MORPHOLOGICAL DIFFERENCES IN PACIFIC COAST POPULATIONS OF GREATER WHITE-FRONTED GEESE[1]

Dennis L. Orthmeyer and John Y. Takekawa
National Biological Survey, California Pacific Science Center,
6924 Tremont Road, Dixon, CA 95620

Craig R. Ely
National Biological Survey, Alaska Science Center, 1011 East Tudor Road, Anchorage, AK 99503

Michael L. Wege
U.S. Fish and Wildlife Service, Yukon Delta National Wildlife Refuge,
P.O. Box 346, Bethel, AK 99559

Wesley E. Newton
National Biological Survey, Northern Prairie Science Center,
8711 37th St. S.E., Jamestown, ND 58401

Abstract. We examined morphological relationships of three Pacific coast populations of Greater White-fronted Geese (*Anser albifrons*). Adult geese were captured and measured at three breeding areas in Alaska and two wintering areas in California, 1980–1991. A two-step discriminant function analysis examined morphological differences among the three populations. Stepwise discriminant function procedures created the simplest measurement models. Each sex was analyzed separately since multivariate analysis of variance indicated that males were significantly larger than females for all three populations. Tule Greater White-fronted Geese (*A. a. gambelli*) were significantly larger than Pacific Greater White-fronted Geese (*A. a. frontalis*), hereafter Pacific Geese. The first step of discriminant function analysis created models to differentiate Tule Geese from the Pacific Geese. Bivariate stepwise discriminant function models consisting of only two measurements correctly classified 92% of males (bill height, bill width) and 96% of females (bill height, culmen) of these subspecies. The second step of discriminant function analysis compared a small population of Pacific Geese from the Bristol Bay Lowlands (BBL) of southwestern Alaska with the large population of Pacific Geese that breed on the Yukon-Kuskokwim River Delta (YKD) of westcentral Alaska. We developed models with three (culmen, diagonal tarsus, midtoe) and five (culmen, diagonal tarsus, midtoe, total tarsus, bill height) measurements from stepwise discriminant function analyses to correctly classify 72% of males and 74% of females of these populations. Thus, morphology of Tule Geese differed highly significantly from Pacific Geese, as expected, but differences between populations from the BBL and YKD areas were also significant. Morphometric analyses as these provided supporting evidence for clinal variation in populations of Greater White-fronted Geese. They also underscore a need for further studies of differences among North American populations of Greater White-fronted Geese to resolve classification and to allow formulation of subpopulation/subspecies management strategies.

Key words: Greater White-fronted Goose; Anser albifrons frontalis; Tule Goose; Anser albifrons gambelli; morphometrics; discriminant function; subpopulations.

INTRODUCTION

Greater White-fronted Geese (*Anser albifrons*) have the largest breeding range of Holarctic nesting geese, and only two North American subspecies are currently recognized (Bellrose 1980, Owen 1980). More than 98% of the half million (U.S. Fish and Wildl. Serv. 1993) Greater White-fronted Geese in North America are classified as

the Pacific Greater White-fronted Goose, *A. a. frontalis* (Bellrose 1980, Wege 1984, Pacific Flyway Study Committee 1991). The majority of the Pacific coast population nests on the Yukon-Kuskokwin River Delta (YKD) of west-central Alaska and winters in the Central Valley of California (Bellrose 1980); however, two other Pacific coast White-fronted populations with different distributions have also been described.

Tule Greater White-fronted Geese (*A. a. gambelli*) breed in the Cook Inlet Lowlands (CIL) of central Alaska (Bellrose 1980, Timm et al. 1982).

