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Adapting in the Arctic: Habitual activity and landscape interaction in Late Holocene hunter-gatherers from Alaska

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Abstract

Objectives: This study compares lower limb diaphyseal robusticity between Native Alaskan hunter-gatherers to reconstruct patterns of mobility and engagement with terrain.

Materials and methods: Ancestral remains included in this study date between 600 and 1800 C.E. and were divided into three regions: Coastal Bay, Far North Coastal, and Inland/Riverine. Cross-sectional properties were determined at femoral and tibial midshafts and standardized by powers of body mass and bone length.

Results: Consistently elevated areas and second moments of area were found in ancestral remains from the Far North Coastal, while the Coastal Bay remains had reduced diaphyseal robusticity. Individuals from the Inland/Riverine region were intermediate in robusticity for male femora, but similar to the Coastal Bay group for females. Sexual dimorphism was greatest in the Inland/Riverine ancestral remains and comparable between Coastal Bay and Far North Coastal regions.

Conclusions: Ancestral remains from the Far North Coastal region have the greatest diaphyseal robusticity in response to intensive hunting and travel over rugged terrain. Reduced sexual dimorphism in the Far North Coastal region suggest female participation in hunting activities. Intermediate diaphyseal robusticity among Inland/Riverine males and increased sexual dimorphism reflects diverse patterns of mobility in relation to the hunting cycle between males and females. Reduced diaphyseal robusticity and sexual dimorphism among the Coastal Bay group is associated with sedentary villages established around net fishing in regions with low relief. Such findings argue against technocentric views of sedentism in hunter-gatherer lifeways and generally reflect diverse adaptive strategies and interaction with local terrain among Indigenous Late Holocene hunter-gatherers of Alaska.

KEYWORDS

arctic mobility, functional adaptation, long bone diaphyseal robusticity, sexual dimorphism

1 | INTRODUCTION

Bone functional adaptation (or “Wolff’s Law”) incorporates the concept that bones subjected to increased loading deposit greater amounts of skeletal tissue on periosteal and endosteal surfaces, while those subjected to strains below optimal levels resorb bone to reduce

tissue maintenance (Frost, 1973; Lanyon, 1982; Li et al., 1990; Peck & Stout, 2009; Robling et al., 2002; Ruff et al., 2006; Schaffler, 1990). Thus, cross-sectional geometric properties of diaphyses (Table 1) may be used to quantify the response of long bones to changes in mechanical loadings (Ruff, 2019). Analyses of athletes report greater diaphyseal robusticity in bones associated with increased intensity and

TABLE 1 Cross-sectional geometric properties measured and compared between samples

Name	Definition/mechanical interpretation
Total Subperiosteal Area (TA)	Area within the outer bone contour
Cortical area (CA)	Axial strength/rigidity
Medullary area (MA)	Area within the medullary cavity
M-L SMA ^a (I_x)	A-P bending rigidity
A-P SMA (I_y)	M-L bending rigidity
Polar SMA (J)	Torsional rigidity/overall rigidity

^aSecond moment of area.

duration of physical activity (Bass et al., 2002; Claussen, 1982; Jones et al., 1977; Kannus et al., 1995; King et al., 1969; Ruff et al., 1994; Shaw & Stock, 2009a, 2009b). Conversely, individuals who experience disruptions in loading or space-related weightlessness show declines in bone strength (Jenkins & Cochran, 1969; Miyamoto et al., 1998; Peck & Stout, 2009).

Bioarchaeological research uses cross-sectional properties of long bones to reconstruct intensity of activity and mobility in the human past (Larsen, 2015; Ruff, 2005, 2019). Reductions in cross-sectional areas and second moments of area in long bone diaphyses are found where intensity of activity and mobility decline, while increases in these values occur among more active and mobile populations (Bridges, 1989; Bridges et al., 2000; Hill et al., 2016; Holt, 2003; Holt et al., 2018; Larsen, 1982; Larsen et al., 1996; May & Ruff, 2016; Ruff, 1999; Ruff et al., 1984; Ruff & Larsen, 1990). Diversity in long bone diaphyseal morphology has been reported among hunter-gatherers from differing biomes and subsistence regimes (Cameron & Stock, 2018; Holt, 2003; Ruff & Holt, 2018; Shackelford, 2014; Stock & Macintosh, 2016; Stock & Pfeiffer, 2001, 2004). Variation in terrain also influences intensity of bone strain (Ruff, 2019). Populations who traversed rugged terrain have greater bone rigidity and strength in the lower limb, while those with reduced intensity of activity from regions with flatter terrain have reduced rigidity/strength (Cameron & Stock, 2018; Holt, 2003; Holt et al., 2018; Holt & Whittey, 2019; Marchi, 2008; Marchi et al., 2011; Ruff, 2019; Ruff & Holt, 2018). Taken together, these results suggest that the contextual study of long bone cross-sectional properties is a useful adjunct to understanding patterns of behavior and landscape usage in past populations.

In addition to overall rigidity or strength, variation in structural properties between different planes of a cross section such as the ratio of anteroposterior (A-P) to mediolateral (M-L) bending rigidity can also provide information on mechanical loadings and behavior (Ruff, 1987). Elevated mobility increases A-P bending of the lower limb bones (see Ruff et al., 2015 and references therein), and thus an increase in the ratio (Cameron & Stock, 2018; Hill et al., 2016; Larsen et al., 1996; Ruff et al., 1984; Ruff & Larsen, 1990, 2014). Greater relative A-P bending rigidity is also found in regions with rugged terrain (Cameron & Stock, 2018; Holt, 2003; Holt & Whittey, 2019;

Marchi, 2008; Marchi et al., 2011; Ruff, 1999; Stock & Pfeiffer, 2004). Sexual dimorphism in these bone shape indices may be used to differentiate logistical and residential mobility patterns (Ruff, 1987, 1999). Logistical mobility is associated with the cyclical movements of task groups in pursuit of resources, while residential mobility references the movement of encampments by entire local populations (Binford, 1981; Kelly, 1992). Elevated levels of sexual dimorphism in mobility indices are observed in populations where task specialization leads to different degrees of logistical mobility between males and females (Ruff, 1987; Ruff & Larsen, 2014).

The Alaskan land-mass and constituent barrier islands incorporate a diverse geographic landscape where Indigenous hunter-gatherer cultures included a broad array of ideological, linguistic, and economic strategies (Friesen & Mason, 2016). The current study uses femoral and tibial midshaft cross-sectional properties to help reconstruct activity patterns of prehistoric Native Alaskan populations employing different subsistence strategies in a variety of environments. Six geographic regions are identified on the Alaskan landmass including North Slope and Arctic Coast, Interior, Bering Sea, Aleutian Islands, Gulf of Alaska, and Southeastern Alaska. These regions act as relatively useful designations for defining unique arrays of culturally and ecologically adaptive behaviors among Native populations (Gillispie, 2018). This study focuses on behavior and mobility in the Late Holocene hunter-gatherer populations established in the North Slope and Arctic Coast, Interior, and Bering Sea regions.

Populations from the North Slope and Arctic Coast experienced subfreezing temperatures, snowfall, extended darkness in the winter, and the existence of permafrost. Sea-ice accumulates as fast and pack-ice throughout the year excepting summer. Pack-ice forms as islets in bodies of water, while fast-ice adheres to the coastline forming a continuous landscape. This region is separated from the interior peninsula by the Brooks and De Long mountain ranges at Barrow and Point Hope respectively, while four mountain ranges are found along the Seward Peninsula (Kigluak, Bendeleben, Darby, and York ranges) in Wales. Late Holocene North Slope and Arctic Coast populations were behaviorally and ideologically diverse (Jensen, 2014, 2016; Mason, 1998). Subsistence economies in this region included hunting of ringed seals, bearded seals, and walrus as well as caribou, polar bear, and wolves (Jensen, 2014, 2016; Mason, 1998; Stanford, 1976). Smaller contributions from fish, deer, and birds were also part of the North Slope and Arctic Coast subsistence strategies (Dumond, 2014; Jensen, 2014; Larsen & Rainey, 1948; Mason, 1998; Mason & Gerlach, 1995). Finally, the Tigara and Late Western Thule communities of this area engaged in intensive whale hunting (Jensen, 2014, 2016; Larsen & Rainey, 1948; Mason, 1998). Evidence for semi-sedentary lifestyles exist in North Slope and Arctic Coast populations, with primary villages occupied year-round combined with seasonal hunting forays (Dumond, 2014; Jensen, 2014, 2016; Larsen & Rainey, 1948; Mason & Gerlach, 1995; Mason & Jordan, 1993). These findings suggest that Late Holocene populations from the North Slope and Arctic Coast were semi-sedentary, though engaged in intensive hunting behavior that included seasonal mobility across diverse forms of rugged terrain.

