GEOGRAPHIC VARIATION IN TOOTH MORPHOLOGY OF THE ARCTIC FOX, *VULPES (ALOPEX) LAGOPUS*

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Data on the shape of teeth can be used to test hypotheses about the relationship between adaptive and stochastic processes involved in morphologic divergence between populations. We used 7 two-dimensional landmarks to quantify shape in the upper 1st molar of the arctic fox (*Vulpes lagopus*, formerly *Alopex lagopus*) and tested for differences in molar shape between populations. The arctic fox is widely distributed throughout the Holarctic region, is found on several Bering Sea islands, and occurs in a range of habitats. This broad geographic and ecological distribution allowed for simultaneous testing of the relationship between molar shape and several factors including environmental parameters, geographic distances, and time since population divergence. We identified 11 populations for comparison, located from Siberia to Greenland, including 4 Bering Sea island populations. We found that shape differed only slightly among mainland populations, whereas island populations differed significantly from each other and from all mainland populations. Divergence in tooth shape was significantly correlated with geographic distance. Because differences in annual temperature and annual rainfall often underlie differences in local environmental conditions, we used these variables to test for differences in tooth shape resulting from local adaptation. Shape did not correlate significantly with either mean annual temperature or precipitation. Observed divergences in tooth shape between populations may be explained by local adaptation, allometry related to between-population size differences, and stochastic processes. The results are most consistent with a combination of allometry and stochastic processes, but local adaptation cannot be excluded.

Key words: arctic fox, island populations, morphologic variation, population divergence, shape divergence, tooth shape, *Vulpes (Alopex) lagopus*

Morphologic data provide important direct evidence for understanding the patterns and rates of evolutionary change that have occurred as biological units diverge from one another. However, it has been difficult to discern population-level patterns of divergence using morphologic data. Recent developments in the field of geometric morphometrics (Bookstein 1986, 1989, 1991; Rohlf 1993, 1995, 1998; Rohlf and Bookstein 1993; Zelditch et al. 2004) provide new tools that allow researchers to document relatively fine-scale patterns of population-level divergence with morphologic data.

Identifying good taxonomic systems, choosing appropriate morphologic character complexes to measure, and using appropriate tools for quantifying shape are necessities for morphologically based population-level analyses. We chose the arctic fox (*Vulpes lagopus*, formerly *Alopex lagopus*) as a study

system for documenting tooth-shape divergence, given the arctic fox's diversity and distribution that includes mainland and island populations. The arctic fox is Holarctic in distribution and occupies arctic, tundra, and alpine zones (Audet et al. 2002). In addition to mainland populations, natural populations are present on several islands of varying size. This is of particular importance because island populations face significant barriers to immigration and emigration, and are thus likely candidates for shape divergence resulting from genetic isolation. Individuals can cover great distances ($\geq$1,000 km) when foraging, and during seasonal and other periodic migrations (Macpherson 1968; Wrigley and Hatch 1976). The range of habitats occupied and the broad geographic range provide the potential to test for morphologic divergences resulting from differing degrees of temporal and geographic isolation.

The character complex we focus on is the mammalian tooth, a structure uniquely suited for examining patterns of population divergence. There is an abundant body of research on evolutionary change in mammalian dental characters based on data from the fossil record (Butler and Clemens 2001; Clyde and Gingerich 1994; Gingerich 1991, 1993, 1996; Gingerich et al.
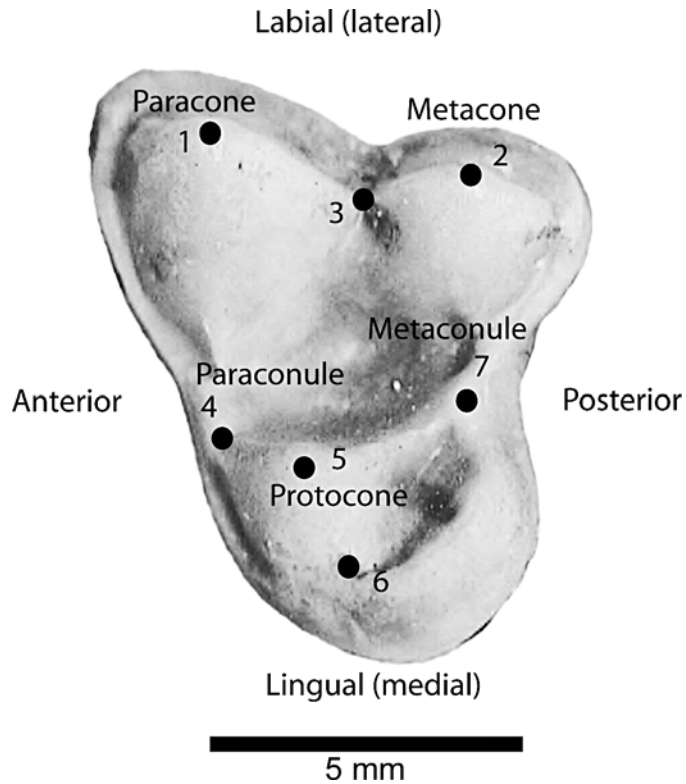
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FIG. 1.—First upper molar of an arctic fox showing tooth orientation, primary cusps, and location of the 7 landmark points used in this analysis.

1991; Gingerich and Gunnell 1995; Polly 1998a, 1998b; Sheets and Mitchell 2001) and modern record (Dayan et al. 2002; Jernvall 2000; Jernvall and Jung 2000; Jernvall et al. 2000a, 2000b; Keranen et al. 1998; Meiri et al. 2004; Salazar-Ciudad and Jernvall 2002; Szuma 2004; Tucker and Sharpe 2004). As a result of this research, there is a rich context within which to interpret dental variation. Polly (2001, 2003a, 2003b, 2004, 2005) in particular has shown that tooth morphology may evolve in a stochastic manner via fluctuating selection such that tooth-shape divergence and population divergence are strongly correlated.