Yukon Kuskokwim
River Delta

Bristol Bay
Lowlands

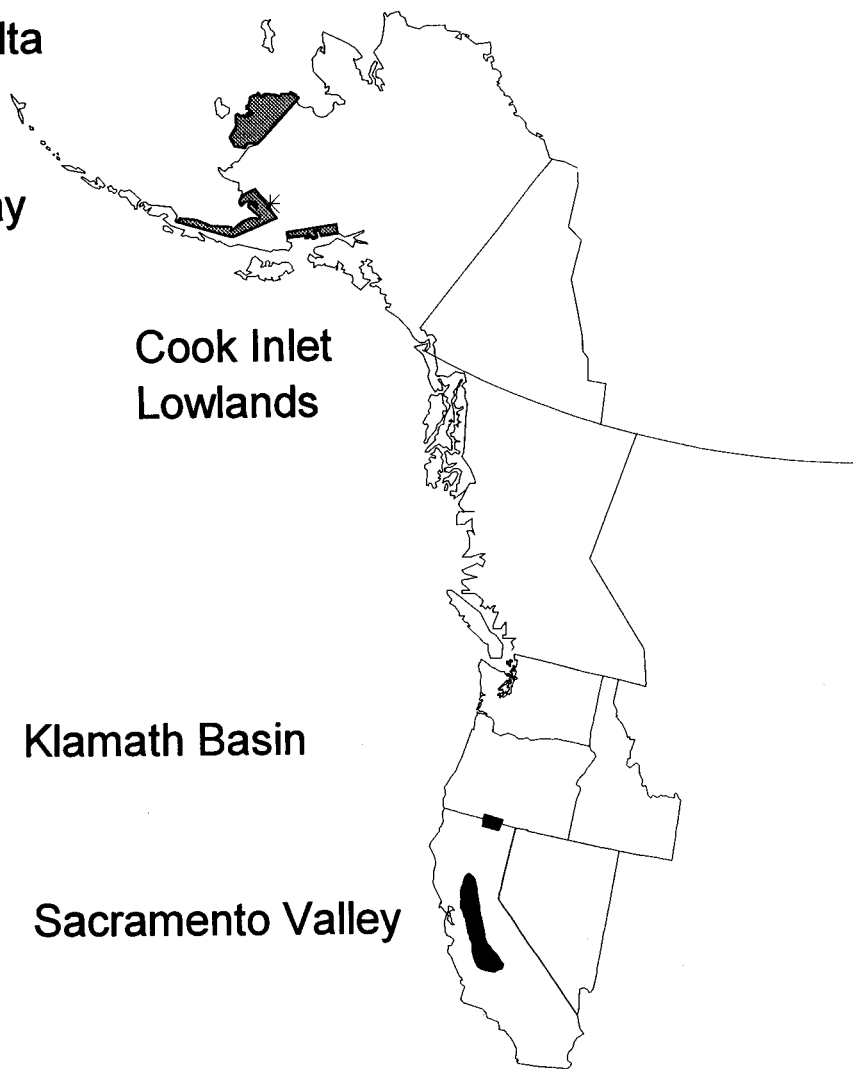Cook Inlet
Lowlands

Klamath Basin

Sacramento Valley

FIGURE 1.   Capture locations on breeding and wintering areas of Greater White-fronted Goose populations on the Pacific coast.

Their winter area is sympatric with Pacific Geese in the Sacramento Valley and Suisun Marsh of California (Bauer 1979, Wege 1984). Tule Geese segregate from Pacific Geese at roost sites and feed in wetland habitats, whereas Pacific Geese feed predominantly in agricultural fields (Moffitt 1926, Bauer 1979, Ely 1992).

Recently, a small population of Greater White-fronted Geese has been described (C. Ely and J. Takekawa, unpubl. data) that breed in the Bristol Bay Lowlands (BBL) of southwestern Alaska. BBL Geese migrate earlier than YKD Geese, arrive in late August and early September to the Klamath Basin of southern Oregon and northern California. Spatial and temporal overlap occur in late September as the remaining BBL Geese depart and the YKD Geese arrive in the Klamath Basin. BBL Geese depart mid-September to winter in central highlands of northern Mexico (Leyva-Espinosa 1993; C. Ely and J. Takekawa, unpubl. data). Winter behavior of BBL Geese is similar to that of Tule Geese (Bauer 1979), feed-

ing primarily in wetland areas although agricultural fields are readily available (Leyva-Espinosa 1993).

Three Pacific coast populations of Greater White-fronted Geese with substantial ecotypic differences have been identified (Bauer 1979; Timm et al. 1982; Wege 1984; Leyva-Espinosa 1993; C. Ely and J. Takekawa, unpubl. data), however, their relationships have not been examined. The objectives of this study are to describe morphological differences in these populations, develop measurement models to assign geese of unknown origin to the correct population, and assess whether the BBL population might represent a distinct subspecies.

METHODS

Study areas. Morphological measurements were taken on 1,142 adult geese at three Alaska breeding areas and two California wintering areas (Fig. 1). Geese were captured on breeding areas which included the Yukon Delta National Wildlife Refuge (NWR) on the YKD (July–August, 1985–1989), Togiak NWR and Alaska Peninsula/Becharof NWR in the BBL (July, 1988–1991), and Redoubt Bay on the CIL (July, 1980–1981). Captured geese were flightless except when trapped on the nest near the end of incubation on the YKD. Wintering areas included the Klamath Basin (September–October, 1987–1989) and the Sacramento Valley (October–January, 1978–1981) in California.