Populations distributed along the Bering Sea coast were active participants in a “tripartite” subsistence economy (Shaw, 1998). The tripartite subsistence economy was focused on sea-mammals, salmon, and caribou. These populations intensively harvested salmonid fish as well as migratory animals such as birds, porpoises, sea lions, and whales (Dumond, 1984, 2000; Gillispie, 2018; Shaw, 1982, 1990, 1998). At estuaries and along coasts, Bering Sea populations were dependent on salmon fishing and seal hunting (Dumond, 1984, 2000; Gillispie, 2018; Shaw, 1982, 1990, 1998). Some evidence for caribou hunting at upland locations is noted although deemphasized, as salmon and aquatic mammals were the most significant contributor to diet (Shaw, 1998). In fact, the expansion of sedentary coastal communities along the Bering Sea coast in Southwestern Alaska during the Norton phase (ca. 400 B.C.E.) is associated with the development of net fishing along coastal embayments and at the mouths of rivers (Dumond, 1984, 2000; Shaw, 1982, 1990, 1998). Later pre- and colonial era cultures of this region engaged in intensive net fishing and include associations with Thule, then Yup'ik cultures (Dumond, 1984, 2000; Shaw, 1998). Sea-ice formation in this region is seasonal, and differentiated as pack-ice (islets of frozen sea) compared with the fast-ice formed along the North Slope and Arctic Coast. The landscape of the Bering Sea region is characterized by relatively flat, lowland tundra abbreviated by rocky shorelines. These findings suggest subsistence economies that included intensive fish harvesting and marine mammal hunting established around sedentary villages, with reduced interaction with rugged terrain.

Late Holocene hunter-gatherers from inland regions around the Bering Sea and Interior portions of Alaska are associated with the establishment of winter villages in mountainous regions, while summer villages were found along rivers (Collins, 2000; Gillispie, 2018; Kofinas et al., 2010). These populations hunted caribou, moose, sheep, bear, beavers, canids, and numerous anadromous species of fish (Collins, 2000; Gillispie, 2018; Kofinas et al., 2010). Stable isotope studies emphasize the importance of salmonid fishing along the Kuskokwim River (Halfman et al., 2015), and ethnographic research points towards winter hunting in mountainous terrain (Sullivan, 1942; VanStone, 1979). Storage cache and tool kit distribution suggests reduced residential and increased logistic mobility into the later Holocene among populations from the Alaskan Interior (Potter, 2008). Diverse hunting strategies may have placed these populations in contact with myriad landscapes including mountainous terrain that borders surrounding rivers, while archaeological evidence points towards high levels of logistical mobility in association with subsistence economies split between two landscapes: riverine fishing and mountain hunting.

Two primary hypotheses are tested in this study. First, populations with greater mobility from regions with rugged terrain should exhibit more robust lower limbs with greater relative A/P bending rigidity than those from sedentary environments with flatter terrain. Here, it is predicted that ancestral remains from the North Slope and Arctic Coast will demonstrate consistently greater long bone diaphyseal robusticity and higher relative A/P bending rigidity when compared the Bering Sea and Interior regions. Ancestral remains from inland regions of the Bering Sea and Alaskan Interior are

predicted to express an intermediate level of diaphyseal robusticity in association with mobile hunting strategies and interaction with mountainous terrain. Populations from coastal areas of the Bering Sea and Gulf of Alaska regions should have the lowest robusticity reflecting a sedentary settlement pattern established around intensive fishing. It is further predicted that sexual dimorphism should be highest among ancestral remains from the inland locales of the Bering Sea and Interior regions, where logistical mobility appears elevated, and the population encountered differing environmental conditions in association with seasonal hunting patterns.

2 | MATERIALS

The skeletal remains used in this study are curated by the Departments of Anthropology within the National Museum of Natural History of the Smithsonian Institution (NMNH) and American Museum of Natural History (AMNH). Detailed information on excavations may be found in Rosa (2019) and Shackelford (2005, 2014). Many ancestral remains included in this study were collected by Ales Hrdlička on several research tours to Alaska affiliated with the United States National Museum between 1925 and 1931. It must be acknowledged that the excavation of ancestral remains by Hrdlička often did not include consultation with descendant populations, and there exist circumstances where verbal objections by community members to the excavation and curation of these remains were documented (Sockbeson, 1995). The ancestral remains included in this study are not part of an ongoing repatriation claim by Indigenous peoples. That said, it remains important to acknowledge that the remains included in this study exist as members of a collective ancestral body within Native historical memory (Bardill et al., 2018; Bear & Jones, 2002; Colwell, 2017; Krmpotich, 2010; Pullar, 1995). As such, this study will briefly address how information collected from these remains may speak to scientific and Indigenous knowledge regarding questions of ancestry.

One area of tension between Western scientific research and Indigenous worldviews may be found in explorations of time perspectivism. Western scientists impose a view of time that is linear, while Indigenous worldviews reconcile time as multi-scalar, and ancestors are active participants in the past, present, and future (Pullar, 1995). Linear time perspectivism is frequently used as an agent of dispossession by emphasizing disconnections between Indigenous communities and prehistoric ancestors (Bardill et al., 2018). In fact, it has been argued that the search for “origins” seeks to justify present social order by suggesting that the past was populated with people moving towards a teleological destiny (Ingold, 2006). This becomes particularly troubling when juxtaposed against the backdrop of settler colonialism and dispossession. In contrast, Ingold (2006) argues that bodies and environments take on meaning through recursive relationships with one another. These relationships develop over the course of a lifetime and become encoded by neurological, muscular, and anatomical systems. This view links generations through time as behaviors are written into the body through interactions between “ascendant” and “descendant” members of a population.

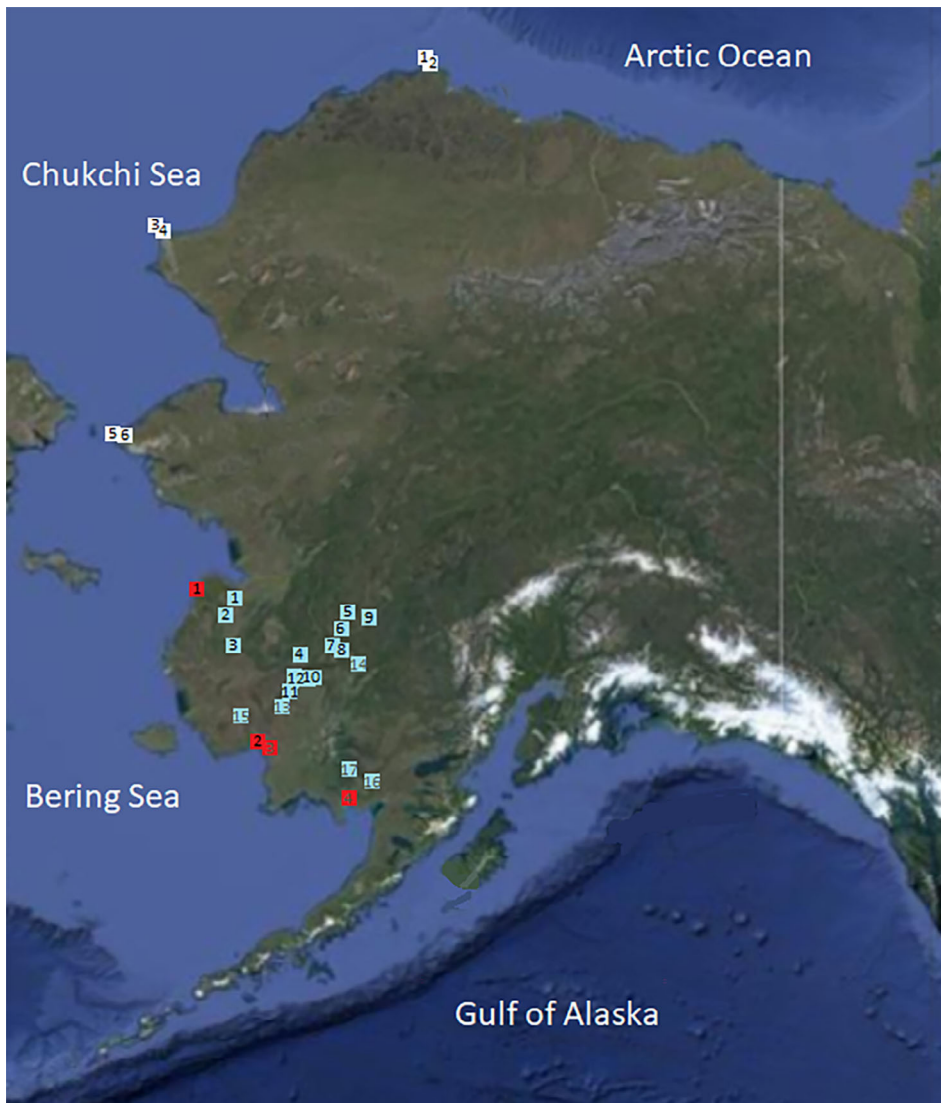


FIGURE 1 Map of archaeological sites yielding human skeletal remains included in this study. White boxes are associated with Far North Coastal sites. Red boxes are affiliated with Coastal Bay sites. Light blue boxes are associated with Inland/Riverine sites. Numbers within each box correspond to site names provided in Table 2

