
Anthropometric Variation Among Bering Sea Natives

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Abstract Recent research indicates that anthropometrics can be used to study microevolutionary forces acting on humans. We examine the use of morphological traits in reconstructing the population history of Aleuts and Eskimos of the Bering Sea. From 1979 to 1981, W. S. Laughlin measured a sample of St. Lawrence Island Eskimos and Pribilof Island Aleuts. These samples included adult participants from St. George and St. Paul in the Pribilof Islands and from Gambell and Savoonga on St. Lawrence Island. The Relethford-Blangero method was used to examine the phylogenetic relationship between Aleuts and Eskimos. Anthropometric measurements for Native North Americans (measured by Boas and a team of trained anthropometrists in 1890–1904) and Native Mesoamericans (compiled from the literature for 1898–1952) were used for comparison. A principal components analysis of means for measurements and a neighbor-joining tree were constructed using Euclidean distances. All these tests revealed the same strong relationship among the focus populations. The *R* matrix from the Relethford-Blangero method clusters Aleuts and Eskimos separately and accounts for 97.3% of the variation in the data. Phenotypic variation within the population is minimal and therefore minimum F_{ST} values are low. Genetic distances were compared to a Euclidean distance matrix of anthropometric measurements using a Mantel test and gave a high but not significant correlation. Our results provide evidence of a close phylogenetic relationship between Aleut and Eskimo populations in the Bering Sea. However, it is apparent that history has affected the relationship among the populations. Despite previous findings of higher European admixture in Gambell (based on blood group markers) than in Savoonga, Savoonga has greater within-group variation in anthropometric measurements. Anthropometrics reveal a close relationship between Gambell and St. Paul as a result of European admixture. The St. George population was the most divergent of the populations, indicating that it diverged from the Eskimos and St. Paul because of the compounding effects of genetic drift and limited European gene flow. These findings are in agreement with previous anthropometric and genetic studies of the Aleut and Eskimo populations and support the utility of anthropometrics in inferring population history and structure.

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Recent studies of both living and ancient populations have indicated that anthropometrics, much like genetic markers, can be applied to the study of microevolutionary forces acting on human groups (Gonzalez-Jose et al. 2007; Relethford 1996; Relethford and Blangero 1990; Relethford and Harpending 1994; Relethford et al. 1980, 1997; Scherer 2007; Williams-Blangero and Blangero 1989). Although anthropometric traits are affected by environmental factors, some have high heritabilities and adequately reflect the phylogenetic histories of populations (Devor et al. 1986a, 1986b). The main goal of this study is to determine the efficacy of anthropometric measurements (collected on the Aleut and Eskimo populations of the Bering Sea) for inferring population history and substructure. The Aleuts and Eskimos offer a unique opportunity to test these claims because much is known about their recent history and because of the growing pool of archaeological data and molecular genetic data that informs researchers of the prehistoric relationship. This efficacy will be tested while answering the following two questions: (1) How have history and evolution shaped the relationship of Aleut and Eskimo populations residing in the Bering Sea? (2) What is the historical and genetic relationship of Aleuts and Eskimos to other Native American populations as inferred from anthropometrics? To answer these questions, we compare anthropometric measurements for Aleuts from the Pribilof islands of St. Paul and St. George with those of Eskimos from the St. Lawrence Island locations of Gambell and Savoonga (Figure 1).

Laughlin and Harper (1979) proposed, on the basis of linguistic, cultural, craniometric, and genetic evidence, that Aleut and Eskimo populations share recent common ancestry. Aleut and Eskimo languages belong to the same language family (Eskimo-Aleut), which, based on glottochronology estimates, diverged between 5,000 and 11,000 years ago (Greenberg et al. 1985). Both groups traditionally relied on open-sea hunting technology and sea mammals for their subsistence, used rain-resistant gut clothing, and shared other technology and cultural items (Laughlin 1980). The Aleuts and Eskimos are similar in appearance and have relatively high sitting heights, medium to submedium stature, and small hands and feet. These physical characteristics are considered cold-climate adaptations that prevent loss of body heat (Laughlin 1980). Aleuts and Eskimos have similar frequencies of blood group markers (ABO, MNS, and Rhesus systems), other classic genetic markers (Laughlin 1980; Rychkov and Sheremetyeva 1972), and molecular genetic markers, including mitochondrial DNA haplogroups A and D (Merriwether et al. 1995; Rubicz et al. 2003; Saillard et al. 2000). The Aleuts exhibit high frequencies of haplogroup D and lower frequencies of haplogroup A, whereas the Eskimos have a high frequency of haplogroup A and a much lower haplogroup D frequency.

Aleuts of the Pribilof Islands: Communities of St. Paul and St. George

At the time of Russian discovery in 1786, the Pribilof Islands were uninhabited (Lantis 1984). However, the Aleuts apparently knew of the existence of



Figure 1. Locations of the St. Lawrence Island Eskimo communities of Gambell and Savoonga and the Aleut communities of St. Paul and St. George in the eastern Bering Sea. Map created using Online Mapping Creation (Weinelt 1996).

these islands, as legends tell of their accidental discovery by the son of an Unimak Island chief (Torrey 1983). As the summer residence and breeding grounds of the northern fur seal, the Pribilof Islands were of great commercial interest to the Russians, particularly after the collapse of the sea otter population in the Aleutians caused by overhunting.

The Russians relocated Aleut hunters from Umnak and Unalaska islands in the eastern Aleutians to the Pribilofs (Black 1983), where they were forced to harvest fur pelts. Fortunes were made by both the fur trading companies operating in the area and the Russian treasury, until 1796 when the fur seal population was nearly decimated (Torrey 1983). The harvest continued indiscriminately until 1848, at which time protection was afforded to female seals to replenish the herds. In 1825, the village of St. Paul was established at its current location, and in 1830 the village of St. George was consolidated at its current location.

In 1867, the United States purchased Alaska from Russia, and with it came the Aleutian and Pribilof islands and their inhabitants (Lantis 1984). The Aleuts

of the Pribilof Islands officially became U.S. citizens, although they were still required to hunt fur seals, first for the Alaska Commercial Company and later for the U.S. Department of Fisheries. By 1874 there were 222 Aleuts living on St. Paul and 118 on St. George. Although the population size has fluctuated over time, St. Paul has always had the larger number of individuals.

At the start of U.S. involvement in World War II in 1942, the Japanese invaded the Aleutian Islands and captured the entire community of Attu. As a result, all remaining Aleut communities in the Aleutians and Pribilofs were evacuated and placed in camps in southeast Alaska. The Pribilof Aleuts, numbering 477, were taken to Funter Bay, located west of Juneau, and placed under the charge of the U.S. Fish and Wildlife Department (Kolhoff 1995). The Office of Indian Affairs was responsible for all other relocated Aleut communities. Conditions in the camps were poor; nonetheless, Aleuts were kept there for the duration of the war. In 1943, Pribilof Aleut men and schoolboys were permitted to return to St. Paul and St. George to do their part for the war effort by participating in the seal harvest. By 1944, all Pribilovians had returned home, and by June 1945 all Aleuts who wished to return were repatriated.