We trapped geese in drive nets on breeding areas and under rocket nets (Dill and Thornsberry 1950) on wintering areas. Dial calipers were used to take length measurements to the nearest 0.1 mm and mass was estimated with a spring scale to the nearest 10 g. Prior to combining the measurement data sets of CIL, BBL, and YKD Geese from different locations, the data were tested for statistical differences. Geese captured in the Klamath Basin prior to 23 September were designated as BBL Geese and geese captured after 14 October were designated as YKD Geese (Ely and Raveling 1989; Takekawa et al. 1990; Leyva-Espinosa 1993; Ely and Takekawa, unpubl. data).

Morphological measurements. Nine structural measurements were taken consistently (Baldwin et al. 1931, Dzubin and Cooch 1992): body mass in grams, length of the flattened wing, length of head from bill tip to hindmost point on occiput, total tarsus length from medial condyle of tarsus to rounded portion of distal condyles of tibia, length of tarso-metatarsus or diagonal tarsus, length of midtoe without nail, length of exposed culmen (culmen length), bill height at base of bill, and bill width at base of bill. Morphology characteristics evaluated subjectively (e.g., plumage color, eye ring color) or measurements that could not be taken during the annual cycle (e.g., primary length and flat wing due to molt) were not included in the analyses.

Statistical analyses. Summary statistics were calculated for each population and sex combination, and simple Pearson correlation coefficients (Steel and Torrie 1980) were computed among measurements. We used two-way multivariate analysis of variance (MANOVA) techniques (Johnson and Wichern 1988, SAS Institute 1990) to compare differences among sexes, populations, and their interaction. Flat wing and head length measurements were excluded from the MANOVA test because of missing values for some combinations. Univariate analysis of variance (ANOVA) tests were conducted for each measurement. Detection of significant ANOVA differences were followed by pairwise comparisons using Fisher's protected Least Squares Difference test (Milliken and Johnson 1984) for effects with more than two levels.

We computed Mahalinobis distances (Johnson and Wichern 1988) to examine differences in sex and population centroids. Canonical variate analysis (Mardia et al. 1979, SAS Institute 1989, Srivastava and Carter 1983) was used to illustrate separation of populations in bivariate plots (Wilkinson 1990).

We took a two-step approach to the discriminant function analysis (Johnson and Wichern 1988), similar to the two-step approach used by Johnson et al. (1979) to examine subspecies differences. In the first step of the discriminant function analysis, Tule Geese were compared with Pacific Geese from the BBL and YKD populations combined. We randomly selected 10 observations from the combined CIL, BBL, YKD data set from each sex and population combination to create the test set. The remaining observations (training set) were used to develop the discriminant function, and the test set was used to test the discriminant functions created by the training set. We used the procedure PROC DISCRIM (SAS Institute 1990) to create three classification error rates (1) train—apparent error rate, (2) train Lachenbruch's holdout—jacknifing, and

(3) test apparent error rate. Prior to beginning the discriminant analysis we excluded observations where morphological measurements were missing.

We used two procedures to select the best discriminant function model. The first was to use stepwise discriminant function techniques (Srivastava and Carter 1983) to determine if a reduction in the number of morphological variables was possible in the discriminant function and yet still obtain good classification based on classification error rates. A variable was included in the stepwise discriminant function procedure if it was significant in the discriminant function model and $R^2 \geq 0.10$. The second, used in conjunction with stepwise selection was to compare the apparent error rate for test and training datasets. Lachenbruch's holdout error rate for the training dataset was also used to compare among discriminant functions (Lachenbruch and Mickey 1968, Lachenbruch 1975).

In the second step of the discriminant function analysis, we compared measurements of Pacific Geese from the BBL and YKD populations. The statistical analyses were the same as in the first step, except that more observations were available for each sex and population combination in the test dataset (50) as we used population means to replace missing measurement values (< 10%) (see Krogman 1973, Miller et al. 1988).

RESULTS

COMPARISONS

No morphological differences in the location and sex interaction were indicated by MANOVA in CIL (Alaska $n = 78$, California $n = 133$; Wilks' $\lambda = 0.9618$; $F = 1.566$, df = 4, 158, $P = 0.1857$), BBL (Alaska $n = 337$, California $n = 1,121$; Wilks' $\lambda = 0.9817$; $F = 0.9503$, df = 5, 256, $P = 0.4490$), and YKD (Alaska $n = 47$, California $n = 426$; Wilks' $\lambda = 0.9748$; $F = 1.495$, df = 5, 290, $P = 0.1913$) measurement data from Alaska and California. Thus, we combined the data sets from different locations of CIL, BBL, and YKD Geese for the following analyses.