Previous research has shown that mammalian teeth provide useful data for population-level analyses because teeth do not remodel after eruption and because tooth morphology is known to be diagnostic to the species level, thus, phenotypic plasticity is limited to prenatal development and population level divergence is likely captured. Additionally, selective pressure for divergence in tooth shape should be minimal when diet is not significantly different between populations. An advantage of using tooth shape is that a single data set enables researchers to examine simultaneously patterns of population-level divergence, potential environmental factors that may explain tooth-shape variation, geographic distance, and temporal separation, so as to tease apart the potentially complex web of factors influencing shape divergence.

The research presented here addresses 4 questions: are tooth shape and size different among arctic fox populations? Are tooth shape and size correlated? Are population-level shape divergences and environmental factors correlated? Are population-level shape divergences and geographic distance correlated? If tooth shape is diverging via stochastic processes (drift or randomly fluctuating selection), then between-population shape divergence is predicted to be greater for populations that have been isolated longer. Additionally, assuming stochastic processes are the main factors driving shape changes, the patterns of shape divergence should not correlate significantly with environmental variables, should be at least roughly concordant with patterns documented in genetic analyses based on presumed neutral markers, and should vary between populations inferred to be genetically isolated from one another.

MATERIALS AND METHODS

Data collection.—The steps to perform a geometric morphometric analysis include imaging of specimens, digitizing, quantification of shape and size, grouping of specimens, and statistical analyses. Digitizing and quantification were done using TPSutil, version 1.33 (Rholf 2004a), TPSdig, version 2.05 (Rohlf 2006), and TPSrelw, version 1.42 (Rohlf 2005).

Imaging.—Data on tooth shape were collected from 410 specimens of *V. lagopus*. These specimens are housed in the collections of the National Museum of Natural History, the American Museum of Natural History, the University of Kansas, the Museum of Vertebrate Zoology, Berkley, and the California Academy of Sciences. The 1st upper molar of each specimen was digitally imaged using a Ward's Digital Stereo Microscope (model DMW143; Ward's Scientific, Rochester, New York) with image capture capability and Motic Images 2000 software version 1.3 (Motic Instruments Inc., Richmond, British Columbia, Canada, http://www.motic.com).

Digitizing and quantifying shape.—Images were digitized by placing landmarks at 7 locations (Fig. 1) and setting scale on the image of each specimen. Two criteria were sufficient for identifying landmark points: the homology of points between specimens and the ability to identify each landmark point consistently on all specimens. Landmarks 1, 2, 5, and 7 are located on top of cusps and the remaining 3 landmarks are located in valleys between cusps at the intersections of mineralized areas of the tooth. The points are considered to be anatomical landmarks in which correspondence between specimens can be made based on previous knowledge. We did not include any obvious pseudolandmarks (i.e., landmarks located in areas on the boundary of a form that would be difficult to relocate across specimens). An initial TPS file was created using TPSutil, version 1.33 (Rohlf 2004a), and images were digitized using TPSdig, version 2.05 (Rohlf 2006).

The x-y coordinate data and scale factors are used to calculate multivariate shape descriptors and a univariate measure of size for each specimen. The x-y coordinates were translated, rotated, and scaled using the Procrustes superimposton method (Rohlf 1999) in TPSrelw, version 1.42 (Rohlf 2005) and a consensus shape was constructed. This hypothetical shape provides the x-y coordinates from which the shape of each
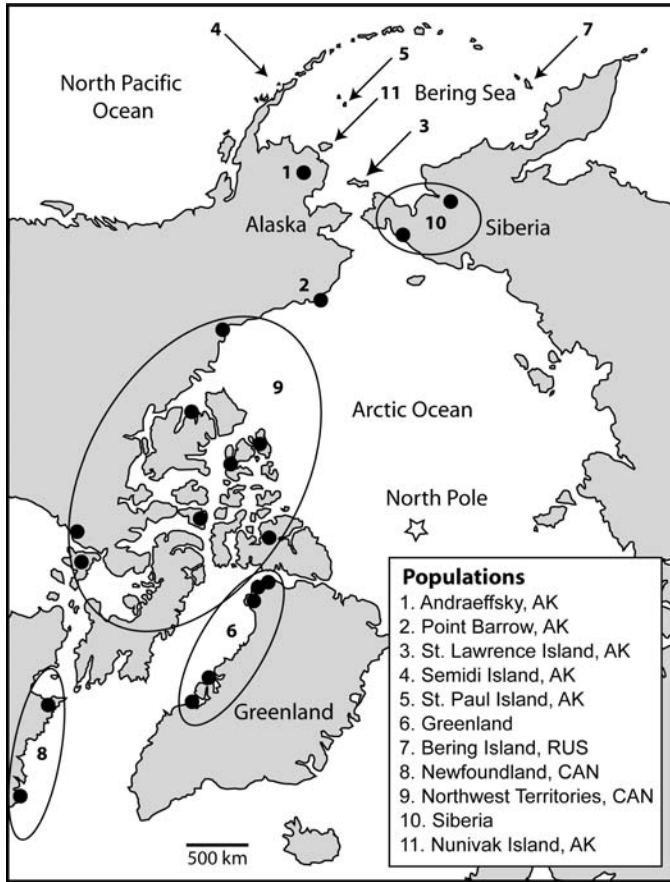
FIG. 2.—Map showing the 11 populations included in this analysis. Black dots represent locations where specimens were collected. Populations composed of specimens from more that a single location are enclosed in an ellipse.

specimen is defined. Multivariate shape descriptors, called partial warp (PW) scores, define the shape of each specimen and are calculated based on the difference between a specimen's coordinates (after translation, rotation, and scaling) and those of the consensus shape. Centroid size, used as our measure of size in the study because it is statistically uncorrelated with shape, is computed as the square root of the sum of the squared distances from all landmarks to the form centroid. Centroid size is a unitless measure of size.