Upon their return, the Pribilof Aleuts struggled for independence, establishing their own village-level governments in the 1960s and gaining legal title to their land in the 1970s (Torrey 1983). By 1970, the Pribilof Aleut communities numbered 613 individuals (428 on St. Paul and 156 on St. George), with only 29 non-Aleut residents. More recently, an estimated 500 individuals have been living on St. Paul and 250 individuals have been living on St. George, with an increasing number of non-Aleuts entering the region as a result of easier access to the islands through commercial air travel and the promise of employment in the crabbing and fishing industries.

The Yupik Eskimos of St. Lawrence Island: Communities of Gambell and Savoonga

St. Lawrence Island, in contrast to the recently settled Pribilofs, has a long prehistory of occupation by sea-mammal-hunting Eskimo peoples. Archaeological excavations indicate that approximately 2,000 years ago the Okvik and Old Bering Sea cultures appeared on St. Lawrence Island, followed by the Punuk culture a few hundred years after that and a more recent intrusion of Thule influences (Hughes 1984). Maritime resources have always been important to the island's inhabitants, although residents appear to have relied increasingly on whaling during the later cultural phases (Collins 1964). Traditionally, and because of their geographic proximity to Siberia, the St. Lawrence Island Eskimos have had closer cultural ties to their Siberian rather than to their Alaskan neighbors. Their linguistic dialect belongs to the Siberian Yupik branch of the Eskimo language. Before European contact, there were about 35 villages and seasonal camps around the island (Byard 1981).

After Vitus Bering's first sighting of St. Lawrence Island in 1728, a number of other Russian and European explorers noted its presence/and or made contact with the island's inhabitants (Hughes 1984). By the mid-1800s commercial whaling stations had been established in and around the North Pacific Ocean and the Bering and Chukchi seas. Commercial whaling had a significant impact on the peoples of St. Lawrence Island. Although it is uncertain whether any shore stations were established on St. Lawrence by the whalers, it is clear that the inhabitants were involved in commerce with whaling vessels. Water, clothing, baleen, and ivory were exchanged for alcohol, firearms, and whaling equipment. Disease was also spread to local populations, often with devastating consequences.

Before 1878, an estimated 1,500 individuals were residing on St. Lawrence Island. A severe famine, which struck in 1878, significantly reduced the population, however (Byard 1981; Hughes 1984). An estimated two-thirds of the island's inhabitants perished. Depletion of whales and walrus by commercial whaling vessels appears largely responsible for the depopulation, but other factors that may have played a role include disease, alcoholism, reliance on trade goods (rather than on storage of local foods), and unique climatic and hunting conditions. The survivors gathered in the village of Sivokak, which was later renamed Gambell, and they recruited additional migrants from mainland Siberia. In 1880, only 500 individuals remained in Gambell, and the St. Lawrence Island population continued to decline until it reached its nadir of 222 people in 1917 (Byard 1981).

Recovery of the population was facilitated by the decline of commercial whaling, which began in the 1880s (Byard 1981). In addition, reindeer were introduced to the island in 1900, and efforts were made to convert the hunters to herders. Younger individuals were chosen for this task, as they were more "progressive." They followed the herds to better pasture, eventually establishing (in 1917) the village of Savoonga 40 mi east of Gambell. By 1920, 183 individuals were living in Gambell and 95 in Savoonga. Despite its lower population size Savoonga had nearly an equivalent breeding size to Gambell, allowing Savoonga's population size to eventually surpass Gambell's. By 1978, there were 402 individuals living in Gambell and 425 in Savoonga.

Analysis of classic genetic markers indicates that the villages of Savoonga and Gambell diverged considerably, likely because of a founder effect compounded by intergenerational drift (Byard and Crawford 1991; Crawford et al. 1981). Genetic drift appears to have had a greater effect on the population of Gambell, resulting in lower average genetic heterozygosity (when considering only nonadmixed individuals). Estimates of European admixture, based on gamma globulin markers, are slightly higher for Gambell than for Savoonga but are small for both communities (8% and 4%, respectively) (Byard et al. 1983). Compared with other populations, Savoonga is closer genetically to the Chaplino Eskimos of northeastern Siberia than to Gambell. This can be explained by the number of Savoonga males obtaining wives from the nearby Siberian community of Chaplino (Crawford et al. 1981). The two (Yupik-speaking) St. Lawrence Island Eskimo communities cluster

closer together than do the Inupik-speaking communities of Wales and King Island, Alaska, from which they are genetically distinct. Overall, the St. Lawrence Island Eskimos show the greatest genetic affinity to the Asian Eskimos, and, as expected, based on language affiliation, geography, and ethnohistory of the circumarctic region, they cluster with the circumpolar group that includes Eskimos, Aleuts, and Chukchi, who differ genetically from other Native American and Siberian populations (Crawford et al. 1981; Ferrell et al. 1981).

Materials and Methods

In 1979 William S. Laughlin measured Eskimo populations from St. Lawrence Island, followed by Aleuts from the Pribilof Islands in 1981. These anthropometric measurements were originally collected as part of a growth and development study of Bering Sea children (Johnston et al. 1982). Original data sheets used by Laughlin were made available to us by the Museum of the Aleutians in Unalaska, Alaska. This analysis of the anthropometric measurements included Aleut participants from the Pribilof Islands [St. George, $N = 165$ (92 males and 73 females); and St. Paul, $N = 65$ (32 males and 33 females)] and Yupik-speaking Eskimo participants from St. Lawrence Island [Gambell, $N = 61$ (29 males and 32 females); and Savoonga, $N = 108$ (51 males and 57 females)]; all participants were over the age of 18. We used the most heritable and informative measurements: linear and cranial measurements, wrist breadth, elbow breadth, and one measurement of body breadth. Table 1 provides the mean values for all variables used for each of these populations. For the statistical analyses used to assess interpopulation variation, we excluded individuals with missing data in most cases. However, total face height and upper face height could not be measured for some participants because of dentures. In these cases mean values were substituted for original data. All measurements were taken by Laughlin; thus there is no interobserver error.

For comparative purposes, we used anthropometric measurements for North Americans and Mesoamericans. North American Natives were measured by Boas and a team of trained anthropometrists in 1890–1904 (Jantz 1995, 2006; Jantz et al. 1992). Measurements of Mesoamericans were collected across a large span of time, ranging from 1898 until 1952. No attempts were made in this study to correct for interobserver error; however, Faulhaber discussed this issue in his original publication (Faulhaber 1970), and Jantz et al. (1992) and Jantz (2006) addressed the same issues regarding Boas's data. Because early data collection was biased toward males (Jantz 2006), many data sets from North America and Mesoamerica are missing measurements for females or the sample sizes for females are much lower than those for males. To increase sample number and use as many measurements as possible for comparison, we used only males. Table 2 lists the populations used in this analysis and provides means for each measurement. The measurements were chosen to maximize the number of variables and sample size of the populations.

