

## SEXUAL DIMORPHISM IN CONTINENTAL STEAMER-DUCKS

BRADLEY C. LIVEZEY

AND

PHILIP S. HUMPHREY

**ABSTRACT.**—Data from 133 specimens of three species of steamer-duck were used to assess sexual size dimorphism in the genus *Tachyeres*. In these three species, males on the average exceed females in all of the 15 external, 30 skeletal, and 2 muscular measurements analyzed, except number of bill lamellae. Sexual dimorphism is proportionately greatest in weights, intermediate in areal variables, and least in linear measurements. With few exceptions, magnitude of univariate sexual dimorphism is equal in the three species and among localities for *T. patachonicus*, although differences in magnitude of multivariate sexual dimorphism are indicated. Multivariate comparisons show that males are not only larger than females but also that, proportionately, males have larger core elements and smaller crania, proximal wing elements, and acetabular widths than females. The robust trunks and proportionately shorter wings of males may reflect structural refinements for combat; relatively large acetabular widths of females may be an accommodation for producing and laying large eggs. We hypothesize that sexual dimorphism of steamer-ducks results from the combined effects of largely linear and environmentally stable habitats; strong selection in males for territorial defense of food supplies, mates, and young; and, possibly, selection for smaller body size in females related to reproductive energetics. The greater number of bill lamellae in females than males probably allows the large, territorially active males to feed more on large food items, whereas females are equipped to utilize smaller food items.

Steamer-ducks (*Tachyeres*) are large diving ducks limited in distribution to southernmost South America. Four species are recognized, of which three are flightless and inhabit sea coasts throughout the year (Weller 1976, Humphrey and Thompson 1981): Magellanic Flightless Steamer-Duck (*T. pteneres*) of southern Chile and Tierra del Fuego; White-headed Flightless Steamer-Duck (*T. leucocephalus*) of Chubut, Argentina; Falkland Flightless Steamer-Duck (*T. brachypterus*) of the Falkland Islands; and Flying Steamer-Duck (*T. patachonicus*) of marine and freshwater habitats throughout southern Argentina, Chile, and the Falkland Islands.

All species of *Tachyeres* are monogamous and form lasting, perhaps life-long, pair bonds in which males remain with females throughout nesting and brood rearing (Humphrey and Livezey, in press). Males are extremely territorial, fight frequently, and often attack non-congeners, sometimes fatally (Livezey and Humphrey, in press). Published weights and standard skin measurements show that male steamer-ducks typically are larger than conspecific females (Murphy 1936, Weller 1976). Little information has been reported, however, on possible sexual differences in bill morphology, skeletal dimensions, muscle weights, or the relative magnitude of sexual dimor-

phism in these ducks as compared to other waterfowl. The combination of intense aggression among males—from which one would expect relatively great, intrasexually selected male size (Selander 1972, Trivers 1972)—and substantial parental investment by males and monogamy—typically associated with reduced sexual size differences (Trivers 1972, Sigurjónsdóttir 1981)—makes steamer-ducks particularly useful for the study of sexual dimorphism. Moreover, sexual differences in morphology may reflect differences in ecological niche (e.g., Selander 1966, Reynolds 1972, Wallace 1974, Snyder and Wiley 1976).

Specimens and related data collected during our research on the systematics, ecology, and flightlessness of steamer-ducks provided an opportunity to study in greater detail the sexual size differences in the genus. In this paper we present analyses of sexual dimorphism in the three continental species of steamer-duck; our data for the Falkland Flightless Steamer-Duck were too few for separate study.

### MATERIALS AND METHODS

#### SPECIMENS

Together with M. C. Thompson, we collected 127 steamer-ducks in Argentina during October–December 1979, December 1980–Feb-

TABLE 1. Univariate comparisons of sexes of *Tachyeres* by species.