Pearson correlation coefficients among measurements were significantly different from zero ($r = 0.50$ to 0.75, $P < 0.0001$); however, correlation coefficients were highly variable among the different sex and population combinations. Since diagonal tarsus and total tarsus were highly correlated ($r > 0.56$, $P < 0.0001$) for all combinations of sex and populations, correlated

measurements were not deleted from the following analyses.

The MANOVA test indicated that morphological differences (Table 1) by sex (Wilks' $\lambda = 0.6233$; $F = 64.34$, df = 6, 639, $P < 0.0001$) and population (Wilks' $\lambda = 0.3106$, $F = 84.57$, df = 12, 1,278, $P < 0.0001$) were significant, whereas their interaction was not (Wilks' $\lambda = 0.9851$, $F = 0.7987$, df = 12, 1,278, $P > 0.6522$). All variables used in the MANOVA differed between sexes and among populations ($P < 0.0001$) in univariate ANOVA tests, and none of the interactions were significant ($P > 0.05$).

Males were consistently larger than females across all measurements ($P < 0.0001$, Table 1). Measurement differences between male and female geese averaged 5.9% including mass (10.4%), flat wing (4.3%), head length (6.4%), total tarsus (4.8%), diagonal tarsus (5.0%), midtoe (4.6%), culmen length (6.2%), bill height (6.2%), and bill width (4.8%). Consequently, separate canonical variate and discriminant function models were done for male and female geese.

Fisher's protected Least Square Difference test indicated there were distinct size differences in geese from each of the three populations ($P < 0.0001$). Geese in the CIL population were 10.8% larger than geese from the BBL and YKD populations (Table 1), especially in mass (24.2%), culmen length (11.3%), bill height (15.4%), and bill width (13.4%). The BBL population was significantly larger than the YKD population by 1.9% inlcuding mass (5.4%), total tarsus (1.9%), diagonal tarsus (1.4%), culmen length (1.4%), and bill height (1.3%), but differences between midtoe measurements were not significant ($P = 0.8105$).

Although mass was significantly different between sexes and among populations (Table 1), mass varied widely among seasons and different days within a season. Ely and Raveling (1989) reported large annual variation in body mass of Greater White-fronted Geese. Therefore, mass was excluded from canonical variate and discriminant function analyses because mass could not be adjusted for seasonal changes. Flat wing and head length measurements also were excluded from further analyses because sufficient samples were not available for every population.

CANONICAL VARIATE ANALYSIS

Canonical variate analysis differentiated the CIL population from BBL and YKD populations for both sexes (Table 2). Canonical variate 1 ac-

TABLE 1.   Measurements (mm) and weights (g) of adult Greater White-fronted Geese from three Pacific Coast populations (1979–1989). Superscript letters following variable names report results of the ANOVA on sex effect, population effect, and their interaction, where A indicates a significant difference ($P \leq 0.05$), and B represents a nonsignificant result ($P > 0.05$). Letters (a, b, c) following means indicate significant differences ($P \leq 0.05$) among populations. If the letters are the same no difference occurred (Fisher's protected Least Square Difference tests). Head length data not collected in earlier studies (CIL).

Area variable	Yukon Kuskokwim Delta			Bristol Bay Lowlands			Cook Inlet Lowlands		
	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD
				Males					
Weight[A,A,A]	217	2,255.0a	179.00	141	2,408.0b	223.00	105	3,010.0c	359.00
Flat wing[A,A,B]	168	431.0a	12.60	65	428.0b	13.10	70	443.0c	11.00
Head length[A,A,B]	—	—	—	72	110.0	3.80	—	—	—
Total tarsus[A,A,B]	152	88.4a	3.81	143	89.4b	3.66	74	91.7c	2.83
Diagonal tarsus[A,A,B]	182	75.8a	3.69	126	76.8b	3.26	98	82.0c	3.39
Mid toe[A,B,B]	147	68.5a	2.94	87	68.6a	2.23	98	74.7b	3.71
Culmen[A,A,B]	201	51.4a	2.57	143	53.0b	2.58	105	58.5c	2.98
Bill height[A,A,B]	150	24.8a	1.52	136	25.3b	1.35	74	28.6c	1.82
Bill width[A,A,B]	152	24.4a	1.08	136	24.7b	1.20	71	27.5c	1.17
				Females					
Weight[A,A,A]	247	2,000.0a	164.00	204	2,114.0b	178.00	83	2,776.0c	217.00
Flat wing[A,A,B]	156	411.0a	14.60	66	413.0b	17.60	39	422.0c	11.60
Head length[A,A,B]	14	102.0a	4.33	86	103.0b	2.89	—	—	—
Total tarsus[A,A,B]	187	83.7a	3.58	206	85.3b	3.45	44	87.6c	2.63
Diagonal tarsus[A,A,B]	178	71.6a	3.00	155	72.6b	2.82	71	78.7c	2.92
Mid toe[A,B,B]	167	65.9a	3.54	121	65.0a	4.23	71	71.1b	2.92
Culmen[A,A,B]	228	48.4a	2.32	206	49.1b	2.36	78	55.3c	2.76
Bill height[A,A,B]	167	23.3a	1.37	171	23.6b	1.35	44	26.9c	1.54
Bill width[A,A,B]	183	23.2a	0.92	171	23.4b	1.01	39	26.3c	1.17