A principal component analysis was performed on the 10 correlated PW scores in TPSrelw, resulting in 10 uncorrelated shape axes called relative warp (RW) scores. RW scores are the geometric morphometric equivalent of principal components. These scores can be visualized as the deformation of a grid that is undeformed for the consensus shape. The greater the deformation of an individual's grid, the more divergent the shape of that specimen is from the consensus shape. This allows one to observe the actual manner in which specimens differ from one another in shape.

Population groupings.—Three hundred seventy of the 410 specimens were grouped into a priori populations to define within-population shape variation and to test for between-population differences in shape. Eleven populations of arctic

foxes were identified from the specimens included in this analysis. Seven of these are mainland populations: Andraeffsky, Alaska ($n = 12$); Point Barrow, Alaska ($n = 68$); St. Lawrence Island, Russia ($n = 41$; this island is icebound for a portion of the year and is thus considered "mainland" for these analyses); Greenland ($n = 19$); Newfoundland, Canada ($n = 41$); Northwest Territories, Canada ($n = 54$); and Siberia, Russia ($n = 10$). Four are island populations: Semidi Islands, Alaska ($n = 24$); St. Paul Island, Alaska ($n = 73$); Bering Island, Russia ($n = 16$); and Nunivak Island, Alaska ($n = 12$; Fig. 2). Population grouping was based on geographic criteria under which a reasonable presumption of isolation can be made. Island populations are isolated from one another by considerable expanses of water. Mainland populations are separated by large geographic distances, the smallest being the approximately 1,600 km between Andraeffsky and Point Barrow, Alaska. In many cases, specimens from specific locations that form a population were all collected during a single year.

Statistical analyses.—Three statistical tests were used to characterize between-population differences in tooth shape. To test for between-population differences in overall tooth shape, PW scores were used in multivariate analyses of covariance (MANCOVAs) with size as a covariate. To test for differences in localized aspects of tooth shape between populations, RW scores were used in univariate analysis of covariance (ANCOVA) with size as a covariate. Multiple discriminant function analyses (MDAs) were performed to determine how well individual specimens could be correctly classified into a priori populations, and resulting canonical function plots were used to visualize the extent of morphologic divergence between populations.

Because shape differences may be allometric in origin, observed sexual dimorphism in size (Ballard et al. 2000; Goltsman et al. 2005; Murry and Larivière 2002; Prestrud and Nilssen 1995; Tannerfeldt and Angerbjörn 1996) and skewed sex ratios in some populations of the arctic fox (Goltsman et al. 2005) need to be considered in the context of population-level differences in tooth shape. Of the 410 specimens in this analysis, 103 were identified as female and 89 were identified as male. The remaining 218 were of unknown sex. Mean tooth size for males, females, and individuals of unknown sex is reported, and compared with that of St. Paul Island (the only island population for which data on sex were available). ANCOVAs were performed on each RW score to test for differences in shape between males and females.

Linear regression analyses were performed to test for correlations between RW scores and mean annual temperature and annual precipitation. Data collected for these analyses included specimens from 49 localities for which latitude and longitude were available, and for which there was available temperature and precipitation data. To avoid the use of non-independent data, a single consensus shape was used for any locality where more than a single specimen was present. Of the 49 localities included in these regression analyses, 26 are represented by a consensus shape of 2 or more specimens. The remaining localities are represented by individual specimens.
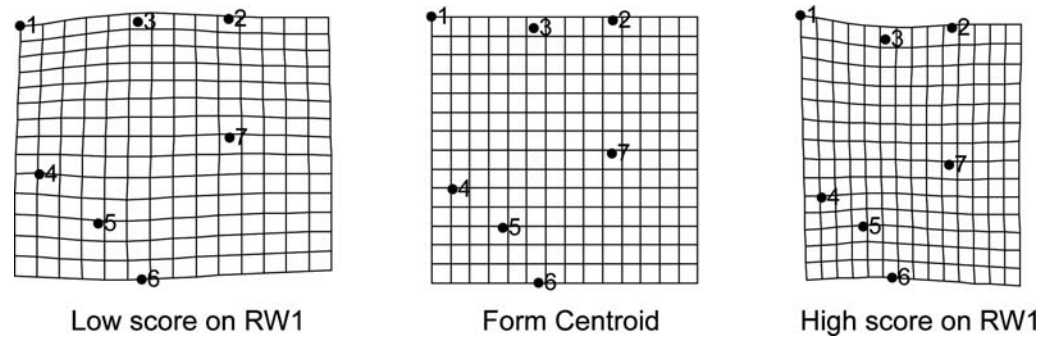
Low score on RW1   Form Centroid   High score on RW1

Fig. 3.—Deformation grids showing undeformed form centroid (center), and deformed grids for high score on relative warp 1 (RW1, right) and low score on RW1 (left). Specimens scoring low on RW1 show anterior–posterior expansion relative to the form centroid, whereas specimens scoring high on RW1 show anterior–posterior compression relative to the form centroid.