Character	Dimorphism ratio ( $\delta$ mean/ $\sigma$ mean) by species ( $n \delta, n \sigma$ ) <sup>a</sup>		
	<i>T. pteneres</i>	<i>T. leucocephalus</i>	<i>T. patachonicus</i>
<b>External</b>			
Culmen length	1.02 (5, 3)	1.03 (8, 8)	1.05** (28, 26)
Nail width	1.11** (5, 3)	1.06* (8, 8)	1.06* (28, 26)
Bill length	1.06* (5, 3)	1.06*** (8, 8)	1.06*** (28, 26)
Bill width	1.16*** (5, 3)	1.08*** (8, 8)	1.09*** (28, 26)
Bill depth	1.16* (5, 3)	1.11*** (8, 8)	1.10*** (28, 26)
Lamellae	0.95 (5, 3)	0.98 (8, 8)	0.97 (28, 26)
Lamellae/bill length	0.90* (5, 3)	0.92*** (8, 8)	0.92*** (28, 26)
Total weight	1.22*** (12, 7)	1.30*** (15, 15)	1.26*** (40, 37)
Cross-sectional area	1.21* (5, 3)	1.22*** (8, 8)	1.19*** (28, 26)
Tarsus length	1.12** (5, 3)	1.03 (8, 8)	1.05*** (28, 26)
Digit-III length	1.07*** (5, 3)	1.02 (8, 8)	1.08*** (28, 26)
Paddle area	1.24** (5, 3)	1.12*** (8, 8)	1.13*** (28, 26)
Wing-arc length	1.06** (8, 2)	1.03 (10, 11)	1.05*** (27, 26)
Wing area	1.08 (10, 5)	1.04 (10, 11)	1.06** (33, 31)
Primary remex length	1.05* (5, 2)	1.03 (5, 8)	1.04** (22, 22)
Secondary remex length	1.04 (5, 2)	1.06* (5, 8)	1.04** (22, 22)
Tail length	—	—	1.05* (14, 9)
<b>Postcranial skeleton</b>			
Humerus length	1.07*** (11, 8)	1.06*** (18, 16)	1.05*** (41, 37)
Humerus width	1.06** (12, 8)	1.05*** (18, 16)	1.07*** (41, 37)
Ulna length	1.06*** (9, 8)	1.05*** (14, 13)	1.04*** (37, 32)
Radius length	1.08*** (9, 8)	1.05*** (14, 13)	1.04*** (37, 31)
Carpometacarpus length	1.08*** (9, 8)	1.06*** (14, 13)	1.06*** (37, 33)
Digit-II length	1.08*** (9, 8)	1.08*** (14, 13)	1.06*** (37, 33)
Femur length	1.06*** (12, 8)	1.05*** (18, 16)	1.05*** (41, 37)
Femur width	1.06*** (12, 8)	1.04** (18, 16)	1.05*** (41, 37)
Tibiotarsus length	1.06*** (9, 8)	1.05*** (14, 13)	1.05*** (37, 33)
Tarsometatarsus length	1.07*** (9, 8)	1.04** (14, 13)	1.06*** (37, 33)
Digit-III length	1.07*** (9, 8)	1.06*** (14, 13)	1.11*** (37, 33)
Sternal keel length	1.08*** (12, 8)	1.07*** (18, 16)	1.09*** (41, 37)
Sternal basin length	1.07*** (12, 8)	1.06*** (18, 16)	1.07*** (41, 37)
Least sternal width	1.03 (12, 8)	1.04*** (18, 16)	1.06*** (41, 37)
Posterior sternal width	1.12*** (12, 7)	1.04 (18, 16)	1.08*** (41, 37)
Sternal keel depth	1.07** (12, 8)	1.05** (18, 16)	1.05*** (41, 37)
Coracoid length	1.07*** (12, 8)	1.08*** (18, 16)	1.07*** (41, 37)
Coracoid width	1.07*** (12, 8)	1.07*** (18, 16)	1.10*** (41, 37)
Acetabular width	1.05* (12, 8)	1.04** (18, 16)	1.07*** (41, 37)
Sacral length	1.05** (11, 7)	1.03* (18, 16)	1.07*** (40, 37)
<b>Cranial skeleton</b>			
Cranial height	1.05** (9, 6)	1.05*** (11, 12)	1.05*** (34, 29)
Cranial length	1.05*** (9, 6)	1.05*** (10, 12)	1.05*** (34, 29)
Interorbital width	1.05 (9, 6)	1.12*** (11, 12)	1.17*** (24, 29)
Postorbital width	1.06*** (9, 6)	1.04** (11, 11)	1.05*** (34, 29)
Antorbital width	1.13*** (9, 6)	1.19*** (9, 11)	1.10*** (32, 28)
Frontonasal width	1.12** (9, 6)	1.10** (10, 12)	1.09*** (34, 29)
Bill height	1.06*** (9, 6)	1.09*** (10, 12)	1.08*** (34, 29)
Bill length	1.04 (9, 6)	1.04*** (10, 12)	1.04*** (34, 29)
Bill width	1.09*** (9, 6)	1.04* (10, 12)	1.05*** (34, 29)
Internarial width	1.08* (9, 6)	1.05 (10, 11)	1.09*** (33, 29)
<b>Muscle weight</b>			
Pectoralis major	1.43** (5, 3)	1.17 (7, 7)	1.26*** (26, 25)
Supracoracoideus	1.27*** (5, 3)	1.14 (7, 7)	1.18*** (26, 25)

<sup>a</sup> Significance level for difference of means of sexes (*F*-test, one-way ANOVA): \*  $P \leq 0.05$ , \*\*  $P \leq 0.01$ , \*\*\*  $P \leq 0.001$ .

ruary 1981, and December 1981–January 1982: 16 *T. pteneres* at Ushuaia, Tierra del Fuego (54°48'S); 34 *T. leucocephalus* at Puerto Melo, Chubut (44°01'S); 20 *T. patachonicus* at Ushuaia, Tierra del Fuego (54°48'S), 34 at Puerto Deseado, Santa Cruz (47°46'S), 3 at Puerto Melo, Chubut, and 20 on freshwater lakes in the Andes of Santa Cruz and Chubut (four localities, 42°48'S to 50°13'S). Specimens

were weighed soon after collection, and measurements made of bill, length and area of wing, and feet. Determination of sexes and ages of birds was based on examination of gonads and cloacal bursa (Humphrey and Livezey 1982a). Birds then were prepared as complete or partial (lacking distal limb elements and skull) skeletons and study skins. Our samples also included two borrowed skeletons of *T. pata-*

*chonicus* (FM104109—male, Rio Caike, Magallanes, Chile; NM491013—male, Staten Island, Argentina) and four of *T. pteneres* (NM536348—male, Bahía Buen Suceso, Tierra del Fuego, Argentina; NM490939—male, Staten Island, Argentina; NM488291—female, Navarino Island, Chile; NM490942—female, Staten Island, Argentina). Only fully ossified skeletons were included in analyses.

#### MEASUREMENTS

External measurements were taken to within 1 mm; skeletal measurements were accurate to within 0.1 mm. Of the 46 numerical variables used in the following analyses (Table 1), the following require description: bill length—distance from gape to tip of upper bill; bill width—distance across gape measured ventrally; bill depth—distance from dorsal-most exposed point of bill to gape; lamellae—count of lamellae on one side of upper bill; cross-sectional area—estimated by  $C^2/4\pi$ , where  $C$  is the circumference of a fresh bird at pectoral girdle; paddle area and wing area—area estimate of tracing of pinned structure, measured to within  $0.1\text{ cm}^2$  with planimeter, and doubled; primary length—arc length of ninth primary remex; secondary length—arc length of distal-most secondary remex; cranial height—maximal distance from dorsum to venter of braincase; cranial length—distance along midline from frontonasal suture to posterior of braincase; postorbital width—maximal width of cranium, measured on the lateral processes of quadratojugal bones; antorbital width—maximal distance across the antorbital processes of the lacrimal bones; frontonasal width—distance across rostrum at frontonasal suture; acetabular width—width of the pelvis between the anterodorsal margins of the acetabula; skeletal height, length, and width of bill—measured as on skin but with the base of bill defined as frontonasal suture. We supplemented these measurements with a qualitative assessment of rugosity and ossification of the skull.