Table 1. Mean Values for 12 Anthropometric Measurements of Pribilof Island Aleuts and St. Lawrence Island Eskimos

Population	N	Stature (cm)	Sitting Height (cm)	Biacromial Breadth (cm)	Elbow Breadth (mm)	Wrist Breadth (mm)	Total		Upper		Minimum		Bizygomatic Breadth (mm)	Bigonial Breadth (mm)
							Face Height (mm)	Face Height (mm)	Head Length (mm)	Head Breadth (mm)	Frontal Breadth (mm)	Head Breadth (mm)		
St. Paul (males)	92	165.907	89.133	40.15	74.473	60.272	123.672	70.871	195.435	157.478	109.163	146.467	111.5	
St. Paul (females)	73	155.873	84.021	36.528	67.479	53.26	115.344	65.617	185.603	149.096	106.164	138.192	106.534	
St. George (males)	32	170.281	90.719	40.853	74.25	61.438	125.875	72.821	196.219	158.75	108.406	148.281	110.844	
St. George (females)	33	158.197	85.436	37.206	67.712	55.242	115.091	66.581	187.303	151.727	106.606	141.364	106.727	
Gambell (males)	28	165.82	89.03	40.32	71.11	59.96	125.21	71.53	194.79	156.54	110.39	148.32	113.57	
Gambell (females)	32	153.131	82.888	36.388	64.844	53.734	116	66.778	184.625	151.344	109.129	141.438	108.563	
Savoonga (males)	51	163.892	87.976	40.19	71.559	60.735	124.686	73.24	193.49	157.824	108.804	149.471	113.863	
Savoonga (females)	57	153.946	83.754	36.702	65.605	54.193	115.158	68.606	185.193	150.316	107.579	141.684	109.86	

Table 2. Mean Values for Five Measurements Used from Comparative Populations of Male Native Americans

<i>Code</i>	<i>Population^a</i>	<i>Region</i>	<i>Stature (cm)</i>	<i>Sitting Height (cm)</i>	<i>Head Length (mm)</i>	<i>Head Breadth (mm)</i>	<i>Bizygomatic Breadth (mm)</i>
WEsk	Western Eskimo	Polar	167.85	88.24	191.84	149.04	151.24
Gam	Gambell	Polar	165.82	89.03	194.79	156.54	148.32
Sav	Savoonga	Polar	163.89	87.98	193.49	157.82	149.47
StP	St. Paul	Polar	165.91	89.13	195.43	157.48	146.47
StG	St. George	Polar	170.28	90.72	196.22	158.75	148.28
EEsk	Eastern Eskimo	Polar	156.74	83.14	192.15	152.12	145.12
TSI	Tsimshian	Northwest Coast	167.22	88.24	196.86	161.37	154.25
CRE	Cree	Subarctic	168.51	86.49	195.51	149.51	148.78
HAI	Haida	Northwest Coast	168.08	87.80	198.31	162.64	153.71
CHI	Chilcotin	Subarctic	164.59	86.35	185.65	158.29	146.03
KWK	Kwakiutl	Northwest Coast	163.33	88.84	193.87	157.89	150.42
SWA	Shushwap	Plateau	166.00	86.68	189.44	158.93	145.99
LIL	Lillooet	Plateau	160.97	84.32	185.59	160.17	148.87
TOM	Thompson	Plateau	161.91	84.61	188.82	156.33	147.15
STL	Stalo	Northwest Coast	163.20	86.37	188.90	165.75	152.66
MAK	Makah	Northwest Coast	164.37	87.91	187.83	160.46	156.35
CHW	Chippewa	Northeast	171.49	88.32	193.56	155.93	144.97
OJB	Ojibwa	Northeast	171.40	87.12	193.54	157.21	146.66
CRW	Crow	Plains	173.13	89.82	196.02	158.39	148.96
SIX	Sioux	Plains	172.32	88.47	194.37	154.95	148.15
MIC	Micmac	Northeast	172.74	88.63	191.55	150.68	143.65
TUS	Tuscarora	Northeast	171.21	88.99	192.97	153.60	143.37
ONE	Oneida	Northeast	171.87	89.97	194.46	154.73	146.22
KLA	Klamath	Plateau	167.88	87.94	182.10	159.34	143.60
HOP	Hoopa	California	166.52	85.54	180.18	152.32	134.56

PAI	Paiute	Great Basin	167.67	87.52	188.65	154.68	146.18
YUK	Yuki	California	161.25	84.06	194.69	149.79	146.66
UTE	Ute	Great Basin	165.32	86.31	191.42	152.47	146.53
YOK	Yokuts	California	170.26	86.20	192.00	162.10	150.19
CKE	Cherokee	Southeast	169.81	86.89	190.81	151.02	143.28
ZUN	Zuni	Southwest	161.77	85.92	181.68	150.92	143.01
KIW	Kiowa	Plains	157.83	82.14	182.03	147.68	138.11
CSW	Chickasaw	Southeast	168.93	87.90	186.93	148.85	141.71
SLR	San Luis Rey	California	169.92	85.84	185.75	161.51	149.48
APC	Apache	Southwest	169.29	88.46	181.79	161.13	149.42
PAP	Papago	Southwest	168.80	87.30	186.70	150.20	142.20
CTW	Choctaw	Southeast	170.92	84.49	186.32	151.11	144.58
YAQ	Yaqui	Southwest	166.70	83.10	183.80	149.20	141.00
TAR	Tarahumara	North Mexico	163.00	83.50	190.00	145.00	140.00
NAH	Nahua	Central Mexico	157.00	84.40	176.00	150.80	139.00
TEP	Tepehua	Central Mexico	157.70	85.70	179.80	153.90	143.90
MAY	Maya	Central Mexico	156.40	80.80	182.60	155.60	142.30
TOT	Totonac	Central Mexico	158.00	83.90	176.60	155.00	141.60
HUA	Huastec	Central Mexico	157.20	83.90	176.70	148.80	141.50
POP	Popoluca	Central Mexico	160.50	83.70	178.90	152.20	143.20
CUI	Cuitlateco	Central Mexico	161.10	85.20	174.90	150.50	138.70
CHL	Chol	Central Mexico	158.50	83.20	185.70	149.60	140.90
MIX	Mixtec	South Mexico	156.10	81.60	182.50	149.40	142.50
TZL	Tzotzil	South Mexico	158.40	84.70	184.20	144.20	130.50
ZAP	Zapotec	South Mexico	155.40	82.20	183.30	148.90	138.90

a. Populations are listed in descending order by latitude.

Analytical Methods. We used the Relethford-Blangero method to examine the phylogenetic relationship between Aleuts and Eskimos of the Bering Sea (Relethford and Blangero 1990). This method is based on Harpending and Ward's (1982) method for examining gene flow based on the frequency of genetic markers. The Relethford-Blangero analysis compares the observed within-group variation with the expected within-group variation based on the distance of each population to the regional centroid (r_{ii}) and the average within-group variance for the populations. The Relethford-Blangero method operates on the assumption that a linear relationship exists between average within-group phenotypic variation and the distance to the regional centroid. Deviations from the models are shown as deviations from the expected within-group phenotypic variance. These estimates are used to create a distance matrix. The eigenvectors are then scaled and weighted using estimations of population size at the time of collection (Relethford 1996; Relethford and Harpending 1994). We performed a principal coordinates analysis on the R matrix to provide a visual representation of the variation based on two axes.

