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Sex Differences in Humeral Bilateral Asymmetry in Two Hunter-Gatherer Populations: California Amerinds and British Columbian Amerinds

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ABSTRACT This study uses two prehistoric Amerindian populations of hunter-gatherer subsistence patterns to determine whether levels of sexual dimorphism in humeral bilateral cross-sectional asymmetry are related to sex-specific differences in activities among these populations. Results confirmed that males of the California Amerind population who engaged in the more unimanual activities of spear hunting and warfare were more asymmetrical than were their female counterparts who engaged in the more bimanual activities of grinding acorns. California Amerind males were also more asymmetrical than British Columbian Amerind males who rowed (using both arms) extensively. Sex differences within British Columbian Amerinds were not statistically significant, nor were female differences between populations. In general, levels of humeral asymmetry appear to be more dependent on sex and population-specific behaviors rather than broad subsistence patterns. Am J Phys Anthropol 140:19–24, 2009. © 2009 Wiley-Liss, Inc.

Directional bilateral asymmetry, which differs from fluctuating asymmetry, is nonpathological in human upper limbs and relates to handedness. Fluctuating asymmetry is defined as the random difference between measures of a bilateral trait that results from disturbances in the environment during growth, which is indicative of pathology, nutritional stress, or other factors affecting health (Fields et al., 1995). Evidence of activity-induced bilateral asymmetry in humeral bones comes primarily from research on athletes (Jones et al., 1977; Krahl et al., 1994; Kannus et al., 1995; Haapasalo et al., 2000; Kontulainen et al., 2003). Haapasalo and coworkers (2000) using computer tomography examined upper limb bilateral humeral asymmetry in male tennis players ($N = 12$) and control subjects ($N = 12$) who were matched for age and weight, and who had all begun their playing careers early in life. Tennis players had greater asymmetry levels in mid- and distal humeral measurements than did the control group. Variation within each group was large, implying that additional factors affect asymmetry. Kannus et al. (1995) studied females by examining bone mineral density using DXA scanners on tennis and squash players ($N = 105$) and a nonplaying female control group ($N = 50$) to determine the effects of activity and age on bone. Levels of upper limb asymmetry were higher in the female athletes compared with the nonplaying females. Athletes who started playing before menarche had two times greater bone remodeling in the playing arm than individuals who started playing after menarche. However, athletes who started playing after the onset of their menstrual cycles still exhibited greater asymmetry values than nonplayers. Kontulainen and coworkers (2003) examined female racquetball players ($N = 36$ for young starters; $N = 28$ for old starters) and a nonplaying control group ($N = 27$) to determine the effect of sports on upper limb cross-sectional shape, which were assessed using peripheral quantitative tomography. Racquetball players had greater asymmetry values compared with the control group and those who started playing at young ages had the greatest degrees of asymmetry. Nevertheless, individuals who started playing racquetball as adults had greater asymmetry levels than those who did not play racquetball.

Thus, research on athletes supports the assumption that activity differences can cause measurable differences in upper limb bone bilateral asymmetry. Based on this, anthropologists have utilized humeral cross-sectional asymmetry to examine the effects of such behavioral distinctions as sexual division of labor and differences in subsistence patterns (e.g., Bridges, 1989, 1996; Fresia et al., 1990; Stock and Pfeiffer, 2004; Westcott and Cunningham, 2006; Maggiano et al., 2008; Sládek et al., 2007; Sparacello and Marchi, 2008).

Fresia and coworkers (1990) found changes in activity patterns among Georgia coast Amerinds who were associated with hunter-gatherer and agricultural subsistence patterns and contact with Europeans by examining precontact and postcontact populations ($N = 51$). Female humeri became less asymmetrical upon the adoption of agriculture (which involved grinding maize with mortars and pestles) while male asymmetry decreased most following Amerind contact with Europeans.

Maggiano and colleagues (2008) linked sex differences in humeral asymmetry of Mayan populations (250–700 AD)—in a location that developed from a salt-producing

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city to a commercial port—to a division of labor. Females (N = 35) had consistently low levels of asymmetry (associated with childcare and food preparation). Males (N = 47) experienced a significant decrease in asymmetry, which may have been related to an increase in administrative work.