#### STATISTICAL ANALYSES

Univariate comparisons of sexes were made using one-way analysis of variance. Two-way analysis of variance was used to test for sexual differences by species and, for *T. patachonicus*, by locality. Variances were compared using Levene's test, a procedure that is robust to departures from normality (Brown and Forsythe 1974).

We used two multivariate techniques: principal components analysis (PCA) and discriminant function analysis (DFA). All PCAs were based on correlation matrices;  $t$ -tests were used to compare factor scores by sex. In DFA, sexes

were contrasted in single-species analyses; variables were added to the discriminant functions in a forward-stepwise fashion based on partial  $F$ -statistics. Selection of final DFA models was based on four criteria: values of Wilk's lambda,  $F$ -statistic for the model, the  $F$ -to-remove of each of the included variables, and the percentage of specimens correctly classified using jackknife techniques. Variables included in the analyses represent those characters that together best distinguished the sexes in each species; most of the excluded variables also differed significantly between the sexes. Canonical axes and associated Mahalanobis'  $D$  were based on variables included in the final DFA models. The magnitudes and signs of the coefficients of variables in canonical axes, weighted by their respective pooled standard deviations, reflect size or shape contrasts in a manner analogous to loadings of variables in PC axes.

In both PCA and DFA, sexes were compared using three different character sets: skull characters (10 variables), postcranial characters (20 skeletal variables and cube root of body weight), and combined skull and postcranial characters. We used the cube root of body weight in multivariate analyses to make it dimensionally comparable to linear measurements of bones. External characters were not used in multivariate analyses because of small sample sizes. Subdivision of characters allowed separate study of dimorphism in the head and body, and permitted multivariate analysis of skeletons for which skulls were lacking. Statistical analyses were performed using BMDP Biomedical Computer Programs (Dixon and Brown 1979).

## RESULTS

#### UNIVARIATE COMPARISONS

*Differences between means.* Most external characters, and all skeletal measurements, were significantly larger in males than in females in the three species. Of the 138 comparisons of variables for the three species, only 20 did not reveal statistically significant differences between the sexes. Thirteen of these were external measurements, which were more variable and were based on smaller samples than skeletal variables; 12 were in *T. leucocephalus* (Table 1).

Degree of dimorphism (mean for males divided by mean for females) for characters was generally between 1.01 and 1.10. However, nine linear measurements (five external, one sternal, and three measures of skull width) showed greater dimorphism in one or more species (Table 1). Cross-sectional area and

TABLE 2. Summary of results of principal component analyses of *Tachyeres* by species and character set.

Character set	Statistic	Species					
		<i>T. pteneres</i>		<i>T. leucocephalus</i>		<i>T. patachonicus</i>	
		PC I	PC II	PC I	PC II	PC I	PC II
Postcranial (21 variables)	sample size: ♂, ♀	9, 6		13, 13		36, 30	
	eigenvalue	15.75	1.59	16.17	1.10	15.40	0.92
	% variance	75.0	7.5	77.0	5.3	73.3	4.4
	<i>t</i> -value <sup>a</sup>	6.822***	0.031	13.878***	1.623	7.309***	3.371*
Cranial (10 variables)	sample size: ♂, ♀	9, 6		9, 9		31, 28	
	eigenvalue	6.68	0.85	6.85	0.98	6.80	0.99
	% variance	66.8	8.5	68.5	9.8	68.0	9.9
	<i>t</i> -value <sup>a</sup>	6.427***	0.035	6.370***	0.669	7.483***	1.198
Combined (31 variables)	sample size: ♂, ♀	9, 5		9, 9		30, 26	
	eigenvalue	21.69	2.07	22.17	1.80	21.25	1.74
	% variance	70.0	6.7	71.5	5.8	68.6	5.6
	<i>t</i> -value <sup>a</sup>	6.462***	0.186	6.247***	1.595	7.148***	2.598*

<sup>a</sup> Significance level of difference in mean component score for males: \*  $P \leq 0.05$ , \*\*  $P \leq 0.01$ , \*\*\*  $P \leq 0.001$ .

paddle area showed consistently greater dimorphism ratios of 1.12 to 1.22, presumably reflecting linear dimorphism of skeletal elements in two dimensions. Dimorphism of wing area, however, was equal in magnitude to that of linear measurements, and probably resulted from the relatively small dimorphism shown by the remiges (Table 1). Body weight and weights of breast muscles, functions of three linear dimensions, showed the greatest sexual differences; dimorphism ratios for weights ranged from 1.14 to 1.43.

Lamellar count showed weak sexual dimorphism in all three species. These differences, in combination with the shorter bills of females, gave significantly more lamellae per unit length of bill in females than males of all species (*t*-test on log-transformed ratios; Table 1).

*Qualitative characters of skulls.* Frontal bones of male steamer-ducks generally were more rugose than those of females of all species, but there was substantial individual variation within both sexes. The antorbital processes of the lacrimal bones of males also tended to be larger, more ossified, and more rugose than those of females. However, both rugosity of the frontals and development of antorbital processes were greater in the larger, flightless species than in *T. patachonicus*, independent of sex.

*Intersexual comparisons of variances.* Certain characters were significantly more variable in one sex than the other in each species. Total weight and cranial length were more variable ( $P \leq 0.05$ ) in females than in males of *T. pteneres*, the only cases in which females exhibited greater variance. Males of *T. pteneres* were more variable than females in length of digit II. Sternal basin length, coracoid width, and interorbital width were more variable ( $P \leq 0.05$ ) in males than in females of *T. patachonicus*. In *T. leucocephalus*, males were more

variable ( $P \leq 0.05$ ) than females in cranial height, humerus width, coracoid width, and four of five sternal measures: basin length, least and posterior width, and keel depth.

*Species differences in univariate size dimorphism.* Magnitude of sexual dimorphism in six variables differed among the species of *Tachyeres*, as indicated by interaction effects in species-sex analyses of variance. Dimorphism of total weight, external tarsus length, paddle area, posterior sternal width, antorbital width, and skeletal bill width was greater in the larger flightless species, *T. pteneres*, than in *T. leucocephalus* or *T. patachonicus*.