counted for 98% of intergroup differences for males and females (Fig. 2). Relative loadings of standardized canonical coefficients for both sexes (Table 2) indicated that all measurement variables except total tarsus contributed to canonical variate 1, while total tarsus contributed to most of the variation explained in canonical variate 2. Significant separation occurred among all three populations for canonical variate 1 means for females (ANOVA $F = 371.18$, df = 2, 320, $P < 0.0001$) and males (ANOVA $F = 296.41$, df = 2, 324, $P < 0.0001$), while the separation for canonical variate 2 means were marginal for females (ANOVA $F = 7.95$, df = 2, 320, $P < 0.0001$) and males (ANOVA $F = 4.64$, df = 2, 324, $P < 0.0103$).

DISCRIMINANT FUNCTION ANALYSIS

No differences were detected between the training and test data sets (Wilks' $\lambda = 0.9955$, $F = 0.4735$, df = 6, 633, $P > 0.8282$), nor did the datasets interact with either sex (Wilks' $\lambda =$

TABLE 2.   Relative loadings of standardized canonical coefficients of canonical variates (CV1) and (CV2) for male and female Greater White-fronted Geese from three populations. Values indicate the relative contribution of a morphological measurement to canonical axes 1 and 2.

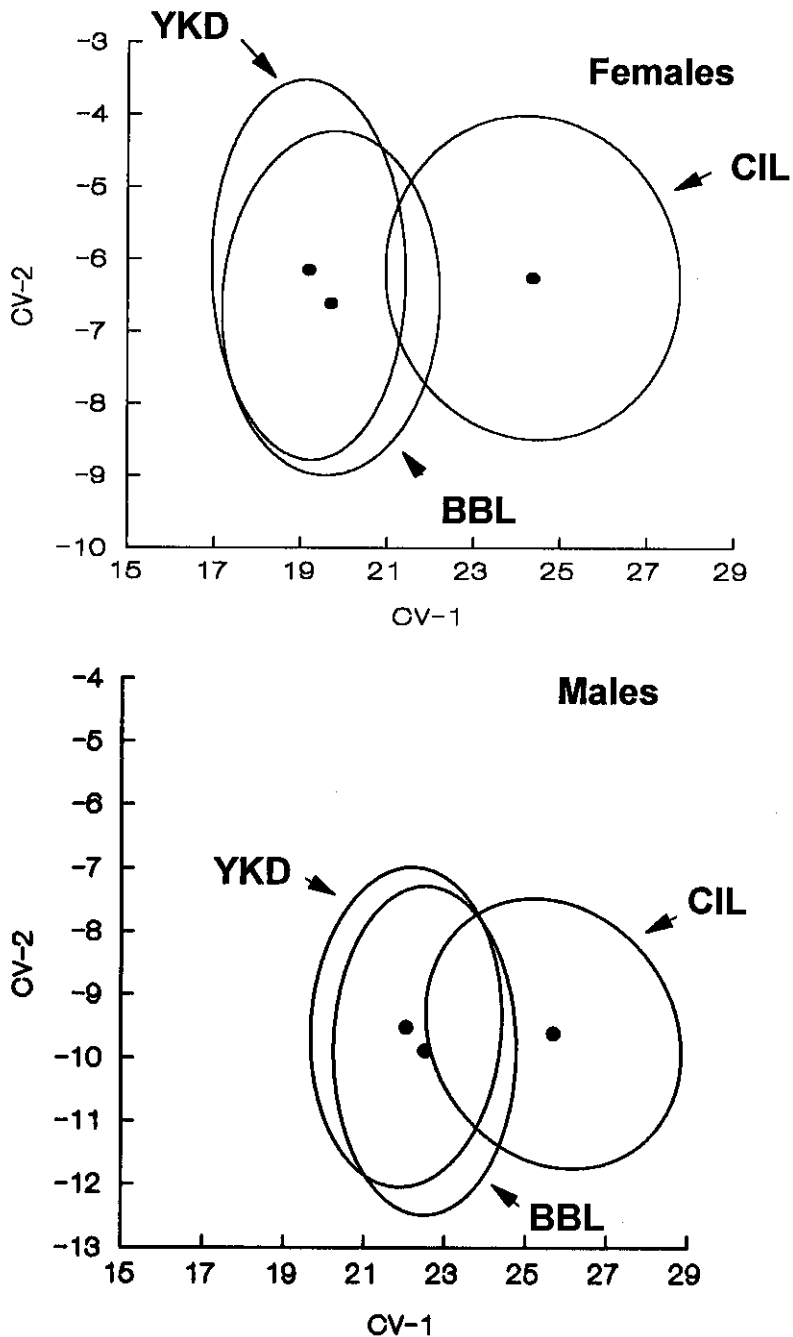| Measurement	Male		Female	
	CV1	CV2	CV1	CV2
Total tarsus	−0.5393	−1.0736	−0.3806	−1.1630
Diagonal tarsus	0.4257	0.4220	0.5562	0.1368
Mid toe	0.2531	0.7334	0.1356	0.6581
Culmen	0.5891	−0.8234	0.5338	−0.1790
Bill height	0.4313	−0.0307	0.4728	0.2025
Bill width	0.7549	0.4300	0.5965	−0.1005