We calculated a minimum F_{ST} value to estimate the degree of population substructure found within the region (Relethford and Blangero 1990; Relethford and Harpending 1994; Relethford et al. 1997; Williams-Blangero and Blangero 1989). F_{ST} can be estimated from r_{ii} , which is inversely related to σ_p^2 , making all estimates of population divergence using phenotypic variance less than or equal to estimates made from an R matrix of genetic variance. Genetic variance estimates can be obtained by scaling the minimum F_{ST} by the heritability (h^2) of the trait under consideration.

Because the Relethford-Blangero method offers to establish the genetic relationship among populations using phenotypic traits, it is important to include heritability when comparing populations with significantly different genetic backgrounds. However, the heritability of each measurement is unknown for the Aleuts of the Pribilof Islands and the Eskimos of St. Lawrence; given that previous studies have found that Alaskan Eskimos and Aleuts are closely related (Jantz et al. 1992; Ousley 1995), it is reasonable to assume that the heritability of these traits is similar. Because the heritability is given as 1, this measure provides a minimum F_{ST} . In addition, previous studies have shown no significant changes in the overall relationship among populations when altering h^2 (Relethford and Blangero 1990; Roseman 2004). For exploratory purposes we used heritability in one instance to examine any possible alterations. A heritability of 0.42 was used because it was estimated from Cherokee, Chippewa, Micmac, Mississauga, and Ojibwa Native Americans using 12 traits (leg length, arm length, shoulder height, finger reach, sitting height, shoulder breadth, head length, head breadth, face height, bizygomatic breadth, nose height, and nose breadth) from Boas's original data (Konigsberg and Ousley 1995). Keep in mind that this heritability estimate may not accurately reflect the heritability of traits in the Aleut and Eskimo communities under study because of the extreme environmental history of these populations (Johnston and Schell 1979).

All analytical methods were performed using the computer program RMET, version 5.0 (Relethford 2003). Before data were entered, each measurement was regressed against age, and the resultant residuals were used to eliminate any effects of age on the variables. To remove any effects of gender, these residuals were then standardized using z scores before pooling males with females. To assess phylogenetic relationships through plots, we plotted the principal coordinates of the R matrices using NTSYSpc, version 2.02h (Rohlf 1998).

To further reveal the relationship of Aleuts and Eskimos to other Native Americans, we performed several additional tests. We constructed Euclidean and geographic distance matrices, calculating the Euclidean distances using NTSYSpc, version 2.02h (Rohlf 1998), and the geographic distance matrix using GEOG, version 2.1 (Relethford 2000). To examine the relationship of phenotypic variation and geography, we ran a Mantel randomization test between the Euclidean distance matrix and the geographic distance matrix. Mantel tests were performed using NTSYSpc, version 2.02h (Rohlf 1998). Because previous studies on North American Indians have not found a strong relationship between geography and phenotypic distance but rather a relationship with distance in longitude (Jantz 2006), we then performed a Mantel test using only North Americans and a separate test on Mesoamericans. We also generated a distance matrix based on latitude and one on longitude and then compared these to Euclidean distance. We constructed a neighbor-joining tree (Saitou and Nei 1987) using the Euclidean distance matrix. To assess the fit of the tree to the original data, we created a cophenetic distance matrix from the tree and then compared this to the original Euclidean distance matrix using a Mantel randomization test. The neighbor-joining tree, cophenetic matrix, and Mantel randomization test were performed using NTSYSpc, version 2.02h (Rohlf 1998). We performed a principal components analysis on the Euclidean distance to provide another means for describing the variation among populations on fewer axes (NTSYSpc, version 2.02h; Rohlf 1998).

Results

Bering Sea Natives. The results of the Relethford-Blangero method are given in Table 3. As expected, the results indicate that little population substructure exists among the females, males, and total populations of this region. Both populations of St. Lawrence Island have a less than average phenotypic variance, whereas the Aleut populations have a greater than expected within-group phenotypic variation. Overall, males seem to have a higher within-group phenotypic variance (0.939) compared to females (0.928). This seems to be mostly due to the high within-group phenotypic variance of males from St. George.

For the R matrix analysis using only females, 97.9% of the variation is accounted for by the first two axes (79.9% and 18.0%, respectively). The R matrix for males accounts for 100% of the variation on the first two axes, with 87% on the first and 13% on the second. The R matrix accounts for 97.3% of the variation

Table 3. Estimates of Within-Group Phenotypic Variance, Distance from the Average Centroid (r_{ii}), and Deviations from Expectation of Phenotypic Variance Using the Relethford-Blangero Method for 12 Measurements

<i>Population</i>	r_{ii}	<i>Observed Variance</i>	<i>Expected Variance</i>	<i>Residual</i>
Males ^a				
St. Paul	0.017028	1.016	0.933	0.083
St. George	0.023836	1.034	0.926	0.108
Savoonga	0.009245	0.922	0.94	-0.018
Gambell	0	0.838	0.949	-0.111
Females ^b				
St. Paul	0.026936	1.02	0.919	0.102
St. George	0.016555	1.192	0.928	0.264
Gambell	0.002988	0.776	0.941	-0.165
Savoonga	0.018873	0.883	0.926	-0.043
Total population ^c				
St. Paul	0.0228	1.014	0.927	0.087
St. George	0.034	1.104	0.921	0.184
Gambell	0.004	0.803	0.942	-0.139
Savoonga	0.0165	0.907	0.93	-0.023

a. Mean phenotypic variance = 0.939; minimum F_{ST} = 0.0106.

b. Mean phenotypic variance = 0.928; minimum F_{ST} = 0.0165.

c. Mean phenotypic variance = 0.931; minimum F_{ST} = 0.0150.

within the data, with 77.3% on the first axis and 20.0% on the second (Figure 2; note that all analyses were performed separately but were plotted in a single figure). In Figure 2 the first axis clearly separates the Aleuts from the Eskimos, and the second axis clusters St. Paul with Gambell and St. George with Savoonga. Gambell is still closest to the centroid, and St. George has the greatest distance from the centroid.

Finally, we used a model that included Konigsberg and Ousley's (1995) estimate of heritability ($h^2 = 0.42$) obtained using Boas's data. This test resulted in an F_{ST} of 0.0475 and an unbiased F_{ST} of 0.0420. This estimate is far lower than any estimate of F_{ST} using Boas's data (this study = 0.0420, Siberia = 0.12, Aleut and Northwest Coast = 0.27, Northwest Coast only = 0.26) (see Ousley 1995, Table 7). This is indicative of the strong phylogenetic relationship between the Aleuts and Yupik Eskimos, resulting in little phenotypic variation. However, as mentioned earlier, heritability of traits varies between populations, especially among those living under extreme environmental conditions (Johnston and Schnell 1979). Because of the inverse relationship between heritability and F_{ST} , the estimates of F_{ST} might be higher if the heritability of physique is lower for the Aleuts and Eskimos compared to that of Southeast Native Americans from which the estimate of heritability was made.