*Geographic differences in univariate dimorphism of T. patachonicus.* Many characters of *T. patachonicus* varied geographically, but most locality effects were independent of sex (Livezey and Humphrey, unpubl.). Only one measure differed geographically in degree of sexual dimorphism; antorbital skull width in *T. patachonicus* was more dimorphic ( $P \leq 0.05$ ) in birds from Andean lakes than in birds from marine localities.

#### MULTIVARIATE COMPARISONS

*Principal component analyses.* The first PC axes in all analyses of species and data sets accounted for most of the total variances, were correlated highly with all variables, and were interpreted as general size axes. Univariate sexual dimorphism in original variables resulted in significant differences between the sexes in scores on PC-I for each species (*t*-tests, Table 2). Sexual differences in PC-I scores generally were greater for postcranial and combined data sets than for cranial variables alone.

Sexual differences on PC-II were significant only for postcranial and combined characters in *T. patachonicus* (*t*-tests, Table 2). Because of their orthogonality with respective PC-I axes, we interpret scores on PC-II axes as indicators

TABLE 3. Factor loadings on PC-II for *T. patachonicus* by data set.

Character	PC-II factor loadings by data set <sup>a</sup>	
	Postcranial characters <sup>b</sup>	All characters <sup>c</sup>
Body weight (cube root)	-0.232*	0.179
Humerus length	0.312*	-0.267*
Humerus width	0.004	0.017
Ulna length	0.345*	-0.344*
Radius length	0.262*	-0.296*
Carpometacarpus length	0.348*	-0.251*
Digit-II length	0.160	-0.225*
Femur length	0.138	-0.218*
Femur width	-0.068	-0.083
Tibiotarsus length	0.133	-0.253*
Tarsometatarsus length	0.098	-0.177
Digit-III length	-0.099	-0.021
Sternal keel length	-0.213*	0.031
Sternal basin length	-0.185	-0.032
Least sternal width	-0.204*	0.040
Posterior sternal width	-0.293*	0.111
Sternal keel depth	-0.151	0.055
Coracoid length	0.017	-0.133
Coracoid width	-0.293*	0.123
Acetabular width	-0.176	-0.085
Sacral length	-0.158	-0.081
Cranial height		0.132
Cranial length		0.014
Interorbital width		0.692*
Postorbital width		0.135
Antorbital width		0.446*
Frontonasal width		0.366*
Bill height		0.148
Bill length		0.039
Bill width		0.003
Internarial width		0.487*

\* Factor loading greater than 0.200 in absolute magnitude and considered significant.

<sup>b</sup> Males tended to have negative scores, females positive.

<sup>c</sup> Females tended to have negative scores, males positive.

of shape or skeletal proportions. Postcranial PC-II for *T. patachonicus* contrasted lengths of four wing elements (carpometacarpus, humerus, ulna, and radius) with those of coracoid width, body weight, and three sternal measures (keel length, least width, and posterior width). Males tended to have larger trunk measurements relative to wing elements than females (Table 3). PC-II for combined data of *T. patachonicus* essentially contrasted four measures of skull width (antorbital, frontonasal, interorbital, and internarial) with lengths of the same four wing elements and the lengths of femur and tibiotarsus (Table 3). This shape axis indicates that the anterior and middle regions of the skulls of male *T. patachonicus* are proportionately more robust, relative to their wing and leg elements, than in females.

*Discriminant function analyses.* Sexual dimorphism is sufficiently great in *Tachyeres* that the DFAs and associated classification functions for all species and data sets correctly determined the sex of at least 88% of the specimens (Table 4). Classification functions for all analyses except that for skulls of *T. patachonicus*

achieved correct sex identification for 93% or more of the specimens. The analyses and classifications based on postcranial and combined character sets generally had preferable summary statistics and higher classification percentages than those based on the smaller and more variable set of cranial characters (Table 4). Moreover, DFAs derived from the 31-character combined data set were superior to postcranial analyses by the same criteria. We will discuss in detail only these combined-data analyses.

The numbers and identities of specific variables included in final DFAs differed greatly among species (Table 5). Four of the seven variables used to discriminate the sexes of *T. pteneres* were appendicular: lengths of the humerus, carpometacarpus, tarsometatarsus, and digit III. The remaining three characters were cranial height, bill height, and acetabular width (Table 5). Canonical coefficients indicated that male *T. pteneres* have proportionately larger skulls and distal limb elements than females, but that humeri of females are longer, relative to other body measures, than those of males (Table 5).

Sexes of *T. leucocephalus* were contrasted most effectively using a combination of body weight, humerus width, three trunk elements, and six skull measurements (Table 5). The trunk elements included measurements from the sternum, coracoid, and synsacrum. Five of the seven skull variables measured width, the other two were length and height of the bill. Canonical coefficients indicated rather different skeletal proportions in the sexes of *T. leucocephalus* compared to those in *T. pteneres*, another flightless species. The skulls of male *T. leucocephalus* tend to be proportionately larger at the base of the bill (antorbital width, bill height) than those of females. Furthermore, females are relatively wider at other points on the skull and have proportionately greater acetabular widths than males (Table 5).

Only six variables were used in the final DFA for *T. patachonicus*; these included two wing elements, two trunk elements, body weight, and interorbital width. The large, negative canonical coefficient for radius length indicated, as in *T. pteneres*, that males had proportionately shorter proximal wing elements than females. The reduced number of useful variables and relatively small values of statistics associated with the model (Table 4) resulted, in part, from the confounding effects of geographic variation in this species.

Separate DFAs for *T. patachonicus* by locality resulted in correct determination of sex for 100% of the specimens (Table 6). Only six variables were entered significantly into the

TABLE 4. Summary of discriminant function analyses for sexes of *Tachyeres* by species and character set.