Sparacello and Marchi (2008) examined 33 humeral pairs from a Neolithic population (6,000–5,500 BP) and a medieval population (10th–15th Century) in Italy and found asymmetry decreased in males, which they tied to stone axe use by Neolithic males. Female asymmetry was low throughout time, which they connected to mortar and pestle use for grinding grains. Another study of remains looked at humeral comparisons between Late Upper Paleolithic and Neolithic Europeans (N = 22) and also found that asymmetry decreased (Marchi et al., 2006). In this case, as well, low asymmetry in females was associated with grinding grains while decrease in males was linked to a concurrent decrease in hunting.

In England, Mays (1999) examined humeri of 111 individuals from the 11th to 16th Centuries to look at sex differences. Males were more asymmetric than females, which Mays coupled with craftsmanship (such as woodworking). Symmetry in females was probably due to their versatility; they created textiles, prepared foods, and engaged in craftsmanship. Monks were less active than laypersons and had accordingly symmetrical humeri.

Bridges and coworkers (2000) looked at humeri of Native Americans (N = 372) who had subsisted in a hunter-gatherer period (50 BC–200 AD), a transitional period when native seeds were ground (600–1050 AD), and a maize agricultural period (1050–1250 AD). Throughout time, male asymmetry decreased slightly, but female asymmetry increased in the maize agricultural period, which may be due to easier processing of maize compared with that of native seeds. Westcott and Cunningham (2006) examined humeri of 16th–19th Century horticultural Great Plaines Amerinds (N = 222) and found a decrease in sex differences as a result of an increase in male asymmetry. Females showed greater asymmetry than males, which could be due to food processing methods without the use of mortars and pestles.

In the current study, two Amerindian prehistoric hunter-gatherer populations were examined to determine whether levels of sexual dimorphism in humeral bilateral cross-sectional asymmetry could be related to differences in activities along sex lines in these populations. It was predicted that the populations would have sex differences in bilateral asymmetry and that these sex effects would be different between the two populations due to cultural differences in activity patterns, which are discussed in detail in the following Materials and Methods section.

MATERIALS AND METHODS

Samples

A skeletal sample of 136 individuals from two populations (British Columbian Amerinds, N = 18 males, 7 females; California Amerinds, N = 47 males, 64 females) was used in this study. Cybulski (1990, 1992) and Jurmain (1990) previously sexed and aged all individuals. Ages were recorded in intervals of 18–29 years, 30–44 years, and 45 years or older (Table 1). Only individuals possessing both humeri, without pathologies, were utilized.

TABLE 1. Age distribution in British Columbian and Californian Amerinds

	British Columbians		Californians		
Age	Males	Females	Males	Females	Total
18–29	6	5	11	22	44
30–44	7	2	33	36	78
45+	5	–	3	6	14
Total	18	7	47	64	136

The British Columbian Amerinds are from Prince Rupert Harbour and come from the Middle Period that dates from 3,500 years BP to 1,300 years BP (Cybulski, 1992). The site is located on British Columbia's northwest coast 50 km south of the Alaska Panhandle. Due to the moderating effect of the Pacific Ocean, the climate is relatively mild year-round compared with the colder and harsher land-locked inland regions of British Columbia. Prince Rupert Harbour lies between the eastern mountains and the Pacific Ocean, an area highly forested on the east, but sparse on the west. For the Amerinds of Prince Rupert Harbour, the habitable land was narrow, lying between the sea and the mountains. On land, the Amerinds gathered berries, edible roots, and tubers similar to potatoes (Drucker, 1955). The coastal waters and nearby rivers were rich in fish, such as salmon, herring, tuna, and trout (Drucker, 1955). Inland, up natural channels and rivers, open forests were home to numerous lakes and a rich wildlife where the Amerinds found and hunted elk, deer, marmot, fox, mink, and many other animals (Brown, 1977; Fladmark et al., 1990). Canoeing was the main form of transportation. The oars used to propel the canoes for coastal and inland travels were of the single bladed variety, which required use of both arms.