Differences in these environmental parameters underlie differences in habitat conditions and were used to test for correlations that would indicate local adaptation to such conditions.

A Mantel test (including a permutation test with 999 replications) was used to test for correlations between Procrustes distance and geographic distance for the populations. A consensus shape for each population was calculated, and the resulting 11 consensus shapes were then realigned using Procrustes superimposition in TPSspline, version 1.20 (Rohlf 2004b), and a Procrustes distance matrix was calculated. The computer program DIVA-GIS (http://www.diva-gis.org/) was used to calculate a geographic distance matrix based on the latitude and longitude data for each population. All statistical analyses except Mantel tests were run in SPSS for Windows, release 14.0 (SPSS Inc. 2005). Mantel tests were run in Passage 1.1 (http://www.passagesoftware.net/).

RESULTS

Differences in shape and associated correlative factors.— The first 5 RW scores from the relative warps analysis explained 73.75% of the variation (RW1, 25.62%; RW2, 16.92%; RW3, 12.25%; RW4, 11.10%; and RW5, 7.86%). Scores on each of the RW axes corresponded to specific variations in shape as described. Because these variations in shape are subtle, and become more subtle as less variation is explained, we limited the descriptions to the first 2 RWs. High scores on RW1 corresponded to an anterior–posterior compression of the tooth, whereas low scores on RW1 corresponded to anterior–posterior expansion of the tooth. Fig. 3 shows the deformation grid for specimens scoring low and high on RW1. High scores on RW2 corresponded to compression around the protocone and a simultaneous arching of the tooth toward the anterior, and low scores on RW2 corresponded to compression around the protocone and a simultaneous arching of the tooth toward the posterior. The remaining RW scores documented relatively slight modifications to tooth shape, such as minor shifts in location of cusps or localized expansion and compression.

Relative warp analyses also were run using PW scores for several subgroupings of the data including all specimens belonging to 1 of the 11 identified "populations" (n = 370),

mainland populations only (n = 245), island populations only (n = 125), and island populations plus Northwest Territories (n = 179; Northwest Territories was included here as a representative of a mainland morphotype, and was chosen because of this population's central geographic location and large sample size). This allowed for examination of specific relationships between populations in these limited subgroups. Percent variation explained by RW scores was not notably different from the data set including all specimens for any of the subgroups. In all cases, the 10 resulting RW scores described essentially the same patterns of variation in shape as described above.

A MANCOVA (design: shape = population + size + (size × population)) with all PW scores, all populations, and size as a covariate documented a significant interaction between size and population. Subgrouping specimens into 3 size classes (centroid size < 7.00, centroid size 7.00–8.00, and centroid size > 8.00) and plotting PW scores against populations for each size class indicated that the interaction was primarily driven by a small number of the smallest specimens in the sample. A regression of all individual RW scores on centroid size found significant correlations (following a sequential Bonferroni correction) with only 3 of the RW (RW1, RW4, and RW7). Of the 3 RWs that were found to correlate significantly with size, RW1 shows the strongest correlation ($R^2 = 0.471$, $P < 0.001$). RW4 and RW7 showed less strong correlations with size ($R^2 = 0.18$, $P = 0.001$ and $R^2 = 0.15$, $P = 0.004$, respectively), but in all cases size explained less than 50% of the variation.

Analyses of covariance with individual RWs, all populations, and size as a covariate showed only 2 of the RWs (RW2 and RW9; see Table 1) to have significant interactions between size and population. Of the remaining 8 RWs, 6 (1, 3, 4, 5, 7, and 8) showed significant differences in shape between populations when controlling for size, and 3 (1, 4, and 6) showed significant differences in size when controlling for shape (Table 1). A MANCOVA including only mainland populations found significant differences in tooth shape between populations when controlling for size (Wilk's lambda = 2.4, d.f. = 60, 1199, $P < 0.001$). A Bonferonni post hoc test was performed to determine which populations differed from one another. Greenland and Siberia differed significantly from

TABLE 1.—*F* and *P* values for ANCOVAs on all populations. Dependent variable = relative warp (RW) scores, independent variable = population, covariate = size. Interaction between size and population is only present in RW2 and RW9. Significant results are indicated in bold.

Axis	Population × size	Population	Size
RW1	$F = 1.22$, *d.f.* = 10, 370, $P = 0.275$	$F = 10.9$, *d.f.* = 10, 370, $P < 0.001$	$F = 49.14$, *d.f.* = 1, 370, $P < 0.001$
RW2	$F = 1.95$, *d.f.* = 10, 370, $P = 0.038$		
RW3	$F = 0.871$, *d.f.* = 10, 370, $P = 0.56$	$F = 3.38$, *d.f.* = 10, 370, $P < 0.001$	$F = 0.86$, *d.f.* = 1, 370, $P = 0.354$
RW4	$F = 1.79$, *d.f.* = 10, 370, $P = 0.062$	$F = 7.66$, *d.f.* = 10, 370, $P < 0.001$	$F = 10.46$, *d.f.* = 1, 370, $P = 0.001$
RW5	$F = 0.713$, *d.f.* = 10, 370, $P = 0.712$	$F = 2.79$, *d.f.* = 10, 370, $P = 0.002$	$F = 0.605$, *d.f.* = 1, 370, $P = 0.437$
RW6	$F = 1.32$, *d.f.* = 10, 370, $P = 0.219$	$F = 1.746$, *d.f.* = 10, 370, $P = 0.069$	$F = 4.51$, *d.f.* = 1, 370, $P = 0.034$
RW7	$F = 0.77$, *d.f.* = 10, 370, $P = 0.658$	$F = 3.77$, *d.f.* = 10, 370, $P < 0.001$	$F = 0.624$, *d.f.* = 1, 370, $P = 0.43$
RW8	$F = 1.319$, *d.f.* = 10, 370, $P = 0.218$	$F = 4.86$, *d.f.* = 10, 370, $P < 0.001$	$F = 0.408$, *d.f.* = 1, 370, $P = 0.523$
RW9	$F = 2.004$, *d.f.* = 10, 370, $P = 0.032$		
RW10	$F = 0.982$, *d.f.* = 10, 370, $P = 0.459$	$F = 1.102$, *d.f.* = 10, 370, $P = .359$	$F = 0.176$, *d.f.* = 1, 370, $P = 0.675$

each other, and from all other mainland populations except St. Lawrence Island. The remaining populations did not differ significantly from one another.