Character set and statistic	Species		
	<i>T. pteneres</i>	<i>T. leucocephalus</i>	<i>T. patachonicus</i>
<b>Postcranial</b>			
No. included variables	9	10	7
Wilk's lambda	0.004	0.047	0.224
<i>F</i> -statistic (df) <sup>a</sup>	137.3 (9, 5)***	30.3 (10, 5)***	28.8 (4, 8)***
Mahalanobis' D	29.87	8.64	3.69
% sexed correctly	100	100	93.9
<b>Cranial</b>			
No. included variables	4	4	6
Wilk's lambda	0.109	0.059	0.323
<i>F</i> -statistic (df) <sup>a</sup>	20.4 (4, 10)***	51.6 (4, 13)***	18.1 (6, 52)***
Mahalanobis' D	5.43	7.52	2.85
% sexed correctly	100	100	88.1
<b>Combined</b>			
No. included variables	7	12	6
Wilk's lambda	0.005	0.001	0.199
<i>F</i> -statistic (df) <sup>a</sup>	159.2 (7, 6)***	508.6 (12, 5)***	32.8 (6, 49)***
Mahalanobis' D	26.33	65.88	3.95
% sexed correctly	100	100	92.9

\*\*\* *F*-value significant,  $P \leq 0.001$ .

DFA for Flying Steamer-Ducks from Ushuaia, eight variables were used for birds from Andean lakes, and 15 characters were significantly incorporated into the DFA for specimens from Puerto Deseado. Despite these differences in numbers and identities of included variables, the canonical coefficients indicated some similarities between localities in sexual differences in skeletal proportions (Table 6). Males from all localities had proportionately longer sterna than females, and at two localities had relatively shorter proximal wing elements and nar-

rower acetabular widths. Males from coastal localities also tended to have proportionately narrower crania but more broadly based bills than females taken on the coast. Leg elements were unimportant in single-locality DFAs for *T. patachonicus* and showed no consistent trends in proportions (Table 6).

Relatively high numbers of variables included in the DFAs, and associated Mahalanobis' distances, indicate a greater multivariate sexual dimorphism in *T. leucocephalus* than in the other two species (Table 4). By the

TABLE 5. Coefficients for variables in canonical axes, standardized through multiplication by pooled standard deviations of original variables. On all axes, males tended to have positive scores and females tended to have negative scores.

Character	Standardized canonical coefficients <sup>a</sup>		
	<i>T. pteneres</i>	<i>T. leucocephalus</i>	<i>T. patachonicus</i>
Body weight (cube root)		5.540***	0.824***
Humerus length	-3.645**		
Humerus width		6.492***	
Radius length			-0.720**
Carpometacarpus length	8.693***		
Tarsometatarsus length	-2.862**		
Digit-III length	3.730***		0.430**
Posterior sternal width			0.314
Sternal keel depth		-2.391**	
Coracoid width		3.833*	0.380*
Acetabular width	-6.221***	-8.295**	
Cranial height	2.198**		
Interorbital width		-3.874*	0.316*
Postorbital width		-2.218*	
Antorbital width		6.356***	
Frontonasal width		-2.997*	
Bill height	1.374*	9.134***	
Bill length		-5.800***	
Internarial width		-1.908	

<sup>a</sup> Significance level for *F*-to-remove of variable in final stepwise DFA model: \*  $P \leq 0.05$ , \*\*  $P \leq 0.01$ , \*\*\*  $P \leq 0.001$ .

TABLE 6. Standardized canonical coefficients and summary statistics for final discriminant function analyses for sexes of *T. patachonicus* by locality. On all axes, males tended to have positive scores and females tended to have negative scores.

Statistic	Locality for <i>T. patachonicus</i>		
	Ushuaia	Puerto Deseado	Andes
Canonical coefficient*			
Body weight (cube root)		1.582*	8.601***
Humerus length			-6.512*
Ulna length		-6.412***	-7.208*
Carpometacarpus length	-3.075*	5.229**	
Digit-II length			6.896**
Femur width		-1.794*	
Tarsometatarsus length	4.034**		
Sternal keel length	8.142***	2.539*	2.711**
Sternal basin length		-3.168*	
Least sternal width		-4.781***	
Coracoid length		5.387***	
Coracoid width		1.640**	
Acetabular width		-1.678*	-5.520***
Sacral length	-5.940***		
Cranial height		-2.556**	
Cranial length	3.143**		
Postorbital width	-6.110***	-2.652**	
Frontonasal width		3.317***	
Bill height		6.723***	
Bill length		-3.275**	
Bill width			-1.176
Internarial width			2.791**
Summary statistics			
<i>n</i> ♂, <i>n</i> ♀	7, 6	12, 14	10, 5
Wilk's lambda	0.004	0.027	0.005
<i>F</i> -statistic (df) <sup>a</sup>	244.5 (6, 6)***	24.4 (15, 10)***	153.3 (8, 6)***
Mahalanobis' D	28.85	11.66	28.24
% sexed correctly	100	100	100

\* Significance level for associated *F*-statistic: \*  $P \leq 0.05$ , \*\*  $P \leq 0.01$ , \*\*\*  $P \leq 0.001$ .

same criteria, of the three populations of *T. patachonicus* analyzed, the overall multivariate dimorphism was least in birds from Puerto Deseado, and higher in those from Ushuaia and the Andes (Table 6).

## DISCUSSION

In contrast to steamer-ducks, House Sparrows (*Passer domesticus*) show consistent sexual dimorphism in their body skeletons, but little size difference between the sexes in skull measurements (Selander and Johnston 1967, Johnston 1969, Johnston and Selander 1971). These authors explained that large body size of males is related to territoriality, small body size in females reflects a thermoregulatory optimum for incubation in enclosed nests, and lack of skull dimorphism suggests that the sexes share a single feeding niche. Johnston and Selander (1973) and Hamilton and Johnston (1978) found that degree of sexual dimorphism in House Sparrows increases with latitude, regardless of absolute body size, and Johnston and Fleischer (1981) and Fleischer and Johnston (1982) concluded that climatic conditions account for latitudinal variation in sexual size differences.