As represented in the ethnographic and archaeological literature, male tasks seemed to include fishing and hunting as well as making tools, such as bolas and harpoons, necessary for subsistence activities (MacDonald and Inglis, 1975; Halpin and Seguin, 1990). Males experienced greater mobility than females and canoed extensively. Females, on the other hand, engaged in weaving, hide cleaning, gathering vegetation (such as tubers and berries), catching small animals, and collecting shellfish (Drucker, 1955; MacDonald and Inglis, 1975; Halpin and Seguin, 1990). Domestic duties have been coupled with low asymmetries in females (e.g., Maggiano et al., 2008), but artisan activities (such as weaving and sewing) are often unilateral due to the coordination required for these tasks. Male activities, such as hunting, have been connected to high levels of asymmetry (Marchi et al., 2006), but as mentioned earlier, rowing requires use of both arms and, therefore, may result in a reduction of asymmetry.

The California site of Ryan Mound (CA-Ala-329) is located on the southeastern side of the San Francisco Bay and contained many indicators of rich natural environmental resources, such as large quantities of shellfish, waterfowl, and mammal bones (Leventhal, 1993). The temporal span of the site is 2,180–250 BP. Leventhal (1993) stated that cultural continuity existed due to similarities in mortuary practices and artifacts. Agriculture was not adopted by these Amerinds and hunting and gathering continued throughout the time span. The entire period encompassed a precontact era.

The Amerinds from CA-Ala-329 were hunter-gatherers with a diet that heavily relied on acorns and was supplemented by game (Jurmain, 1990, 1993; Leventhal, 1993). Obsidian points, shafts, hooks, and harpoons were in abundance at CA-Ala-329 (Leventhal, 1993). Sex differences in burial goods were evident: harpoons, hooks, and obsidian points were associated with male burials, and females were buried with pestles (Leventhal, 1993). This indicates a clear emphasis on hunting as a male activity, while gathering and grinding acorns were activities closely linked to females.

In summary, both Amerind populations occupied locations of rich resources. Males from both populations hunted and fished, although uses of marine resources and travel by canoes were far more extensive among the British Columbian Amerind population. Females from both populations were gatherers. In California, females utilized acorns as a staple food and ground acorns with mortars and pestles. Females of the British Columbian population had no evidence of mortar and pestle use, but did engage in activities of gathering, preparing hides, and weaving.

Cross-sectional measurements

To obtain cross-sectional data, the British Columbian Amerinds' humeri were radiographed at the Canadian Museum of Civilization in Hull, Quebec and the California Amerinds' humeri were radiographed by the Health Center at San Jose State University in San Jose, California. Following Ruff and Larsen (1990), humeral lengths were used to mark 35% of the bone length (where 100% is the proximal end), at which point cross-sectional geometries were calculated. Humeri were arranged on film in the anteroposterior orientation (i.e., the anterior side of the bone faced upward); then, they were arranged in the mediolateral orientation (i.e., the medial side of the bone faced upward). Both left and right humeri were radiographed in these orientations. Magnification errors were removed using the formula:

$$\text{Source to film distance}/(\text{source to film distance} - \text{object center to film distance})$$

Biplanar radiographs are likely to overestimate true cross-sectional values (see O'Neill and Ruff, 2004), but other methods for obtaining cross-sectional data, such as CT scans, were not available. Correction formulae for biplanar radiograph data are currently unavailable for humeral properties. Nonetheless, O'Neill and Ruff (2004) stated that the values produced by biplanar radiographs can be used in research as long as one does not compare the calculated data using biplanar radiographs with data collected by different methods.

Each radiographed humerus was measured for inner and outer diameters and the values were used to calculate the derived values: total cross-sectional area (TA), cortical cross-sectional area (CA), area moment of inertia about the mediolateral plane (Iml), area moment of inertia about the anteroposterior plane (Iap), and polar moment of inertia (J). Total area was calculated with the formula:

$$\text{TA} = \text{II} \times (\text{ML outer diameter} \times \text{AP outer diameter}/4)$$

Medullary area (MA) was calculated with the formula:

$$\text{MA} = \text{II} \times (\text{ML inner diameter} \times \text{AP inner diameter}/4)$$

Then, CA was calculated by subtracting the medullary area from the total area (CA = TA − MA) (Biknevicius and Ruff, 1992).

