

MORPHOMETRIC VARIATION IN TUNDRA SWANS: RELATIONSHIPS AMONG SEX AND AGE CLASSES¹

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Abstract. Variation in 36 morphometric variables among 82 Tundra Swans (*Cygnus columbianus*) wintering in Humboldt County, California, was evaluated; 15 variables were analyzed in detail to identify patterns of morphometric variation and differences among sex-age classes. Adult males were the largest class, and males had a significant positive covariation between wing length and other external and internal morphological features. There was no such covariation among females. When 15 morphological variables were evaluated with a principal components analysis, seven components accounted for 74% of the observed variation. Only the first component, associated with external body size and heart weight, was aligned with sex and age differences. There was some sex-age variation associated with viscera weights, and to a lesser extent with tarsus size in relation to bill length. There was little sex-age variation among most bill measures, body fat measures, or spleen weight. Based on a discriminant function analysis, five of the 15 variables discriminated the morphologies of the sex-age groups. Our data suggest that sexual dimorphism is minor in immatures, but pronounced in adults. This increase of dimorphism with age occurred for most external and internal characters, but was not apparent for bill dimensions. We believe that Tundra Swans can be classified into three distinct groups on the basis of internal and external morphological features: (1) adult males have a relatively large body size but are similar in viscera weight and foot length to immature swans; (2) adult females are intermediate in body size, small in viscera weight, and smaller in foot length than adult and immature males; and (3) immature swans are relatively small-bodied, but similar in viscera weights and foot length measures to adult males.

Key words: California; *Cygnus columbianus*; evolution; maturation; morphology; multivariate analysis; sexual dimorphism; Tundra Swans.

INTRODUCTION

Knowledge of morphometry is important for determining patterns of growth in an animal species, especially as it may affect the biology and behavior of that species. It also is valuable in delineating the major differences among various populations over a species' geographic range, and providing reference values for determining the impact of disease, toxic agents, or nutritional stress. While a number of studies have been conducted on Tundra Swans (*Cygnus columbianus*) in North America (Bellrose 1976, p. 94-101; Palmer 1976, p. 72-88), only limited information is available on their morphometry, and there has been little attempt to relate variation in swan morphometry to their biology and behavior.

Tundra Swans rarely wintered along the north-

west coast of California prior to the late 1940s, but have since increased. During a U.S.F.W.S. survey on 3 January 1984, an estimated 860 swans were observed on the Eel River delta in Humboldt County. On 7 January 1984, approximately 135 Tundra Swans were found dead at the mouth of the Eel River. After a thorough analysis, the birds were diagnosed as having died from drowning (Miller et al. 1986).

This mortality provided a unique opportunity to compare morphometric variation among the sex-age groups of a wintering population of Tundra Swans taken at a single point in time. Our purposes were to: (1) identify the morphological relationships within and between the four sex-age groups, (2) clarify the major sources of morphological variation, and (3) determine the morphological features best discriminating the sex-age groups of wintering Tundra Swans.

One concern in the present study is that drowning might have resulted in a nonrandom

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sample of birds in our collection. Some biases would have no effect on the findings reported in this study. For example, the sample sizes of birds for each sex-age class in our collection might not be representative of their proportional occurrence in the population. This sort of bias would not affect any analyses of morphometry within and between sex-age classes. More serious would be any bias resulting in differential mortality within a sex-age class because of morphological differences. An example would be if the drowning tended to select for immature males with a smaller body size, or a reduced wing span, or shorter tarsi. Our assumption in these analyses is that the likelihood of death due to drowning was not related to morphology within a sex-age class.

MATERIALS AND METHODS

COLLECTIONS AND NECROPSY

Tundra Swan carcasses were collected on 10 January 1984 from the mouth of the Eel River and frozen. The sex of each bird was determined internally.

Swans were classified as immature (6–7 months old in January) if gray plumage was present on the head and neck, and adult (> 18 months of age) if gray was absent (Palmer 1976, p. 73). If our aging technique was faulty, we believe it would have introduced substantial variance heterogeneity among the sex-age groups for the majority of morphological characters. However, based on Levene's tests for variance heterogeneity (Levene 1960, p. 278), only two of the 15 morphological characters we discuss were significantly heterogeneous. This finding supports our belief that aging by plumage reliably discriminated first year birds from older swans. Thus, four sex-age classes were considered: immature females, immature males, mature females, and mature males.

For birds with yellow lores, lore dimensions were recorded to the nearest 0.1 mm with calipers. The presence of pink pigmentation on the upper or lower mandibles of the bill and rust stains on the head and neck also was noted.

Total weight and eviscerated weight (ECW) were determined to the nearest 0.01 kg. Eviscerated weight was defined as the total weight after all internal organs were removed. The esophagus and trachea were cut just above the tracheal bifurcation. The large intestine was cut as close to the cloaca as possible and removed.

The heart, liver, spleen, gizzard, and right and left lungs were detached along their natural contours, rinsed, blotted dry, and weighed separately to the nearest 0.1 g. All fat from the outer surface of the gizzard, and the gizzard contents were removed before the gizzard was weighed.

The following external measures were taken on each bird (Baldwin et al. 1931). Total length with feathers (total length), body girth, and length of closed wing (wing length) were measured to the nearest 1 mm. Left foot lengths were measured to the nearest 1 mm with calipers. Tarsus length was defined as the length from back of the tarsus to the front metatarsus joint. Diagonal tarsus length was measured from the lower part of the tarsus joint to the metatarsus joint; this measure is called length of tarsus by Baldwin et al. (1931, p. 107). Length of middle toe and length of middle toe with claw also were measured. Bill length measurements, to the nearest 1 mm, included length of exposed culmen, length of bill from nostril (bill–nostril length), and length of bill from gape (bill–gape length). Bill width measurements, to the nearest 0.1 mm, included greatest width of nail of bill (nail width), width of bill at posterior end of nail, and width of bill directly behind the nares.

