

## RESEARCH ARTICLE

# Adapting in the Arctic II: Upper limb diaphyseal robusticity and habitual activity in Late Holocene hunter-gatherers from Alaska

Daniel H. Temple<sup>1</sup>  | Emily Rosa<sup>1</sup> | David R. Hunt<sup>2</sup> | Christopher B. Ruff<sup>3</sup> 

<sup>1</sup>Department of Sociology and Anthropology, George Mason University, Fairfax, Virginia, USA

<sup>2</sup>National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia, USA

<sup>3</sup>Center for Functional Anatomy and Evolution, Johns Hopkins University, Baltimore, Maryland, USA

## Correspondence

Daniel H. Temple, Department of Sociology and Anthropology, 6260 Horizon Hall, George Mason University, 4400 University BLVD, Fairfax, VA 22030-444, USA.  
Email: [dtemple3@gmu.edu](mailto:dtemple3@gmu.edu)

## Abstract

**Objectives:** This study compares humeral diaphyseal robusticity and asymmetry between Late Holocene hunter-gatherers from Alaska with the goal of reconstructing habitual activity in relation to culture and environment.

**Materials and Methods:** Ancestral remains from four geographic regions of Alaska were divided into five site groups defined by subsistence strategies and technology: Aleutian Islands, Coastal Bay, Far North Coastal, Inland/Riverine, and Tikeraq. Mid-distal humeral diaphyseal robusticity was quantified using cross-sectional geometric properties standardized by estimated body mass and bone length.

**Results:** Humeral strength and bilateral asymmetry were greatest in Aleutian Island males, moderate in Far North Coastal and Tikeraq males, and reduced in Inland/Riverine males. Left-biased directional asymmetry and reduced humeral strength were found in Coastal Bay males. Aleutian Island males had relatively mediolaterally strengthened humeri compared with other groups. Aleutian Island females had elevated humeral strength, while humeral asymmetry among females was moderate and did not vary between groups. Humeri were relatively round among Aleutian Island and Tikeraq females and anteroposteriorly (A-P) strengthened among Coastal Bay, Far North Coastal, and Inland/Riverine females.

**Conclusions:** These results suggest elevated humeral strength and asymmetry in males that engaged in rowing and unimanual projectile hunting, while reduced humeral strength and asymmetry may reflect bow-and-arrow or ensnarement technologies. Left-biased humeral asymmetry may be associated with net-fishing. Humeral strength and asymmetry are consistent with select instances of unimanual projectile hunting in females, while differences in humeral A-P/mediolateral strength may reflect variation in butchery and processing of prey versus rowing and throwing behaviors.

## KEYWORDS

activity reconstruction, Arctic, bioarcheology, functional adaptation, humeral robusticity, hunter-gatherers

## 1 | INTRODUCTION

### 1.1 | Upper limb bone structure and behavior

Studies of bone functional adaptation explore the structural properties of skeletal elements in relation to mechanical demand (Ruff et al., 2006). The functional adaptation paradigm argues that variation in long bone diaphyseal morphology reflects its mechanical environment: bone adapts to mechanical demands during ontogeny through periosteal expansion, and later, endosteal deposition, and modifies or maintains these properties in adulthood (Ruff et al., 1994; Warden et al., 2014). This paradigm has garnered substantial clinical support in studies of the human upper limb. For example, increases in average cortical thickness and periosteal expansion have been documented in the playing versus nonplaying arms of female and male athletes (Bass et al., 2002; Claussen, 1982; Jones et al., 1977; King et al., 1969; Shaw & Stock, 2009). These findings are consistent with increasing humeral robusticity (strength or rigidity relative to body size) in relation to habitual activity and level of mechanical loading.

Shape ratios such as the distribution of bone in the anterior-posterior (A-P) relative to mediolateral (M-L) plane may also be used to reconstruct patterns of activity (Ruff et al., 2022; Trinkaus et al., 1991). Circular humeral diaphyses are associated with a variety of behaviors that involve multidirectional or torsional loading, including throwing and rowing (Schmitt et al., 2003; Shaw & Stock, 2009; Warden et al., 2014). By contrast, A-P reinforced humeri may be associated with high bending loads along a singular directional plane such as during spear thrusting or hide scraping (Schmitt et al., 2003; Shaw et al., 2012). Here, we use the ratio of A-P/M-L second moments of area in the distal humerus as a cross-sectional “shape” index, with higher indices indicating relatively increased A-P bending strength, lower indices relatively increased M-L bending strength, and indices close to 1.0 a relatively circular cross section with approximately equivalent A-P and M-L bending strengths. (Second moments of area technically measure bending rigidity, not strength (Ruff, 2019), but we use the term “strength” here in a broader sense.) As shown later, this simplifies true cross-sectional shape of the distal humerus, which varies along a continuum that includes more triangular and circular morphologies, but is a useful heuristic device for summarizing the relative magnitudes of mechanical properties along anatomically defined axes.

Bilateral (i.e., right-left) asymmetry in diaphyseal dimensions also reflects behavior by highlighting unimanual versus bimanual use of the upper limbs (Churchill and Formicola, 1997; Rhodes & Knüsel, 2005; Schmitt et al., 2003; Trinkaus et al., 1994). Demonstration of greater directional asymmetry in upper limb bone cross-sectional diaphyseal dimensions compared with more developmentally constrained features such as joint surface area and length further suggests a strong role for behavior in producing bilateral asymmetry in long bone diaphyseal properties (Auerbach & Ruff, 2006; Reeves et al., 2016; Sládek et al., 2016, 2018; Trinkaus et al., 1994; Zelazny et al., 2021). Research in living human subjects has also shown that activities such as thrusting and throwing are associated with

considerable directional asymmetry of upper limb mechanical loadings and bone strength (Schmitt et al., 2003; Shaw, 2011; Shaw & Stock, 2009; Warden et al., 2014).

Bioarchaeological studies provide evidence for a variety of upper limb bone adaptations in response to changes in subsistence strategy, behavior, and technological innovation. There is a modest decline in humeral robusticity (strength relative to body size) with the transition from hunting and gathering to agricultural economies in Europe and parts of North America (Holt et al., 2018; Ruff et al., 2015; Ruff & Larsen, 1990), though this trend is contingent on local context and technological innovations related to grinding stone usage and toughness of cultigens (Bridges, 1989; Bridges et al., 2000). Increases in humeral robusticity and changes in bone shape are found following European colonization of North America and associated with shifting labor demands under settler colonialism (Rogers, 2020; Ruff & Larsen, 2001).

Diversity in upper limb robusticity is also noted in relation to general subsistence behavior and environment among hunter-gatherers in global settings (Cameron & Stock, 2018; Hill et al., 2020; Ruff & Holt, 2018; Stock et al., 2010; Stock & Pfeiffer, 2004). Reliance on projectile weapons compared with bow-and-arrow or ensnarement technology is associated with greater humeral robusticity, diaphyseal circularity, and right-dominant directional asymmetry (Cameron & Stock, 2018; Churchill et al., 1996, 2000; Hill et al., 2020; Sakaue, 1997; Sládek et al., 2016, 2018; Stock & Pfeiffer, 2004). Hunter-gatherers involved in open-ocean rowing also have increased humeral robusticity when compared with communities engaged in terrestrial hunting or riverine rowing, though directional asymmetry remains moderate as this behavior was primarily a bimanual activity (Knobbe, 2010; Stock et al., 2010; Stock & Pfeiffer, 2001; Weiss, 2003). More recently, A-P strengthening of humeral diaphyses has been observed in relation to hide processing in groups with documented emphases on this behavior (Cameron et al., 2018).

### 1.2 | Ecology and behavior of Alaskan Indigenous populations

The Alaskan landmass and constituent barrier islands are occupied by Indigenous populations where traditional lifeways are associated with hunting and gathering economies (Gillispie, 2018). Alaska can be divided into six geographic regions, including North Slope and Arctic Coast, Interior, Bering Sea, Gulf of Alaska, Aleutian Islands, and South-eastern Alaska, with archeological research arguing for unique arrays of socioecological and ideological behaviors within each of these regions (Friesen & Mason, 2016; Gillispie, 2018). This study focuses on humeral diaphyseal morphology in ancestral remains from four geographic regions (Aleutian Islands, Bering Sea Coast, Interior, and North Slope and Arctic Coast), which were subdivided into five site groups associated with variation in habitual activity/subsistence ecology and hunting technology (Table 1, Figure 1).

The Aleutian Islands are a chain of volcanic mountains in the Northern Pacific Ocean, beginning with the Fox Island group in

**TABLE 1** Geographic regions and site groups combined with summaries of habitual activity for Indigenous Alaskan ancestral remains included in this study.

Geographic region	Site group	Subsistence ecology/ hunting technology
Aleutian Islands	Aleutian Islands	Intensive open-ocean rowing; aquatic hunting: cetaceans, pinnipeds, fissionpeds, aves; harpoons, spears
North Slope and Arctic Coast	Far North Coastal	Intensive terrestrial and fast ice hunting: pinnipeds, caribou, aves; bow and arrow, harpoons, spears
North Slope and Arctic Coast	Tikeraq	Occasional open-ocean rowing; aquatic, fast ice, and terrestrial hunting: cetaceans, aves, pinnipeds, caribou, sea mammal hunting; bow and arrow, harpoons, spears
Bering Sea Coast	Coastal Bay	Occasional open-ocean rowing; fishing; sea mammal hunting: cetaceans, pinnipeds, aves; net fishing, spears, harpoons, bolas
Interior	Inland/Riverine	Riverine net fishing, terrestrial hunting: caribou, moose, aves, sheep; net snares, bow and arrow, net fishing

Southwestern Alaska and ending at the Commander Islands. Late Aleutian (50 B.C.E.–C.E. 1780) and Aleutian (C.E. 1780–present) traditions represent 4000 years of continuous occupation in this region, though it remains possible that this continuity dates 7000 years into the past (Corbett & Yarborough, 2016; Davis et al., 2016; Dumond, 2001; Maschner, 2016). Reviews of archeological and ethnographic research suggests that the populations occupying the Aleutian Islands engaged in intensive<sup>4</sup> hunting of marine mammals on the open ocean, fishing, and shellfish harvesting (Corbett & Yarborough, 2016). Maritime mammal hunting included sea lions, seals, and otters (Corbett & Yarborough, 2016). Cetacean hunting in the Western Aleutian Islands has been debated (Black, 1987). Mortuary practices included the residual elements of cetaceans, while debates address ethnographic and archeological documentation of harpoon usage on Umnak and Kagamil islands (Black, 1987). Recent stable isotope analysis suggests consumption of foods from elevated trophic levels, including cetaceans and pinnipeds (Byers et al., 2011).



**FIGURE 1** Map indicating location of sites included in this study. Green squares: Aleutian Islands; Red squares: Coastal Bay; White squares: Far North Coastal; Blue squares: Inland/Riverine; Black square: Tikeraq. Site names and corresponding numbers are listed in Table 2.

These behaviors suggest intensive aquatic mobility that required open-ocean rowing and unimanual projectile usage.

Communities from the Bering Sea Coast experienced increased sedentism around 400 B.C.E. with the advent of the Norton cultural phase (Jensen, 2016). Settlement size and numbers suggest increasing sedentism and population density along the southwestern Alaskan landmass around 2400 BP, and the distribution of stone weights for net fishing suggests concurrent expansion of this technology (Shaw, 1982, 1998). Zooarcheological and ethnohistoric research further indicate that seal hunting and fishing on the open ocean were also part of the local subsistence economy in this region (Dumond, 2000; Fitzhugh & Kaplan, 1982; Shaw, 1982, 1998). Historic and modern inhabitants of this landscape are affiliated with Yup'ik cultural groups. These populations engaged similarly with net fishing along coastal embayments, hunted whale and seal on the open ocean, and participated in deep sea fishing (Fienup-Riordan, 1986; Fitzhugh & Kaplan, 1982). Overall, Bering Sea Coast cultures appear to have established a sedentary lifestyle around embayment fishing, with increases in population density supported by this economic system with reduced investment in projectile hunting.