Weight is probably the best single measure of size dimorphism (Amadon 1977), despite substantial variability of body weights in birds (Clark 1979). A histogram of dimorphism ratios (Fig. 1) and a linear regression of mean male body weight (g) on mean female weight for 86 taxa of waterfowl (Frith 1967; Bellrose 1976; Weller 1967, 1976; Kear and Berger 1980; unpubl. data) show remarkable constancy in sexual dimorphism and provide a basis for interspecific comparisons:

$$\text{Male Wt.} = -73.732 + 1.211 (\text{Female Wt.}); \\ R^2 = 0.9907.$$

A slightly more precise model included an additional significant term, approximately  $10^{-9}$  (Female Wt.)<sup>3</sup>, resulting in  $R^2 = 0.9911$ . A 95% confidence interval for the slope in the simple model is (1.186, 1.236). The maximum-likelihood estimate for the slope (principal-axis slope) of this line, assuming both male and female weights were measured with some error and that their variances are equal, is 1.233. The largest dimorphism ratios for these anatids, *Biziura* (1.55) and *Bucephala* (up to 1.68), closely approximate the extreme for birds cited

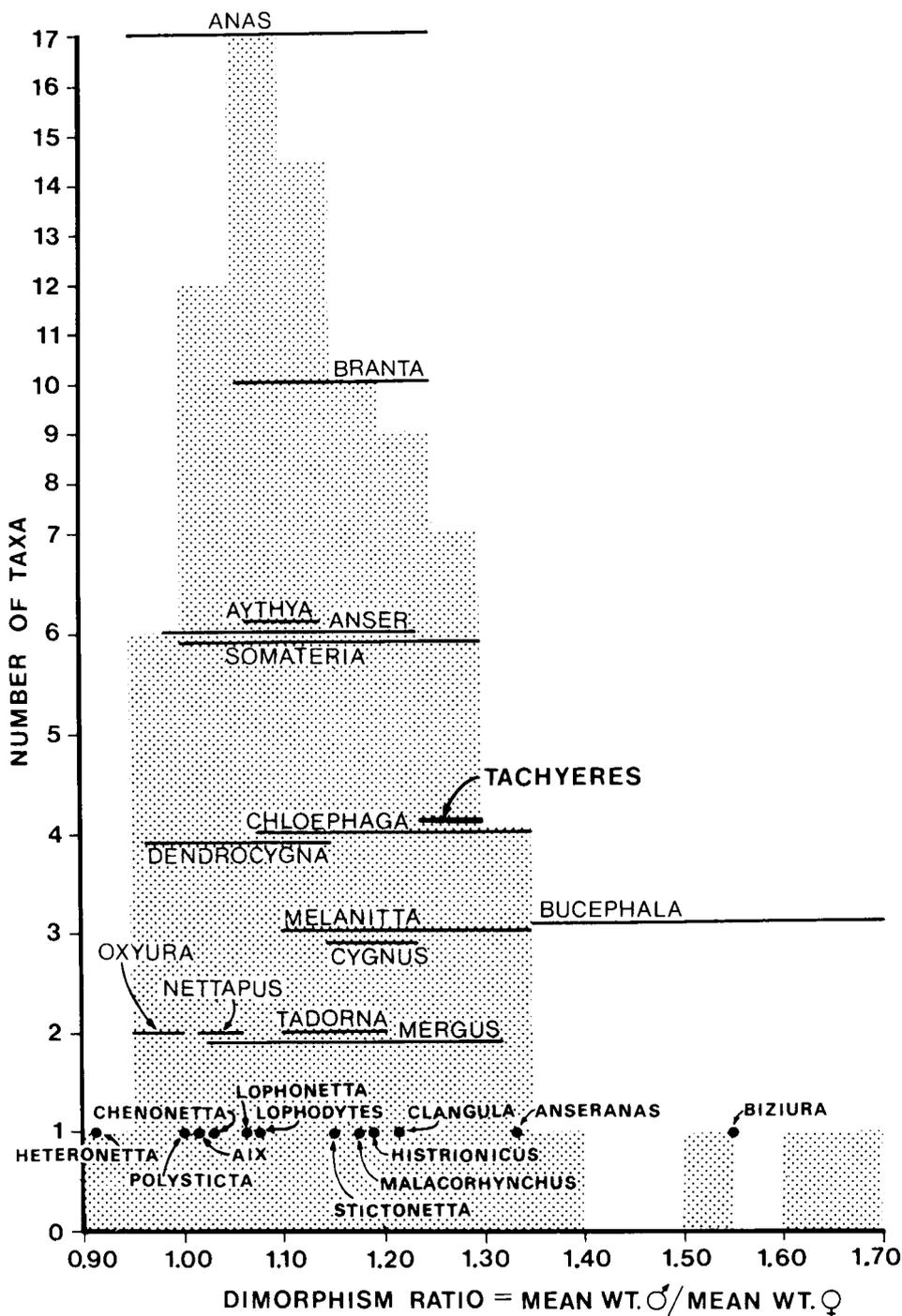


FIGURE 1. Ratios of sexual dimorphism in body weight for 86 taxa of waterfowl. Shaded histogram depicts overall distribution of dimorphism ratios. Generic ranges are based on ratios calculated for species individually, except for *Branta canadensis* (eight subsp.), *Somateria mollissima* (four subsp.), *Anser albifrons* and *A. caerulescens* (two subsp. each) for which separate ratios were calculated for each subspecies. Sources of data were Frith (1967), Weller (1967, 1976), Bellrose (1976), Kear and Berger (1980), and the present study.

by Amadon (1977) for the sexual dimorphism in weights of certain species of *Accipiter*.

Our data on weights and those compiled by Weller (1976) show that all species of steamer-ducks have approximately equal dimorphism ratios: *T. patachonicus*, 1.26 ( $n = 96$ ); *T. leu-*

*cocephalus*, 1.30 (30); *T. brachypterus*, 1.28 (9); and *T. pteneres*, 1.27 (25). Compared to the slope of the overall regression for waterfowl, steamer-ducks show relatively high sexual size dimorphism (Fig. 1), but do not show, as concluded by Weller (1976), that magnitude

of dimorphism within the genus increases with body weight.