An MDA of all populations with only shape data resulted in low classification success (44.9% correctly classified, and 35.9% after cross validation), with slight improvement when size data were added (47% correctly classified, and 38.1% after cross validation). However, plots of shape data on the first 2 canonical functions (Fig. 4B) show all mainland populations and Nunivak Island grouping tightly, whereas Semidi Island, Bering Island, and St. Paul Island all show notably different scores on 1 or both of these functions. When size is included, both Siberia and Nunivak Island (the 2 populations showing the largest mean sizes) also score notably different on these functions (Fig. 4A). When only mainland populations are included in a MANCOVA with size as a covariate, there is no significant difference in shape between populations ($P = 0.312$), and size is only marginally significant ($P = 0.038$). MDA results for mainland-only populations score very low classification success (34.3% correctly classified, 28.6% correctly classified after cross validation) and group tightly when plotted on the first 2 functions (Fig. 4D).

Differences in shape among island populations.—Analyses of covariance including the 4 island populations and Northwest Territories with size as a covariate show significant interactions between size and population in only 2 of the RWs (RW4 and RW9), and of the remaining 8 RWs only 1 (RW10) showed no significant difference in shape between populations when controlling for size (Table 2). In only 1 (RW1) of these same 8 RWs was size found to be significantly different between populations when controlling for shape (Table 2). An MDA with these same 5 populations greatly improved the classification success over that for all populations, with 72.6% of cases correctly classified (65.9% after cross validation) and these populations show notable divergence when plotted against the first 2 canonical functions (Fig. 4C). Classification improved further when only the 4 island populations were included, with 80% of cases correctly classified and 76% after cross validation.

Correlations between shape and environmental parameters.—Relative warp scores of specimens from 49 localities were regressed against both mean annual temperature and annual precipitation to test for relationships between shape and environmental conditions. After a sequential Bonferroni correc-

tion no RW scores correlated significantly with either mean annual temperature or with mean annual precipitation.

Correlations between shape divergence and geographic distance.—Procrustes distances between consensus shapes for the 11 populations were correlated with between-population geographic distance using a Mantel test with 999 replications. Procrustes distance and geographic distance are significantly correlated for all populations ($r = 0.456$, $P = 0.002$). A Mantel test also was performed on a reduced data set including only the 7 mainland populations. Procrustes distance and geographic distance were found to correlate significantly among the mainland populations ($r = 0.688$, $P = 0.003$).

Sexual dimorphism and differences in shape between sexes.—For the overall sample, males were significantly larger than females (mean tooth size of males = 7.99; mean tooth size of females = 7.62; $P < 0.001$). Mean tooth size of specimens with unknown sex was 7.77. ANCOVAs for each RW score documented a significant difference in tooth shape between males and females in RW3 only.

Size differences among populations.—An ANOVA documented significant difference in tooth size among all populations ($F = 14.285$, *d.f.* = 370, 10, $P < 0.001$). A Bonferroni post hoc test was used to identify which populations were significantly different in size. Foxes from Semidi Island had significantly smaller teeth than all other populations. Foxes from St. Paul Island had significantly smaller teeth than all other populations except Greenland and Newfoundland, and significantly larger than Semidi. Foxes from Siberia had significantly larger teeth than all populations except Andraeffsky, St. Lawrence Island, Bering Island, and Nunivak Island. Foxes from Nunivak Island had significantly larger teeth than those from Semimdi Island, St. Paul Island, and Greenland. A significant difference in tooth size among island populations was documented ($F = 30.56$, *d.f.* = 124, 3, $P < 0.001$). A pattern of increase in tooth centroid size with island area is observed; however, a Bonferroni post hoc test indicated no significant difference in tooth size between the Nunivak and Bering island populations.