Populations from the North Slope and Arctic Coast were involved in intensive hunting economies that included predation of aquatic and terrestrial mammals. Zooarcheological assemblages and lithic technology suggest that Ipiutak (400–950 C.E.) and Birnirk (500–1000 C.E.)

populations from the North Slope and Arctic Coast hunted caribou across rugged arctic landscapes as well pinnipeds across pack ice (Jensen, 2014, 2016; Larsen & Rainey, 1948; Mason, 1998; Stanford, 1976). Terrestrial mammal hunting utilized bow-and-arrow technology, while spears, harpoons, and bow and arrow technology were used for hunting pinnipeds (Larsen & Rainey, 1948). Smaller contributions from fish, deer, and birds were also part of the North Slope and Arctic Coast subsistence strategies (Dumond, 2014; Gerlach & Mason, 1992; Jensen, 2014; Larsen & Rainey, 1948). Later coastal occupations in this region affiliated with Late Western Thule culture yielded faunal and material evidence for cetacean hunting around 1200 C.E., with evidence for continuity in modern Inupiat speaking groups, including the Tikeraq site in the Point Hope region (Jensen, 2014, 2016; Larsen & Rainey, 1948; Mason, 1998). Technological innovations included bow-and-arrow usage for caribou and harpoons/spears for aquatic mammal hunting (Larsen & Rainey, 1948; Rainey, 1947). The two contrasting subsistence economies suggest complexity in manual activity between North Slope and Arctic Coast populations, with one economic structure focused on hunting on pack ice and in mountainous landscapes and another that included seasonal hunting of cetaceans on the open ocean.

Ethnohistoric accounts of hunter-gatherers from the Interior regions of the Bering Sea Coast describe a mixed subsistence economy, with seasonal encampments and fishing along rivers in the summer, with migration toward villages near mountains for fall, winter, and early spring hunting (Collins, 2000; Kofinas et al., 2010). Stable isotope studies indicate strong reliance on anadromous fish in the Upper Kuskokwim River region dated to 1000 BP (Halfman et al., 2014). Caribou, moose, sheep, bear, beaver, canids, and numerous species of anadromous fish formed the primary components of diet in the Interior and inland areas of the Bering Sea regions. Net capture technologies were widespread in these communities, with net fishing in riverine communities and net snares combined with bow-and-arrow usage documented in terrestrial mammal hunting (Collins, 2000; VanStone, 1979).

In a previous study, femoral and tibial diaphyseal morphologies were compared between ancestral remains from three of these regions: Northern Slope and Arctic Coast, Interior, and Bering Sea Coast (Temple et al., 2021). In this study, the Tikeraq (Tigara) site group was included within the Northern Slope and Arctic Coast regional group, while ancestral remains from the Aleutian Islands were not available for study. Elevated femoral and tibial diaphyseal robusticity was found in ancestral remains from the Northern Slope and Arctic Coast compared with Bering Sea Coast and Interior groups. These results are consistent with archeological and ethnographic studies that suggest higher terrestrial mobility and interaction with rugged terrain along the Arctic Slope and North Coast of Alaska (Mason, 1998) as well as the evolution of sedentary economies supported by net-fishing along the Bering Sea Coast (Dumond, 2000; Shaw, 1982, 1998). Intermediate femoral robusticity combined with higher levels of sexual dimorphism (see below) found in the Interior region partially supports archeological hypotheses that suggest the establishment of net fishing in riverine environments was associated with increasing

sedentism (Temple et al., 2021). The present study extends these analyses to comparisons of upper limb diaphyseal morphology in relation to local ecology and behavior, and includes an additional group (Aleutian Islanders). This work also focuses on variation within Alaska, rather than between select regions of Alaska and other globally distributed samples.

In addition to comparisons between populations, studies of diaphyseal morphology help clarify the sexual division of labor in past communities by reporting embodied evidence for differences or similarities in habitual activity between females and males (Cameron & Stock, 2018; Carlson et al., 2007; Hill et al., 2020; Stock & Pfeiffer, 2004; Ruff et al., 2015). Two interpretations of the sexual division of labor among Indigenous communities from Alaska are commonly promoted. First, ethnohistoric sources link females to butchery, hide processing, transportation of prey, and shell fish gathering, while males engaged in the tracking and immobilization of prey, suggesting a relatively binary division of labor (Hrdlička, 1945; Rainey, 1947; VanStone, 1979). One study of long bone cross-sectional geometry further emphasized these distinctions based on differences in humeral robusticity between the sexes in the Aleutian Islands (Weiss, 2003). Other ethnohistoric sources provide a more nuanced approach, valuing all aspects of the hunting cycle, documenting female tracking and immobilization of prey, and challenging binary attributions of gendered behavior (Laughlin, 1968; Murdoch, 1892; Murray, 2002; Ray, 1885). Similarly, archeological mortuary practices identify projectile weapons in female graves and suggest that gendered behavior in relation to the immobilization of prey may have been more complex than binary attributions (Crass, 1998). Biomechanical studies have also supported this viewpoint, suggesting that female/male mobility and interaction with terrain was diverse across regions (Berget & Churchill, 1994; Collier, 1993; Temple et al., 2021). On this basis, a complementary goal of this study is to understand differences in female and male contributions to the hunting cycle through analysis of cross-sectional geometric properties of the upper limb bones within each sex.

### 1.3 | Predictions

This study tests the null hypothesis that humeral diaphyseal morphology among Indigenous Alaskans will not be related to habitual activities proposed by archeological and ethnographic research (see Table 1) for each site group. Within this context, three alternate hypotheses are tested: First, it is expected that populations engaged in open-ocean rowing will have elevated right and left humeral diaphyseal robusticity and reduced humeral diaphyseal strength ratios. Aleutian Island, Coastal Bay, and Tikeraq groups will have the greatest levels of upper limb bone robusticity for both right and left humeri. Robusticity is expected to be moderate in Far North Coastal groups, who engaged in an intensive hunting economy but did not row on the open ocean. Upper limb diaphyseal robusticity will be reduced in Inland/Riverine groups where open ocean rowing is not documented. Second, increased bilateral asymmetry and circular AP-ML bending

strength ratios will be observed among ancestral remains that utilized unimanual projectile weapons, rejecting the null hypothesis that there is no relationship between humeral diaphyseal morphology and habitual activity. More specifically, bilateral asymmetry combined with equivalent diaphyseal strength ratios will be most strongly pronounced in the Aleutian Islands, where use of dart boards is documented in marine mammal hunting. Intermediate levels of asymmetry combined with circular diaphyses will be observed in Coastal Bay, Far North Coastal, and Tikeraq remains owing to occasional use of unimanual projectile weapons. Reduced levels of asymmetry and circular AP-ML strength ratios will be found in Inland/Riverine communities due to reliance on bow/arrow and ensnarement hunting technologies.

Finally, humeral strength and shape will reveal complex interactions between socioecological systems and the sexual division of labor, again rejecting the initial null hypothesis and illustrating relationships between sex, gender, behavior and diaphyseal morphology. It is expected that behavioral reconstructions from humeral cross-sectional geometry will indicate diverse female involvement in the immobilization, processing, and transportation of prey between site groups. More specifically, it is expected that females from sites that more frequently used projectile weapons and engaged in open ocean rowing will have increased humeral strength, asymmetry and circular shape ratios reflecting these behaviors. Those from sites focused on ensnarement technology or terrestrial hunting will have reduced humeral strength and asymmetry as well as A-P oriented humeri, possibly reflecting greater roles in processing and transportation of prey.

## 2 | MATERIALS AND METHODS

### 2.1 | Ancestral remains

Ancestral remains included in this study are curated by the Departments of Anthropology at the National Museum of Natural History of the Smithsonian Institution and American Museum of Natural History. Many of the remains from the National Museum of Natural History were excavated by Ales Hrdlička between 1925 and 1938. Earlier work provides an ethical statement regarding the excavation and use of these remains (Temple et al., 2021), but a brief statement here is still required. No repatriation claim existed for these ancestral remains at the time of study. However, it is important to emphasize that collections accumulated by Hrdlička were often collected without descendant permission, and in some cases, removed over local objection (Sockbeson, 1995). While this work cannot redress grievances associated with these practices, it is important to emphasize that studies of cross-sectional geometry follow methodological and theoretical pathways that allow for greater integration with Indigenous knowledge. One point of tension between Western Science and Indigenous knowledge is a focus on linear temporality by the former and an emphasis on continuity in the latter (Pullar, 1995). Western Science repeatedly disembodies ancestral remains from communal memory by emphasizing genetic relationships (Bardill et al., 2018): population histories are consistently studied in terms of origins which has the

consequence of acting as a justification for modern socio-political structures, including inequality and settler colonialism (Ingold, 1998). By contrast, studies of cross-sectional geometry emphasize the embodiment of habits, dispositions, and practices of individuals (Ruff, 2019; Ruff et al., 2006). Here, behavior literally becomes encoded into skeletal remains through systemic interaction (Frost, 1973; Pearson & Lieberman, 2004; Ruff et al., 2006) and in ways that allow modern populations to see how ancestral knowledge of local environments was transmitted to future generations. Site dates are described below to document consistency in relation to site occupation and habitual activity rather than population origins.

Ancestral remains from the Western Aleutian Islands were recovered from Kagamil, Shiprock, and Unmnak Islands (Hrdlička, 1945) (Figure 1). Individuals were originally divided into Aleut and Pre-Aleut physical categories based on cranial morphology (Hrdlička, 1945); however, these categories were not biologically meaningful (Churchill, 1994). Excavation practices did not provide reliable dates, though material culture associated with the burials is consistent with pre- and early Russian colonial times, approximately 1500–1750 C.E. (Hrdlička, 1945). Radiocarbon dates largely confirm these findings, though they suggest a slightly earlier occupation between 1100 and 1700 C.E. (Byers et al., 2011). All individuals were associated with the Late Aleut and Aleut phases of cultural occupation, which is continuous with contemporary Indigenous populations in the region (Gillispie, 2018).

Ancestral remains from three coastal archeological sites in the Bering Sea region were placed into a Coastal Bay group (Figure 1; Tables 1 and 2). Geographically speaking, ancestral remains from the Coastal Bay group were recovered from three 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, 1930a). 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 originating from the North Slope and Arctic Coastal region were placed into two groups due to differences in habitual manual activity. The first includes a Far North Coastal site group comprised of six archeological sites affiliated with Birnirk and Ipiutak cultures (Figure 1; Tables 1 and 2). Far North Coastal site groups hunted aquatic and terrestrial mammals on sea ice and across arctic tundra (see: Section 1.2). Ancestral remains from the Birnirk cultural occupation were excavated from the Kugok, Kugusugaruk, and Nunavak sites in the Point Barrow Region of Alaska and date between C.E. 500 and 900 based on mortuary practices and cultural affiliation (Hollinger et al., 2004). Remains from the Ipiutak site were excavated from the Point Hope region of Alaska and date between C.E. 400 and 900 C.E. based on radiocarbon dating, mortuary practices, and cultural affiliation (Gerlach & Mason, 1992; Giddings, 1964; Larsen & Rainey, 1948; Mason & Gerlach, 1995). Another set of remains were

**TABLE 2** List of sites by geographic designation.

Site group	Site/location	Number <sup>a</sup>
Aleutian Islands	Umnak Island	1
Aleutian Islands	Kagamil Island	2
Aleutian Islands	Shiprock Island	3
Coastal Bay	Kwiguk Pass	1
Coastal Bay	Kuskogamut	2
Coastal Bay	Nushagak	3
Far North Coastal	Kugok	1
Far North Coastal	Kugusugaruk	2
Far North Coastal	Nunavak	3
Far North Coastal	Ipiutak	4
Far North Coastal	Wales	5
Far North Coastal	Sand Mound	6
Inland/Riverine	Ekwok	1
Inland/Riverine	Kokwok	2
Inland/Riverine	Anvik	3
Inland/Riverine	Bonasila	4
Inland/Riverine	Greyling River	5
Inland/Riverine	Shageluk	6
Inland/Riverine	Refuge Creek	7
Inland/Riverine	Ghost Creek	8
Inland/Riverine	Okahamute	9
Inland/Riverine	Bogus Creek	10
Inland/Riverine	Kwethluk	11
Inland/Riverine	Akiak	12
Inland/Riverine	Bethel	13
Inland/Riverine	Hamilton	14
Inland/Riverine	Old Andreafsky	15
Inland/Riverine	Paimiut	16
Inland/Riverine	Georgetown	17
Inland/Riverine	Horse Island	18
Tikeraq	Tikeraq	1

<sup>a</sup>Numbers correspond to numerical locations depicted on the map in Figure 1.

excavated from the Sandmound Site on the Seward Peninsula approximately two miles north of Wales and also attributed to the Birnirk culture (Collins, 1937). An additional set of remains were excavated from a site identified as Wales by Hrdlička (1930a) and not attributed to a specific cultural occupation. However, ethnographic analysis indicates that this region is associated with sea mammal hunting on frozen ice (Ray, 1964).