Biomechanical studies of long bones help dislodge linear temporality by illustrating links between ancestral remains and interactions with the natural environment—how bodies *are shaped by* and how bodies *shape* local landscapes. Long bone diaphyseal morphology is produced through the daily habits and practices of individuals, where behavior enters into a mutual relationship with underlying systemic processes (Frost, 1973; Pearson & Lieberman, 2004; Ruff, 2019; Ruff et al., 2006). Here, habitual activity becomes part of an embodied landscape, where ancestral habitus comes alive in the present and persists into the future. It should, however, be readily acknowledged that this perspective may not serve as adequate reason for study of ancestral remains to many descendant communities (Colwell, 2017). Bringing Indigenous knowledge to bear on these questions is important and necessary, and while it addresses one aspect of dispossession (in an epistemological or ontological sense), bioarchaeologists must remain mindful of other histories of dispossession in which ancestral remains were collected.

Approximate dates for ancestral remains used in this study are described. The inclusion of these dates is geared toward

understanding that the individual remains included in this study were members of communities that overlapped in time and space. Ancestral remains originating from the North Slope and Arctic Coastal region were placed into a Far North Coastal geographic group (Figure 1; Tables 2 and 3). The Far North Coastal group comprises ancestral remains from six archaeological sites distributed from the northern Kotzebue Sound region of the Bering Strait to Point Barrow (Figure 1). Far North Coastal sites are dated between 600 and 1500 C.E. based on artifact and grave good affiliations as well as radiocarbon methods (Collins, 1937; Gerlach & Mason, 1992; Giddings, 1964; Hollinger et al., 2004; Larsen & Rainey, 1948). Far North Coastal archaeological sites are affiliated with the Birnirk, Ipiutak, and Tigara cultures (Hollinger et al., 2004; Larsen & Rainey, 1948). This group represents an economically and ideologically diverse set of populations, but may be defined through economic systems focused on intensive hunting across comparable terrain, as discussed above (Dumond, 2014; Jensen, 2014, 2016; Larsen & Rainey, 1948; Mason, 1998). Recent studies found few differences in lower limb diaphyseal morphology among Far North

TABLE 2 List of sites by geographically-specific designation, excavator, and accession year

Geographic designation	Site	Site Number ^a	Excavator: Publication year
Coastal Bay	Kwiguk Pass	1	Hrdlička, 1930
Coastal Bay	Kuskogamut	2	Hrdlička, 1931
Coastal Bay	Nushagok	3	Hrdlička, 1932
Coastal Bay	Beacon Point	4	Hrdlička, 1932
Far North Coastal	Birnirk	1	Ford, 1959; Van Valin, 1917-1919
Far North Coastal	Koguk	2	Ford, 1959; Van Valin, 1917-1919
Far North Coastal	Point Hope Ipiutak	3	Larsen & Rainey, 1948
Far North Coastal	Point Hope Tigara	4	Larsen & Rainey, 1948
Far North Coastal	Shishmaref	5	Hrdlička, 1927; Collins, 1937
Far North Coastal	Kurkusuk	6	Hrdlička, 1927; Collins, 1937
Inland/Riverine	Kotlik	1	Hrdlička, 1930
Inland/Riverine	Hamilton	2	Hrdlička, 1930
Inland/Riverine	Old Areafsky	3	Hrdlička, 1930
Inland/Riverine	Paimiut	4	Hrdlička, 1930
Inland/Riverine	Grayling River	5	Hrdlička, 1927, 1930, 1931
Inland/Riverine	Anvik	6	Hrdlička, 1931
Inland/Riverine	Ghost Creek	7	Hrdlička, 1927, 1930, 1931
Inland/Riverine	Holy Cross	8	Hrdlička, 1927, 1930, 1931
Inland/Riverine	Shageluk	9	Hrdlička, 1927, 1930, 1931
Inland/Riverine	Bogus Creek	10	Hrdlička, 1931
Inland/Riverine	Kwethluk	11	Hrdlička, 1931
Inland/Riverine	Akiak	12	Hrdlička, 1931
Inland/Riverine	Bethel	13	Hrdlička, 1931
Inland/Riverine	Georgetown	14	Hrdlička, 1931
Inland/Riverine	Okahamut	15	Hrdlička, 1931
Inland/Riverine	Ekwok	17	Hrdlička, 1931
Inland/Riverine	Kokwok	18	Hrdlička, 1931

^aSite number corresponds to numerical locations indicated on the map referenced in Figure 1.

TABLE 3 Sex-specific sample sizes for each geographically specific locale

Geographic type	N male femora	N female femora	N male tibiae	N female tibiae
Coastal Bay	12	19	11	17
Far North Coastal	47	37	35	45
Inland/River	46	59	43	53
Σ	105	115	89	115

Coastal remains suggesting that it is reasonable to combine these remains (Shackelford, 2014).

Ancestral remains recovered from the Bering Sea region were placed into a Coastal Bay group (Figure 1; Tables 2 and 3). Geographically speaking, ancestral remains from the Coastal Bay region were recovered from four sites distributed at coastal embayments or at the mouths of rivers along the Bering Sea Coast of the Yukon-Kuskokwim Delta (Figure 1). Burials from this region are dated to the time just prior to and following Russian colonialism based on association with funerary items and artifacts, suggesting a period between 1500 and 1800 C.E. (Hrdlička, 1930). The burials from the Bering Sea region are

unaffiliated with any particular ethnic or linguistic population owing to a lack of context in the original site reports. However, this region is associated with Central Yup'ik ethnic and linguistic groups (Pratt, 1984).

Ancestral remains recovered from the inland and riverine regions of the Bering Sea and Interior regions of Alaska were placed into an Inland/Riverine group. Ancestral remains from the Inland/Riverine region were recovered from 17 archaeological sites located along the banks of the Kuskowkwim, Nushagok, and Yukon rivers as well as the inland delta regions surrounding these bodies of water (Figure 1; Tables 2 and 3). More specifically, these sites are located directly within

the Deg Xit'an (Ten'a or Ingalik) cultural region. These cultural traditions date between 300 C.E. and the present (Gillispie, 2018). Notes from Hrdlička (1927, 1930, 1931) suggest that some individuals were buried with coffins and included items associated with Russian traders. As a whole, colonial burials were differentiated from those of the pre-Russian era based on above-ground interment (Hrdlička, 1931). Grave goods and coffin design suggest that ancestral remains from the Inland/Riverine region likely date between 1500 and 1800 C.E.

3 | METHODS

Sex was determined using morphological variation of the *ossa coxae* and skull. Morphological features of the greater sciatic notch, ventral arc, subpubic concavity, and medial aspect of the ischiopubic ramus were recorded according to reference standards (Buikstra & Ubelaker, 1994). In addition to the pelvic girdle, or in cases where the *ossa coxae* were poorly preserved or absent, morphological features of cranial elements, including the nuchal crest, mastoid process, supraorbital margin, glabella, and mental eminence were recorded using standard protocols (Buikstra & Ubelaker, 1994). Sex was determined using morphological features, and this method does not speak to the diverse array of social and biological factors that are reflected in gender and sex. That said, explorations of sexual dimorphism in diaphyseal morphology in relation to morphological sex has the capacity to identify habitual activity patterns that question binary understandings of sex and gender in the past.

Fusion of all long bone epiphyses was used as a minimum age criterion for inclusion in this study. In addition, to counteract the impact of age-related bone loss, individuals estimated to be older than 55 years of age were not included in this analysis. Age estimation in adults relied on the degeneration and wear of skeletal elements including the pubic symphysis, auricular surfaces, enamel surfaces, cranial sutures, and sternal rib ends; phases of degeneration and wear were recorded according to standard protocols (Buikstra & Ubelaker, 1994).