Relationship Among Bering Sea Natives and Other North American Natives. The Euclidean distance matrix was compared to a geographic distance

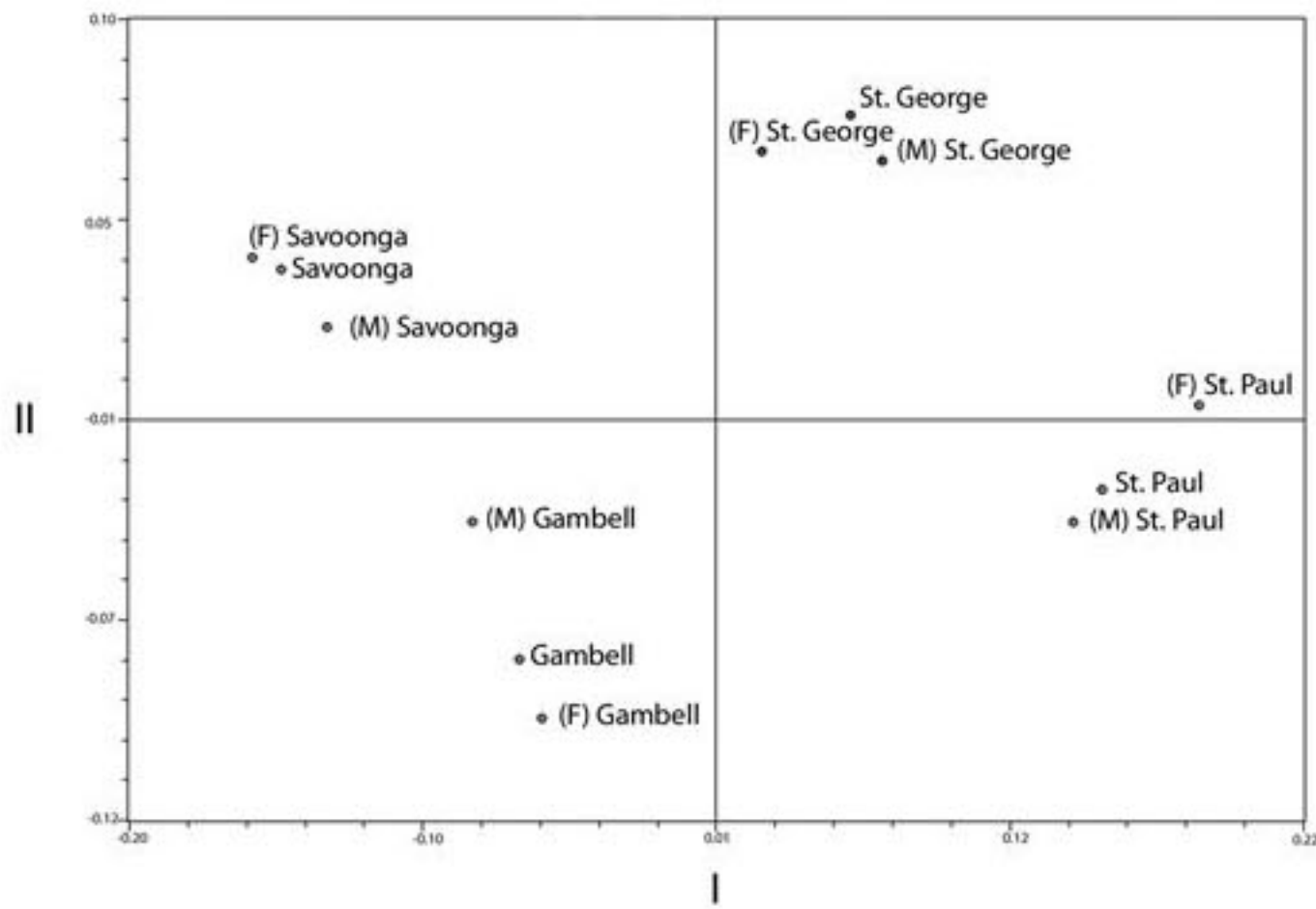


Figure 2. Plot of first two principal coordinates from an *R* matrix analysis performed using 12 variables on males, females, and the whole population. Analyses were performed separately but are plotted together in a single diagram for easier comparison.

matrix using a Mantel randomization test. The results (Table 4) reveal statistically significant correlations between anthropometric distance, geographic circumferential distance, distance in latitude, and distance in longitude. Although geography and physique are significantly related, the relationship is not a strong one. The Mantel test comparing Euclidean distance to latitude reveals the strongest correlation of 0.5324. However, previous studies have found a pattern of change in stature and sitting height from east to west among North American Natives (Jantz 2006). Given that the results of this study contradict previous studies, we separated the Mesoamerican populations and performed distance matrix and Mantel tests again to ensure that the populations' inclusion was not concealing any association between longitude and physique in northern North America. However, we found no significant correlation between anthropometric distance and distance based on circumference or longitude among North Americans, but we did find a small, marginally significant correlation between latitude and morphology.

Table 5 reports the eigenvectors and eigenvalues for the first three components. The first component roughly separates North America from Mesoamerica with the exception of the Eastern Eskimo, Zuni, Hoopa, Kiowa, and Yaqui (originally from northern Mexico), which cluster with the Mesoamericans (see Figure 3). St. Paul, Gambell, and Savoonga all cluster closely along the first axis. St. George has a slightly higher score along the first component, causing it to cluster closer to the Crow. This component appears to be a size component, with populations possessing the largest overall size occupying the right side of this axis and populations with the smallest overall size occupying the left. The second component is a shape component contrasting length and width of the

Table 4. Results of Mantel Randomization Test Comparing Anthropometric Distance to Geographic Distance^a

	<i>All North American Indians</i>	<i>Only North Americans</i>
Circumferential distance (<i>p</i> value)	0.38392 (0.001)	0.1612 (0.065)
Latitude (<i>p</i> value)	0.5324 (0.033)	0.1403 (0.0427)
Longitude (<i>p</i> value)	0.11519 (0.033)	0.0004 (0.469)

a. Anthropometric distance was calculated using Euclidean distance on the means, and geographic distance was calculated using circumferential distance, distance in latitude, and distance in longitude.

body. Although the first component clusters Gambell, Savoonga, and St. Paul together, St. Paul and Gambell are slightly closer to St. George than to Savoonga on the second axis. Together, these axes represent 82.3% of the variation, and they fail to cluster St. Paul and Gambell closely with the other focus populations. Instead, St. George appears to be closely related to Crow, St. Paul and Gambell to Ojibwa, and Savoonga to Kwakiutl. The eigenvectors reveal that those populations with the largest linear measurements are being pulled to the upper-right quadrant. This explains why Savoonga is being pulled to the lower-right quadrant, as Savoonga is the shortest in all linear measurements among the focus populations (Table 5). The third principal component (Figure 3) represents an additional shape component, contrasting heights and head breadth with head length and bizygomatic breadth. On this third component, the Alaskans maintain similar trajectories with one another and with the Western Eskimo and Kwakiutl. Savoonga is closer to St. Paul and Gambell on the third axis than is St. George, which still clusters closely with the Crow. The most notable change on this component is that the Yuki and Eastern Eskimo now separate from the other Americans. This eigenvector highlights the contrasting relationship of head length to head breadth and the linear measurements.