A second group from this general region includes ancestral remains from a single site affiliated with what Larsen and Rainey (1948) reference as the Tigara culture, named in relation to a local village (Figure 1; Tables 1 and 2). Ancestral remains from this site group were excavated from the Tikeraq site in the Point Hope region and date between C.E. 1200 and 1780 (Jensen, 2014; Larsen &

Rainey, 1948). Material artifacts and zooarcheological evidence suggest that the Tikeraq occupants engaged in intensive whale hunting and were likely continuous with Late Western Thule cultures (see: Section 1.2).

Ancestral remains recovered from the Interior region of the Yukon and Kuskokwim Delta were placed into an Inland/Riverine group (Figure 1; Tables 1 and 2). Ancestral remains from the Inland/Riverine group were recovered from 16 archeological sites located along the banks of the Kuskokwim, Nushagak, and Yukon rivers as well as the inland delta regions surrounding these bodies of water (Figure 1). These sites are located directly within the Deg Xit'an (Ten'a) cultural region. Deg Xit'an cultural traditions date between 300 C.E. and the present (Gillispie, 2018). Notes suggest that the sites included in this study date between 1500 and 1800 C.E. (Hrdlička, 1930b), while mortuary practices and taphonomic analysis indicate that some interments date between 1800 and 1850 C.E. (Lippert & Dudar, 2021). Three individuals from the Ghost Creek site were identified as possible victims of a smallpox epidemic in AD 1900 (Lippert & Dudar, 2021), despite claims by Hrdlička (1930b) that the remains dated to an earlier period. Ancestral remains identified as potential victims of this epidemic were not included in the analysis.

## 2.2 | Methods

Detailed descriptions of the measurement and scanning of ancestral remains were included in previous work on these samples (Churchill, 1994; Rosa, 2019; Shackelford, 2005, 2007; Temple et al., 2021). Briefly, sex was estimated on the basis of cranial and pelvic morphology (Buikstra & Ubelaker, 1994). Determination of sex using morphological features does not acknowledge the diverse expression of sex and gender in biological and cultural context, but does provide some information regarding the ways behavioral practices differed between individuals within these morphological designations. Fusion of all long bone epiphyses was used as a minimum criterion for inclusion in this study. Age was estimated using pubic symphysis and auricular surface morphology, cranial suture closure, and sternal rib morphology (Buikstra & Ubelaker, 1994). Individuals with ages estimated as greater than 55 years were not included in the study, to minimize age-related effects on cortical geometry.

Linear long bone measurements were collected according to standard protocols (Buikstra & Ubelaker, 1994; Ruff, 2002). Body mass was estimated using maximum diameter of the femoral head and an equation derived from a diverse geographic sample of contemporary humans (Ruff et al., 2018). Cross sections were measured in the mid-distal humeral diaphysis, at a location 35% of length from the distal end for the Aleutian Island and Point Hope ancestral remains and 33% of length for all other remains.<sup>2</sup> This anatomical location remains the most common target for cross-sectional geometric analysis of humeral diaphyses (Ruff, 2019). However, we acknowledge that other locations, including the humeral midshaft, may also provide information on habitual behavior (Stock & Pfeiffer, 2001). Scans for all ancestral remains excepting those from the Aleutian Islands and Point Hope

**TABLE 3** Cross-sectional geometric properties.

Property	Abbreviation	Units	Definition
Total subperiosteal area	TA	mm <sup>2</sup>	
Cortical area	CA	mm <sup>2</sup>	Axial rigidity
Medullary area	MA	mm <sup>2</sup>	
SMA about the x-axis	$I_x$	mm <sup>4</sup>	Anteroposterior bending rigidity
SMA about the y-axis	$I_y$	mm <sup>4</sup>	Mediolateral bending rigidity
Polar second moment of area	$J$	mm <sup>4</sup>	Torsional/ Twice average bending rigidity

Abbreviation: SMA, second moment of area.

**TABLE 4** Number of individuals included in the comparisons of unilateral and asymmetric analysis listed according to skeletally identified sex.

Site group	N left humeri	N right humeri	N asymmetry
Aleutian Island Female	15	16	14
Aleutian Island Male	24	24	24
Coastal Bay Female	17	10	10
Coastal Bay Male	8	6	4
Far North Coastal Female	22	20	20
Far North Coastal Male	28	27	27
Inland/Riverine Female	39	31	31
Inland/Riverine Male	33	27	27
Tikeraq Female	10	10	10
Tikeraq Male	12	12	12

(see below) were performed on a SOMATOM Emotion 6 CT Scanner (Siemens USA, Washington) at the National Museum of Natural History of the Smithsonian Institution. Scans were completed in standard anatomical position using foam wedges to aid in placement (Ruff, 2002). Machine settings of 80 kV and 110 mAs with a reconstruction kernel at u90s ultra sharp were found to produce adequate thresholds distinguishing between bone and air. Images were saved as DICOM files and converted to TIF files. TIF files were uploaded into Image J (National Institute of Health, Bethesda) and cross-sectional properties were calculated using *MomentMacro* (Ruff, 2016). Cross-sectional images from the Aleutian Island and Point Hope ancestral remains were obtained through external periosteal molds and biplanar x-rays (Churchill, 1994; Shackelford, 2005). Cross-sectional properties were then calculated using the SLICE program (Eschman, 1990; Nagurka & Hayes, 1980). Areal and second moment of area measurements have been compared between the external molding/biplanar radiography and CT-scan techniques, and results suggest that these measurements produce comparable results (O'Neill & Ruff, 2004). Areal measurements were standardized by body mass and second moments of area were standardized by body mass  $\times$  bone length<sup>2</sup> (Ruff, 2019). A list of cross-sectional properties and their geometric/mechanical interpretation is given in Table 3.

Table 4 lists the total number of right and left humeri for each group and total number of individuals that had both sides available for assessment of bilateral asymmetry. Standardized areal and second moments of area measurements were compared between samples using one-way ANOVA with Games-Howell pairwise tests. Upper limb A-P/M-L bending rigidity ratios ( $I_x/I_y$ ) were compared using a Kruskal-Wallis test combined with Dunn's pairwise test. Right and left humeri were analyzed separately. Outliers were retained in all comparisons:

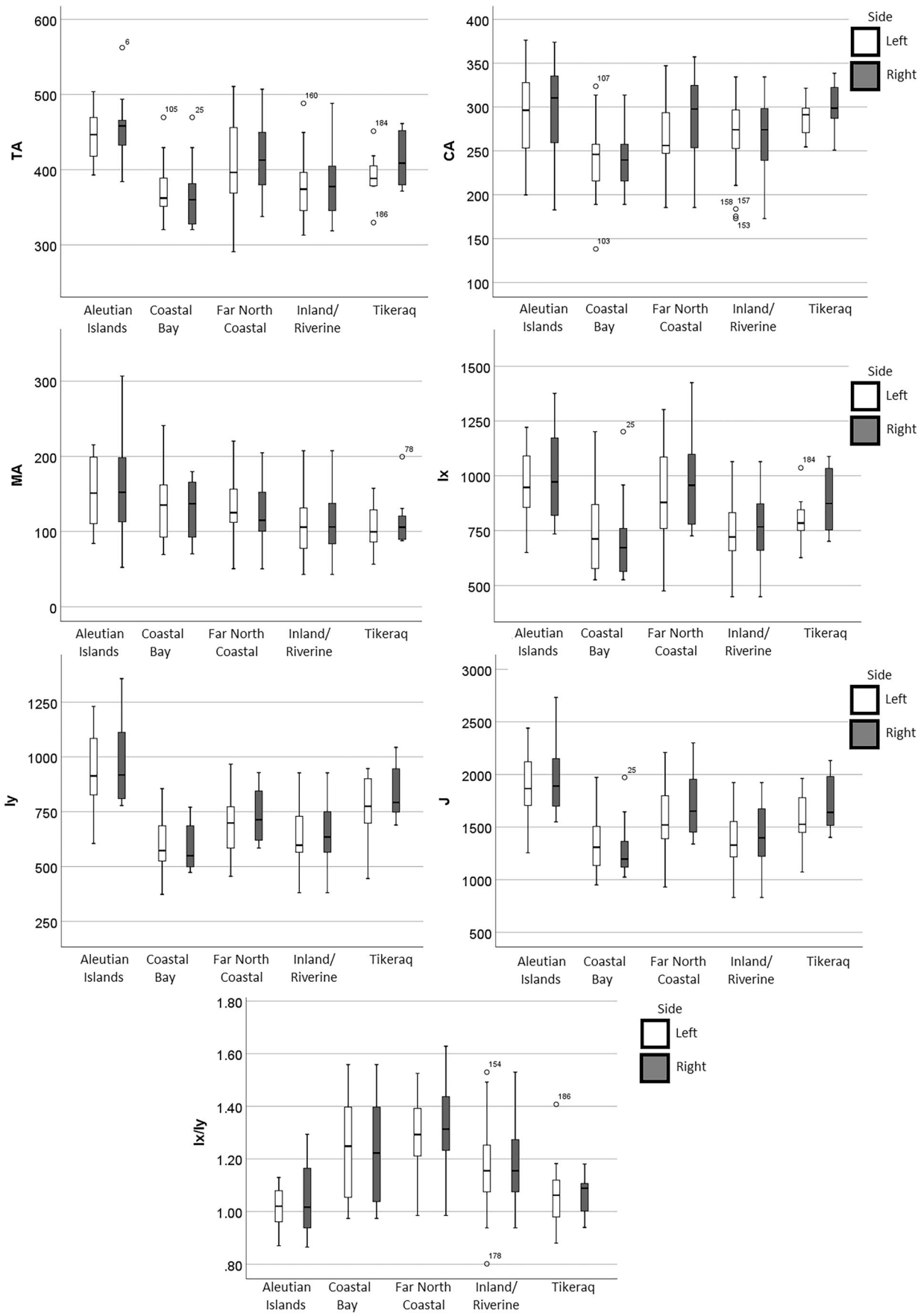
in most cases, these values do not surpass the 90% confidence intervals for each site group. In cases where these values exceed the 90% confidence intervals, they are still distributed within the normal range of human variation and are retained. Null hypotheses for all statistical tests were rejected at a significance level of 0.05 or less.