Back fat was defined as the greatest depth of fat over the sacral vertebrae. Heart fat was the width of the heart fat band at the widest point. Pectoralis depth was the greatest depth of the pectoralis muscles as measured by a sharp probe. Back fat, heart fat, and pectoralis depth were measured to the nearest 1 mm. Gizzard fat weight was defined as the total weight of all fat removed from the surface of the gizzard, to the nearest 0.1 g. A gizzard fat index was calculated by dividing the gizzard fat weight by the weight of the gizzard without fat.

Penis length, as well as testes and lore dimensions were measured to the nearest 1 mm with calipers. Ovaries were weighed to the nearest 0.1 g. Bursa depth was determined to the nearest 1 mm with a dull probe. Any weights and measurements affected by scavenging were excluded from the analyses.

UNIVARIATE STATISTICAL ANALYSES

Means and standard deviations for 36 variables were calculated for each sex-age class. After excluding variables with a large number of missing data points, and those that were highly redundant (determined from simple and multiple cor-

relation patterns), a subset of 15 variables was retained. Each of these 15 variables was tested for a goodness of fit to a normal distribution. No significant deviations from normality were found, precluding any need for transformations.

Tests of the null hypothesis of no difference in the means, by sex-age group, for each morphological variable were conducted using Welch's ANOVA model (Brown and Forsythe 1974) which does not assume homogeneity of group variances. Pair-wise contrasts based on Bonferroni confidence intervals were calculated only after a significant overall ANOVA was found.

BIVARIATE STATISTICAL ANALYSES

We examined the relationships between internal and external morphological features (dependent variables) and wing length (independent variable) using least squares regression models. Since total weights were not available for all birds because of scavenging, wing length was chosen as the best index of overall body size because of its high correlation with total weight ($r = 0.72$). For each analysis, regression lines were estimated separately for males and females and tested to determine if their slopes differed significantly from zero. We computed Pearson's product-moment correlation coefficients (Sokal and Rohlf 1981) among all 15 morphological variables for 82 swans, based on untransformed data.

MULTIVARIATE STATISTICAL ANALYSES

In order to conduct the multivariate analyses, missing data among the 15 variables were estimated. Randomly generated values were produced based on sampling from a normal distribution with a mean and standard deviation, by sex-age group, specific to each variable with missing data. No more than 12 generated values were needed for any one morphometric variable among the 82 swans considered. By sex and age group, the maximum numbers of generated values for any variable were two for the 11 juvenile females, two for the 21 juvenile males, six for the 27 adult females, and four for the 23 adult males, respectively. Missing data values were independently generated and analyzed on four separate occasions; all analyses were consistent with the results reported below.

Principal components analysis. The correlation matrix computed from the 15 morphometric variables was evaluated further by a principal components analysis (PCA) (Green 1978, chap-

ter 8). Our goal was to estimate the major axes of morphological variation and then ordinate the sex-age groups along these dimensions. After initial extraction of the principal components, these orthogonal factors were rotated using the varimax criteria; interpretations of principal components were based on the dominant factor loadings.

Tests of the null hypothesis of no difference in means, by sex-age group, for each principal component (PC) axis were based on Welch's ANOVA model. The significance of each a posteriori pair-wise contrast was based on Bonferroni confidence intervals.

Discriminant function analysis. To more specifically address the hypothesis of morphological equality among the sex-age groups, we analyzed these same data with discriminant function analysis (DFA) using stepwise inclusion of variables. The estimated canonical variates were given biological interpretations according to their structure coefficients (Green 1978, p. 309). Pair-wise comparisons to test for the equality of the groups in the canonical variates space were based on Mahalanobis distances. The posterior pattern of correct classifications was tested for a significant deviation from chance-corrected classifications using Cohen's Kappa test statistic (Titus et al. 1984).

Tests of the null hypothesis of no difference in means, by sex-age group, for each canonical variate were based on Welch's ANOVA model. The significance of each a posteriori pair-wise contrast was based on Bonferroni confidence intervals.

PCA and DFA often provide complementary inferences from the same data set. PCA incorporates no information on group membership; labeling principal component scores by sex-age group occurs a posteriori. DFA specifically incorporates information on group memberships to test the equality of group centroids. Both statistical models are based on eigenanalyses and estimate a set of new "axes." In PCA, these axes correspond to the major axes of variation in the data independent of group membership. In DFA the canonical axes are estimated so as to maximize overall group separation. The two statistical models may be similar in their first or second axes if the major sources of variation in the data corresponds to differences among the group means.

Confidence limits about mean PC-scores and

TABLE 1. New means and standard deviations after missing data generated, for 15 morphological variables among 82 Tundra Swans collected January 1984, Humboldt County, California.