Long bone measurements were collected according to standard procedures and include femoral head breadth, bicondylar femoral length, maximum femoral length, and tibial maximum length (Buikstra & Ubelaker, 1994). Superior-inferior diameter of the femoral head was used to estimate body mass. Several formulae for estimating the body mass of bioarchaeological and paleoanthropological samples from femoral head breadth have been developed (Grine et al., 1995; McHenry, 1992; Ruff et al., 1991). This study employed updated body mass estimation equations that were derived from a larger, more diverse set of reference samples (Ruff et al., 2018).

Only complete femora and tibiae were used for scanning. Left sided elements were preferentially chosen for scanning, though right sided elements were included when the left side was unavailable. Scanning was completed at 50% of bicondylar femoral length and 50% of total bone length for the tibia. These scan locations differ slightly from those used in previous research (e.g., Ruff, 2002; Ruff & Hayes, 1983), which utilize scans taken at 50% of biomechanical length; this difference should be noted if the results of this study are compared with other research.

Images for all ancestral remains excepting the Point Hope site complex (see below) were generated using a SOMATOM Emotion 6 CT Scanner (Siemens USA) at the Natural Museum of Natural History, Smithsonian Institution. Bones were placed in standard anatomical position on the scanning bed (Ruff, 2002). Foam wedges were used under the proximal and distal portions of all bones for purposes of stabilization and to ensure proper alignment of diaphyses for scanning.

Each long bone was scanned individually at the 50% level using a 2 mm slice. Machine settings of 80 kilovolts (kV) and 110 milliamperes-seconds (mAs) with a reconstruction kernel at u90s ultra sharp were found to produce adequate thresholds distinguishing between bone and air. Images obtained from CT scanning were saved as DICOM files on the Smithsonian Institution server and transferred via external hard drive to a personal computer. *MicroDicom Viewer*, a freely available software program, was used to convert each DICOM image into a TIF file for purposes of obtaining geometric measurements (see below). Cross-sectional images of femora and tibiae from the Point Hope site complex were collected by Dr. Laura Shackelford and kindly shared with this study. Cross-sectional images for the Point Hope ancestral remains were obtained using external molds of periosteal contours combined with biplanar radiography (Shackelford, 2005; Shackelford, 2014). Areal and second moment of area measurements have been compared between external contour molds, biplanar radiography, and CT-scans (O'Neill & Ruff, 2004; Stock & Shaw, 2007). These methods produce comparable results, and are therefore, possible to combine in this study.

TIF files of scans were uploaded into the free software *ImageJ* (National Institute of Health), and diaphyseal cross-sectional properties were calculated using the macro plugin *MomentMacro* (Ruff, 2016). *MomentMacro* generates TA, CA, I_x , I_y , and J, directly from each scanned image. MA was calculated by subtracting CA from TA. Definitions for each of these measurements is provided in Table 1. Cross-sectional properties for the Point Hope material were calculated using the SLICE program (Shackelford, 2005, Shackelford, 2014). All femoral and tibial section areas were standardized by body mass, and all femoral and tibial second moments of area were standardized by body mass * length² (Ruff, 2019).

Comparisons of TA, CA, MA, I_x , I_y , and J involve two or more dependent, continuous variables (geometric properties), an independent variable divided into two or more groups (site types), and independence of observations between and within groups. As such, cross-sectional properties were compared using an analysis of variance (ANOVA) test with Games-Howell pairwise comparisons. The Kruskal-Wallis test combined with Dunn's pairwise comparisons and a Bonferroni correction were used to evaluate differences in the mean ranks between regions for the I_x/I_y measurement as these observations represent non-normally distributed ratio data. All of these comparisons were performed in the SPSS 27 software program.

Sexual dimorphism was evaluated by plotting sexual dimorphism ratios ($[(\text{male} - \text{female})/\text{female}] \times 100$) in A-P/M-L femoral bending rigidity among the Alaskan ancestral remains and a broad group of individuals from hunter-gatherer, agricultural, and industrial settings (reported in Ruff, 1987, 2005, 2019; Ruff & Larsen, 2014).

Magnitudes of sexual dimorphism for femoral I_x , J , and I_x/I_y between the three Alaskan regions were compared statistically using a one-way analysis of variance (ANOVA) with a Bonferroni post hoc test. This method is an extension of a t-statistic that is produced through an analysis of covariance where sex is treated as a dichotomous variable and cross-sectional properties are the dependent variable (Bassam et al., 2002; Konigsberg, 1991; Relethford & Hodges, 1985). These calculations were performed using TestDimorph (Bassam et al., 2002) (<https://cran.rproject.org/web/packages/TestDimorph/index.html>) in the R programming space. An alpha level of 0.05 was considered significant in all tests.

4 | RESULTS

Male and female femoral and tibial cross-sectional properties show a general trend where ancestral remains from the Far North Coastal region have consistently significantly larger areas, second moments of area, and diaphyseal shape ratios compared with Inland/Riverine region and Coastal Bay regions, while Coastal Bay and Inland/Riverine are similar to one another. Box plots for male and female femoral cross-sectional properties are displayed in Figure 2a–g for ancestral remains from the Coastal Bay, Far North Coastal, and Inland/Riverine regions. ANOVA results indicate significant variation among males and females of the three groups for each cross-sectional property ($p < 0.01$). Results of the pairwise comparisons for male and female femoral cross-sectional properties are listed in Table 4. In both sexes, ancestral remains from the Far North Coastal region demonstrate significantly greater total subperiosteal area (TA) than remains from the Coastal Bay and Inland/Riverine regions; TA in the Inland/Riverine remains is also greater than in the Coastal Bay group among males. In addition, male and female femoral CA is significantly greater among the Far North Coastal compared with Inland/Riverine and Coastal Bay groups, which do not significantly differ from each other. Far North Coastal male MA is also significantly greater than males from Inland/Riverine sites. These results indicate that the femoral midshaft is externally expanded in the Far North Coastal group in both sexes, and is smallest in Coastal Bay males. Far North Coastal male and female femora demonstrate consistently greater A-P bending rigidity (I_x), M-L bending rigidity (I_y), and torsional rigidity (J) than Inland/Riverine and Coastal Bay ancestral remains, while Inland/Riverine male I_x and J is also significantly greater when compared to Coastal Bay males.

Kruskal-Wallis tests found significant differences in the rank distribution of femoral A-P/M-L bending rigidity between regions for males ($H = 7.3$, $p = 0.025$) and females ($H = 8.4$, $p = 0.014$). Results of the pairwise comparisons of femoral A-P/M-L bending rigidity are listed in Table 5 and depicted in Figure 2g. Among males, I_x/I_y is significantly smaller in ancestral remains from Coastal Bay sites than in either the Far North Coastal or Inland/Riverine groups, which do not differ significantly from each other. Among females, the only significant difference is between the Far North Coastal and Inland/Riverine groups, with Far North Coastal larger.

Box plots of tibial cross-sectional properties for the Coastal Bay, Far North Coastal, and Inland/Riverine regions are displayed in Figure 3a–g. Significant dependence between tibial cross-sectional parameters and group were found for all male measurements ($p < 0.01$) excepting MA. Significant dependence between all tibial cross-sectional parameters and group were found for all female measurements ($p < 0.01$). Results of pairwise comparisons for males and females from these regions are listed in Table 6. Results generally parallel those found in the femur, with Far North Coastal males and females usually larger in TA and second moments of area than Coastal Bay, and often Inland/Riverine groups. The only exception is female TA, which is nonsignificantly different between Far North Coastal and Coastal Bay ancestral remains. Male tibial I_x is near significantly greater in Far North Coastal compared with Inland/Riverine and Coastal Bay groups ($p < 0.10$). Differences between Coastal Bay and Inland/Riverine are nonsignificant in all comparisons. Neither the Kruskal-Wallis test nor any of the pairwise differences between groups within sex for tibial I_x/I_y were significant (data not shown).