Comparisons of bilateral asymmetry focused on the polar second moment of area ( $J$ ), as the best single indicator of (twice) average bending and torsional rigidity (Ruff, 2019), and include measures of absolute and directional asymmetry. Absolute asymmetry was calculated as  $[(\text{maximum} - \text{minimum})/((\text{maximum} + \text{minimum})/2)] \times 100$ , while directional asymmetry was calculated as  $[(\text{right} - \text{left})/((\text{right} + \text{left})/2)] \times 100$  (Auerbach & Ruff, 2006; Sládek et al., 2018). Right dominance (or positive asymmetry) was defined as directional asymmetry values favoring the right side and greater than 0.5%, while left dominance (or negative asymmetry) refers to values less than  $-0.5\%$  (Auerbach & Ruff, 2006). Bilateral asymmetry was compared using methods that capture both the magnitude of directional asymmetry and percentage of right dominance within a sample (as in Auerbach & Ruff, 2006). Directional asymmetry was compared between groups using a Kruskal-Wallis test with Dunn's pairwise comparisons, while the prevalence of right-dominant individuals was compared between groups using a Fisher's exact test.

### 3 | RESULTS

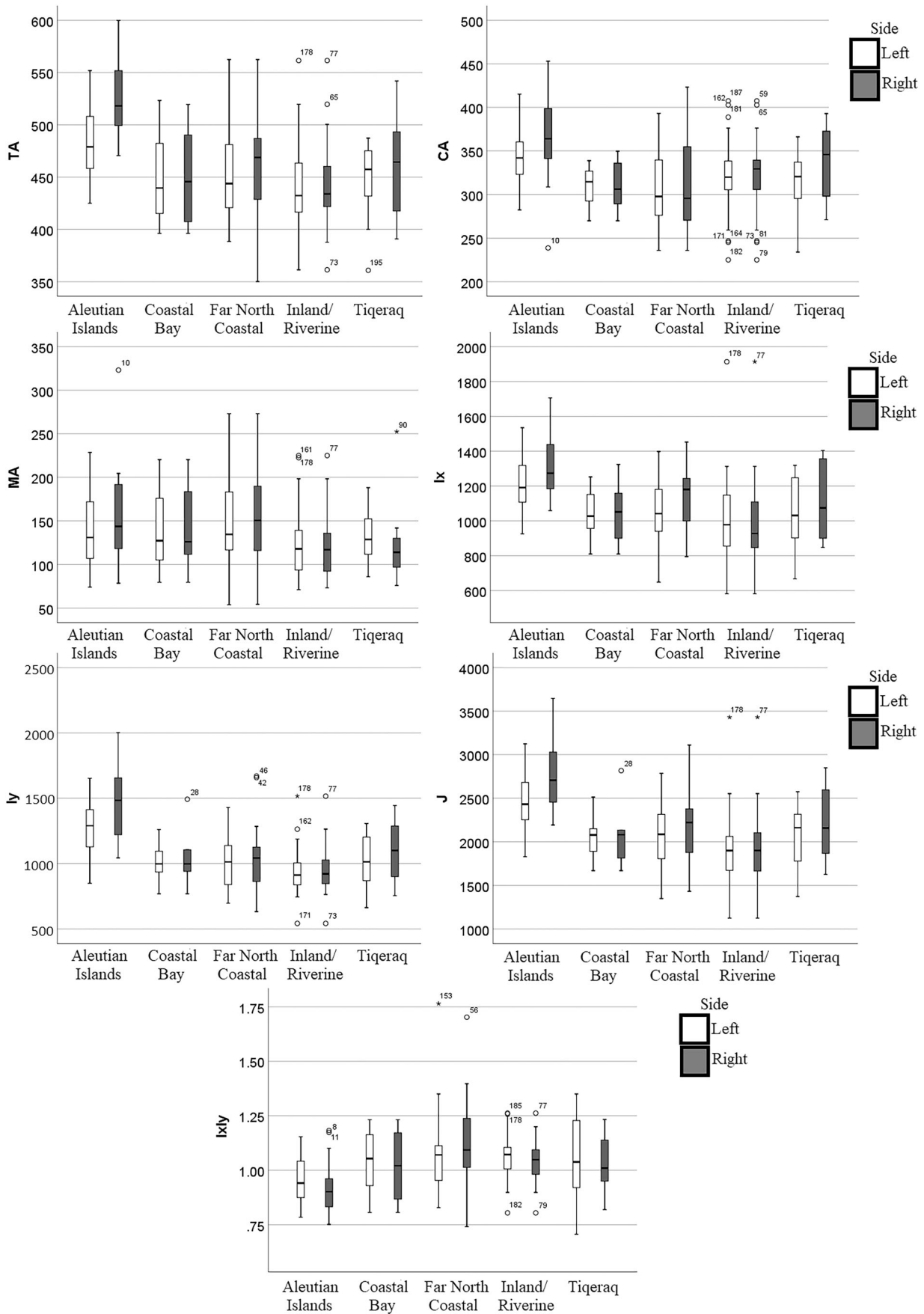
#### 3.1 | Areas and second moments of area

Box plots of cross-sectional properties for females and males are depicted in Figures 2 and 3, respectively. Results from the ANOVA and Games-Howell comparisons of humeral robusticity for females



**FIGURE 2** Box plots for female-identified humeral diaphyseal areas, second moments of area, and shape indices listed by right and left sides.





**FIGURE 3** Box plots for male-identified humeral diaphyseal areas, second moments of area, and shape indices listed by right and left sides.

**TABLE 5** Mean differences in left and right humeral diaphyseal cross-sectional properties for females.

Group	Mean left difference <sup>a</sup>	Group	L difference	Group	Mean right difference <sup>b</sup>	Group	R difference
<b>TA</b>		<b><math>I_x</math></b>		<b>TA</b>		<b><math>I_x</math></b>	
AI <sup>c</sup> - CB <sup>d</sup> ****	71.5	AI - CB**	217.6	AI - CB**	87.3	AI - CB*	283.9
AI - FNC <sup>e*</sup>	41.1	AI - FNC	51.1	AI - FNC*	43.3	AI - FNC	30.3
AI - IR <sup>f</sup> ****	66.6	AI - IR**	213.6	AI - IR***	77.4	AI - IR**	238.5
AI - TQ <sup>g</sup> **	51.3	AI - TQ	152.6	AI - TQ*	43.9	AI - TQ	112.8
CB - FNC	-30.3	CB - FNC	-166.5	CB - FNC	-44.5	CB - FNC*	-253.6
CB - IR	-4.9	CB - IR	-4.1	CB - IR	-10.4	CB - IR	-45.4
CB - TQ	-20.1	CB - TQ	-65.0	CB - TQ	-43.9	CB - TQ	-171.1
FNC - IR	25.5	FNC - IR*	162.4	FNC - IR	34.1	FNC - IR**	208.2
FNC - TQ	10.2	FNC - TQ	101.5	FNC - TQ	0.7	FNC - TQ	82.5
IR - TQ	-15.3	IR - TQ	-60.9	IR - TQ	-33.4	IR - TQ	-125.7
<b>CA</b>		<b><math>I_y</math></b>		<b>CA</b>		<b><math>I_y</math></b>	
AI - CB	48.0	AI - CB****	343.9	AI - CB**	57.4	AI - CB****	379.6
AI - FNC	19.7	AI - FNC**	249.5	AI - FNC	9.5	AI - FNC***	226.8
AI - IR	23.6	AI - IR****	305.2	AI - IR	33.9	AI - IR****	305.4
AI - TQ	2.6	AI - TQ	182.5	AI - TQ	-0.1	AI - TQ	127.7
CB - FNC	-28.3	CB - FNC	-94.4	CB - FNC*	-48.0	CB - FNC	-152.8
CB - IR	-24.4	CB - IR	-38.6	CB - IR	-23.5	CB - IR	-74.1
CB - TQ	-45.5	CB - TQ	-161.4	CB - TQ**	-57.4	CB - TQ	-251.9
FNC - IR	3.9	FNC - IR	55.8	FNC - IR	24.4	FNC - IR	78.7
FNC - TQ	-17.1	FNC - TQ	-67.0	FNC - TQ	-9.5	FNC - TQ	-99.1
IR - TQ	-21.1	IR - TQ	-122.7	IR - TQ	-33.9	IR - TQ	-177.7
<b>MA</b>		<b>J</b>		<b>MA</b>		<b>J</b>	
AI - CB	23.4	AI - CB****	561.5	AI - CB	30.4	AI - CB****	663.5
AI - FNC	21.4	AI - FNC	300.7	AI - FNC	33.9	AI - FNC	257.1
AI - IR*	42.9	AI - IR****	518.9	AI - IR	43.5	AI - IR****	544.0
AI - TQ**	48.8	AI - TQ	335.2	AI - TQ	44.0	AI - TQ	240.5
CB - FNC	-2.0	CB - FNC	-260.9	CB - FNC	3.5	CB - FNC*	-406.4
CB - IR	19.5	CB - IR	-42.7	CB - IR	13.1	CB - IR	-119.5
CB - TQ	25.4	CB - TQ	-226.3	CB - TQ	13.6	CB - TQ*	-423.0
FNC - IR	21.6	FNC - IR	218.2	FNC - IR	9.7	FNC - IR**	286.9
FNC - TQ	27.4	FNC - TQ	34.5	FNC - TQ	10.1	FNC - TQ	-16.5
IR - TQ	5.8	IR - TQ	-183.7	IR - TQ	0.5	IR - TQ*	-303.4

<sup>a</sup>Mean difference between left humeri; <sup>b</sup>Mean difference between right humeri; <sup>c</sup>Aleutian Island; <sup>d</sup>Coastal Bay; <sup>e</sup>Far North Coastal; <sup>f</sup>Inland/Riverine;

<sup>g</sup>Tikeraq; \* $p \leq 0.05$ , \*\* $p \leq 0.01$ , \*\*\* $p \leq 0.001$ , \*\*\*\* $p \leq 0.0001$ ; light gray highlights significant differences in areal measurements; dark gray highlights significant differences in second moments of area. See Table 3 for abbreviations and descriptions of properties.

and males are shown in Tables 5 and 6. To aid in visualizing differences between groups and the sexes, representative right humeral section line drawings from Aleutian Island, Coastal Bay, Far North Coastal, and Inland/Riverine females and males are shown in Figure 4. Individuals were chosen to be of similar body size (body mass  $\times$  bone length<sup>2</sup>) within sex.