Steamer-ducks are well known for their violent, sometimes fatal defense of territories; these areas are probably held year-round and perhaps for life (Livezey and Humphrey, in press). Territorial combat typically involves surface rushes, dives, biting, and blows with the well-developed wing knobs. We conclude that unusually great dimorphism in *Tachyeres* results primarily from selection for large body size in males for combat related to maintenance of territories and defense of mates and young. The importance of large body size in males is probably greatest for flightless species and marine *T. patachonicus*, for which stability of territories and threat of predation on adults and young are greatest. This may explain in part the occurrence of permanent flightlessness in 25% of male Flying Steamer-Ducks at marine localities (Humphrey and Livezey 1982b). In contrast to the situation in polygamous icterines (Searcy 1979, Searcy and Yasukawa 1981), the larger body size of male steamer-ducks probably does not significantly increase their vulnerability to predation, costs of territorial defense, or impair foraging efficiency. The upper limit for body size in male *Tachyeres* may be related to thermodynamics or availability of food.

Sexual differences in body proportions do not reflect simple allometric increase of linear skeletal elements with cubic differences in body weight because body weights were transformed to cube roots for analysis. Consequently, we interpret these differences in shape as sex-related morphological adaptations. The proportionately deep, broadly based bills and relatively short proximal wing elements of males may be structural refinements related to combat. Similarly, the proportionately larger sterna and coracoids of males may provide more structural support for pectoral musculature associated with pursuit and fighting.

Adult male *T. patachonicus* acquire a conspicuous, largely white, supplemental head plumage during the breeding season, which presumably serves as a warning or threat coloration in territorial defense (Humphrey and Livezey 1982a). Sexual dichromatism of head plumage is also marked in *T. leucocephalus* and *T. brachypterus* during courtship and nesting (Humphrey and Thompson 1981). The selective advantage of both large body size and plumage differences in male steamer-ducks probably is enhanced by assessment and choice of mates by females. The characters that endow males with superior paternal abilities logically would become criteria of mate choice.

Sexual differences in size of steamer-ducks

may be increased to some extent through selection for smaller body size in females. Downhower (1976) reasoned that smaller females of two species of Darwin's finches (*Geospiza*) could accumulate and mobilize energy for reproduction more quickly than larger females. The proportionately larger acetabular widths of female steamer-ducks presumably represent an accommodation to the production and laying of the large eggs typical of the genus (Humphrey and Livezey, in press).

*Tachyeres* is clearly an exception to the generalization of Sigurjónsdóttir (1981) that sexual dimorphism in waterfowl is inversely related to parental investment by males. Sigurjónsdóttir's (1981) observation does apply to two exceptionally dimorphic genera, *Bucephala* and *Biziura*, although increased dimorphism probably arose for different reasons in these two genera. Dimorphism in *Bucephala* is probably related to the constraints of hole-nesting on females and sexual selection on males (Bergmann 1965), whereas that in *Biziura* probably resulted from unusually potent sexual selection by females associated with promiscuous mating by males (Lack 1974).

Number of bill lamellae is the only character we found in which sexual differences probably are related to intersexual niche differences. Jenkin (1957) related interspecific differences in lamellar structure of flamingoes to differences in size of ingested organisms. Bill lamellae are also essential for retention of food by filter-feeding waterfowl (Zweers et al. 1977). The closer spacing of lamellae on bills of female steamer-ducks undoubtedly enables females to retain and ingest smaller food particles than males. Smaller body size of females may make the greater use of smaller food items energetically favorable. Fewer bill lamellae in males may reflect an adaptation for handling large food items in order to meet the energy demands of sexually-selected large body size and territoriality. This interpretation is supported by the similar inverse relationship between lamellar density and body size among the species (sexes pooled) of *Tachyeres* (unpubl. data). Intersexual niche separation achieved by sexual dimorphism of the bill is probably especially important for birds that feed on tidal flats and freshwater lakes, and may be enhanced by sexual differences in feeding behavior. We currently are studying this and other aspects of the feeding ecology of steamer-ducks.

#### ACKNOWLEDGMENTS

This study was supported by National Science Foundation grant DEB-8012403, the Kansas University Endowment Association, Southwestern College, W. Saul, M. C.

Thompson, L. A. Osborne, R. T. Peterson, T. Mastin, R. Hamilton, and the Humphrey family. Collecting permits were issued by E. O. Gonzalez Ruiz (Dirección Nacional de Fauna Silvestre), L. O. Saigó de Chialva (Protección Ambiental, Chubut), and D. H. Soria (Ganadería, Santa Cruz). Field work in Argentine national parks was made possible by A. Tarak (Dirección Nacional de Parques Nacionales). Logistic support was provided by J. M. Gallardo, R. A. Bockel, and J. Navas of the Museo Argentino de Ciencias Naturales. G. A. Giaroli, F. Lötbe and F. Villar made essential arrangements for our work. Housing and laboratory facilities were arranged by O. Kühnemann, P. Medina, and J. Sesti; B. Mayer and F. V. T. J. Fauring provided us a home and field support at Puerto Melo. We are also grateful for the assistance and hospitality of B. de Ferradas, L. Orquera, E. Piana, G. Piacentino, J. E. Bonczak, R. E. Caferata, A. Fernandez, R. Landivar, G. C. Sarceda, F. Erize, R. Straneck, W. Conway, Y. Lucero, P. Canevari, M. A. E. Rumboll, and the Gibson family. Specimens were loaned to us by the Field Museum of Natural History (FM) and National Museum of Natural History (NM). We also thank R. Mengel, M. Jenkinson, and their colleagues for preparation of specimens; K. McManness for typing; R. F. Johnston and H. Levinson for reviewing the manuscript; and D. Bennett for graphical help.