DISCUSSION

Size differences among populations.—Differences in tooth size among populations were primarily between the populations
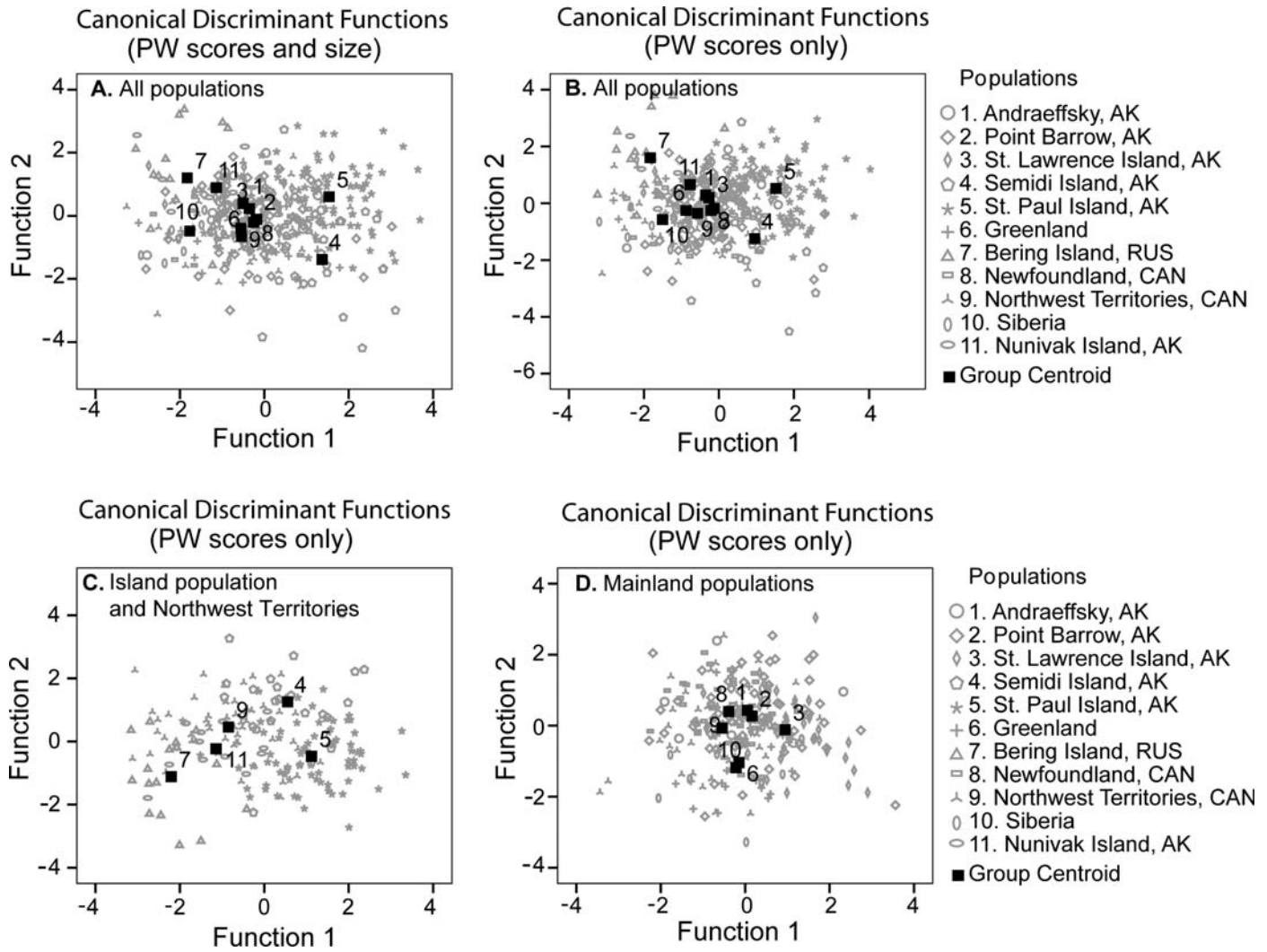
Fɪɢ. 4.—Specimens plotted against the first 2 canonical discriminant functions by population. A) Both size and all partial warp scores were used in the calculation of canonical functions for this plot of all populations; B) only partial warp scores were used for this plot of all populations; C) only islands and Northwest Territories (as a mainland representative); D) only mainland populations. Individual specimen points (identified by population symbols) are not intended to be distinguishable from one another. Numbered points represent the plotted location of the group centroid for the corresponding numbered population.

of Semidi Island and St. Paul Island with the smallest mean tooth size, and the populations of Bering Island, Nunivak Island, and Siberia with the largest mean tooth size (Fig. 5). All other populations were not notably different from one another in tooth size.

Factors influencing shape differences among populations.— Tooth shape differed significantly among populations of arctic fox (Tables 1 and 2). Based on the canonical functions plots (Fig. 4), these divergences were dominated by the St. Paul Island, Bering Island, and Semidi Island populations. Divergence in shape is particularly surprising in the Semidi Island population, because the arctic fox population present on this island was introduced by fur traders in the middle 19th century (Bailey 1993), originating from populations present on St. Paul Island. Mainland populations differed significantly in tooth shape from one another, but to a much lesser degree than that observed in the islands (Fig. 4D). We observed very little

divergence in tooth shape between mainland populations separated by distances of up to, and more than, 5,000 km, with Siberia and Greenland having the only significant divergences. However, a significant correlation between Procrustes distance and geographic distance was recorded for the mainland populations, indicating some degree of isolation by distance.

Differences in tooth shape may be nothing more than allometric patterns resulting from tooth size differences among these islands. Tooth size was found to differ significantly between some island populations, and tooth-shape differences might be explained by these size differences. However, this explanation fails to account for the notable differences in tooth shape between the Nunivak and Bering island populations (similarly large mean sizes), and between the Semidi and St. Paul island populations (similarly small mean sizes). If allometry alone were responsible for the observed divergences in tooth shape, Nunivak and Bering island populations (and the

Table 2.—*F* and *P* values for ANCOVAs on island populations and Northwest Territories. Dependent variable = relative warp (RW) scores, independent variable = population, covariate = size. Interaction between size and population is only present in RW4 and RW9. Significant results are indicated in bold.