Females from the Aleutian Islands have generally more robust humeral diaphyses than those of other groups, with greater total subperiosteal area (TA) and bending and torsional rigidity ( $I_x$ ,  $I_y$ ,  $J$ ) on both sides (Figure 4), although rigidity comparisons do not always reach

significance with the Far North Coastal and Tikeraq groups (Figure 2, Table 5). Coastal Bay and Inland/Riverine females are the least robust, reaching significance in comparisons with Far North Coastal and Tikeraq groups for average bending/torsional rigidity ( $J$ ) on the right side. Cortical (CA) and medullary (MA) areas are more similar between groups, showing that the differences in rigidity are mainly dependent on the degree of outward expansion of the cortex (Figure 4). Data distributions overlap between groups, but in most cases where significant differences were observed there is little overlap in interquartile ranges, and where overlap occurs, it is mainly limited to the second

**TABLE 6** Mean differences in left and right humeral diaphyseal cross-sectional properties for males.

Group	L Difference <sup>a</sup>	Group	L difference	Group	R Difference <sup>b</sup>	Group	R difference
<b>TA</b>		<b>I<sub>x</sub></b>		<b>TA</b>		<b>I<sub>x</sub></b>	
AI <sup>c</sup> - CB <sup>d</sup>	33.5	AI - CB	166.0	AI - CB	71.3	AI - CB	276.8
AI - FNC <sup>e*</sup>	30.5	AI - FNC*	149.2	AI - FNC****	60.2	AI - FNC**	204.1
AI - IR <sup>f**</sup>	38.5	AI - IR**	203.6	AI - IR****	77.3	AI - IR****	329.5
AI - TQ <sup>g</sup>	35.4	AI - TQ	166.6	AI - TQ*	63.0	AI - TQ	214.5
CB - FNC	-3.1	CB - FNC	-16.8	CB - FNC	-11.1	CB - FNC	-72.7
CB - IR	4.9	CB - IR	37.5	CB - IR	6.1	CB - IR	52.8
CB - TQ	1.9	CB - TQ	0.6	CB - TQ	-8.2	CB - TQ	-62.2
FNC - IR	3.1	FNC - IR	54.4	FNC - IR	17.2	FNC - IR	125.3
FNC - TQ	5.0	FNC - TQ	17.4	FNC - TQ	2.8	FNC - TQ	10.4
IR - TQ	-3.0	IR - TQ	-36.9	IR - TQ	-14.3	IR - TQ	-115.0
<b>CA</b>		<b>I<sub>y</sub></b>		<b>CA</b>		<b>I<sub>y</sub></b>	
AI - CB*	33.2	AI - CB**	264.8	AI - CB*	59.5	AI - CB*	418.7
AI - FNC*	36.5	AI - FNC****	269.1	AI - FNC**	55.7	AI - FNC****	432.6
AI - IR	24.4	AI - IR****	333.4	AI - IR**	47.8	AI - IR****	518.6
AI - TQ	27.1	AI - TQ**	265.7	AI - TQ	32.1	AI - TQ**	374.8
CB - FNC	3.4	CB - FNC	4.3	CB - FNC	-3.8	CB - FNC	13.9
CB - IR	-8.8	CB - IR	68.6	CB - IR	-11.7	CB - IR	99.8
CB - TQ	-6.0	CB - TQ	0.9	CB - TQ	-27.4	CB - TQ	-44.0
FNC - IR	-12.1	FNC - IR	64.3	FNC - IR	-7.8	FNC - IR	86.0
FNC - TQ	-9.3	FNC - TQ	-3.4	FNC - TQ	-23.6	FNC - TQ	-57.9
IR - TQ	2.8	IR - TQ	-67.7	IR - TQ	-15.7	IR - TQ	-143.8
<b>MA</b>		<b>J</b>		<b>MA</b>		<b>J</b>	
AI - CB	0.4	AI - CB**	430.8	AI - CB	11.8	AI - CB*	695.5
AI - FNC	-6.1	AI - FNC***	418.3	AI - FNC	4.5	AI - FNC****	636.7
AI - IR	14.1	AI - IR****	537.0	AI - IR	29.5	AI - IR****	848.1
AI - TQ	8.3	AI - TQ*	432.3	AI - TQ	31.0	AI - TQ****	589.3
CB - FNC	-6.4	CB - FNC	-12.6	CB - FNC	-7.2	CB - FNC	-58.8
CB - IR	13.6	CB - IR	106.1	CB - IR	17.8	CB - IR	152.5
CB - TQ	7.9	CB - TQ	1.5	CB - TQ	19.2	CB - TQ	-106.3
FNC - IR	20.1	FNC - IR	118.7	FNC - IR	25.0	FNC - IR	211.3
FNC - TQ	14.3	FNC - TQ	14.1	FNC - TQ	26.5	FNC - TQ	-47.5
IR - TQ	-5.8	IR - TQ	-104.6	IR - TQ	1.4	IR - TQ	-258.8

<sup>a</sup>Mean difference between left humeri; <sup>b</sup>Mean difference between right humeri; <sup>c</sup>Aleutian Island; <sup>d</sup>Coastal Bay; <sup>e</sup>Far North Coastal; <sup>f</sup>Inland/Riverine; <sup>g</sup>Tikeraq; \**p* ≤ 0.05, \*\**p* ≤ 0.01, \*\*\**p* ≤ 0.001, \*\*\*\**p* ≤ 0.0001; light gray highlights significant differences in areal measurements; dark gray highlights significant differences in second moments of area. See Table 3 for abbreviations and descriptions of properties.

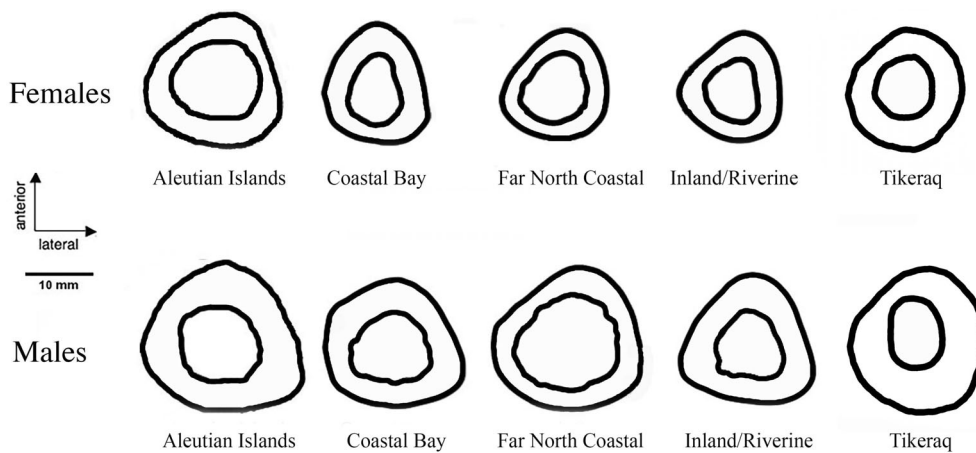
quartile of the smaller group overlapping with the first quartile of the larger group.

Male Aleutian Island humeri have significantly greater average bending/torsional rigidity (*J*) than those of all other groups (Figure 3, Table 6). This is characteristic of both sides, although right side differences are larger (Figure 4). The same is true for M-L bending rigidity (*I<sub>y</sub>*). Differences between Aleutian Island males and other groups in A-P bending rigidity (*I<sub>x</sub>*) are somewhat smaller, reaching significance only in the pairwise comparison of Far North Coastal and Inland/Riverine groups. Aleutian Island males also have generally larger CA

and TA than other groups (Figures 3 and 4; Table 6). Again, as with females, there is overlap between groups, but where groups show significant differences interquartile ranges are usually distinct, or overlap is limited to that between second and first quartiles.

### 3.2 | Diaphyseal shape

Box plots of humeral diaphyseal shape (*I<sub>x</sub>/I<sub>y</sub>*) are shown in Figures 2 and 3 for females and males, respectively, while results from the



**FIGURE 4** Line drawings of mid-distal CT-slices from the right humeri of Aleutian Island, Coastal Bay, Far North Coastal, Inland/Riverine, and Tikeraq females and males. Within sex, individuals are of comparable body size (body mass  $\times$  bone length<sup>2</sup>).

Kruskal–Wallis comparisons of humeral diaphyseal shape ratios are shown in Table 7. Aleutian Island and Tikeraq females have cross sections with the most equivalent A-P and M-L bending rigidities ( $I_x/I_y$  closest to 1.0), and Far North Coastal and Coastal Bay females the most A-P oriented sections (highest  $I_x/I_y$  ratios) (Figures 2 and 4), with differences between groups reaching significance in several comparisons, although interquartile ranges often overlap (Table 7). Aleutian Island males have a relatively more mediolaterally reinforced humerus (lower  $I_x/I_y$ ) than most other groups, again with overlap in interquartile ranges (Table 7, Figure 4). All other males have relatively equal A-P and M-L bending rigidities (Figures 3 and 4), and no additional significant differences between groups were found.

### 3.3 | Bilateral asymmetry

Box plots for directional bilateral asymmetry are shown in Figure 5. A scatterplot of directional asymmetry and percentages of right and left-dominant individuals in each group is shown in Figure 6. Table 8 lists the Kruskal–Wallis results comparing directional asymmetry between groups. Table 9 provides the results of Fisher's exact tests comparing the frequency of right dominance between groups. Variation between groups in median directional asymmetry (2%–7%) and percentage of right dominance (57%–70%) is low and nonsignificant in females. It is, however, important to emphasize that the distribution of asymmetry in female samples shows that some individuals from each group had levels of directional asymmetry that were greater than 15%.

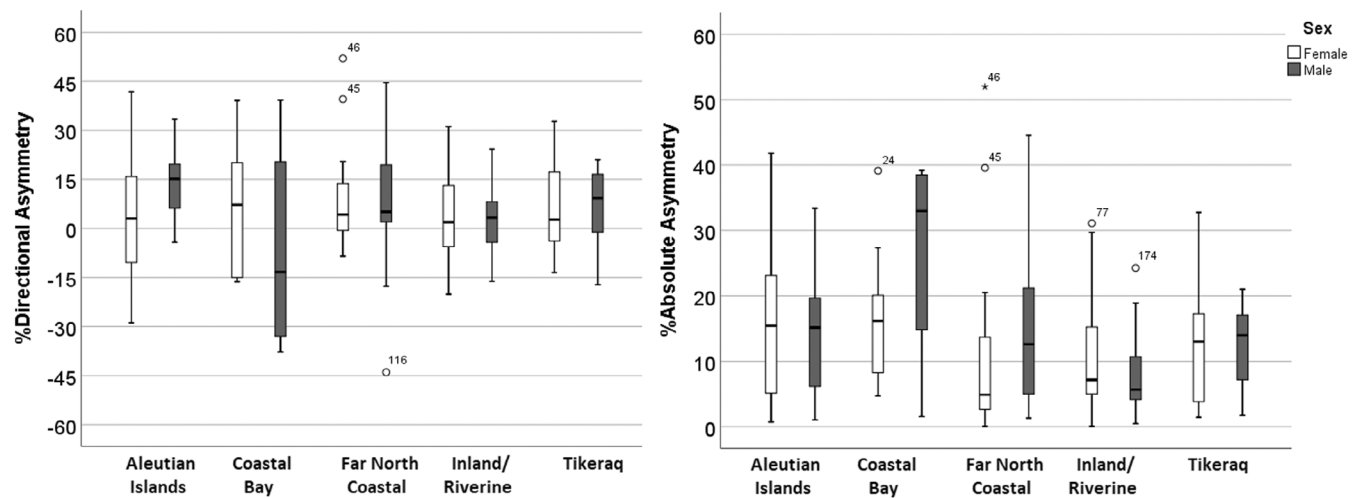
Variation between groups in median directional asymmetry among males is wider than among females (–13%–15%). The small Coastal Bay male sample has two strongly left-dominant individuals and one strongly right-dominant individual (along with one almost symmetric individual) (Figure 6). As a result, the Coastal Bay males are the only group with an average left bias in directional asymmetry (Figure 5) and have the lowest prevalence of right dominance (Figure 6). Directional asymmetry favoring the right side is highest for

**TABLE 7** Kruskal–Wallis comparisons of humeral  $I_x/I_y$  for females and males.

Female comparison	Left ( $p \leq$ )	Right ( $p \leq$ )
AI <sup>a</sup> – CB <sup>b</sup>	0.001	0.015
AI – FNC <sup>c</sup>	0.001	0.0001
AI – IR <sup>d</sup>	0.001	0.009
AI – TQ <sup>e</sup>	0.333	0.682
CB – FNC	0.231	0.149
CB – IR	0.443	0.613
CB – TQ	0.048	0.068
FNC – IR	0.22	0.010
FNC – TQ	0.002	0.0001
IR – TQ	0.164	0.081
Male comparison	Left	Right
AI – CB	0.067	0.131
AI – FNC	0.006	0.0001
AI – IR	0.002	0.022
AI – TQ	0.047	0.033
CB – FNC	0.955	0.264
CB – IR	0.798	0.697
CB – TQ	0.928	0.897
FNC – IR	0.76	0.227
FNC – TQ	0.853	0.206
IR – TQ	0.673	0.750

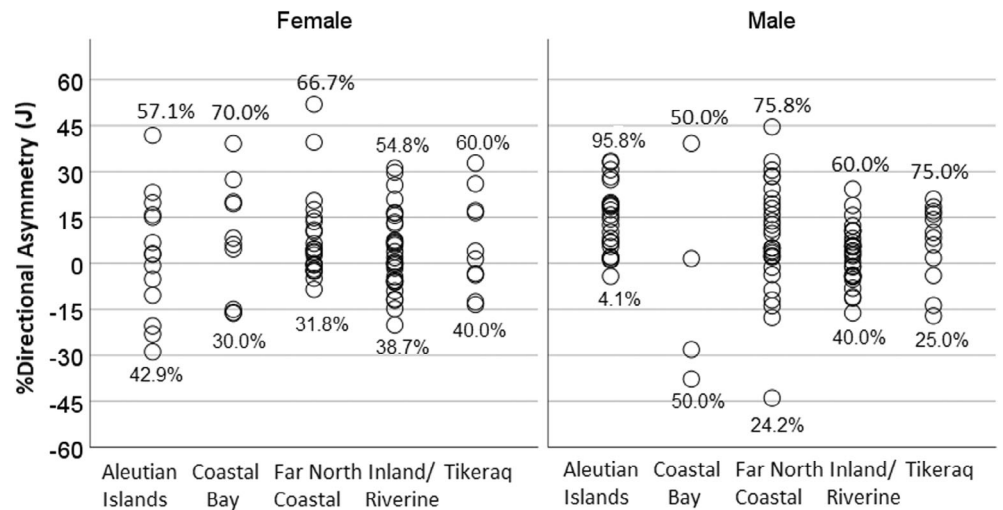
<sup>a</sup>Aleutian Island; <sup>b</sup>Coastal Bay; <sup>c</sup>Far North Coastal; <sup>d</sup>Inland/Riverine; <sup>e</sup>Tikeraq; gray highlight indicates significant differences.