Variable	Immature females <i>n</i> = 11		Immature males <i>n</i> = 21		Adult females <i>n</i> = 27		Adult males <i>n</i> = 23		ANOVA results*
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	
External (mm)									
Total length	1,215.0	40.0	1,213.0	42.0	1,231.0	36.0	1,280.0	49.0	$P < 0.001$
Wing length	504.5	20.2	509.1	15.4	511.4	15.5	540.9	11.0	$P < 0.001$
Diagonal tarsus length	112.8	5.8	113.5	5.5	109.7	5.9	114.7	3.8	$P < 0.01$
Middle toe length	123.0	7.1	122.1	5.6	119.5	5.0	127.3	4.7	$P < 0.001$
Exposed culmen length	90.7	7.6	94.3	6.5	102.5	5.4	108.8	13.0	$P < 0.001$
Bill-nostril length	42.5	2.9	43.0	2.7	42.6	3.1	44.2	2.1	ns
Nail width	18.4	1.7	18.0	2.6	17.4	2.6	17.6	1.6	ns
Bill width behind nares	30.8	2.7	31.3	1.1	31.3	1.0	31.8	1.1	ns
Internal									
Gizzard weight (g)	213.4	29.9	208.3	20.2	166.7	36.6	216.6	21.7	$P < 0.001$
Spleen weight (g)	4.3	1.3	3.9	1.6	4.0	2.2	4.4	1.6	ns
Liver weight (g)	99.1	14.0	101.9	31.5	86.1	14.1	104.4	14.4	$P = 0.01$
Heart weight (g)	61.8	8.0	64.7	10.9	76.0	9.0	89.8	10.9	$P < 0.001$
Gizzard fat weight (g)	11.2	4.2	13.2	6.7	12.8	6.2	14.8	6.7	ns
Depth of back fat (mm)	6.0	3.9	7.0	4.7	7.2	3.6	7.3	2.6	ns
Pectoralis depth (mm)	32.5	7.5	36.0	6.2	36.4	8.2	36.4	6.5	ns

* Calculated prior to generation of missing data.

mean DFA-scores are based on separate rather than pooled variances for each sex-age group.

RESULTS

UNIVARIATE STATISTICAL ANALYSES

A total of 89 swans was necropsied: 23 adult males, 27 adult females, 21 immature males, and 11 immature females; the sex of six additional swans and the age of another swan could not be determined because of damage by scavengers. Generally, adult male swans were heaviest, followed by adult females, immature males, and immature females (Appendix). A similar order was noted for heart weight and wing length; however, the rankings for other weights and lengths varied (Appendix, Table 1). The ANOVA results reported in Table 1 were calculated prior to the generation of missing data points.

Yellow lores were completely absent in only five adults and absent on one side in four additional adult swans. Five immature males also had yellow lores. Lore dimensions were greater for adult males compared to immature males with yellow lores (Appendix).

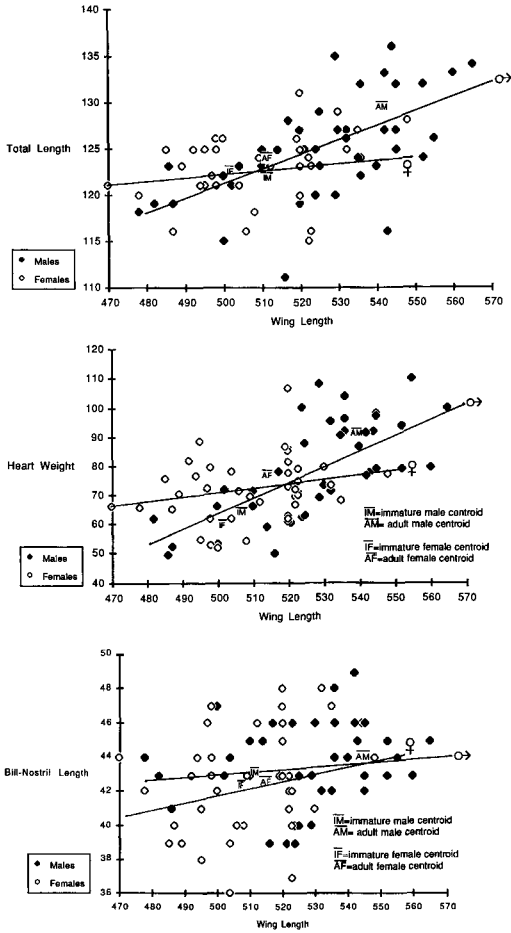
A greater frequency of immature birds (32 of 37, 87%) had pink pigmentation on the upper mandible of the bill compared to adults (3 of 50, 6%). Also, a greater proportion of adults (37 of 50, 74%) had rust stains on the head compared to immature birds (17 of 37, 46%).

The sex-age groups differed in both external and internal morphology (Table 1). Three of seven internal features and five of eight external features showed significant between-group differences. A posteriori pair-wise comparisons indicated that rejection of the null hypothesis usually was attributable to differences between adult males and adult females, and less frequently to differences between immatures and adults.

BIVARIATE STATISTICAL ANALYSIS

Most correlations indicated positive covariance among morphological features, and none of the correlations exceeded 0.62 (Table 2). Those characters with strong covariance were primarily external features related to body size. One internal morphological character, heart weight, also covaried with general measures of body size. The overall pattern of the correlation matrix suggests that we retained relatively independent aspects of the species' morphology for subsequent analysis. Estimated squared multiple correlations of each variable with the remaining 14 variables again emphasized the distinctness of these morphological characters, as only one exceeded 0.55.

Wing length in males was significantly ($P < 0.001$) and positively related to both total length and heart weight (Figs. 1a, b). In contrast, females had no significant ($P > 0.10$) association between wing length and these two characters.



Males and females were similar, however, in that no significant ($P > 0.05$) variation between wing length and bill length occurred for either sex (Fig. 1c).

Collectively, the results of the ANOVA and regression analyses suggest that the dimorphism between males and females became more pronounced as the birds matured. Bill characters were an exception to this pattern, as they did not differ among the sexes and showed no relationship to age or wing length.