Axis	Population × size	Population	Size
RW1	$F = 0.573$, *d.f.* = 10, 370, $P = 0.683$	**$F = 15.1$, *d.f.* = 10, 370, $P < 0.001$**	**$F = 22.00$, *d.f.* = 1, 370, $P < 0.001$**
RW2	$F = 2.28$, *d.f.* = 10, 370, $P = 0.062$	**$F = 3.75$, *d.f.* = 10, 370, $P = 0.006$**	$F = 2.72$, *d.f.* = 1, 370, $P = 0.101$
RW3	$F = 0.738$, *d.f.* = 10, 370, $P = 0.567$	**$F = 12.16$, *d.f.* = 10, 370, $P < 0.001$**	$F = 0.066$, *d.f.* = 1, 370, $P = 0.798$
RW4	**$F = 2.58$, *d.f.* = 10, 370, $P = 0.039$**		
RW5	$F = 0.633$, *d.f.* = 10, 370, $P = 0.64$	$F = 0.663$, *d.f.* = 10, 370, $P = 0.64$	$F = 0.46$, *d.f.* = 1, 370, $P = 0.498$
RW6	$F = 1.319$, *d.f.* = 10, 370, $P = 0.265$	**$F = 3.866$, *d.f.* = 10, 370, $P = 0.005$**	$F = 2.18$, *d.f.* = 1, 370, $P = 0.142$
RW7	$F = 1.54$, *d.f.* = 10, 370, $P = 0.192$	**$F = 3.967$, *d.f.* = 10, 370, $P = 0.004$**	$F = 0.468$, *d.f.* = 1, 370, $P = 0.495$
RW8	$F = 1.47$, *d.f.* = 10, 370, $P = 0.213$	**$F = 5.116$, *d.f.* = 10, 370, $P = 0.001$**	$F = 0.15$, *d.f.* = 1, 370, $P = 0.699$
RW9	**$F = 2.94$, *d.f.* = 10, 370, $P = 0.045$**		
RW10	$F = 1.992$, *d.f.* = 10, 370, $P = 0.098$	$F = 1.38$, *d.f.* = 10, 370, $P = 0.242$	$F = 1.376$, *d.f.* = 1, 370, $P = 0.242$

Siberian population) should be similar in shape based on their similarity in size. Additionally, the significant relationship between geographic distance and Procrustes distance (a raw measure of distance in shape space) also indicates shape divergence independent of size differences.

All mainland populations were similar in tooth size except for the Siberian population, which had the largest mean size of all populations examined. This was consistent with previous findings (Frafjord 1993), although Frafjord (1993) also documents a reduction in skull size with increasing latitude. We found a significant positive relationship between tooth size and latitude, but the relationship was so weak ($R^2 = 0.015$) as to be of little interest.

One issue of concern is that of observed sexual dimorphism in size in these data, and the skewed sex ratios of some island

Fig. 5.—Error-bar plot of tooth size of arctic foxes for all populations.

populations of arctic fox (Goltsman et al. 2005). Because more than half of the specimens included in these analyses did not have information on sex, there is a potential for shape differences that are allometric in origin (and result from differences in sex ratios between populations) to be incorrectly inferred as population differences. The mean tooth size of unknown specimens was 7.77, roughly intermediate between mean tooth size of males (7.99) and mean tooth size of females (7.62). We take this to indicate that our sample of unknown individuals was roughly equal in males and females, and thus our overall sample was as well. Only a single island population (St. Paul) had specimens with available data on sex. On St. Paul Island the mean tooth size of males (7.66) was close to the overall mean tooth size of females, and the mean tooth size of females on the island (7.48) was notably smaller than the overall mean size of females. This indicates that the small mean tooth size of this population was not an artifact of skewed sex ratios. ANOVA results that indicated few shape differences between males and females (significant differences between sexes documented for RW3 only) are further evidence against shape differences caused by skewed sex ratios.

One potential selective force on tooth shape is diet. Arctic foxes rely heavily on small mammals (voles and lemmings in particular) across much of their range; however, when rodents are in low abundance, diets of foxes also may include birds and bird eggs, fish, marine invertebrates, and carcasses of large marine mammals (Audet et al. 2002). Additionally, arctic foxes will follow wolves and polar bears to scavenge from kills (Chesemore 1968). Braestrup (1941) described a distinction in diet between arctic foxes that have lemmings available to them (''lemming'' foxes), and those that do not (''coastal'' foxes). Coastal foxes rely on a marine-based diet including seabirds, fish, invertebrates, and marine mammal carcasses. Recent work by Goltsman et al. (2005) on Mednyi Island (one of the Commander Islands) was consistent with the findings of Braestrup (1941). Foxes residing on Mednyi Island fed primarily on seabirds, marine mammal carcasses, fish, and invertebrates.