Aleutian Island males (15.0%) and lowest for Inland/Riverine males (3.3%), with intermediate values for Far North Coastal (8.3%) and Tikeraq males (6.6%) (Figure 5). Rank sum values for directional asymmetry are significantly greater in Aleutian Island versus Coastal Bay and Inland/Riverine males, and in Far North Coastal compared with Inland/Riverine males (Table 8). Prevalence of right dominance is highest in Aleutian Island males (95%) (Figure 6) and varies from 60% to



**FIGURE 5** Box plots for directional and bilateral asymmetry of humeral diaphyses listed by skeletally identified sex and region.

**FIGURE 6** Distribution and percentages of individuals with directional asymmetry each region. Percentages at the top of the distributions indicate the frequency of individuals with greater than 0.5% (right biased) directional asymmetry in each site group, while percentages at the bottom of the distributions indicate the frequency of individuals with directional asymmetry scores less than -0.5% (left biased).



**TABLE 8** Kruskal–Wallis comparisons of directional asymmetry of humeral J for females and males.

Directional asymmetry		Directional asymmetry	
Female comparison	Significance	Male comparison	Significance
AI <sup>a</sup> - CB <sup>b</sup>	NS <sup>f</sup>	AI - CB	0.041
AI - FNC <sup>c</sup>	NS	AI - FNC	0.116
AI - IR <sup>d</sup>	NS	AI - IR	0.001
AI - TQ <sup>e</sup>	NS	AI - TQ	0.158
CB - FNC	NS	CB - FNC	0.210
CB - IR	NS	CB - IR	0.730
CB - TQ	NS	CB - TQ	0.296
FNC - IR	NS	FNC - IR	0.053
FNC - TQ	NS	FNC - TQ	0.849
IR - TQ	NS	IR - TQ	0.219

<sup>a</sup>Aleutian Island; <sup>b</sup>Coastal Bay; <sup>c</sup>Far North Coastal; <sup>d</sup>Inland/Riverine; <sup>e</sup>Tikeraq; <sup>f</sup>Kruskal–Wallis test not significant, pairwise comparisons not calculated; gray highlight indicates significant differences.

76% in the other groups (except Coastal Bay). Median absolute asymmetry is highest in Coastal Bay males (33.0%) (Figure 5), which is consistent with the strongly left or right-dominant directional asymmetry

in three out of four Coastal Bay male humeri. Median absolute asymmetry between other groups and among females varies between 5% and 17%.

**TABLE 9** Fisher's exact comparisons of right dominance between groups.

Female comparison	Significance	Male comparison	Significance
AI <sup>a</sup> - CB <sup>b</sup>	0.678	AI - CB	0.045
AI - FNC <sup>c</sup>	0.737	AI - FNC	0.052
AI - IR <sup>d</sup>	0.999	AI - IR	0.003
AI - TQ <sup>e</sup>	0.999	AI - TQ	0.010
CB - FNC	0.999	CB - FNC	0.295
CB - IR	0.711	CB - IR	0.999
CB - TQ	0.999	CB - TQ	0.547
FNC - IR	0.778	FNC - IR	0.267
FNC - TQ	0.999	FNC - TQ	0.999
IR - TQ	0.999	IR - TQ	0.485

<sup>a</sup>Aleutian Island; <sup>b</sup>Coastal Bay; <sup>c</sup>Far North Coastal; <sup>d</sup>Inland/Riverine; <sup>e</sup>Tikeraq; gray highlight indicates significant differences.

## 4 | DISCUSSION

### 4.1 | Rowing

The null hypothesis of this work predicted that no relationships between archeologically and ethnographically identified behaviors and site groups would be found, while one alternate hypothesis predicted that humeral robusticity and strength indices would be associated with rowing. The null hypothesis is rejected, and the alternate hypothesis is supported. Elevated humeral strength is found in males who engaged in intensive open-ocean rowing. Aleutian Island males have significantly greater humeral strength than males who did not engage in open-ocean rowing as well as males who occasionally engaged in open-ocean rowing. This pattern is observable on left and right sides, though more pronounced on the right side. These differences are driven by higher  $I_x$  and  $I_y$  values when Aleutian Island males are compared with Far North Coastal and Inland/Riverine males, while significantly greater  $I_y$  but not  $I_x$  is observed in Aleutian Island males when compared with those from Coastal Bay and Tikeraq sites. These results support the general observation that Aleutian Island male humeri are comparatively robust (Churchill et al., 1996, 2000; Laughlin et al., 1979; 1991) and that populations engaged in intensive open-ocean rowing have greater humeral strength (Stock et al., 2010; Stock & Pfeiffer, 2001; Weiss, 2003). In the Aleutian Islands, kayaks were used for combinations of fishing, hunting, and long-distance trade (Corbett & Yarborough, 2016). Instruction for this activity began in late childhood and included weight-training for the upper body, sitting for extended periods of time, and exposure to cold water (Laughlin, 1968). In adulthood intensive open-ocean rowing occurs in one- to three-person kayaks that move at speeds ranging between 11 and 16 km/h (Beaglehole, 1967), with ethnohistorically documented distances of 1600 km over a 64-day period (Pinart, 1873). On average, open-ocean rowing in kayaks is documented for periods of 12–14 h while hunters remained on the water for 6–10 days. By contrast, Coastal Bay and Tikeraq communities participated in open-ocean rowing in a seasonal capacity and much of this activity is documented near shore (Fitzhugh & Kaplan, 1982; Rainey, 1947).

In addition, Aleutian Island males had significantly lower left and right humeral diaphyseal shape ( $I_x/I_y$ ) indices compared with males that did not engage in open-ocean rowing (Far North Coastal and Inland/Riverine), but did not differ in humeral diaphyseal shape when compared with other populations engaged in occasional open-ocean rowing (Coastal Bay, Tikeraq). This trend is associated with stronger mediolateral reinforcement of humeri in Aleutian Island males (Figure 4). Reduced A-P/M-L bending rigidity ratios ( $I_x/I_y < 1.0$ ) have been documented among other communities engaged in intensive open-ocean rowing including Jomon hunter-gatherers from Japan (Knobbe, 2010; Shackelford, 2014). Biomechanical studies of Indigenous ancestral remains from the Timucuan Ossuary in Florida found reduced rigidity ratios ( $I_x/I_y < 1.0$ ) to be associated with pronounced medial and lateral bony projections at the origin sites for forearm flexor and extensor muscles (Ruff & Larsen, 2001). Flexion and extension of the shoulder and elbow should increase A-P bending of the humerus, but simultaneous activation of forearm flexors and extensors should also promote enlargement and proximal extension of the flexor and extensor ridges (particularly the extensor ridge), resulting in mediolateral expansion and elevated  $I_y$  values in the distal diaphysis. Extensive kayak usage involving double-bladed paddles is likely to have produced such loadings. Musculoskeletal injuries of the forearm represent one of the most oft-reported hazards among kayak paddlers (Pelham et al., 2020). More specifically, enthesitis at the extensor/flexor origins in the distal humerus is a common injury in paddlers due to high levels of strain in these muscles during the stroke cycle of paddling (Kramer & Wilson, 2016). EMG studies find substantial engagement of forearm extensors and flexors during the stroke cycle, especially in countercurrents (Skopek et al., 2009). Analyses of enthesophytes reveal elevated expression for shoulder and forearm musculature in hunter-gatherers that used double-bladed paddles (Hawkey & Merbs, 1995; Lieverse et al., 2009). Larger forearm musculature has been noted in studies of enthesophytes among Tikeraq populations who engaged in whaling, while larger shoulder musculature characterizes Far North Coastal populations who engaged in terrestrial projectile hunting (Steen, 2003). Greater expression in shoulder and forearm enthesophytes are also observed in ancestral remains from the

Aleutian Islands (Churchill, 1994). These findings suggest that reduced  $I_x/I_y$  ratios may reflect substantial engagement of forearm musculature in Aleutian Island kayaking, and variation in these values are dependent on the frequency of rowing.

## 4.2 | Unimanual projectile weapon use and hunting technology

A second alternate hypothesis predicted that relationships between hunting technology and bilateral asymmetry would be found in contrast to the null hypothesis that predicted no relationship between diaphyseal morphology and archeologically and ethnographically documented behaviors. The null hypothesis is again rejected, and the second alternate hypothesis is supported. Humeral robusticity and bilateral asymmetry are greater in site groups where unimanual projectile weapons are archeologically and ethnographically documented and thus our results do not falsify these parts of the second hypothesis. Aleutian Island males, who combined frequent ocean rowing with unimanual projectile use, are differentiated from all Native Alaskan groups, with the largest humeral robusticity and directional asymmetry values for humeral J, and percentage of individuals with right dominance. Among males, Far North Coastal and Tikeraq samples, who also engaged in these behaviors, show the next highest directional asymmetry and percentage of right dominance, while Inland/Riverine males are lower in both respects.

Reduced diaphyseal robusticity combined with negative (left-dominant) median directional asymmetry is observed in four Coastal Bay males. The finding of negative median directional asymmetry is unusual (Cameron & Stock, 2018; Churchill et al., 1996, 2000; Stock et al., 2010; Trinkaus et al., 1994) and differs from all other Native Alaskan site groups included in this study. This also differs more generally from hunter-gatherers who engaged in habitual throwing, bimanual processing, or bow-and-arrow usage where moderate or pronounced directional asymmetry is right-dominant (Auerbach & Ruff, 2006; Churchill et al., 1996, 2000; Sládek et al., 2016, 2018; Trinkaus et al., 1994; Zelazny et al., 2021), as well as ethnohistoric sources that document low frequencies of left-handedness among Native Alaskans (Murdoch, 1892; Nelson, 1900). Higher levels of left dominance have been observed in humeral diaphyses from hunting and gathering communities that engaged in intensive net fishing (Ruff & Holt, 2018; Sparacello & Marchi, 2008). When combined with studies that report reduced femoral robusticity in Coastal Bay ancestral remains (Temple et al., 2021), these findings provide tentative support for hypotheses that suggest net fishing may have formed the basis for reduced residential and logistical mobility in the region (Shaw, 1982, 1998). However, larger numbers of humeral diaphyses are needed to establish such relationships between directional asymmetry and net fishing among Indigenous Alaskans.