MULTIVARIATE STATISTICAL ANALYSES

Principal components analysis. Based on a minimum eigenvalue of 1.0, seven principal components (PC) together accounted for 74% of the observed variation among the 15 variables (Table 3). PC-1 (18% of the variance) was charac-

FIGURE 1. Top. Relationship between total length and wing length. The lines are least squares regressions, where $y = 45.64 + 0.15x$, $r^2 = 0.31$, $F_{1,42} = 18.74$, $P < 0.001$ (male), and $y = 95.37 + 0.05x$, $r^2 = 0.06$, $F_{1,36} = 2.13$, $P > 0.10$ (female). Middle. Relationship between heart weight and wing length. The lines are least squares regressions, where $y = 214.47 + 0.56x$, $r^2 = 0.48$, $F_{1,42} = 38.77$, $P < 0.001$ (male), and $y = -8.44 + 0.16x$, $r^2 = 0.06$, $F_{1,36} = 2.35$, $P > 0.10$ (female). Bottom. Relationship between bill–nostril length (measure from the tip to the anterior end of nares) and wing length. The lines are least squares regressions, where $y = 29.03 + 0.03x$, $r^2 = 0.05$, $F_{1,42} = 2.37$, $P < 0.01$ (male), and $y = 18.42 + 0.05x$, $r^2 = 0.07$, $F_{1,36} = 2.78$, $P > 0.10$ (female).

TABLE 2. Simple correlation coefficients of 15 morphometric variables from 82 Tundra Swans collected January 1984, Humboldt County, California.

	Gizzard weight	Spleen weight	Liver weight	Heart weight	Total length	Wing length
Gizzard weight	1.000					
Spleen weight	0.146	1.000				
Liver weight	0.427	0.196	1.000			
Heart weight	0.039	0.217	0.241	1.000		
Total length	0.260	0.076	0.200	0.559	1.000	
Wing length	0.293	0.089	0.296	0.575	0.489	1.000
Diagonal tarsus length	0.256	0.163	0.304	0.251	0.336	0.306
Middle toe length	0.412	0.218	0.381	0.338	0.533	0.498
Exposed culmen length	-0.040	0.140	0.159	0.478	0.430	0.384
Bill–nostril length	0.075	0.066	0.160	0.229	0.348	0.292
Nail width	-0.020	0.193	0.054	-0.037	0.005	-0.014
Bill width behind nares	0.021	0.195	0.048	0.131	0.198	0.089
Gizzard fat weight	-0.061	0.039	0.017	0.160	0.062	0.105
Depth of back fat	-0.026	-0.028	0.189	0.207	0.033	0.211
Pectoralis depth	-0.002	-0.097	0.129	0.155	0.109	0.064

terized by extensive variation in heart weight, exposed culmen length, wing length, and total length (Table 3), PC-2 (12%) by gizzard weight and liver weight, PC-3 (11%) by diagonal tarsus length and middle toe length and to a lesser extent by bill-nostril length, PC-4 (10%) by back fat and gizzard fat, PC-5 (8%) by bill width behind nares and spleen weight, PC-6 (<8%) by pectoralis depth and bill-nostril length, and PC-7 (<8%) by nail width (Table 3). With the exception of bill-nostril length in PC-6, all factor loadings were positive.

It has been observed that if the first component of a PCA adequately characterizes size variation, subsequent components often represent residual shape variation (Flessa and Bray 1977, Grant 1986), and that such variation in shape is largely independent of size (Mosimann and James 1979, Humphries et al. 1981). Based on an examination of the factor pattern matrix, we interpret the first two components to represent body size: PC-1 as an axis of variation in general body size, and PC-2 as an axis of variation in internal body size (viscera weight). We interpret PC-3 as a shape axis representing variation in tarsus length relative to bill length, and PC-4 to be an axis of body fat. PC-5 through PC-7 appear to be additional axes of general body shape (Table 3).

Only PC-1, the primary component, was distinctly aligned along sex and age differences (Fig. 2). For PC-2, adult females varied significantly from all other groups (Fig. 2). For PC-3, adult females were significantly different from both immature and adult males. No other significant differences were found among the sex and age groups for PC-4 through PC-7.

In sum, there were significant differences in the patterns of variation among the sex-age classes with regard to body-size characteristics, viscera

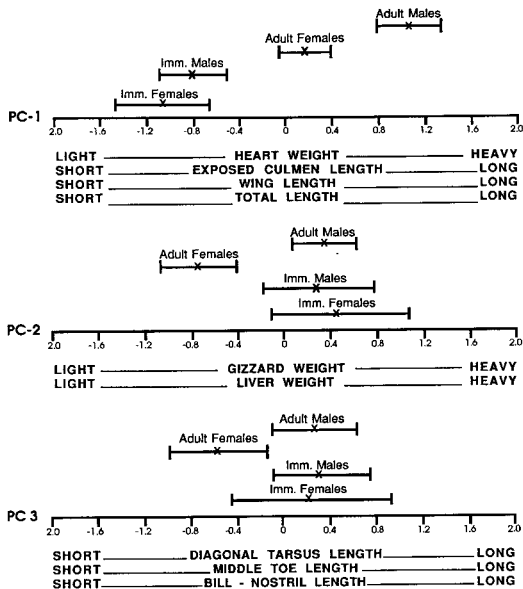


FIGURE 2. Ordination of morphometric variables along the first three principal components, partitioned by Tundra Swan sex-age groups. The mean and 95% confidence interval are illustrated for each sex-age group. Axes PC 1 and PC 2 represent gradients of body size. Axis PC 3 represents a gradient in body shape.

weights, and to a lesser extent, foot-length measures. Generally, there was little variation among the sex-age classes in bill sizes, body fat/condition (back fat, gizzard fat weight, pectoralis depth), or spleen weight.

Discriminant function analyses. A subset of five of the original 15 morphological variables was selected by the stepwise procedure (Table 4). This subset of variables, prior to the removal of any canonical variates (CV), significantly discriminated the four sex-age classes (Bartlett's $V = 103.97$; $df = 8$; $P < 0.001$; Table 5). A test of

TABLE 2. Extended.