Figure 4 plots sexual dimorphism in femoral A-P/M-L bending rigidity among the ancestral remains from Alaska compared with hunter-gatherers and agriculturalists from North America, and individuals from industrial contexts. Sexual dimorphism in ancestral remains from the Inland/Riverine are most similar to hunter-gatherers. Ancestral remains from the Far North Coastal region are comparable with agricultural populations, and individuals from the Coastal Bay region fall below industrial groups, that is, females have larger values than males. Table 7 lists sexual dimorphism ratios for midshaft femoral J , I_x , and I_x/I_y , with results of associated statistical tests shown in Table 8. Sexual dimorphism in all parameters (males larger) is greatest in the Inland/Riverine group. These differences are significant for I_x ($F = 3.84$, $p = 0.023$) and J ($F = 3.12$, $p = 0.046$) and near significant for I_x/I_y ($F = 2.41$, $p = 0.094$). Pairwise differences reach statistical significance in comparisons of I_x between Inland/Riverine and Far North Coastal as well as Inland/Riverine and Coastal Bay. Near-significance ($p < 0.10$) differences in J were found between Far North Coastal and Inland/Riverine groups and in I_x/I_y between Inland/Riverine and Coastal Bay groups.

5 | DISCUSSION

This study tested the hypothesis that ancestral remains from rugged arctic terrain with elevated terrestrial mobility would demonstrate greater femoral and tibial robusticity than sedentary individuals from flatter terrain. This hypothesis is widely supported within each sex. Among the Native Alaskan remains, individuals from the Far North Coastal region have the highest total subperiosteal areas and second moments of area, standardized for body size, for both males and females. Ancestral remains from the Inland/Riverine region are intermediate, though often statistically undifferentiated from the Coastal Bay region. Males and females from Far North Coastal sites also have the greatest relative A-P/M-L bending rigidities for femora.

Overall, these results are consistent with previous studies that demonstrated increased femoral and tibial areas and second moments

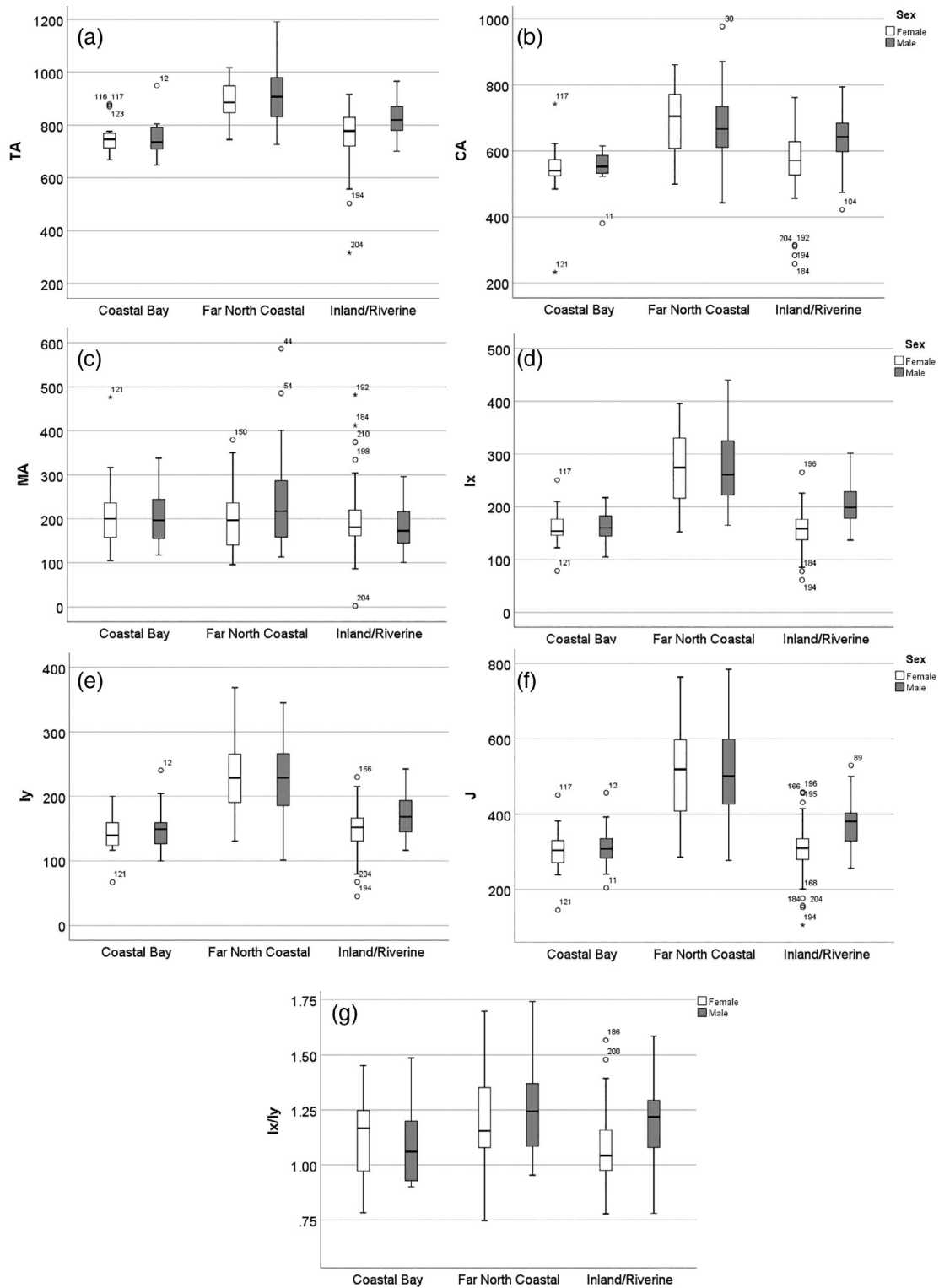


FIGURE 2 Box plots depicting the interquartile range and medians for midshaft femoral cross-sectional properties by sex and site group. Open boxes: Females; filled boxes: Males

of area as well as greater A-P/M-L bending rigidity in the lower limb of hunter-gatherers with higher terrestrial mobility, and specifically, higher mobility across rugged terrain (Cameron & Stock, 2018; Holt, 2003; Holt et al., 2018; Holt & Whittey, 2019; Macdonald et al., 2009; Ruff, 1999; Stock & Pfeiffer, 2001, 2004). Several

examples are of particular relevance to the results reported from Alaska. First, human remains from the forested regions of South Africa had higher femoral and tibial moments and second moments of area when compared with coastal groups from the Andaman Islands (Stock & Pfeiffer, 2001). These results are associated

TABLE 4 Pairwise comparisons for male and female midshaft femoral diaphyseal properties between geographic regions

Comparison	Mean difference		Mean difference	
	TA (male)	Significance (p)	TA (female)	Significance (p)
<i>FNC^a-CB^b</i>	159.8	0.0001	141.3	0.0001
<i>FNC-IR^c</i>	93.7	0.0001	133.9	0.0001
<i>IR-CB</i>	65.9	0.043	7.4	0.922
	CA (male)	Significance (p)	CA (female)	Significance (p)
<i>FNC-CB</i>	126.8	0.0001	152.2	0.0001
<i>FNC-IR</i>	35.5	0.149	129.9	0.0001
<i>IR-CB</i>	91.3	0.0001	22.4	0.649
	MA (male)	Significance (p)	MA (female)	Significance (p)
<i>FNC-CB</i>	32.9	0.361	-10.8	0.881
<i>FNC-IR</i>	58.2	0.003	4.2	0.96
<i>IR-CB</i>	-25.3	0.422	-15.0	0.771
	I _x (male)	Significance (p)	I _x (female)	Significance (p)
<i>FNC-CB</i>	116.9	0.0001	112.6	0.0001
<i>FNC-IR</i>	76.3	0.0001	115.7	0.0001
<i>IR-CB</i>	40.6	0.002	-2.9	0.954
	I _y (male)	Significance (p)	I _y (female)	Significance (p)
<i>FNC-CB</i>	75.7	0.0001	86.4	0.0001
<i>FNC-IR</i>	57.8	0.0001	80.8	0.0001
<i>IR-CB</i>	17.9	0.326	5.6	0.842
	J (male)	Significance (p)	J (female)	Significance (p)
<i>FNC-CB</i>	192.8	0.0001	199.0	0.0001
<i>FNC-IR</i>	134.2	0.0001	196.3	0.0001
<i>IR-CB</i>	58.6	0.033	27.0	0.986

Note: *Italic text indicates statistically significant difference.*

^aFar North Coastal.

^bCoastal Bay.

^cInland/Riverine.

TABLE 5 Results of the Kruskal-Wallis pairwise tests for differences in A-P/M-L bending rigidity of males and females at the femoral midshaft

Comparison	H	Significance (p)
<i>Male pairwise</i>		
<i>FNC^a-CB^b</i>	-26.0	0.02
<i>FNC-IR^c</i>	-4.8	0.455
<i>IR-CB</i>	21.3	0.02
<i>Female pairwise</i>		
<i>FNC-CB</i>	10.3	0.806
<i>FNC-IR</i>	-20.4	0.011
<i>CB-IR</i>	10.1	0.736

Note: *Italic text highlighting indicates statistically significant difference.*

^aFar North Coastal.