We argue that this information provides indirect evidence that adaptation to different food types is likely not driving divergence in tooth shape. If adaptation to specific available
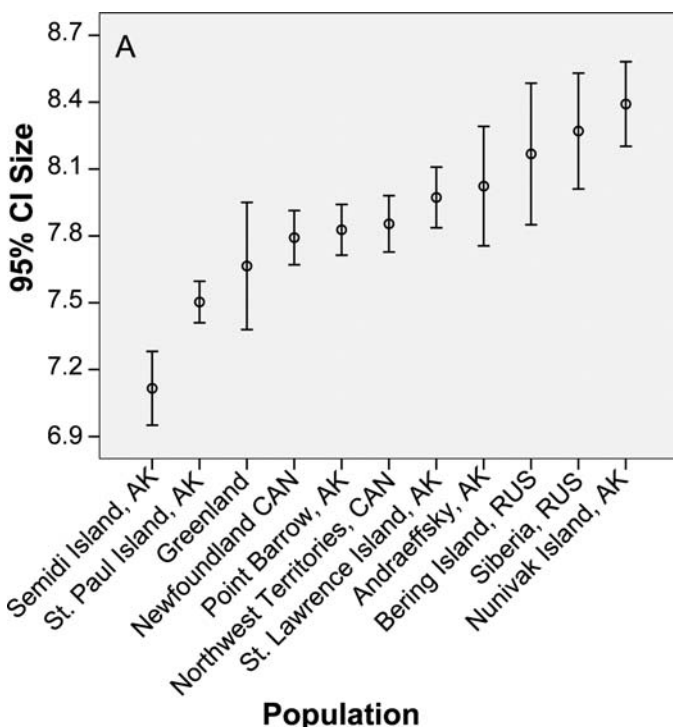
food types was driving divergence in tooth shape, we would expect to see similar tooth morphologies among "coastal" or "lemming" fox populations and differing morphologies between them. However, populations inhabiting islands differ from one another in tooth shape as much, or more than they differ from mainland populations. Additionally, the population from Greenland also would fall under the "coastal" ecotype (Braestrup 1941), yet this population is only moderately different in tooth shape from other mainland populations, but is notably different from the other "coastal" ecotypes. Unfortunately, a lack of specific information on diets of arctic foxes for any of the 4 island populations, and the lack of accurate faunal lists for these islands, prevents us from testing statistically the relationship between diet and tooth shape. Therefore, we were unable to statistically exclude local dietary adaptation as a possible explanation for the tooth-shape divergence observed among the island populations in particular. No significant relationship was found between tooth shape and mean annual temperature, or between tooth shape and annual precipitation, suggesting that adaptation to local habitat conditions does not explain the observed patterns of tooth-shape divergence.

The arctic fox is a highly mobile species and genetic isolation is unlikely in mainland populations. Dispersal of individuals of distances up to, and greater than, 1,000 km has been documented (Eberhardt and Hanson 1978; Macpherson 1968; Wrigley and Hatch 1976). This highlights the degree to which gene flow between mainland populations of arctic foxes is possible, and contrasts with the degree to which island populations of arctic foxes are likely genetically isolated. The island populations included in this analysis all represent populations that face significant zoogeographic barriers that require glacial expansion or rare rafting events to maintain a genetic connection with mainland populations.

Dalen et al. (2005) documented current gene flow between all populations of arctic foxes (except Iceland) included in their analyses, with little phylogeographic structure, concluding that this species has intermediate gene flow and no long-term zoogeographic barriers. Additionally, they found no evidence for genetic isolation by distance. Our results are roughly consistent with those of Dalen et al. (2005), although examination of data on tooth shape from our study suggests some degree of isolation by distance. However, Dalen et al. (2005) did not examine specimens from any of the islands included in our analysis. Mainland populations, although not strictly isolated from one another, diverge with geographic distance, indicating stochastic processes of tooth-shape differentiation.

Our results indicate that the observed differences in tooth shape among island populations result from a combination of long-term genetic isolation and among-population differences in tooth size. Island populations differed in size, and allometric changes in tooth shape, particularly those characterized by RW1, explained some of the divergences observed among island populations. However, the notable divergence in tooth shape among populations from similar-sized islands, with similar mean tooth size, in conjunction with the inferred geographic isolation (reducing genetic flow) of these islands

are indicators of divergence resulting from stochastic processes. For example, the similarity in tooth shape of the Nunivak Island population to that of its nearest neighbor population of Andraeffsky, Alaska, is probably a result of an increased likelihood of gene flow between these populations. The proximity of the Nunivak Island population to both the mainland and the winter ice sheet potentially explains why the Nunivak population shows the least divergence from mainland tooth shape of all island populations; rafting events are more likely for this island than for others. Alternatively, the Bering Island population, with tooth shapes divergent from both the mainland populations and Nunivak island population, is the least likely to maintain a genetic connection with mainland populations because of the low likelihood of rafting events. These findings are consistent with those of Szuma (2004) for the red fox (*Vulpes vulpes*), and we concur that geographic differentiation in tooth shape is probably a result of differing Pleistocene histories among populations.

CONCLUSIONS

We found that both tooth size and tooth shape differed significantly among populations of arctic foxes and these divergences were most notable in island populations. Significant differences in the shape of teeth among mainland populations were limited to the Greenland and Siberia populations. Mantel tests indicated isolation by distance in mainland populations alone, as well as for mainland and island populations together. We found no significant correlations between tooth shape and the environmental variables of mean annual temperature or annual precipitation. Superficially, differences in diet did not appear to explain the observed divergences in tooth shape. Unfortunately, sufficient documentation of the diets of arctic foxes was not available to test statistically for a relationship between diet and tooth shape, and thus it remains possible that dietary adaptation is a factor in tooth-shape divergence.

Island populations of arctic foxes that we inferred to have become genetically isolated from mainland populations after the last glacial maximum (or possibly earlier in the case of Bering Island) showed the greatest divergence in tooth shape. Both the Bering Island population and Nunivak Island population showed large mean tooth size, yet differed notably in shape. Populations on Nunivak Island, where genetic interchange with the mainland is more likely, had tooth shapes more similar to nearest neighbor mainland forms than to Bering Island forms (where rafting is likely a rare event), despite their similarity in tooth size. St. Paul Island and Semidi Island populations both showd small mean tooth sizes, and also were significantly divergent in tooth shape. The St. Paul Island population has likely been isolated from other populations since the last glacial maximum, whereas the Semidi Island population can only have been isolated from the St. Paul populations for approximately 150 years. Shape divergences observed in this population may be driven by patterns of decreases in body size (possibly related to small island size). Based on these results, allometric changes in tooth shape

resulting from changes in tooth size and random divergences in tooth shape after genetic isolation are the most consistent explanations for the observed data.

ACKNOWLEDGMENTS

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