Diagonal tarsus length	Middle toe length	Exposed culmen length	Bill-nostril length	Nail width	Bill width behind nares	Gizzard fat weight	Back fat	Pectoralis depth
1.000								
0.620	1.000							
0.171	0.373	1.000						
0.248	0.283	0.245	1.000					
-0.065	0.171	-0.021	0.021	1.000				
0.114	0.074	0.222	0.077	0.058	1.000			
0.298	0.194	0.178	-0.073	-0.010	0.038	1.000		
0.174	0.131	0.019	0.054	-0.166	-0.153	0.424	1.000	
0.147	0.231	0.188	-0.100	-0.108	0.000	0.157	0.110	1.000

TABLE 3. Rotated loadings of seven factors for 15 morphometric variables from 82 Tundra Swans collected January 1984, Humboldt County, California.

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6	Factor 7
Heart weight	0.841	0.000 ^a	0.000	0.000	0.000	0.000	0.000
Exposed culmen length	0.727	0.000	0.000	0.000	0.000	0.000	0.000
Wing length	0.713	0.315	0.000	0.000	0.000	0.000	0.000
Total length	0.696	0.000	0.394	0.000	0.000	0.000	0.000
Gizzard weight	0.000	0.801	0.272	0.000	0.000	0.000	0.000
Liver weight	0.000	0.750	0.000	0.000	0.000	0.000	0.000
Diagonal tarsus length	0.000	0.262	0.760	0.287	0.000	0.000	0.000
Middle toe length	0.392	0.390	0.646	0.000	0.000	0.000	0.253
Depth of back fat	0.000	0.000	0.000	0.809	0.000	0.000	0.000
Gizzard fat weight	0.000	0.000	0.260	0.785	0.000	0.000	0.000
Bill width behind nares	0.000	0.000	0.000	0.000	0.832	0.000	0.000
Spleen weight	0.000	0.367	0.000	0.000	0.575	0.000	0.379
Pectoralis depth	0.000	0.000	0.000	0.000	0.000	0.864	0.000
Bill-nostril length	0.411	0.000	0.480	0.000	0.000	-0.501	0.000
Nail width	0.000	0.000	0.000	0.000	0.000	0.000	0.940
Eigenvalue	2.690	1.752	1.626	1.544	1.218	1.163	1.153
Percent variance	17.9	11.7	10.8	10.3	8.1	7.8	7.7
Cumulative variance	17.9	29.6	40.4	50.7	58.8	66.6	74.3

^a Loadings less than 0.250 have been replaced by zero.

the overall significance of V is also a test for the significance of the first canonical variate (CV-1) (Green 1978, p. 304). Therefore, we proceeded to test the significance of CV-2 and CV-3 separately. Of the remaining canonical variates, only CV-2 was significant (Table 5). To measure the extent of sex-age group separation, we computed the W^2_{multi} index (Tatsuoka 1970). Over 83% of the total variability in the three canonical variates was attributable to between group differences ($W^2_{\text{multi}} = 0.832$).

The apportionment of discriminatory power across the three variates was highly inequitable. About 74% of the discriminatory power of the five predictor variables was accounted for by CV-1, 26% by CV-2, and <1% by CV-3 (Table 5). We therefore confined ourselves to an examination of the first two variates.

Nonoverlap of the confidence regions among

the adult ellipses, and among the adult and immature ellipses, indicated the pattern of group separation in the CV-1, CV-2 plane (Fig. 3). The extent of separation in this plane reflected the degree to which the sex-age groups differed in their morphologies. A posteriori, pair-wise comparisons of the equality of group centroids indicated that all groups, except immature males and females, were distinct ($P < 0.001$; $df = 5, 74$).

To further examine the pattern of group separation, all possible pairs of sex-age centroids were tested separately for equality along each canonical variate axis. Along CV-1, significant separation occurred between adult males and adult females, and between adults and immatures. However, immature males and immature females were statistically indistinguishable (Fig. 3). Adult males and adult females also were significantly separated along CV-2 (Fig. 3), adult

TABLE 4. Importance of functions in stepwise discriminant analysis for 15 morphometric variables among 82 Tundra Swans collected January 1984, Humboldt County, California.

Variable	Structure coefficients		Standardized coefficients	
	Discriminant function		Discriminant function	
	I	II	I	II
Heart weight	-0.876	0.059	-0.677	-0.121
Wing length	-0.747	0.452	-0.510	0.254
Exposed culmen length	-0.723	-0.084	-0.510	0.156
Diagonal tarsus length	-0.080	0.538	0.373	0.403
Gizzard weight	0.001	0.923	0.095	0.809

TABLE 5. Summary of multiple step-wise discriminant analysis for 15 morphological variables among 82 Tundra Swans collected January 1984, Humboldt County, California.

Characteristic	Discriminant function		
	I	II	III
Eigenvalue	2.398	0.832	0.006
Percent of eigenvalue associated with the function	74.1	25.7	<1
Cumulative percent of eigenvalue	74.1	99.8	100.0
Bartlett's <i>V</i> -statistic	103.97	51.76	0.01
Degrees of freedom	15	8	3
Significance	$P < 0.001$	$P < 0.001$	ns

females were distinct from both classes of immatures, but no other pair-wise comparisons were significant—immatures were again indistinguishable.

The biological interpretation of group separation, based on the structure coefficients, indicates that heart weight, wing length, and exposed culmen length were the key variables characterizing CV-1 (Table 4). Negative scores on this axis occurred for individuals with high values for these variables (Fig. 3). Collectively, these variables indicated a gradient of decreasing body size moving from left (negative scores) to right (positive scores). The most negative values occurred for the large-bodied adult males, and the most positive were for the relatively smaller immature birds. CV-2 also can be characterized as a body-size gradient dominated by among-group variation in gizzard weight, diagonal tarsus length, and again wing length. This axis separated adult females from all other sex-age classes primarily on the basis of their smaller gizzard weights, and additionally separated them from male swans on the basis of shorter diagonal tarsus lengths.