^bCoastal Bay.

^cInland/Riverine.

with greater terrestrial mobility in hunter-gatherers reliant upon terrestrial versus aquatic resources. In addition, differences in terrain must also be considered when comparing femoral and tibial

cross-sectional properties between ancestral remains from Alaska. Individuals from the Ligurian coast of northwest Italy who engaged in animal herding across rugged terrain had significantly greater lower limb diaphyseal robusticity when compared with sedentary Neolithic and coastal fishing communities (Marchi, 2008; Marchi et al., 2011; Sparacello et al., 2011, 2015). In Alaska, Shackelford (2014) compared femoral cross-sectional properties of Tigara and Ipiutak hunter-gatherers from Point Hope, Alaska with those of five Holocene populations¹ with differing subsistence strategies and landscape interaction. Relative to Holocene hunter-gatherers, both males and females from Point Hope demonstrated high levels of femoral midshaft robusticity and were comparable only to the hyper-robust Jomon hunter-gatherers from Japan. Robust femora of males and females Point Hope were attributed to increased mobility across the rugged terrain at Point Hope (Shackelford, 2014).

While some communities included in the Far North Coastal group participated in offshore whaling, all individuals hunted aquatic and terrestrial mammals. These behaviors occurred over rugged terrain including the hunting and transportation of mammal remains over

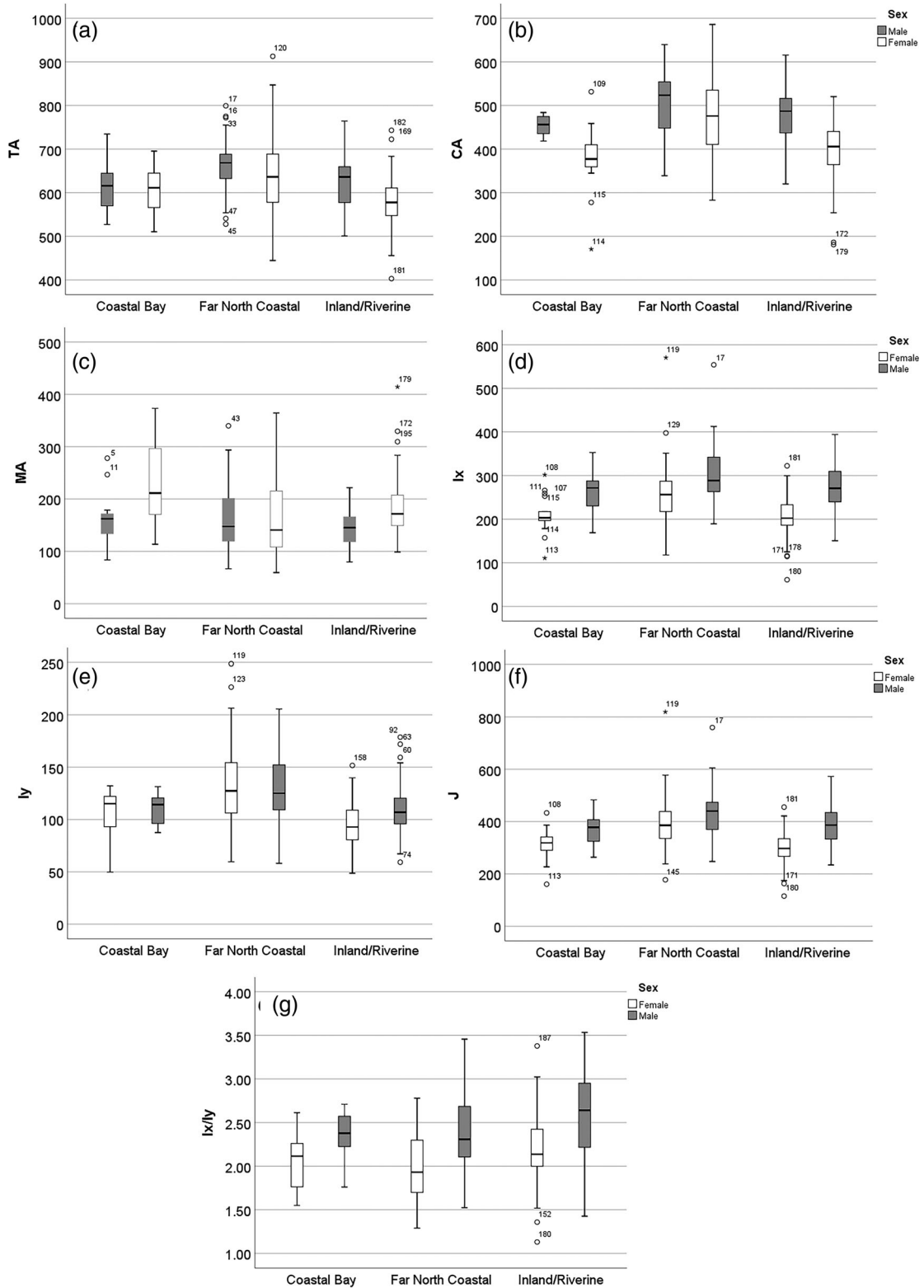


FIGURE 3 Box plots depicting the interquartile range and medians for midshaft tibial cross-sectional properties by sex and site group. Open boxes: Females; filled boxes: Males

sea-ice and across extensive mountain ranges. By contrast, reduced terrestrial mobility and interaction with lowland terrain is reported for Coastal Bay populations, where net fishing and marine mammal hunting formed the primary economic base. A combination of riverine

fishing and terrestrial mammal hunting among Inland/Riverine groups, which would therefore be expected to result in intermediate femoral and tibial robusticity between individuals from the Far North Coastal and Coastal Bay. These differences in hunting practice and landscape

TABLE 6 Pairwise comparisons for male and female midshaft tibial diaphyseal properties between geographic regions

Comparison	Mean difference		Mean difference	
	TA (male)	Significance (p)	TA (female)	Significance (p)
FNC ^a -CB ^b	45.3	0.142	38.0	0.214
FNC-IR ^c	42.5	0.006	63.7	0.004
IR-CB	2.8	0.992	-25.7	0.288
CA (male)		Significance (p)	CA (female)	Significance (p)
FNC-CB	47.4	0.002	108.0	0.0001
FNC-IR	25.6	0.214	87.9	0.0001
IR-CB	21.7	0.176	20.2	0.603
MA (male)		Significance (p)	MA (female)	Significance (p)
FNC-CB	-2.0	0.994	-69.9	0.007
FNC-IR	16.9	0.257	-24.1	0.235
IR-CB	-18.9	0.542	-45.9	0.071
I _x (male)		Significance (p)	I _x (female)	Significance (p)
FNC-CB	46.2	0.058	52.5	0.008
FNC-IR	30.5	0.057	57.7	0.001
IR-CB	15.6	0.665	-5.2	0.909
I _y (male)		Significance (p)	I _y (female)	Significance (p)
FNC-CB	22.0	0.010	30.6	0.005
FNC-IR	23.0	0.002	41.1	0.0001
IR-CB	-1.0	0.986	-10.5	0.28
J (male)		Significance (p)	J (female)	Significance (p)
FNC-CB	68.2	0.026	83.1	0.004
FNC-IR	53.5	0.011	98.8	0.0001
IR-CB	14.7	0.795	-15.7	0.658

Note: Italic text indicates statistically significant difference.

^aFar North Coastal.

^bCoastal Bay.

^cInland/Riverine.