Our prediction of greater circularity of humeral diaphyses in site groups who engaged frequently in unimanual projectile use is not supported by our results, at least for males, with most groups falling within a relatively narrow range of variation in this characteristic, and

Aleutian Island males showing less circular diaphyses than some other groups. This may be due in part to the confounding effects of flexor/extensor ridge development (increasing mediolateral rigidity), as discussed above, and more generally to the combined effects of rowing and hunting on loading of the distal humerus in different directions.

When compared with Holocene hunter-gatherers outside of Alaska, median directional asymmetry values in humeral J are pronounced in Aleutian Island males and moderate in the other samples. Mean directional asymmetry in J reported for Holocene hunter-gatherers outside of Alaska varies between about 5% and 10% (Trinkaus et al., 1994: our calculations from data presented in their Table 4), while Aleutian Island males have median values of 15% and other site groups (except Coastal Bay males) fall between 2% and 10%. These results add complexity to biomechanical studies of bimanual behaviors such as rowing and swimming that report moderate levels of bilateral asymmetry (Shackelford, 2014; Shaw & Stock, 2009; Stock et al., 2010) and emphasize the additional influence of unimanual projectile hunting on humeral strength and asymmetry (Bridges et al., 2000; Cameron & Stock, 2018; Churchill et al., 1996, 2000; Hill et al., 2020; Sládek et al., 2016, 2018; Stock & Pfeiffer, 2004; Trinkaus et al., 1994; Zelazny et al., 2021). While Aleutian Island males had pronounced humeral directional asymmetry for Holocene hunter-gatherers, average asymmetry in humeral section moduli (measures of bone strength related to J) reached between 30% and 40% in Upper Paleolithic males (Ruff, 2019). These results suggest a considerable possible range for humeral directional asymmetry when considered across larger spans of time and behaviorally diverse populations.

Aleutian Island males engaged in year-round hunting of whale, seals, sea lions, and otters using darts and throwing boards, harpoons, and spears (McCartney & Veltre, 1999; Veniaminov, 1984). This emphasis on unimanual hunting during intensive periods of rowing likely explains the elevated humeral strength combined with directional asymmetry and pronounced right-biased humeral strength observed in this group. These findings also suggest that there may be interactions between humeral strength and asymmetry in populations engaged in bimanual rowing combined with projectile hunting: directional asymmetry and humeral strength may both be pronounced in cases where frequent rowing and throwing behaviors occur. By contrast, Far North Coastal and Tikeraq communities engaged in seasonal hunting strategies that relied on diverse technology. Both of these groups used unimanual projectiles to hunt seal, but also targeted caribou using bow-and-arrow technology (Larsen & Rainey, 1948; Rainey, 1947). Tikeraq communities hunted whale using harpoons, though this behavior was seasonal and restricted to select individuals (Rainey, 1947). By contrast, Inland/Riverine communities hunted terrestrial mammals and trapped anadromous fish using ensnarement, bow-and-arrow, and basket weir technology and infrequently relied on projectile hunting (VanStone, 1979). These findings provide embodied evidence for habitual activity in relation to the record of material culture and ethnohistoric documentation in these regions, demonstrating how human technological innovation and interactions with the living environment are encoded in ancestral remains.

### 4.3 | Complicating the sexual division of labor

Finally, the null hypothesis predicting no relationship between archaeologically and ethnographically documented behaviors and diaphyseal morphology is rejected, and a third alternate hypothesis predicting relationships between sex, gender, and behavior is supported. Elevated humeral strength combined with circular diaphyseal rigidity ratios and reduced bilateral asymmetry were found in Aleutian Island and Tikeraq females (Figure 4). Studies of musculoskeletal stress markers emphasize behaviors such as hide preparation and sewing among females in these regions (Hawkey & Street, 1992; Steen, 2003). Previous studies also document lower female compared with male humeral robusticity in the Aleutian Islands and argue that this reflects an emphasis on rowing in males and shellfish collecting in females (Weiss, 2003). While these behaviors are ethnographically documented among Aleutian Island females (Coxe, 1803; Hrdlička, 1945; Osborn, 1990), recent studies have found that elevated humeral robusticity in Neolithic and Medieval European females was comparable to modern semi-elite athletes, suggesting that females engaged in substantial levels of mechanical loading in the recent past (Macintosh et al., 2017). While humeral robusticity among Aleutian Island females is lower than Aleutian Island males, it is comparable to our sample of Inland/Riverine male hunter-gatherers and to male hunter-gatherers from North America who engaged in open-ocean rowing (Weiss, 2003). These results suggest elevated levels of mechanical loads in female upper limbs and do not falsify female participation in rowing.

As noted above, shellfish digging has been suggested as a contributor to humeral diaphyseal robusticity among females in the Aleutian Islands (Weiss, 2003). Elevated A-P relative to M-L bending strength and reduced humeral bilateral asymmetry is found in hunter-gatherers from South Africa and Australia who habitually used digging sticks for shellfish collecting (Cameron & Stock, 2018; Hill et al., 2020; Stock & Pfeiffer, 2004). Aleutian Island females do show reduced bilateral asymmetry, but also a circular humeral shape, suggesting that shellfish digging was unlikely to be an important contributor to diaphyseal morphology. Similar results were found for Tikeraq females—diaphyseal robusticity is elevated and humeral AP/ML strength ratios are relatively circular (close to 1.0). These results suggest that the sexual division of labor in these regions was more complex than binary attributions of labor. Specifically, the possibility of rowing or paddling among females must be considered. In the Aleutian Islands, kayaks became sacred objects once the outset skin was affixed to the frame, and male usage was ideologically proscribed (Lantis, 1984; Turner, 2008; Veniaminov, 1984). By contrast, *angyaq*, *nixilax*, and *umiak* were larger water craft that were used by six to eight individuals including females and males for hunting and fishing (Anichtchenko, 2012; Turner, 2008). Similarly, female watercraft usage is documented during whale hunting across the North American Arctic, including communities surrounding the Tikeraq site (Jenness, 1957; Nansen, 1893; Rainey, 1947). These findings indicate that elevated robusticity and/or low  $I_x/I_y$  ratios (as in male Aleuts) among Aleutian Island and Tikeraq females provides embodied evidence for behaviors that include rowing.

Greater A-P relative to M-L strengthening and comparable bilateral asymmetry is observed in females from Coastal Bay, Far North Coastal, and Inland/Riverine regions. Increased humeral diaphyseal robusticity is observed among Far North Coastal compared with Coastal Bay and Inland/Riverine females. These results are consistent with similar patterns of activity between females from the three site groups, but greater magnitudes of loading in Far North Coastal female remains. Bioarcheological and experimental research documents a bilaterally symmetrical A-P direction of mechanical loading and orientation of humeral diaphyseal shape in cases where bimanual hide scraping is experimentally induced or archeologically documented (Cameron et al., 2018; Shaw et al., 2012). Bilateral hide scrapers were reported from Coastal Bay and Far North Coastal sites (Fitzhugh & Kaplan, 1982; Larsen & Rainey, 1948). Ethnographic and ethnohistoric evidence for a sexual division of labor is documented in each of these three communities, specifically behaviors where females engaged in butchery and processing and males engaged in immobilization of other-than-human agents (Fienup-Riordan, 1986; Fitzhugh & Kaplan, 1982; Jolles, 2006; VanStone, 1979). These results suggest activity patterns for females from these site groups that emphasize butchery and processing of prey.

Accentuated A-P orientation and robusticity of humeral diaphyses suggests that these behaviors may have been more pronounced in Far North Coastal compared with Coastal Bay and Inland/Riverine females and is consistent with earlier studies that report elevated humeral robusticity in females from the Far North Coastal region (Collier, 1993). Variation in A-P orientation and humeral robusticity may reflect differences in the intensity of processing and scraping the hides of large game. Females from Coastal Bay and Inland/Riverine communities processed and scraped hides from a diverse group of animals including seal and reindeer, but also birds, fish, and smaller mammals (Fitzhugh & Kaplan, 1982). By contrast, females from Far North Coastal site groups primarily engaged in processing and scraping hides from larger animals with tougher skin, including caribou, seal, and polar bear (Fitzhugh & Kaplan, 1982; Murdoch, 1892; Rainey, 1947). While results from our biomechanical analyses are consistent with the sexual division of labor identified by ethnographic and ethnohistoric research in these regions, it is important to point out that these results also suggest regional diversity in habitual activity among females and challenge assertions that situate female behavior outside of the hunting cycle.

Traditional interpretations of the sexual division of labor represent colonized world-views where males acted as primary producers and females were passive contributors (Mihsuah, 2003). Binary gendered behaviors were often introduced through colonial practices that targeted and erased complex gendered identities among Indigenous communities (Geller, 2008, 2017; Mihsuah, 2003; Smith, 2021). These are well illustrated in Western conceptualizations of hunting that establish humans as dominant over animals and prioritize the act of immobilization of prey over relational behaviors associated with the hunting process (Fienup-Riordan, 1990; Laughlin, 1968). Relational behaviors are, however, part of an interconnected cycle in many Indigenous Arctic communities where human interaction with other-



than-human-agents collectively ordain relationships with the natural world through tracking, immobilization, and butchering (Bodenhorn, 1990; Fienup-Riordan, 1990; Fienup-Riordan, 1994; Jarvenpa & Brumbach, 2006; Lantis, 1947; Laugrand & Oosten, 2015; Rainey, 1947; Turner, 1990). In addition, butchery and processing helped preserve foodstuffs in communities that relied on hunting for more than 80% of protein intake (Binford, 2001; Kelly, 1998), and who stored food and utilized hides as risk minimization strategies (Fitzhugh & Kaplan, 1982; Murdoch, 1892; Rainey, 1947; VanStone, 1979). In this sense, biomechanical evidence for processing and scraping of animal remains challenge interpretations that insist on dichotomous sexual divisions of labor among Indigenous Alaskans. Instead, these results suggest that the sexual division of labor in these communities may be contextualized within a series of interdependent and flexible behaviors that maintained ideological relationships between humans and nature, while ensuring caloric return and survival in harsh climates.

Directional asymmetry in *select* females from each region is pronounced and comparable to unimanual projectile hunters (Figures 5 and 6). These results are consistent with mortuary practices and studies of musculoskeletal stress markers that suggest individuals that were skeletally identified as female engaged in immobilization of prey (Crass, 1998; Steen, 2003). While behaviors such as whale hunting may be male oriented (Rainey, 1947), gendered identities across the Arctic were fluid. Individuals inherit the name of deceased relatives as well as the habits, dispositions, and practices of those ancestors, regardless of age or sex (Saladin d'Angulure, 1994). Fluidity in gendered behavior and identities in relation to hunting are further noted across the Arctic (Murray, 2002; Nansen, 1893). Traces of this fluidity may be observed in the embodied evidence of habitual activity and mortuary ritual, where skeletal phenotypes suggest complex relationships between sex and gender. In Alaska, these results reflect complex world views, gender ideologies, and habitual activity patterns in relation to interactions with other-than-human agents.

#### 4.4 | Study limitations

The present study has several limitations. We consider only mechanical (behavioral) effects on bone structural properties, while bone structure is in fact also influenced by other environmental factors such as diet (Ruff et al., 2006), which varied between the populations included in this study (Byers et al., 2011; Larsen & Rainey, 1948; VanStone, 1979). However, such systemic influences are likely to be reflected more in overall skeletal size rather than specific localized structural features. The determination of bone structure also has a genetic component, and is influenced by the age during which environmental influences act (Agostini et al., 2018; Pearson & Lieberman, 2004; Ruff et al., 2006, 2013; Temple et al., 2013). These may complicate interpretations, but do not erase the signature of mechanical loading effects during life (Agostini et al., 2018; Ruff et al., 2006). The size of some of our geographic site groups (e.g., Coastal Bay males) was relatively small, although our total sample

of more than 200 individuals, most represented by both right and left humeri, is by far the largest ever analyzed for the Alaskan region. This allowed us to consider variation in both long bone diaphyseal dimensions and archeologically and ethnographically documented behaviors within a relatively circumscribed yet diverse set of populations.