In summary, the adults of both sexes were clearly distinct in terms of both internal and external morphological characters, with males larger than females. The immatures differed from adults in most aspects, but not from each other.

Thus, based on the DFA, the degree of sexual dimorphism became more pronounced as the birds matured.

A direct way to test the power of the discriminating variables is to determine their accuracy in correctly predicting group membership. The power of the discriminating variables then can be determined empirically by the proportion of correct classifications.

The jack-knifed, percent correct classification was 67.1% (Table 6). Cohen's Kappa statistic ($P < 0.001$) indicated that the classification functions predicted 55% better than chance predictions based on relative group sizes. Despite the significant improvement over a chance model, the classification accuracy was highly inequitable across the sex-age classes. Adult males and adult females were accurately classified, 91.3% and 74.1%, respectively. However, immature males and immature females were poorly classified (52.4% and 27.3%, respectively). Thus, classification functions based on these five discriminating variables would perform well at classifying unknown adult samples, but would poorly classify unknown immature birds. Although the classification pattern based on external features alone was similar, the discrimination between sex-age groups was not as clear as when both external and internal features were considered.

TABLE 6. The jack-knifed, percent correct classification of Tundra Swans collected January 1984, Humboldt County, California.

	Percent correct	Immature females	Immature males	Adult females	Adult males
Immature females	27.3	3	6	1	1
Immature males	52.4	8	11	1	1
Adult females	74.1	1	4	20	2
Adult males	91.3	0	1	1	21
Total	67.1	12	22	23	25

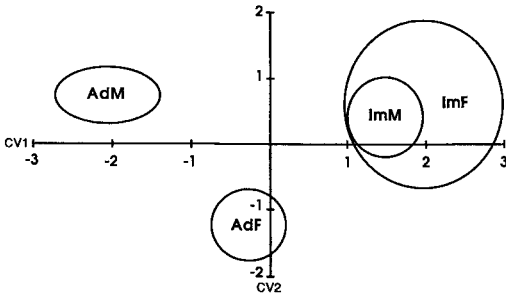


FIGURE 3. Sex-age centroids with 95% confidence ellipses of discriminant function analysis for Tundra Swans collected January 1984, Humboldt County, California. AdM = adult males, AdF = adult females, ImM = immature males, ImF = immature females.

DISCUSSION

Overall, the average sizes and weights among the Tundra Swans wintering along the north coast of California were greater than those reported for Tundra Swans wintering in other areas of North America (Nelson and Martin 1953; Banko 1960, p. 63–64; Tate 1966; Sladen et al. 1981; Limpert et al. 1987), as well as those reported for the Eurasian subspecies, Bewick's Swans (*Cygnus columbianus bewickii*), wintering in Europe (Scott 1972, p. 198–200; Evans and Kear 1978). Sexual dimorphism among adults also was noted in these reports, with adult males consistently being heavier. We are aware of no information on morphometric variation among the sex-age groups of swans on their breeding grounds.

Adult Tundra Swans, particularly adult males, were large-bodied (Fig. 2, Appendix). Large size generally appears to reduce the susceptibility of swans to most predators (Scott 1972, p. 101). Male swans usually are responsible for nest protection (Scott 1972, p. 101) and sometimes incubate the nest as a protective response against egg predators (Scott 1977, Hawkins 1986). Scott (in press) also found evidence that large male size is crucial in determining the long-term breeding success among pairs of breeding Bewick's Swans. In a brief comparative study, Scott (1980) found that parent-offspring behavior of adult and juvenile Tundra Swans was not distinguishable from that of Bewick's Swans.

Variation in body size also may affect feeding ecology. Although swans of all ages often feed together, the distinctive body sizes, particularly total length, among adult males, adult females, and immatures may help them to partition sub-

mergent food resources. There is little evidence for consistent differences in the foods used by different sex-age groups (Stewart and Manning 1958, Sherwood 1960, Nagel 1965, Tate and Tate 1966, Munro 1981). However, the greater foot lengths (tarsus, middle toe) of adult males may help partition food resources by allowing access to vegetation at depths greater than available to adult females. These morphological differences may be relevant in light of the similarity of bill dimensions among the sex-age groups.

Of all bill measures, only exposed culmen length differed consistently among any of the sex-age classes, varying significantly between immature and adult birds. This occurs because feathering extends farther forward on the top midline of the bill in young birds compared to adults (Palmer 1976, p. 73). Since exposed culmen length is measured from the tip of the bill to the first plumage on the head, it reflects changes in the pattern of feathering as the birds mature rather than variation in the size of the bill itself. Thus, Scott (1972, p. 199) found relatively large differences in culmen length between adult and immature Bewick's Swans, but only minor differences in head size (bill tip to back of skull) for the same set of birds.

Bill-size variables were similar among adult males and females, which represented an exception to the sexual dimorphism noted for most other morphological features. In contrast to our findings, Tate (1966) found a significant difference between male and female Tundra Swans for juvenile culmen length, bill-nostril length, and bill-commissural length; this was after combining adult and immature birds for each sex. However, no significant differences by sex were found for adult culmen length, nostril length and width, and bill-eye length.

If foraging has been the primary selective force influencing bill shape, as we speculate, then the common diets of the different sex and age classes should account for the observed similarities in bill dimensions.