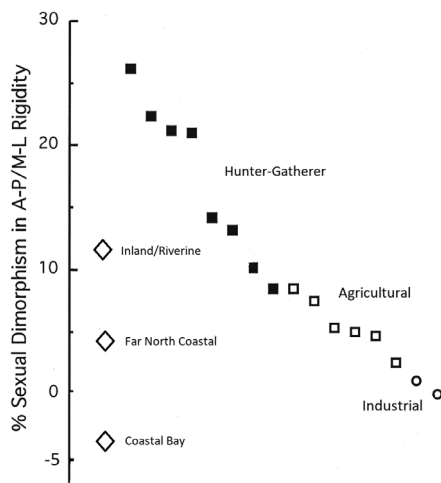


FIGURE 4 Sexual dimorphism in A-P/M-L bending rigidity for the Coastal Bay, Far North Coastal, and Inland/Riverine site groups compared with native American and modern industrial samples associated with hunter-gatherer, agricultural, and industrial economies. Adapted from Ruff (1987, 2005) and Ruff and Larsen (2014)

TABLE 7 Sexual dimorphism indices for midshaft femoral cross-sectional parameters in the native Alaskan samples

Group	N	J	I _x	I _x /I _y
Coastal Bay	31	2.96	0.63	-3.5
Far North Coastal	84	0.60	2.2	4.2
Inland/Riverine	105	21.5	21.5	11.1

interaction very likely contributed to the pattern of greater diaphyseal robusticity observed in the Far North Coastal compared with Coastal Bay and Inland/Riverine, and (in some properties) the intermediate robusticity found in ancestral remains from the Inland/Riverine region. This supports previous studies that have found evidence for adaptive variation in long bone cross-sectional properties among closely related populations, reflecting exploitation of different ecosystems across a diversity of landscapes (e.g., Cameron & Stock, 2018; Ruff et al., 1984; Sparacello & Marchi, 2008; Stock & Pfeiffer, 2004). In addition, these findings are consistent with archaeological studies of economy and mobility in Late Holocene Alaska (Dumond, 1984, 2000;

TABLE 8 Results of the Bonferroni pairwise tests for differences in the magnitude of sexual dimorphism between samples in femoral properties

Comparison	Mean difference	F	p
<i>Ix/Iy</i>			
FNC ^a –CB ^b	0.09	–1.11	0.803
FNC–IR ^c	–0.07	–1.26	0.63
IR–CB	0.16	2.19	0.089
<i>Ix</i>			
FNC–CB	4.3	–0.16	0.99
FNC–IR	–39.2	2.38	0.018
IR–CB	43.5	2.78	0.006
<i>J</i>			
FNC–CB	–6.2	0.158	0.99
FNC–IR	–62.2	2.74	0.071
IR–CB	56.0	2.07	0.122

^aFar North Coastal.^bCoastal Bay.^cInland/Riverine.

Halfman et al., 2015; Jensen, 2014, 2016; Larsen & Rainey, 1948; Mason, 1998; Potter, 2008; Shaw, 1982, 1990, 1998).

Observed sexual dimorphism in femoral diaphyseal robusticity supports the second hypothesis of this study, while suggesting further complexity in habitual behavior. Sexual dimorphism in femoral A-P/M-L bending rigidity in ancestral remains from Inland/Riverine regions is comparable to that observed in hunter-gatherers from North America (Ruff, 1987, 2005; Ruff & Larsen, 2014), and is greater than the Far North Coastal or Coastal Bay groups. Sexual dimorphism in femoral A-P/M-L bending rigidity among ancestral remains from Far North Coastal and Coastal Bay regions is similar to agricultural and industrial populations, respectively (Ruff, 1987, 2005; Ruff & Larsen, 2014). Differences in A-P/M-L bending rigidity in the femur and tibia reflect (in part) A-P forces transmitted through the knee joint (Pauwels, 1980; Ruff, 2005). Elevated sexual dimorphism in A-P/M-L bending rigidity is, therefore, attributed to greater mobility among males including activities involving engagement with more rugged terrain (Ruff, 1987, 2005, 2019; Ruff & Larsen, 2014). These findings are, therefore, consistent with a sexual division of labor in the Inland/Riverine region where males were more engaged in long distance travel over rugged terrain (also see below). However, results from this study also demonstrate that sexual dimorphism in A-P/M-L bending rigidity among hunter-gatherers may show substantial variation and be comparable to more sedentary agricultural and industrial populations. Comparisons of sexual dimorphism between regions in Alaska provide greater insight into the behavioral context for this variability.

Sexual dimorphism of femoral diaphyseal robusticity in ancestral remains from the Coastal Bay region is reduced and most similar to that found in industrial populations. General economic models of hunter-gatherers emphasize a routine division of labor between males and females (e.g., Kelly, 1995; Winterhalder, 2001) suggesting that

sexual dimorphism in skeletal indicators of habitual activity should be significant in these groups. Sexual dimorphism in lower limb diaphyseal morphology is pronounced among coastal hunter-gatherers from South Africa (Stock & Pfeiffer, 2004), the Andaman Islands (Stock & Pfeiffer, 2001), and Japan (Kimura, 2006), while large-scale reviews find that this trend is apparent across North America (Ruff, 1987, 2005; Ruff & Larsen, 2014). However, reduced sexual dimorphism among coastal hunter-fisher-gatherer communities from Mesolithic Europe has been reported, especially when compared with riverine sites surrounded by mountainous landscape (Ruff & Holt, 2018). This suggests that the behavioral environment of each group must be carefully considered in exploring factors that contribute to sexual dimorphism in lower limb diaphyseal morphology.

Recent theoretical work critiques the techno-centric argument that agriculture exists as a prerequisite to sedentism and sociopolitical complexity, specifically advocating that evolutionary studies break with this teleological thinking by recognizing the vast socioecological complexity and diversity in hunter-gatherer communities (Arnold, 1996; Arnold et al., 2015; Temple & Stojanowski, 2019). These theoretical contributions may be observed in the Coastal Bay populations, where sedentism appears tethered to economic structures established around net fishing (Shaw, 1982, 1990, 1998). Large-scale villages were supported by these practices around 400 B.C.E., and these behaviors persisted into the colonial period (Shaw, 1998). Ethnographic research among Yup'ik communities documents comparable investment in fishing by males and females (Fienup-Riordan, 1986), a point emphasized across Native Alaskan fishing traditions (Murdoch, 1892; Rainey, 1947; VanStone, 1979). Within Yup'ik ethnography, females heavily engage with processing fish, a practice requiring considerable skill and importance for maintaining reciprocal relationships with nature (Frink, 2009). Results from the Coastal Bay region indicates that specific hunting and gathering economies that include equivalent mechanical contributions from males and females may produce patterns of sexual dimorphism in long bone diaphyseal properties that are comparable to industrial populations under circumstances where these behaviors are associated with sedentary lifestyles centered around stable economic structures. Such findings imply great complexity in occupational task differentiation in hunter-gatherer communities that may be revealed using long bone cross-sectional properties.

The magnitude of sexual dimorphism was also reduced in the Far North Coastal group when compared with Inland/Riverine group, and was more similar to the Coastal Bay sites. This result was somewhat surprising among ancestral remains from the Far North Coastal region, where elevated diaphyseal robusticity is repeatedly found, suggesting high levels of mobility over rugged landscapes. Lower levels of sexual dimorphism, but greater diaphyseal robusticity is observed in Early compared with Late Neolithic populations in the Cis-Baikal region of Siberia suggesting that sexual dimorphism may be reduced under circumstances of elevated terrestrial mobility in males and females (Stock & Macintosh, 2016). Diaphyseal robusticity among females from agricultural Europe (ca. 5300 B.C.E. through 850 C.E.) is comparable to contemporary semi-elite male athletes, suggesting substantial

female contributions to labor in past populations (Macintosh et al., 2017). Given the higher level of lower limb robusticity repeatedly observed among both males and females from the Far North Coastal region compared other areas, it is possible that similar levels of strain may have reduced sexual dimorphism in lower limb diaphyseal robusticity in this region.

Among Far North Coastal sites, females have substantially greater A-P bending rigidity, areas, and second moments of area when compared with Inland/Riverine and Coastal Bay males and females (Figures 2 and 3). The ethnographic record documents intensive female labor in Far North Coastal populations including the transportation of caribou, seal, and whale meat from hunting locales to residential communities (Murdoch, 1892; Nelson, 1899; Rainey, 1947; Steffánsson, 1919). These behaviors require the movement of heavy remains over large distances (some estimated at ~5 km) and across rugged arctic terrain (Murdoch, 1892; Nelson, 1899; Rainey, 1947). The retrieval and processing of meat has immense symbolic value among Far North Coastal populations as these interactions help ordain spiritual communications that influence the success of future hunts (Fienup-Riordan, 1994; Lantis, 1947; Laugrand & Oosten, 2014; Rainey, 1947). In addition, while hunting is often referenced as a “male” activity in the ethnographic record, it remains important to emphasize that this gendered distinction does not preclude female participation. Gendered identities in Far North Coastal populations are fluid rather than binary and chosen in association with the habits, dispositions, and practices of the individual, including beliefs about ancestral spirits that inhabit the body (Saladin d’Angulure, 1994). In this sense, Far North Coastal females were deeply engaged in the socioecological systems of this region. Results from this study provide evidence that reduced sexual dimorphism *combined with* increased areas and second moments of area in femoral and tibial cross-sectional properties among Far North Coastal populations are consistent with elevated levels of diaphyseal strain for both sexes, specifically owing to female participation in intensive hunting practices.