The neighbor-joining tree roughly separates Mesoamericans from the other North American Natives with few exceptions. Therefore, for ease of

Table 5. Results of the Principal Components Analysis Including the Three Significant Eigenvectors and Eigenvalues

<i>Variable</i>	<i>PC1</i>	<i>PC2</i>	<i>PC3</i>
Stature	0.7915	0.4681	0.245
Sitting height	0.8558	0.298	0.251
Head length	0.7945	0.2281	-0.535
Head breadth	0.7106	-0.6162	0.253
Bizygomatic breadth	0.8244	-0.4474	-0.198
Eigenvalue	3.175	0.94	0.5125
Proportion	0.635	0.188	0.102
Cumulative	0.635	0.823	0.925

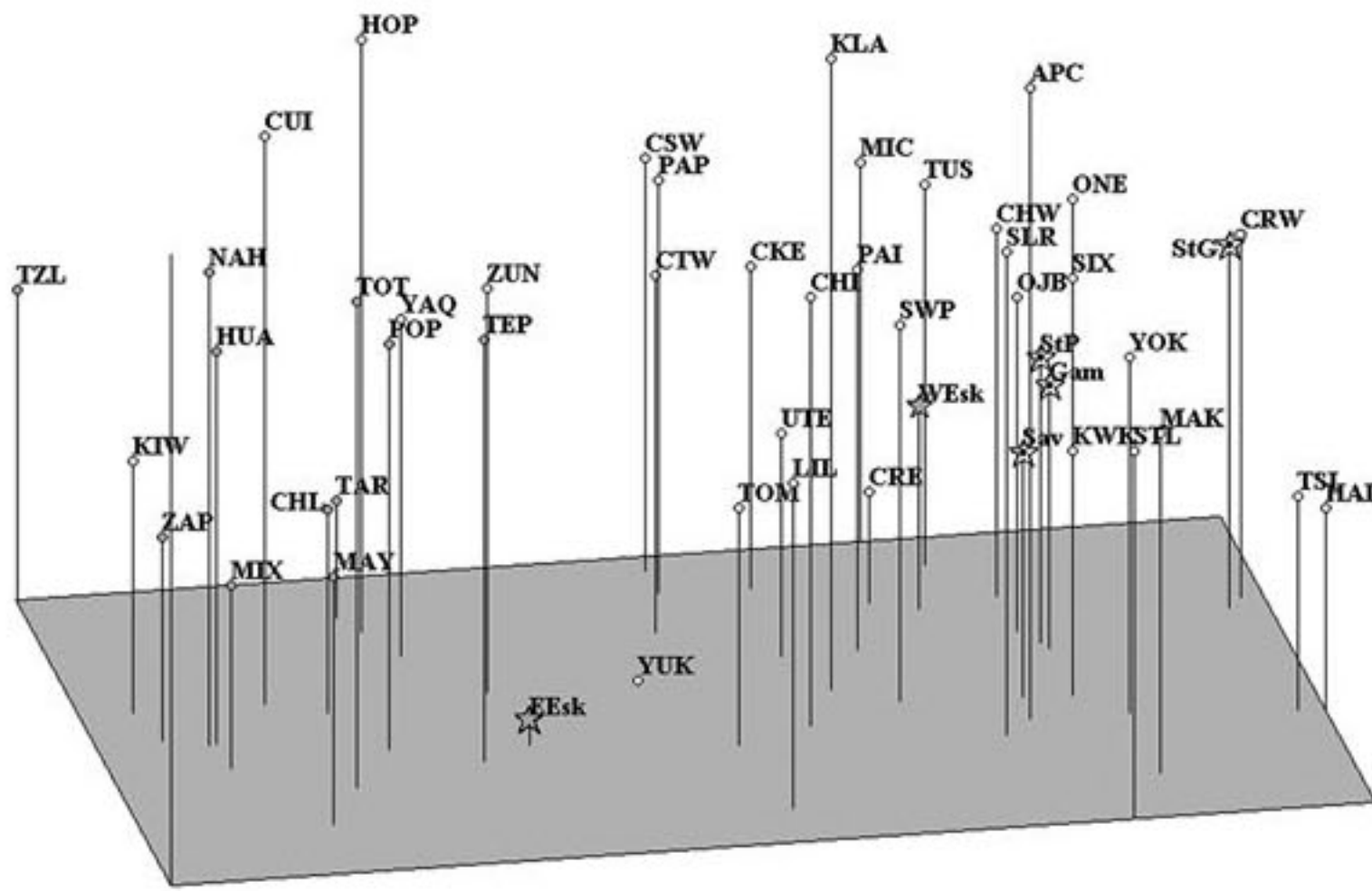


Figure 3. Plot of the first three components of the principal components analysis for the anthropometric variation among North American Natives. Total variation, 92.54%. Dotted stars, focus populations; gray stars, other polar populations; open circles, northern North Americans; gray circles, Mexican populations. For other population codes, see Table 2.

viewing, only the North American branch is shown (Figure 4). In the neighboring tree of northern North Americans, Gambell, Savoonga, and St. Paul all cluster together on a branch with the Kwakiutl (node 1 in Figure 4), similar to the relationships shown in the principal components analysis. Savoonga and Kwakiutl are operational taxonomic units on a single branch, as are St. Paul and Gambell. St. George again clusters with the Crow on node 2. Also, node 2 contains all the East Coast Native Americans and Plains Indians, except the Kiowa, which cluster with the Mesoamericans. The branch marked node 3 contains all West Coast Indians, with the subbranch marked node 6 clustering all Northwest Coast Indians exclusive of the Kwakiutl, which cluster with the focus populations. The Eastern Eskimo cluster with the Yuki, a Central California population, and represent the most divergent node among the northern North Americans. As shown by node 5, the Eastern Eskimo are intermediate between the Mesoamericans and other North Americans.

Similar to what was found in the principal components analysis, the Kiowa and Hoopa cluster with the Mesoamericans. In addition, two of the Southwest populations, Zuni and Yaqui, share branches with Mesoamerican Natives. It is not surprising that the Yaqui cluster with the Mesoamericans, because they migrated to the Southwest from northern Mexico after the Spanish arrived in Mexico. All central Mexicans cluster together. It is surprising that the Hoopa cluster closely with the Tarahumara and Tzotzil, because all these populations are geographically distant. However, the Hoopa tend to have shorter stature, smaller overall body