One distinctive feature of the Humboldt County swans was the number of principal components necessary to describe the morphometric variation observed. In some bird populations, two to four components often account for 80% or more of the observed variation (Grant et al. 1985, Niemi 1985); yet, seven components accounted for less than 75% of the variation evaluated among the swans. Three possible reasons

for this observation are: (1) we compared more variables than was done in other studies, (2) swans have more independent aspects to their morphological variation, or (3) growth and maturation is a more prolonged process in swans.

PC-1, representing variation in overall body size variables, was aligned with differences among the sex-age groups, and component scores generally increased as the swans matured to adults. PC-2, representing variation in two viscera weights (liver weight, gizzard weight), was not strongly aligned with the sex-age groups. These variables attained their maximum values in immatures; among males there was no further increase, whereas there was a decline in component scores for adult females (Fig. 2). Among Canada Geese (*Branta canadensis minima*), Sedinger (1986) found that the gizzard and liver developed quickly, and reached adult sizes in goslings prior to fledging.

Unexpectedly, scores on the third principal component, represented by foot length in relation to bill length, were smallest in adult females. However, it should be noted that these scores were affected by variables other than foot and bill length (Table 3). In addition, there were no significant differences between adult and immature females for any foot or bill-size measures, except for exposed culmen length as discussed above.

The two DFA canonical variates allow a high degree of confidence in distinguishing between males and females of unknown adult birds, but do not provide much confidence in differentiating between the sexes of immature birds. Based on the DFA, immature birds, particularly females, showed a great deal of morphological variation (Fig. 3). Although it is unusual to find adult females having some bill and foot measurements with smaller reported values than found among immature females, we believe these differences are due simply to sampling variation. The small sample size ($n = 11$) of immature females may have resulted in chance collection of a few unusually large birds.

This variation in immature birds also may have been affected by environmental factors. For example, an early fall freeze would select against immature swans that hatched late or were in poor condition for other reasons. Without sufficient reserves, these birds might not survive the migration. This would tend to decrease the morphological variation among immatures. In con-

trast, with a late winter, many of these same birds may survive the migration, increasing the variation observed on the wintering grounds. Cooke et al. (1984) found that early hatched Lesser Snow Geese (*Chen caerulescens caerulescens*) goslings had significantly higher recruitment rates into the population than later hatched goslings, in 3 of 7 years.

Based on our analyses, we conclude that sexual dimorphism is minor in immatures, but pronounced in adults. We believe Tundra Swans can be classified into three morphologically distinct categories. Adult males have a relatively large body size, and are intermediate in viscera weight and foot length. Adult females are intermediate in body size, small in viscera weights, and smaller in foot lengths than adult and immature males. Immature swans are relatively small-bodied, intermediate in viscera weights, and intermediate in foot-length measures.

The patterns of dimorphism we observed were similar to those reported among Bewick's Swans in England (Scott 1972, p. 199) and among Mute Swans (*Cygnus olor*) from the west coast of Sweden (Mathiasson 1981, table 1). One important difference, however, was the more distinctive sexual dimorphism Mathiasson (1981) observed among immature Mute Swans.

Our data suggest that growth rates from immature to adulthood were significantly greater in males (Figs. 1a, b). Ricklefs (1968) reported sexual dimorphism in the growth rates of several species. Among waterfowl, published values suggest that males may grow faster in Bewick's Swans (Evans and Kear 1978), Black Swans (*Cygnus atratus*) (Braithwaite 1981), Lesser Snow Geese (Ankney 1980), and Canada Geese (Sedinger 1986).

It has been noted that, in general, the growth rates of large birds are slower than small birds (Ricklefs 1973). In the initial stages of life of relatively large-bodied birds such as swans, one would expect that not all growth needs could be met simultaneously. Available energy resources probably are directed first to meeting needs critical to survival. Ricklefs (1968) pointed out that factors affecting the survival of offspring during the growth period must constitute a strong selective force. Foot size, bill size, and gizzard size appeared to develop quickly in cygnets (Fig. 2). These body parts are most critical for effectively reaching and assimilating food resources.

In contrast, characteristics of general body size

such as total length or wing length appeared to develop more slowly. We would expect that growth of these body features can reasonably be delayed to a later time. The extensive protection of the young provided by the parent birds would reduce the immediate need for the competitive advantage conferred by a larger body size.

In summary, we speculate that the variation in body morphometry seen among the sex-age groups of Tundra Swans is a function of differential growth strategies designed to maximize the survival, and eventual reproductive success, of these birds. The degree of dimorphism observed among adult birds is apparently the result of sex-specific selection for large body size in males. Similarities in bill morphology among the sex-age groups may be a consequence of parallel selective pressure to exploit a common food resource.

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APPENDIX. Body and organ weights of Tundra Swans found dead at the mouth of the Eel River, Humboldt County, California, January 1984. Weights are in g, except total weight and eviscerated weight which are in kg; linear measurements are in mm; \bar{x} = mean; n = sample size; SD = standard deviation.