Despite comparatively intermediate levels of diaphyseal robusticity, sexual dimorphism appears higher in the Inland/Riverine region than the Far North Coastal or Coastal Bay areas. This pattern of sexual dimorphism is comparable to hunter-gatherers from North America (Ruff, 1987, 2005; Ruff & Larsen, 2014). There may also be specific parallels with hunter-gatherers from other lacustrine and riverine contexts. For example, a general reduction in mobility has been observed between the Early and Late Neolithic occupants of the Cis-Baikal region of Siberia (Stock & Macintosh, 2016). Interestingly, the reduction in mobility at Cis-Baikal was accompanied by an increase in sexual dimorphism, where female mobility reduced over time. Another study found that male femoral A-P bending strength was consistently higher at the Schela Cladovei site in the Iron Gates region of the Danube River when compared with other Mesolithic coastal hunter-fisher-gatherers across Europe, though female A-P bending strength at Schela Cladovei fell within the range of European coastal Mesolithic females (Ruff & Holt, 2018). These results are consistent with a higher magnitude of sexual dimorphism among riverine hunter-gatherers. Occupants of Schela Cladovei are differentiated from European coastal Mesolithic groups by a reliance on anadromous

fish and likely forays into surrounding mountains on hunting excursions suggesting higher levels of logistical mobility. It is possible that the reliance on both fishing and hunting accentuated differences in mobility in relation to the hunting cycle, with males participating more heavily in seasonal long-distance travel.

Results are also comparable to studies from the Roonka site of the Murray River region of Southwestern Australia (Hill et al., 2020). Ancestral remains from the Roonka site express elevated levels of sexual dimorphism in lower limb diaphyseal morphology, though female cross-sectional properties are smaller than hunter-gatherers from arid environments in Africa. These results suggest greater mobility among males compared with females at Roonka. One difference between the Roonka results and those obtained from the Inland/Riverine Alaskan and Schela Cladovei ancestral remains is associated with terrain. Despite originating from a region with relatively low topographic relief, sexual dimorphism remained elevated at Roonka, suggesting that these patterns of variation may be observed in riverine hunter-gatherers from diverse landscapes, and especially, under circumstances where sexual division of labor may engender risk minimization in regions with seasonally available resources.

Archaeological and ethnographic research provide evidence explaining how these patterns of sexual dimorphism emerged among the Inland/Riverine region. First, populations from the Inland/Riverine region exploited large numbers of anadromous fish (Brelsford et al., 1987; Collins, 2000; Gillispie, 2018; Halffman et al., 2015; Kofinas et al., 2010). However, the broad hunting spectrum of these populations also included birds, caribou, moose, and sheep (Brelsford et al., 1987; Collins, 2000; Gillispie, 2018), with seasonal expeditions into mountainous terrain to engage these prey animals (Brelsford et al., 1987; Kofinas et al., 2010; Sullivan, 1942; VanStone, 1979). Zooarchaeological analysis along the Kuskokwim River documents evidence for consumption of small mammals, birds, and caribou at around 1 CE (Hays et al., 2010). Ethnographic studies of Deg Xit’an fishing suggests that these activities occurred at specialized camps during the spring, summer, and early fall, and participation in this behavior incorporated the entire community (Sullivan, 1942; VanStone, 1979). By contrast, a component of Deg Xit’an hunting required forays into the surrounding mountains during the late winter, early spring, and fall (Sullivan, 1942; VanStone, 1979). Hunting behavior included movement across rugged terrain, and frequently required persistence tracking in deep snow. These mobility patterns in relation to hunting were predominantly engaged by males. Female contributions to the hunting cycle included processing of meat (VanStone, 1979). Handling the residual elements of animals is of substantial importance to the hunting cycle and maintenance of reciprocal relationships with nature (Fienup-Riordan, 1994; Lantis, 1947; Laugrand & Oosten, 2014; Rainey, 1947). These findings indicate that sexual dimorphism within the Inland/Riverine area reflects a pattern of logistical mobility that differs from Far North Coastal and Coastal Bay populations, with males and females participating in the hunting cycle, but greater mobility among males.

Results from this study suggest differences in habitual activity in ancestral remains associated with Late Holocene hunter-gatherers in

Alaska. These behaviors are consistent with landscape interaction as well as archaeologically and ethnographically documented habitual activity in each region, though some limitations should be acknowledged. First, there is some unevenness in the number of individuals from the Coastal Bay region. While statistical methods take this into consideration, sample size and comparative methods remain an important question opening up a role for maximum likelihood inferences in future research. As noted above, these ancestral remains were collected with very little archaeological context, and sometimes, under questionable ethical circumstances. As a result, there exist questions regarding temporal alignment of the samples. In addition, ancestral remains were drawn from a series of sites that were homogenized for purposes of broad comparison. It is likely that the level of diversity in habitual behaviors is far greater than that captured using cross-sectional geometric measurements of the lower limb. Future studies of long bone diaphyseal morphology that include the upper limb bone remains will augment results from this study by exploring variation in manual activity.

6 | CONCLUSIONS

This work explored variation in the structural properties of lower limb bone diaphyses among Late Holocene Native Alaskan hunter-gatherers in relation to mobility and terrain. The general predictions of this study are largely supported by the results, demonstrating a clear pattern of increased diaphyseal robusticity among males and females in the Far North Coastal compared with Inland/Riverine and Coastal Bay regions. Far North Coastal populations were engaged in an intensive hunting economy that required traversing long distances of arctic tundra and fast-ice. While ancestral remains from the Inland/Riverine region were occasionally more robust than individuals from the Coastal Bay region (especially in male femora), the general trend is that the two groups appear to have comparable lower limb diaphyseal robusticity, and thus, similar patterns of lower limb bone mechanical loading.

Sexual dimorphism in lower limb diaphyseal robusticity was highest in the Inland/Riverine group and lowest in the Far North Coastal and Coastal Bay areas. Far North Coastal males and females engaged with rugged arctic terrain as part of an intensive economic structure that included hunting marine mammals on sea-ice, caribou across arctic tundra, and transporting the remains of these animals over this challenging landscape. By contrast, Coastal Bay populations were comparatively sedentary, engaging in intensive net fishing with reduced interaction with rugged terrain. These results challenge previous assertions surrounding labor and mobility in hunter-gatherers by demonstrating comparable lower limb strain between males and females from intensive hunting environments and supports the argument that more homogeneous mechanical loading of the lower limb in hunter-gatherer communities can evolve independent of agricultural technology.

Sexual dimorphism in lower limb robusticity was substantially higher among Inland/Riverine groups. Inland/Riverine populations thrived along river corridors within mountainous landscape. Greater sexual dimorphism in this region may be associated with increased logistical

mobility and occupational differentiation where males engaged in hunting activities across more rugged terrain. These differences highlight variation in male and female mobility in relation to hunting, though emphasize that both were active participants in the hunting cycle.

Taken as a whole, results from this study demonstrate consistency between known activities, landscape, and lower limb diaphyseal robusticity. This variation reflects long-standing adaptations to unique and challenging ecological contexts that further portend great diversity within hunter-gatherer ecosystems. Findings from this study also point towards important interactions between the ideological landscape of these populations and behavior suggesting that long bone diaphyseal morphology helps build knowledge of recursive relationships between people and place. In this sense, the patterns of behavior revealed through cross-sectional geometry in this study may be seen as part of a broader ideological-ecological system that helped ordain reciprocal relationships within the hunter-gatherer world.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

ENDNOTE

¹ Late to Final period Jōmon, Andaman Islanders, Semi-nomadic Libyan Sahara herders, sedentary agricultural Egyptians, and contemporary Kenyans

AUTHOR CONTRIBUTIONS

Daniel Temple: Conceptualization; formal analysis; investigation; methodology; supervision; writing-original draft; writing-review & editing. **Emily Rosa:** Conceptualization; formal analysis; investigation; methodology; writing-original draft. **David Hunt:** Data curation; formal analysis; investigation; methodology; resources; supervision; writing-review & editing. **Christopher Ruff:** Conceptualization; formal analysis; investigation; methodology; supervision; writing-review & editing.

DATA AVAILABILITY STATEMENT

The data in this project were collected as part of a Masters thesis conducted at George Mason University. Please contact the authors for access to the data.

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