FIGURE 2.   Plots of centroids on two canonical variate axes (CV1, CV2) for female and male Greater White-fronted Geese on the Pacific coast. Centroids for populations from three breeding areas in Alaska are represented including the Cook Inlet Lowlands (CIL), Bristol Bay Lowlands (BBL), and Yukon Kuskokwim River Delta (YKD). Canonical variate axes are derived from six morphological measurements.

FEMALES

CULMEN (mm)

BILL WIDTH (mm)

Columns: 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60
Rows: 21 22 23 24 25 26 27 28 29 30

MALES

BILL HEIGHT (mm)

BILL WIDTH (mm)

Columns: 20 21 22 23 24 25 26 27 28 29 30 31 32
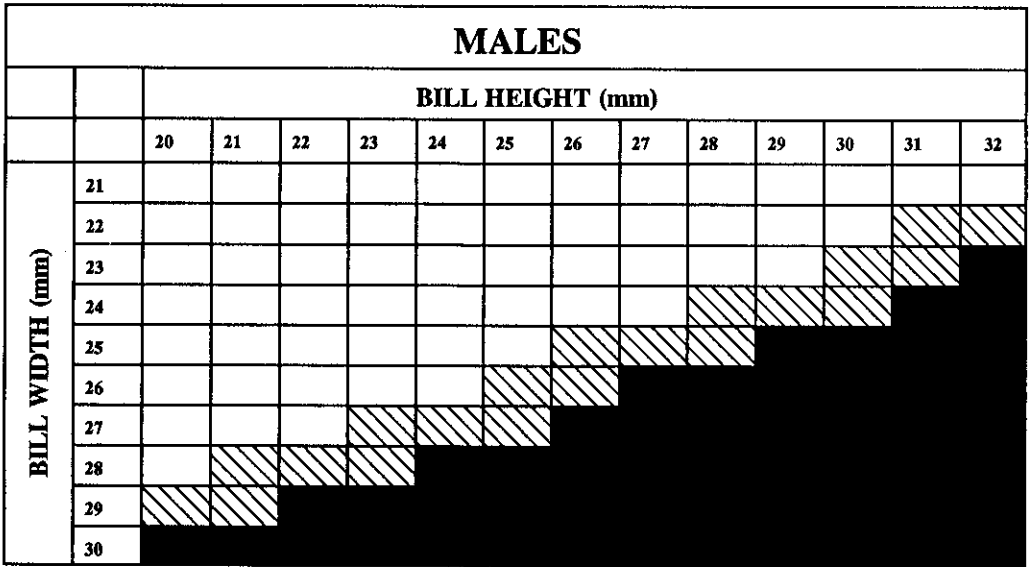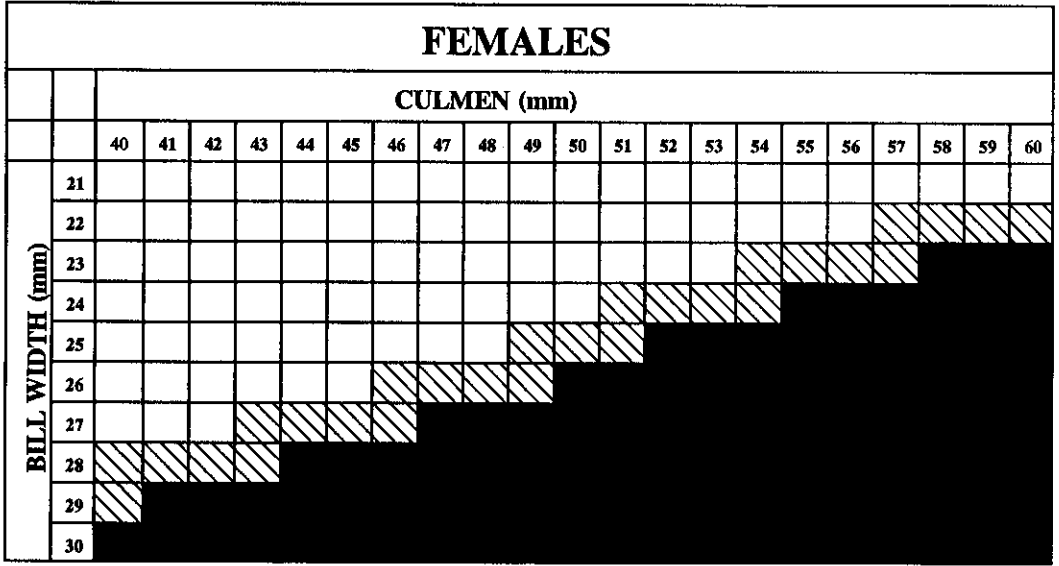Rows: 21 22 23 24 25 26 27 28 29 30