Measurement	Adult male				Adult female			
	\bar{x}	n	SD	Range	\bar{x}	n	SD	Range
Total weight	8.59	17	0.80	7.40–9.58	7.29	10	0.74	6.48–8.80
Eviscerated weight	7.40	18	0.70	6.31–8.39	6.33	11	0.67	5.69–7.70
Gizzard weight*	217.4	21	22.0	185.2–258.0	167.7	23	38.4	74.8–220.0
Spleen weight*	4.3	23	1.6	1.3–8.8	4.1	25	2.3	1.1–9.2
Liver weight*	104.5	22	14.6	74.0–135.0	86.0	26	14.4	67.9–122.1
Heart weight*	89.8	23	10.9	71.5–110.3	76.3	26	9.1	62.2–106.7
Left lung weight	66.7	22	12.2	43.3–97.4	50.3	25	13.5	29.5–94.6
Right lung weight	66.0	20	10.4	52.7–93.4	51.6	23	9.8	34.8–74.1
Total length*	1,281.4	22	15.5	1,160–1,360	1,230.3	26	12.0	1,150–1,310
Wing length*	541.5	22	11.0	520–565	511.4	27	15.5	478–535
Tarsus length	139.4	23	5.1	129–150	131.89	27	4.4	125–145
Diagonal tarsus length*	114.7	23	3.8	107–123	109.7	27	5.9	94–122
Middle toe length*	127.3	23	4.7	120–136	119.5	27	5.0	107–132
Middle toe and claw length	147.0	23	6.1	132–159	137.9	27	6.0	127–155
Girth	587.3	20	32.7	528–653	551.5	20	42.8	490–690
Bursa length	13.5	20	9.4	0–30	15.9	22	12.8	0–45
Exposed culmen length*	108.8	23	13.0	98–159	102.5	27	5.4	93–116
Bill-nostril length*	44.2	23	2.1	40–49	42.6	27	3.1	36–48
Bill-gape length	93.7	23	2.9	89–101	90.3	27	5.2	82–103
Nail width*	17.7	22	1.6	14.6–21.1	17.4	27	2.6	13.9–25.7
Bill width behind nail	32.8	23	1.5	30.2–35.3	31.3	27	3.4	17.4–33.8
Bill width behind nares*	31.8	23	1.1	28.5–33.2	31.2	25	0.94	29.1–33.2
Left lore length	19.8	20	7.9	8.2–35.5	15.8	21	7.5	7.4–32.5
Left lore width	9.1	20	3.3	4.1–15.1	9.0	21	3.6	3.0–16.9
Right lore length	18.3	22	7.8	8.0–35.0	15.8	23	8.1	7.4–39.5
Right lore width	8.5	22	3.5	3.0–16.5	7.3	23	2.7	3.8–11.4
Penis length	21.1	15	12.6	2–45	—	—	—	—
Right testes length	13.2	22	4.2	1–21	—	—	—	—
Right testes width	4.0	22	1.3	2–7	—	—	—	—
Left testes length	14.7	22	3.1	10–22	—	—	—	—
Left testes width	4.7	22	1.2	3–7	—	—	—	—
Ovary weight	—	—	—	—	1.0	24	0.83	0.4–4.3
Gizzard fat weight*	14.3	22	6.4	5.4–32.0	12.9	25	6.4	3.9–31.0
Back fat depth*	7.4	21	2.6	3–12	7.0	26	3.6	0–17
Heart fat width	29.4	23	14.5	2.4–73.5	34.6	27	17.4	16.8–85.0
Pectoralis depth*	36.4	19	6.7	26–52	35.6	21	8.7	21–51

* Morphological variables considered in subsequent analyses.

APPENDIX. Extended.

Immature male				Immature female			
\bar{x}	<i>n</i>	SD	Range	\bar{x}	<i>n</i>	SD	Range
7.17	9	0.99	5.5-8.4	6.87	7	0.83	5.4-7.9
5.94	10	0.73	4.7-6.9	5.75	7	0.77	4.8-6.8
208.7	19	21.1	152.7-246.3	215.3	9	32.0	143.6-258.0
3.9	21	1.6	1.7-7.0	4.3	11	1.3	2.2-6.3
102.6	20	32.1	22.5-170.6	100.0	10	14.4	74.4-119.1
64.7	21	10.9	49.7-99.9	61.8	11	8.0	51.8-77.0
52.1	19	10.8	28.9-73.9	46.6	9	9.8	30.4-59.8
53.8	19	13.6	34.9-80.5	46.9	9	14.5	32.4-81.8
1,214.7	19	41.9	1,110-1,280	1,220.0	10	11.9	1,160-1,280
509.1	21	15.4	478-529	505.2	10	21.2	470-548
136.8	21	6.0	126-148	134.1	11	6.1	122-144
113.5	21	5.5	102-121	112.8	11	5.8	104-123
122.1	21	5.6	111-131	123.0	11	7.1	115-135
139.2	21	6.0	127-150	139.4	11	9.3	127-159
540.1	17	40.6	475-634	539.6	9	44.8	480-610
33.6	17	13.7	0-60	35.2	11	12.0	11-55
94.3	21	6.5	81-106	90.7	11	7.6	79-101
42.9	21	2.7	39-47	42.5	11	2.9	38-47
91.6	21	6.2	81-105	91.6	11	4.2	85-99
18.0	21	2.6	14.5-26.5	18.4	11	1.7	16.0-21.5
31.8	21	1.5	28.2-34.2	31.2	11	2.3	28.0-35.5
31.3	20	1.1	29.4-33.5	30.7	11	2.7	24.6-34.1
17.5	5	5.8	12.7-27.4	—	—	—	—
8.0	5	1.9	5.4-9.8	—	—	—	—
16.6	5	5.6	13.0-26.4	—	—	—	—
7.9	5	2.3	5.5-10.5	—	—	—	—
5.3	9	3.1	3-12	—	—	—	—
10.8	19	3.2	5-17	—	—	—	—
2.4	20	0.08	1-4	—	—	—	—
14.2	20	0.82	7-26	—	—	—	—
3.3	20	3.9	1-7	—	—	—	—
—	—	—	—	0.6	9	0.33	0.2-1.3
13.4	20	6.8	4.2-25.9	10.4	9	4.3	3.3-19.0
6.9	20	4.8	0-19	5.9	10	3.0	3-11
22.4	20	7.5	8.2-42.0	20.9	11	14.0	10.8-58.9
36.0	20	6.4	24-45	32.1	10	7.8	17-44