The formulas used for calculating Iml and Iap were:

$$\text{Iml} = \Pi/64 \times (\text{Tml} \times \text{Tap}^3 - \text{Mml} \times \text{Map}^3)$$
$$\text{Iap} = \Pi/64 \times (\text{Tap} \times \text{Tml}^3 - \text{Map} \times \text{Mml}^3)$$

where, Tml = total mediolateral breadth; Tap = total anteroposterior breadth; Mml = medullary mediolateral breadth; and Map = medullary anteroposterior breadth (Biknevicius and Ruff, 1992).

Polar moment of area was calculated using the formula:

$$J = \text{Iml} + \text{Iap}$$

Cortical area value reflects compressive strength. Total area value provides information on relative distribution of bone within cross-sections. Inertial values (Iml, Iap, J) reflect bending and torsional strength.

Bilateral cross-sectional asymmetries were then calculated by using the above data and the below formula provided by Auerbach and Ruff (2006):

$$100 \times [(\text{right value} - \text{left value})/(\text{right value} + \text{left value})/2]$$

Bilateral asymmetry calculations do not need to be standardized for body size since within-individual ratios make up the asymmetry comparisons (Trinkaus et al., 1994; Ruff, 2000).

Statistical analysis

Data were analyzed using the statistical software program SPSS version 16.0. All of the measures met the assumptions required to run parametric tests, and the relationships between variables were linear. Levene tests were run to determine homogeneity of variance. Keeping in mind that significance levels less than 0.05 indicate nonhomogeneous variance, all variables were homogeneously varied (significances of 0.06–0.78). Kolmogorov-Smirnov tests were run to determine whether data were normally distributed. As significance levels less than 0.05 indicate that the data differs from normal distribution, all variables were normally distributed (significances of 0.52–0.77).

Means and standard errors were calculated for bilateral asymmetry data. t-Tests were run on sex differences within populations and population differences within sexes. In addition, a two-factor analysis of variance (ANOVA) design was used to analyze the data. The two independent factors were population and sex. The dependent variables were CA asymmetry, TA asymmetry, Iap asymmetry, Iml asymmetry, and J asymmetry. Interactions between the factors were also examined with significant interactions being examined via box plots. The critical α levels were set at 0.05.

RESULTS

Table 2 presents the means and standard errors for asymmetry variables in percentage difference between left and right cross-sectional scores for British

TABLE 2. Comparisons of bilateral asymmetry (%) within and between population samples

	Differences between sexes, within population								Differences between populations, within sex	
	British Columbia				California					
	Males (N = 18)		Females (N = 7)		Males (N = 47)		Females (N = 64)			
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Males	Females
TA	3.215	1.613	5.686	3.302	8.518	1.204	3.808*	1.141	*	
CA	4.264	1.925	8.290	5.582	8.459	1.523	4.631	1.690		
Iap	3.764	3.671	15.219	9.373	17.555	2.749	8.890*	2.484	*	
Iml	9.749	3.330	9.099	6.271	16.197	2.337	7.033*	2.644		
J	6.667	3.244	12.081	7.311	16.841	2.403	7.946*	2.415	*	

*$P < 0.05$, t-tests.

TABLE 3. 2-factor ANOVA significance levels bilateral asymmetry variables

Variable	Sex	Population	Sex-population
TA	0.590	0.410	0.086
CA	0.973	0.927	0.179
Iap	0.765	0.426	0.033[a]
Iml	0.275	0.626	0.344
J	0.686	0.484	0.098

[a] Sum of squares = 1,718.816, df = 1, F = 4.625.

Columbian and Californian Amerinds, and separately for both males and females. Significant results are asterisked for sex differences within populations and within-sex population differences. There are significant sex differences in the California population. California males are more asymmetrical than their female counterparts on four out of five dimensions (Table 2). When looking at sex differences between populations, California Amerind males are more asymmetrical than British Columbian males in TA, Iap, and J (Table 2). No significant sex differences are present in the British Columbian population, but there is a trend of higher female asymmetry values compared with British Columbian male asymmetry values. Additionally, no significant results appear between British Columbian and California females, but there is a trend of higher asymmetry values in British Columbian females compared with California females. The lack of significant results in these mentioned trends may be the result of the small sample size of British Columbian females.

There are no significant sex or population differences in the two-way ANOVA. However, there is a significant sex-population interaction for Iap (Table 3). This reflects the greater asymmetry of California males compared with females, and a reversal of this pattern in the British Columbian sample (Figure 1). While this same general contrast is evident for other variables (Table 2), as mentioned before, sample size constraints may explain the lack of statistical significance.