## LITERATURE CITED

- AMADON, D. 1977. Further comments on sexual size dimorphism in birds. *Wilson Bull.* 89:619-620.
- BELLROSE, F. C. 1976. Ducks, geese and swans of North America. Stackpole Books, Harrisburg, PA.
- BERGMANN, G. 1965. Der Sexuelle Grossdimorphismus der Anatiden als Anpassung an des Hohlenbruten. *Commentat. Biol. Soc. Sci. Fenn.* 28:1-10.
- BROWN, M. B., AND A. B. FORSYTHE. 1974. Robust tests for the equality of variances. *J. Am. Stat. Assoc.* 69:364-367.
- CLARK, G. A., JR. 1979. Body weights of birds: a review. *Condor* 81:193-202.
- DIXON, W. J., AND M. B. BROWN [EDS.]. 1979. BMDP-79: biomedical computer programs. Univ. of California Press, Berkeley.
- DOWNHOWER, J. F. 1976. Darwin's finches and the evolution of sexual dimorphism in body size. *Nature* 263:558-563.
- FLEISCHER, R. C., AND R. F. JOHNSTON. 1982. Natural selection on body size and proportions in House Sparrows. *Nature* 298:747-749.
- FRITH, H. J. 1967. Waterfowl in Australia. East-West Center Press, Honolulu, HI.
- HAMILTON, S., AND R. F. JOHNSTON. 1978. Evolution in the House Sparrow—IV. Variability and niche width. *Auk* 95:313-323.
- HUMPHREY, P. S., AND B. C. LIVEZEY. 1982a. Molts and plumages of Flying Steamer-Ducks (*Tachyeres patachonicus*). *Univ. Kans. Mus. Nat. Hist. Occas. Pap.* No. 103:1-30.
- HUMPHREY, P. S., AND B. C. LIVEZEY. 1982b. Flightlessness in Flying Steamer-Ducks. *Auk* 99:368-372.
- HUMPHREY, P. S., AND B. C. LIVEZEY. In press. Nest, eggs, and downy young of the White-headed Flightless Steamer-Duck. In *Neotropical ornithology*. *Ornithol. Monogr.*
- HUMPHREY, P. S., AND M. C. THOMPSON. 1981. A new species of steamer-duck (*Tachyeres*) from Argentina. *Univ. Kans. Mus. Nat. Hist. Occas. Pap.* No. 95:1-12.
- JENKIN, P. M. 1957. The filter-feeding and food of flamingoes (Phoenicopter). *Philos. Trans. R. Soc. Lond. (Ser. B, Biol. Sci.)* 240:401-493.
- JOHNSTON, R. F. 1969. Character variation and adaptation in European sparrows. *Syst. Zool.* 18:206-231.
- JOHNSTON, R. F., AND R. C. FLEISCHER. 1981. Overwinter mortality and sexual size dimorphism in the House Sparrow. *Auk* 98:503-511.
- JOHNSTON, R. F., AND R. K. SELANDER. 1971. Evolution in the House Sparrow. II. Adaptive differentiation in North American populations. *Evolution* 25:1-28.
- JOHNSTON, R. F., AND R. K. SELANDER. 1973. Evolution in the House Sparrow. III. Variation in size and sexual dimorphism in Europe and North and South America. *Am. Nat.* 107:373-390.
- KEAR, J., AND A. J. BERGER. 1980. The Hawaiian Goose. Buteo Books, Vermillion, SD.
- LIVEZEY, B. C., AND P. S. HUMPHREY. In press. Territoriality and interspecific aggression in steamer-ducks. *Condor*.
- LACK, D. 1974. Evolution illustrated by waterfowl. Blackwell Scientific Publ., Oxford.
- MURPHY, R. C. 1936. Oceanic birds of South America. Vol. 2. American Museum of Natural History, New York.
- REYNOLDS, R. T. 1972. Sexual dimorphism in accipiter hawks: a new hypothesis. *Condor* 74:191-197.
- SEARCY, W. A. 1979. Sexual selection and body size in male Red-winged Blackbirds. *Evolution* 33:649-661.
- SEARCY, W. A., AND K. YASUKAWA. 1981. Sexual size dimorphism and survival of male and female blackbirds (Icteridae). *Auk* 98:457-465.
- SELANDER, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* 68:113-151.
- SELANDER, R. K. 1972. Sexual selection and dimorphism in birds, p. 180-230. In B. Campbell [ed.], *Sexual selection and the descent of man*. Aldine Publ. Co., Chicago.
- SELANDER, R. K., AND R. F. JOHNSTON. 1967. Evolution in the House Sparrow. I. Intrapopulation variation in North America. *Condor* 69:217-258.
- STURJÓNSDÓTTIR, H. 1981. The evolution of sexual size dimorphism in gamebirds, waterfowl and raptors. *Ornis Scand.* 12:249-260.
- SNYDER, N. F. R., AND J. W. WILEY. 1976. Sexual size dimorphism in hawks and owls of North America. *Ornithol. Monogr.* 20:1-96.
- TRIVERS, R. L. 1972. Parental investment and sexual selection, p. 136-179. In B. Campbell [ed.], *Sexual selection and the descent of man*. Aldine Publ. Co., Chicago.
- WALLACE, R. A. 1974. Ecological and social implications of sexual dimorphism in five melanerpine woodpeckers. *Condor* 76:238-248.
- WELLER, M. W. 1967. Notes on plumages and weights of the Black-headed Duck, *Heteronetta atricapilla*. *Condor* 69:133-145.
- WELLER, M. W. 1976. Ecology and behaviour of steamer ducks. *Wildfowl* 27:45-53.
- ZWEERS, G. A., A. F. C. GERRITSEN, AND P. J. VAN KRANENBURG-VOOGD. 1977. Mechanics of feeding of the Mallard (*Anas platyrhynchos* L.; Aves, Anseriformes). *Contrib. Vertebr. Evol.* 3. S. Karger, Basel, Switzerland.

*Museum of Natural History and Department of Systematics and Ecology, University of Kansas, Lawrence, Kansas 66045. Received 11 March 1983. Final acceptance 9 April 1984.*