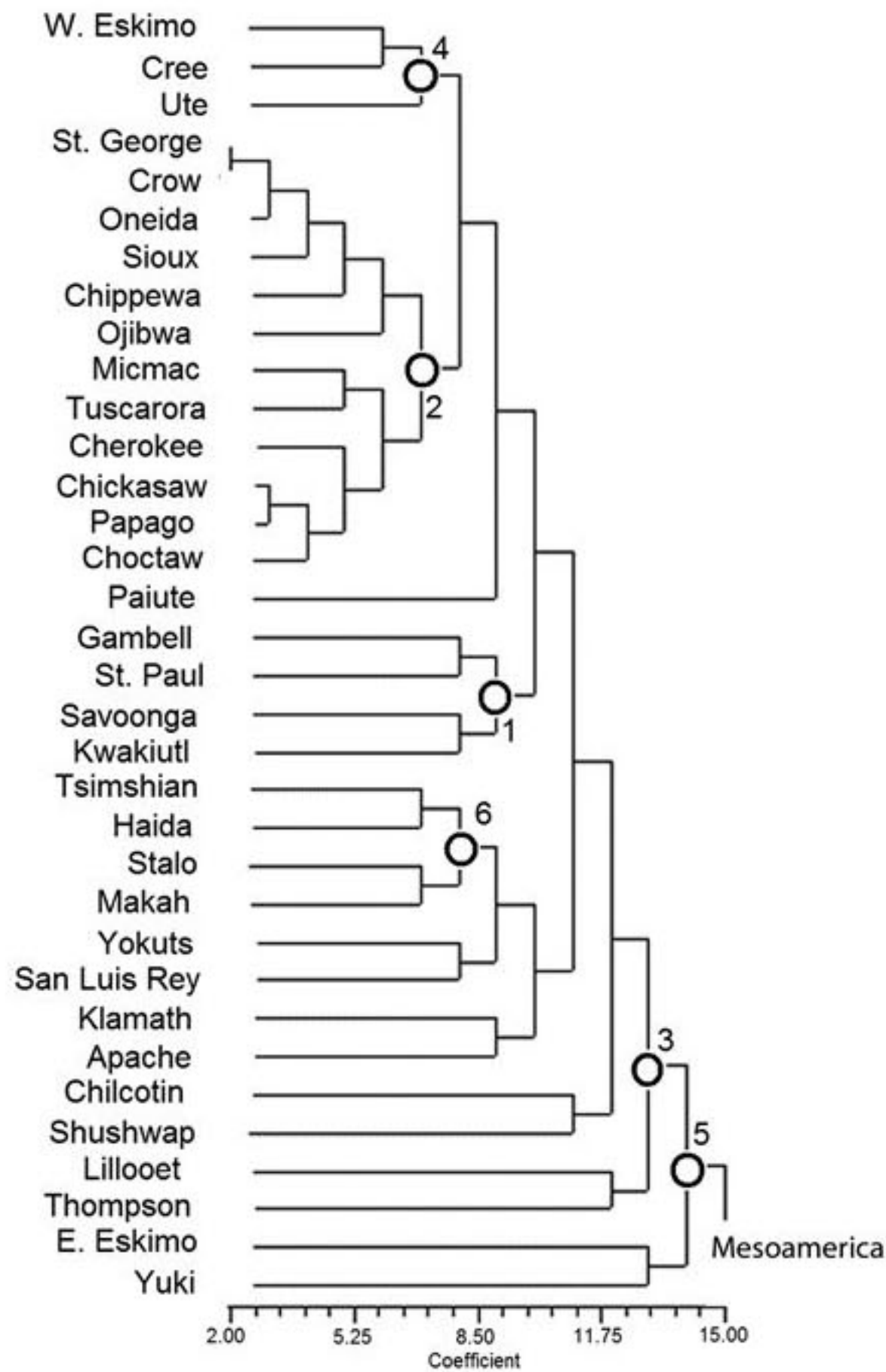


Figure 4. Neighbor-joining tree created from the Euclidean distance matrix showing the phylogenetic relationship among North American Indians. Only North American populations are shown, but the branch that connects the North American tree to Mesoamerica is shown.

size, and a narrow face (see Table 2) compared to other northern North Americans, as do the Tzotzil and Tarahumara. Similar to the results of the principal components analysis, the Kiowa cluster with the Zapotec and Mixtec, likely because of their overall small body size.

We performed a Mantel randomization test to compare a cophenetic matrix created from the neighbor-joining tree and the original Euclidean distance matrix. The test revealed a correlation of 0.6674, with $p = 0.0007$. Although there is a significant correlation between the two matrices, it is not strong, indicating that the neighbor-joining tree may not be the best method to examine the relationship among Native Americans.

Discussion

Despite a longer history of occupation on St. Lawrence Island, it appears that recent demographic events have had a greater negative effect on the phenotypic variation of St. Lawrence Eskimos than on the Pribilof Island Aleuts. It is clear from the deviation from expected within-group variation for the Aleut and Eskimo populations that famine, population relocation, and admixture have had an effect on their genetic structure. This may also be the result of the parental populations of St. Paul and St. George coming from multiple islands, thus giving the Pribilofs an increased amount of variation to start with (Rubicz 2007). Also, the great famine and disease that decimated the population of St. Lawrence Island from 1878 to 1920 may have caused a bottleneck effect, reducing the variation on the island.

The current estimate for population substructure among the Aleuts and Eskimos is far lower than any previous estimate of F_{ST} using Boas's anthropometric data (this study = 0.0420, Siberia = 0.12, Aleut and Northwest Coast = 0.27, Northwest Coast only = 0.26) (see Ousley 1995, Table 7). This is indicative of the strong phylogenetic relationship between Aleuts and Eskimos, resulting in little phenotypic variation. However, as mentioned earlier, heritability may be different in populations living in extreme environments, in which case the estimates of F_{ST} may change.

Within the Pribilof Islands, St. Paul has experienced greater recent male immigration (90% non-Native male lineages) compared to St. George (89% non-Native Y chromosomes) (Rubicz 2007), but males in St. Paul have lower variation than those found on St. George. Similarly, the females of St. Paul have less variability than do females of St. George. When males and females are examined together, St. George exhibits the greatest positive deviation from expectation. Gambell and St. Paul had close to the same population size at the time of data collection, but Gambell has probably experienced less non-Native gene flow than has St. Paul, and the smaller effective population size made Gambell more subject to the effects of genetic drift. St. Paul and St. George have also had an increasing number of non-Aleuts entering the region as a result of easier access to the islands through commercial air travel and the promise of employment in the crabbing and fishing industries.

These patterns are also discernible in the R matrices and principal components analysis results. In all R matrices, Savoonga clusters with Gambell and St. Paul clusters with St. George, showing the similarity within each group and morphological differences between Aleuts and Eskimos. On the second axis of all these tests and on the principal components plots, St. Paul and Gambell cluster together. This is indicative of Russian and European American gene flow into Gambell and St. Paul. Both of these populations have tended not to increase in size as quickly as their counterparts, although they have accumulated more non-Native gene flow. The St. Lawrence Island Eskimos have less phenotypic variation than

the Pribilof Island Aleuts. Reduction in variation can be attributed to a population bottleneck caused by famine and disease from 1878 to 1917.

The Relethford-Blangero method revealed differences in the variability of physical traits between males and females among Bering Sea populations. Males overall have a higher average within-group variation. Most of this variability can be attributed to the sample from St. George. The variation in St. George for males and for the population considered as a whole deviates from expected phenotypic variance in a visibly positive pattern because of admixture. Body proportions are similar among the St. Lawrence Island Eskimos and Pribilof Aleuts.