DISCUSSION

Studies have found that mechanical stress due to activity (in conjunction with other uncontrolled factors) affects upper limb bone bilateral asymmetry (Jones et al., 1977; Krahl et al., 1994; Kannus et al., 1995; Haapasalo et al., 2000; Kontulainen et al., 2003). Here, levels of sexual dimorphism in humeral bilateral cross-sectional asymmetry were examined to determine if asymmetry in two hunter-gatherer Amerind populations were related to differences in activities along sex lines in these populations. Statistically significant results showed male California Amerinds to be more asymmetrical than their female counterparts and more asymmetrical than male British Columbian Amerinds. In addition, trends indicated that British Columbian females were more asymmetrical than both their male counterparts and females from California. These trends do not reach statistical significance likely due to the small sample size of British Columbian females.

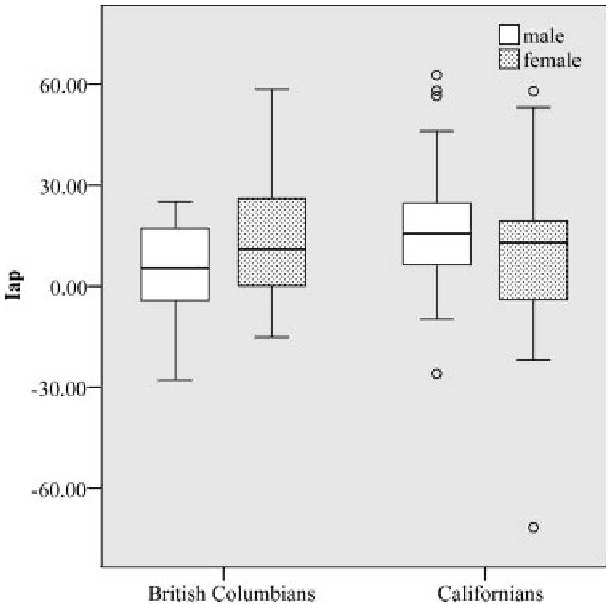

Fig. 1. Iap asymmetry (%) in British Columbian and Californian samples, male data are displayed in white boxes and female data are displayed in speckled boxes. Box represents the interquartile range; horizontal line within the box represents the median value.

It should be mentioned that Ruff and Jones (1981) and Trinkaus et al. (1994) also examined bilateral asymmetry of Amerinds from Ryan Mound; these remains were housed at Stanford University and have since been reburied. Ruff and Jones (1981) examined total area and cortical area asymmetry; the averages were close to the results reported here. For example, males had an average asymmetry in TA of 7.1% and the California males in the current sample had a TA asymmetry of about 8.5%. Additionally, in both total area and cortical area asymmetry, females of the current study and the earlier Ruff and Jones (1981) study showed less asymmetry than the males. Trinkaus et al. (1994) reported similar findings for CA and *J* asymmetries, but medians rather than means were published. These similarities in results are reassuring, and further support the findings here for Ryan Mound.

In comparison with other previously published data, British Columbian males seem to have low levels of asymmetry. Maggiano et al.'s (2008) data on Mayan populations located at a commercial port (250–700 AD) have the most comparable asymmetry levels with the British Columbian males. For example, the Mayan males had an average CA asymmetry of 4.3% for the earlier period examined, which is the same as the British Columbian male CA average. California Amerind males, on the other hand, have values similar to Georgia Coast Amerinds and Italian Neolithic populations. For example, in both the California sample and in Georgia Coast agriculturalists TA measures of asymmetry are about 8% (Fresia et al., 1990). The males in the Italian Neolithic population have an average asymmetry in *J* of 15.8% while the California Amerind males have an average asymmetry in *J* of 16.8% (Marchi et al., 2006). California females have values similar to agricultural Georgia Coast Amerinds; for example, the average TA and CA asymmetries for both populations are around 4% (Fresia et al., 1990; Trinkaus et al., 1994). British Columbian females have asymmetry values that fall between the lower asymmetries published (e.g., those of Georgia agriculturalists) and the higher asymmetries published (e.g., those of South African hunter-gatherers) (Fresia et al., 1990; Ledger et al., 2000). In summary, broad subsistence categories alone are not sufficient for predicting levels of bilateral asymmetry or sexual dimorphism in bilateral asymmetry; as detailed below, these asymmetries appear to be more dependent on population-specific differences in behavior.