FIGURE 3.   Simple classification chart to separate adult male and female Tule Geese from other Greater White-fronted Geese with two structural measurements. Geese with two measurements which intersect in the shaded area are Tule Geese. Geese with measurements intersecting in the hatched area should be identified with the appropriate discriminant function model (see text).

0.9930, $F = 0.7397$, df = 6, 633, $P > 0.6178$) or population (Wilks' $\lambda = 0.9872$, $F = 0.6780$, df = 12, 1,266, $P > 0.7739$).

First discriminant function analysis. Only two measurements were required to separate Tule Geese and Pacific Geese in the stepwise discrim-inant analysis. The highest classification was pro-vided by the bill width and culmen length model for females, while a bill width and bill height model was used for males. Thus, we developed the following discriminant function models to distinguish Tule Geese from Pacific Geese:
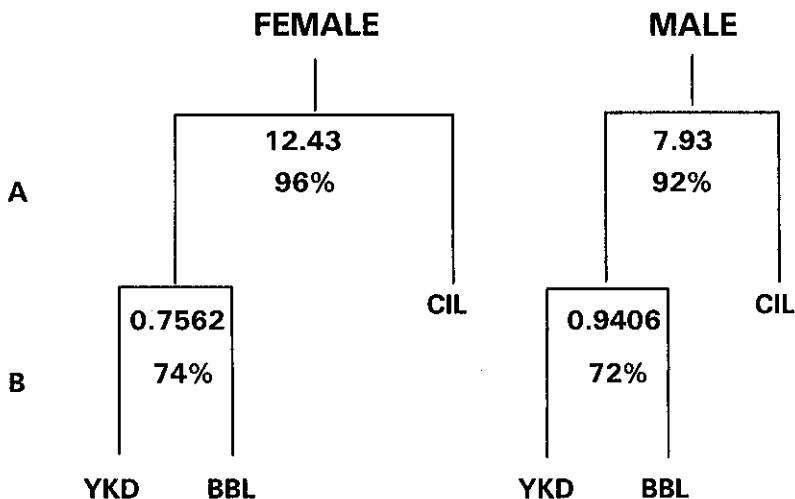
FIGURE 4. Overall correct classification rates (%) and relative Mahalanobis distances for two discriminant function models separating Pacific coast populations of Greater White-fronted Geese. Alaskan breeding areas include the Cook Inlet Lowlands (CIL), Bristol Bay Lowlands (BBL), and Yukon Kuskokwin River Delta (YKD). The first model (A) depicts separation of Tule and Pacific Goose subspecies, while the second model (B) depicts differences between Pacific Goose populations. Relative separation of Mahalinobis distances are not comparable between models.

$$Y_{female} = 2.479(\text{bill width}) + 0.889(\text{culmen length}) - 108.045$$

$$Y_{male} = 1.692(\text{bill width}) + 0.986(\text{bill height}) - 70.417$$

where $Y \geq 0$ if the individual is a Tule Goose.