In addition, Gambell and Savoonga have experienced less non-Native, non-Siberian gene flow than have St. Paul and St. George. Despite measurable amounts of European gene flow and other Native American gene flow as a result of adoption practices in Gambell, Gambell's small effective breeding population has resulted in restricted variability. Conversely, mating patterns in Savoonga combined with a larger effective breeding size have resulted in greater within-group phenotypic variance compared to Gambell. Gambell was used as a military (air force) base during World War II and thus has experienced recent non-Native admixture. These factors have resulted in Gambell having more non-Eskimo gene flow (8.1%) than Savoonga (4.3%) based on immunological markers (Byard et al. 1983). Byard and Crawford (1991) found that heterozygosity was reduced in Gambell when comparing only "native" Eskimos. Our results conform to the expectation of reduced variation in Gambell as a result of reduced effective breeding size, as seen in classical genetic markers. Savoonga's greater within-group variation is the result of several factors. First, Savoonga was founded by the younger generation from Gambell, resulting in a large breeding population in Savoonga relative to the total population. Second, Savoonga experienced greater population increase within the few generations following the migration, but with less European admixture than Gambell. Third, Savoonga's phenotypic variation is slightly higher for females than in Gambell, likely a result of men importing Siberian wives to St. Lawrence Island after Savoonga males split from Gambell to become reindeer herders, taking few women with them (Crawford et al. 1981).

St. George is the most divergent of the Bering Sea populations, as can be seen using the Relethford-Blangero method, principal components analysis, and neighbor-joining tree. St. George has higher than expected phenotypic variance. For females only, St. George has a smaller r_{ii} value than St. Paul; for males and combined males and females, St. George has a greater r_{ii} than does St. Paul. These two pieces of data are contradictory, because high r_{ii} values are normally indicative of greater genetic drift, whereas higher variation is indicative of greater gene flow. However, previous research has found that genetic variation may not be highly correlated with gene flow if many forces of evolution are operating on small populations (Byard et al. 1983). As mentioned, all R matrices presented in this study were scaled by the population census sizes. This scaling diminishes the effects of genetic drift on variation within populations, allowing the investigator to infer past relationships that are not affected by stochastic processes, that is,

gene flow (Relethford 1996). The unscaled R matrices (results not shown) reveal that St. George does not cluster closely with the other Alaskan Natives, the same pattern present in the principal components plots.

Current studies using molecular evidence have found differences between paternal and maternal markers (Rubicz 2007; Zlojutro et al. 2009), where mtDNA diversity is greatly reduced in St. George compared to St. Paul but Y-chromosome data show evidence of approximately equal admixture between St. George and St. Paul (89% non-Native and 90% non-Native respectively). Based on the analysis of blood group markers (Majumder et al. 1988) and results of the principal components analysis and neighbor-joining tree on anthropometrics, it is likely that St. George had a significant amount of Russian and European American gene flow, which resulted in greater changes in physique because of smaller population size. St. George has always been the smaller of the two Aleut groups, further influencing the development of population structure within the Aleut populations. Therefore it is likely that because of the interaction of many forces of evolution, St. George has differentiated from the other Bering populations.

As a result, although the St. George population appears to be morphologically similar to the Crow Indians, this does not reflect a phylogenetic relationship. Based on morphology, St. George clusters with the Crow in the principal components plots and neighbor-joining tree. St. George has the highest mean stature among Aleuts and Eskimos, but the Crow have the highest mean stature across all populations in the study. Therefore, because of the confounding effects of small population size and differential non-Native gene flow, the St. George Aleuts have differentiated from St. Paul and the St. Lawrence Island Eskimos and appear to be morphologically similar to the Crow Indians.

The only clearly discernible relationship to geography across North America is seen in the separation of North Americans and Mesoamericans. However, geography plays a more important role in determining anthropometric distance in Mesoamericans rather than northern North Americans. The lack of fit to geography indicates that the physique of Native American populations has been affected by a combination of migration and non-Native gene flow across North America. Mesoamerica seems less affected by these factors, thus maintaining a closer resemblance in morphological traits. Similar to other findings, Aleuts and Yupik Eskimos have a close phylogenetic relationship with Northwest American Indians. St. Paul and the St. Lawrence Island Eskimo tend to form a cluster along with Native Americans from the northwest and northeast coasts. This would seem to lend itself to the previous assumptions regarding environmental pressures associated with Bergman's and Allen's rules and relationships among the Native Americans (Holliday and Hilton 2010). However, geographic distance in latitude showed little correlation to Euclidean distance among northern North American Natives in the Mantel tests. The neighbor-joining tree showed an alternative relationship, roughly grouping western Native Americans together and eastern Native Americans together. Previous studies have also found a pattern in morphology from east to west (Jantz 2006), which would be expected if a single migration moved down

the West Coast and populated the United States from west to east. Again, the Mantel tests revealed no significant relationship between longitude and Euclidean distance for populations north of Mexico. However, the relationship between longitude and phenotypic variation may be affected by a higher concentration of European admixture in the northeast. A secular trend of increased height and increased leg length has been noted in the eastern United States (Jantz 2006). However, these tests showing a relationship between anthropometrics and longitude used Boas's data grouped into major geographic regions and incorporated a more complete set of populations than found in the current study. Cavalli-Sforza et al. (1994) detected a similar pattern of interpopulation relationships in the Northeast when examining genetic markers, which he attributed to the colonization of North America and the movement of Europeans into the West. These factors may have influenced our findings.

The Eastern Eskimo were the most divergent of the northern North American populations on the neighbor-joining tree, and they failed to cluster with the other circumpolar populations in the principal components analysis as well. This may be due to a combination of a more distant phylogenetic relationship with the other Eskimos and Aleuts and differential gene flow. Although the Eastern Eskimo have undergone European American admixture, estimates using both mtDNA and Y-chromosome data indicate far less admixture than that found in the Aleuts. Bosch et al. (2003) found that only 58% of the Y-chromosome lineages came from European gene flow in Greenlandic Eskimos compared to estimates of 73–90% for Aleut populations (Rubicz 2007). Also, in previous anthropometric studies, the Eastern Eskimo clustered with Siberian populations (Jantz et al. 1992; Ousley 1995) that were not used in this analysis, likely causing the unexpected pattern of Eastern Eskimo relationships. These results would also explain the discrepancy with previous studies that found little relationship between Aleuts and Eskimos, because only Inupik Eskimos were used for comparison, but a greater relationship exists among Aleuts and Yupik-speaking Eskimos. These results highlight the complicated relationship among North American Natives residing in the United States and Canada, as noted elsewhere (Jantz et al. 1992).

The results of this study provide evidence that secular trend has not affected these Native populations, even though data collection occurred over seven decades between Boas's and Laughlin's expeditions. In addition, this study supports claims that environmental plasticity is not great enough to obscure relationships among populations resulting from population history. In line with previous studies, these results challenge Boas's original claims concerning the magnitude and influence of plasticity on anthropometric traits (Gravlee et al. 2003; Relethford 2004; Sparks and Jantz 2002). As investigators have shown in recent publications, multivariate methods can be applied to anthropometrics and used to infer population history and substructure (Gonzalez-Jose et al. 2007; Jantz 1995, 2006; Jantz and Owsley 2001; Nystrom 2006; Ousley 1995; Relethford and Blangero 1990; Relethford and Harpending 1994; Relethford et al. 1997; Scherer 2007; Sparks and Jantz 2002; Williams-Blangero and Blangero 1989). Our results show

a relationship linking geography, history, and underlying genetic relationships of the Amerindian populations.

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