Examining the present results in detail with specific attention to previously published material and knowledge of the populations' artifacts can explain why asymmetry is higher in certain groups of individuals compared with other groups of individuals. Starting with the most robust finding, male Californian Amerinds were more asymmetrical than were their female counterparts on four out of five asymmetry variables (TA, Iap, Iml, *J*). The California hunter-gatherer males at Ryan Mound expended much of their physical energy hunting and engaging in warfare with the use of spears. Leventhal (1993) and Jurmain and Bellefemine (1997) found males to be most often buried with obsidian arrowheads, and victims of these weapons were commonly males. Previously published data support the view that hunters who used primitive weaponry were prone to having asymmetrical humeri (e.g., Ledger et al., 2000). California males were about twice as asymmetrical as California females, who had low levels of asymmetry with ranges of 4–9% differences between left and right humeral cross-sections. Anthropologists have found similar low levels of asymmetry in other hunter-gatherer and agricultural populations where females used mortars and pestles to grind grains (e.g., Fresia et al., 1990; Bridge et al., 2000). The California Amerinds staple food was acorn, which required the use of mortars and pestles, and mortuary practices support the female link to such tools (Leventhal, 1993). Females participated in grinding acorns requiring the use of both arms. Thus, mortar and pestle use seems to reduce bilateral asymmetry in humeral cross-sections regardless of whether a population is hunter-gatherer or agricultural.

Further support for the mortar and pestle connection comes from studies that have found high asymmetry levels in populations where grinding is not an activity. Westcott and Cunningham (2006), as mentioned earlier, found higher levels of asymmetry in female Arikara Amerinds than in their male counterparts. These females were not engaged in grinding grains. Ledger and colleagues (2000) found highly asymmetrical humeri in females of South Africa who employed digging sticks and pulling out tubers, which requires one arm for the majority of the labor. In the current study, the asymmetry differences between females of the California population and the British Columbian population were in the predicted direction, but did not reach statistical significance (likely due to small sample size). The trend showed more asymmetry in British Columbian females than in California females for all the variables, which may relate to the fact that British Columbian females did not use mortars and pestles. British Columbian females wove baskets, mats, nets, and clothing from bark and other fibers (Halpin and Seguin, 1990). The females of the British Columbian population also cleaned and sewed hides for clothing or trade. The labor intensive artisan activities mentioned above were likely unilateral due to the skills needed to complete them; for example, when sewing hides for clothing most individuals are not ambidextrous enough to sew with both hands.

Within the male populations, California Amerinds had more asymmetry in TA, Iap, and *J* measures than did British Columbian Amerinds. British Columbian males actually had lower levels of bilateral asymmetry in Iap than California females (Table 2; Fig. 1). These low levels of asymmetry are likely linked to the rowing that British Columbian males engaged in. They spent much time rowing on streams and in the ocean, which required use of both limbs (especially when boating alone or in small groups such as in a canoe) (Brown, 1977; Cybulski, 1992; Dawson, 1992). As an aside, the British Columbian females were more asymmetrical than were their male counterparts, but this difference did not reach statistical significance likely due to sample size constraints. Nonetheless, this trend may be due to a combination of the female activities that required skilled unilateral labor rather than the use of both arms as in rowing.

CONCLUSIONS

Specific activities between the two examined populations differed (as evidenced by the archaeological record) although both populations occupied areas of rich environmental resources and did not adopt agriculture. The cultural variation between the two populations best explains the humeral asymmetry patterns found in the current study. Low levels of bilateral asymmetry were found in California female Amerinds who ground acorns with the use of both hands. Low levels of asymmetry also were found in British Columbian males, who utilized both arms in rowing canoes, compared with California males. Higher asymmetry values were found in California male Amerinds whose activities were dominated by hunting and warfare with spears. British Columbian females who did not use mortars and pestles showed an overall trend of greater asymmetry compared with both California females who ground acorns with mortars and pestles and British Columbian males who canoed extensively, but ultimately these results were not statistically significant.

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