TABLE 3. Percentage of male and female Greater White-fronted Geese from the Bristol Bay Lowlands (BBL), Cook Inlet Lowlands (CIL), and Yukon-Kuskokwim Delta (YKD) areas classified correctly in discriminant function models. Error rates included test error rate (TER), apparent error rate (AER), and holdout or Lachenbruch error rates (LER). Model 1 compared the CIL population with BBL and YKD populations from two measurements for both sexes. Model 2 compared BBL and YKD populations from five measurements for males and three measurements for females.

Model	Population	Sex	% Classified correctly		
			TER	AER	LER
1	CIL	Male	100	90	90
		Female	100	96	96
	BBL and YKD	Male	95	94	94
		Female	99	97	97
2	BBL	Male	74	75	74
		Female	68	75	75
	YKD	Male	63	70	70
		Female	76	75	74

Classification charts (Fig. 3) were produced from discriminant function models. Classification error rates (Table 3: Model 1) determined from test datasets varied from 0–10%, but correct classification averaged 96% for females and 92% for males. Mahalinobis distances computed for the group centroids (Fig. 2) indicated a greater separation for females (12.4) than for males (7.9).

Second discriminant function analysis. Several measurements were required to separate Pacific Geese populations with stepwise discriminant analysis. Models with three (culmen length, diagonal tarsus, midtoe) and five (culmen length, diagonal tarsus, midtoe, total tarsus, bill height) measurements were developed from stepwise discriminant analyses to separate males and females of these populations. The discriminant function models which distinguished Pacific Geese from BBL and YKD populations were:

$$Y_{female} = 0.121(\text{culmen length}) + 0.131(\text{diagonal tarsus}) + 0.075(\text{total tarsus}) + 0.174(\text{midtoe}) + 0.252(\text{bill height}) - 18.732$$

$$Y_{male} = 0.278(\text{culmen length}) + 0.128(\text{diagonal tarsus}) - 0.080(\text{midtoe}) - 18.801$$

where $Y \geq 0$ if the goose was from the BBL population. The overall correct classification rate (Table 3: Model 2) for this discriminant function

model was 74% for females and 72% for the males. Mahalinobis distances computed for the group centroids indicated a greater separation for males (0.94) than for females (0.76), but separation between these two populations was an order of magnitude smaller than the subspecies separation.

DISCUSSION

The Tule Goose subspecies was morphologically distinct from other Pacific Geese for more than 90% of the observations. Correct classification by the discriminant function models exceeded 75%, a level of taxonomic separation which has been used to distinguish subspecies in the past (Amadon 1949). Tule Geese were successfully separated from other Pacific Geese with only two structural measurements.

Morphological differences between these subspecies were previously reported by Krogman (1973, 1979). However, Krogman's (1979) analysis was completed prior to discovery of the Tule Goose breeding area (Timm et al. 1982), and it relied on a small number of samples and few live specimens. Krogman's model also was difficult to use because it included subjective measurements such as plumage coloring, and he did not report misclassification error rates for the analysis.

Our discriminant function analyses were limited to six measurements. Similar morphometric analyses on Canada Goose subspecies (Johnson et al. 1979, Moser and Rolley 1990) and Mallard (*Anas platyrhynchos*) strains (Byers and Carey 1991) were successful in discriminating populations when limited to five measurements or less. These analyses showed that taking basic measurements consistently among populations was more important than acquiring numerous additional measurements. More birds should be measured in areas where more than one population (Tules, BBL, or YKD) may be sympatric such as the Innoko River of central Alaska and the Old Crow Flats (Elgas 1970) in the Yukon.

We also detected significant differences in all nine morphometric variables between BBL and YKD populations of Pacific Geese, although differences were relatively small (< 2%). We correctly classified 72–74% of the BBL and YKD observations in discriminant function models with three or five measurements (Fig. 3), but correct classification rates may have been related to large sample sizes (Lachenbruch 1975). When

supported by ecotypic differences including discrete breeding, migration, and wintering areas (Ely and Takekawa, unpubl. data), differing habitat use (Leyva-Espinosa 1993), and body mass differences (Ely and Raveling 1989), the BBL population seems to be a distinct subspecies from the YKD population (Mayr and Ashlock 1991, Ratti 1980).

However, recent discussions about the biological species concept (O'Brien and Mayr 1991) recommend including genetic testing prior to delineating new subspecies. We agree that delineation of Greater White-fronted Goose subspecies should include genetic analysis, either protein electrophoresis or restriction enzyme analysis of mitochondrial DNA (see Cronin 1993). Classification of Holarctic Greater White-fronted Goose populations will not be resolved without systematic studies throughout the range of the species (Johnson et al. 1979) including morphometric, genetic and ecologic investigations (Wilson 1992) that verify intergradation or clinal variation (Endler 1977). Our analysis of Pacific coast population morphometrics is a first step in that process.

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