## 5 | CONCLUSIONS

Humeral diaphyseal strength among Aleutian Island males was greater than that observed in all other groups. A-P/M-L bending rigidity ratios were also reduced in males from the Aleutian Islands, which we interpret as reflecting greater development of forearm flexor/extensor ridges. Directional asymmetry was greatest in Aleutian Island followed by Far North Coastal and Tikeraq groups, and reduced in Coastal Bay and Inland/Riverine groups. These results are consistent with intensive rowing behavior among Aleutian Island males combined with unimanual activity among males from groups with a focus on projectile hunting. Coastal Bay males showed more evidence for left-biased asymmetry. Similar results have been observed in some riverine fishing communities that utilized net-capture technology (Ruff & Holt, 2018; Sparacello & Marchi, 2008), and when combined with studies of lower limb diaphyseal morphology (Temple et al., 2021), is consistent with archeological research that suggests sedentism in the region was supported by intensive net fishing (Shaw, 1982, 1998).

Females from the Aleutian Islands had greater humeral robusticity when compared with Coastal Bay and Inland/Riverine females and were comparable in humeral robusticity to females from Far North Coastal and Tikeraq groups. Females from the Aleutian Island and Tikeraq groups had circular humeral diaphyses, while those from Coastal Bay, Far North Coastal, and Inland/Riverine groups had humeral diaphyses with greater A-P reinforcement. These results are consistent with rowing behaviors among females from the Aleutian Islands and Tikeraq sites and reflect emphases on processing and scraping behaviors among females from Coastal Bay, Far North Coastal, and Inland/Riverine regions. A close evaluation of directional asymmetry shows that select females from each group may have engaged in unimanual projectile hunting. Such results portend complexity in the sexual division of labor, which may be attributed to flexibility in gendered behavior and identities in these regions.

#### AUTHOR CONTRIBUTIONS

**Daniel Howard Temple:** Conceptualization (lead); data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); writing – original draft (lead); writing – review and editing (lead). **Emily Rae Rosa:** Conceptualization (equal); formal analysis (equal); investigation (equal); methodology (equal); writing – original draft (supporting); writing – review and editing (supporting). **David R. Hunt:** Conceptualization (supporting); data curation (supporting); formal analysis (supporting); investigation (supporting); methodology (supporting); resources (lead); writing – original draft (supporting); writing – review and editing (supporting). **Christopher B. Ruff:** Conceptualization (supporting); formal analysis (equal); investigation (equal); methodology

(equal); writing – original draft (equal); writing – review and editing (equal).

## ACKNOWLEDGMENTS

Steven Churchill and Laura Shackelford kindly allowed use of humeral cross-sectional data from the Aleutian Island and Point Hope ancestral remains and provided the outlines that were used for the Aleutian Island and Tikeraq cross sections in Figure 4. We thank J. Christopher Dudar for assistance with repatriation reports and original documentation of site excavations. Comments from the editorial board members and reviewers greatly improved this work.

## DATA AVAILABILITY STATEMENT

Data included in this study, Temple et al. (2021), and cross-sectional images of radii (not included in this work) are available upon reasonable request to the corresponding author.

## ORCID

Daniel H. Temple  <https://orcid.org/0000-0003-4582-3978>

Christopher B. Ruff  <https://orcid.org/0000-0002-2932-3634>

## ENDNOTES

<sup>1</sup> Intensive refers to an increasing focus on specific activities. Higher levels of bone mechanical loading may be associated with intensification of a particular behavior, but may also result from a diverse array of activities that increase overall mechanical loads on the bone.

<sup>2</sup> Cross-sections for Point Hope (Shackelford, 2014) and Aleutian Island (Churchill, 1994) remains were measured at 35% of humeral length\* (see Ruff, 2002 for the definition of length\*). Sections for all other samples were measured at 33% of maximum humeral length (Rosa, 2019). The difference in location is trivial in terms of morphology, with cross-sectional size and shape properties likely varying by less than 2% (Mongle et al., 2015).

## REFERENCES

- Agostini, G., Holt, B. M., & Relethford, J. H. (2018). Bone functional adaptation does not erase neutral evolutionary information. *American Journal of Physical Anthropology*, 166(3), 708–729.
- Anichtchenko, E. (2012). Open skin boats of the Aleutians, Kodiak Island, and Prince William Sound. *Études/Inuit/Studies*, 36(1), 157–181.
- Auerbach, B. M., & Ruff, C. B. (2006). Limb bone bilateral asymmetry: Variability and commonality among modern humans. *Journal of Human Evolution*, 50(2), 203–218.
- Bardill, J., Bader, A. C., Garrison, N. A., Bolnick, D. A., Raff, J. A., Walker, A., & Malhi, R. S. (2018). Advancing the ethics of paleogenomics: Ancestral remains should be regarded not as artifacts but as human relatives who deserve respect. *Science*, 360(6387), 384–385.
- Bass, S. L., Saxon, L., Daly, R. M., Turner, C. H., Robling, A. G., Seeman, E., & Stuckey, S. (2002). The effect of mechanical loading on the size and shape of bone in pre-, peri-, and postpubertal girls: A study in tennis players. *Journal of Bone and Mineral Research*, 17(12), 2274–2280.
- Beaglehole, J. C. (Ed.). (1967). The journal of Captain James Cook voyages of discovery. In *The voyage of the resolution and discovery* (Vol. 3, pp. 1776–1780). Cambridge University Press.
- Berget, K. A., & Churchill, S. A. (1994). Subsistence activity and humeral hypertrophy among Western Aleutian islanders. *American Journal of Physical Anthropology Supplement*, 18, 55.
- Binford, L. R. (2001). *Constructing frames of reference: An analytical method for archaeological theory building using ethnographic and environmental data sets*. University of California Press.
- Black, L. T. (1987). Whaling in the Aleutians. *Études/Inuit/Studies*, 11(2), 7–50.
- Bodenhorn, B. (1990). “I’m not the great hunter, my wife is”: Inupiat and anthropological models of gender. *Études/Inuit/Studies*, 14(1/2), 55–74.
- Bridges, P. S. (1989). Changes in activities with the shift to agriculture in the Southeastern United States. *Current Anthropology*, 30(3), 385–394.
- Bridges, P. S., Blitz, J. H., & Solano, M. C. (2000). Changes in long bone diaphyseal strength with horticultural intensification in west-central Illinois. *American Journal of Physical Anthropology*, 112(2), 217–238.
- Buikstra, J. E., & Ubelaker, D. H. (1994). *Standards for data collection from human skeletal remains* (Vol. 44). Arkansas Archaeological Survey Research Series.
- Byers, D. A., Yesner, D. R., Broughton, J. M., & Coltrain, J. B. (2011). Stable isotope chemistry, population histories, and Late Prehistoric subsistence change in the Aleutian Islands. *Journal of Archaeological Science*, 38, 183–196.
- Cameron, M. E., Lapham, H., & Shaw, C. N. (2018). Examining the influence of hide processing on Native American upper limb morphology. *International Journal of Osteoarchaeology*, 28, 332–342.
- Cameron, M. E., & Stock, J. T. (2018). Ecological variation in Later Stone Age southern African biomechanical properties. *Journal of Archaeological Science: Reports*, 17, 125–136.
- Carlson, K. J., Grine, F. E., & Pearson, O. M. (2007). Robusticity and sexual dimorphism in the postcranium of modern hunter-gatherers from Australia. *American Journal of Physical Anthropology*, 134(1), 9–23.
- Churchill, S. E. (1994). Human upper body evolution in the Eurasian Later Pleistocene (Ph.D. dissertation). University of New Mexico, Albuquerque.
- Churchill, S. E., & Formicola, V. (1997). A case of marked bilateral asymmetry in the upper limbs of an Upper Palaeolithic male from Barma Grande (Liguria), Italy. *International Journal of Osteoarchaeology*, 7(1), 18–38.
- Churchill, S. E., Formicola, V., Holliday, T. W., Holt, B. M., & Schumann, B. A. (2000). The Upper Paleolithic population of Europe in an evolutionary perspective. In J. Svoboda & K. Fenema (Eds.), *Hunters of the golden age: The Mid Upper Paleolithic of Eurasia 30,000–20,000 BP* (pp. 31–57). European Science Foundation.
- Churchill, S. E., Weaver, A. H., & Niewoehner, W. A. (1996). Late Pleistocene human technological and subsistence behavior: Functional interpretations of upper limb morphology. *Quaternaria Nova*, 6, 413–447.
- Claussen, B. F. (1982). Chronic hypertrophy of the ulna in the professional rodeo cowboy. *Clinical Orthopaedics and Related Research*, 164, 45–47.
- Collier, S. (1993). Sexual dimorphism in relation to big-game hunting and economy in modern human populations. *American Journal of Physical Anthropology*, 91(4), 485–504.
- Collins, H. B. (1937). Archaeological excavations at Bering Strait. In W. P. True (Ed.), *Explorations and fieldwork of the Smithsonian Institution in 1936* (pp. 63–68). The Lord Baltimore Press.
- Collins, R. L. (2000). *Dichinaneq Hwt ana: A history of the people of the Upper Kuskokwim River who live in Nikolai and Telida*. Alaska Department of Fish and Game. Division of Subsistence. Edzeno Native Council. Telida Tribal Council.
- Corbett, D., & Yarborough, M. (2016). The Aleutian tradition: The last 4000 years. In T. M. Friesen & O. K. Mason (Eds.), *The Oxford handbook of the prehistoric Arctic* (pp. 607–629). Oxford University Press.
- Coxe, W. (1803). *Account of Russian discoveries between Asia and America*. J. Nichols.
- Crass, B. A. (1998). Gender and mortuary analysis: What can grave goods really tell us? In B. Arnold & N. L. Wicker (Eds.), *Gender and the archaeology of death* (pp. 105–118). Alta Mira Press.

- Davis, R., Knecht, R., & Rogers, J. (2016). First maritime cultures of the Aleutians. In T. M. Friesen & O. K. Mason (Eds.), *The Oxford handbook of the prehistoric Arctic* (pp. 279–302). Oxford University Press.
- Dumond, D. E. (2000). The Norton tradition. *Arctic Anthropology*, 37(2), 1–22.
- Dumond, D. E. (2001). Toward a (yet) newer view of the (pre)history of the Aleutians. In D. E. Dumond (Ed.), *Archaeology in the Aleut zone of Alaska: Some recent research* (Vol. 58, pp. 289–309). University of Oregon, Anthropological Papers, Museum of Natural and Cultural History.
- Dumond, D. E. (2014). Point Hope in certain contexts: A comment. In C. E. Hilton, B. M. Auerbach, & L. W. Cowgill (Eds.), *The foragers of Point Hope: The biology and archaeology of humans on the edge of the Alaskan Arctic* (pp. 291–307). Cambridge University Press.
- Eschman, P. N. (1990). SLCOMM. Eschman Archeological Services.
- Fienup-Riordan, A. (1986). *When our bad season comes: A cultural account of subsistence harvesting and harvest disruption on the Yukon Delta*. Aurora Monography Series, Alaska Anthropological Association.
- Fienup-Riordan, A. (1990). Eskimo iconography and symbolism: An introduction/iconographie et symbolisme eskimo: Une introduction. *Études/Inuit/Studies*, 14(1/2), 7–22.
- Fienup-Riordan, A. (1994). *Boundaries and passages: Rule and ritual in Yup'ik Eskimo oral tradition*. University of Oklahoma Press.
- Fitzhugh, W. W., & Kaplan, S. A. (1982). *Inua: Spirit world of the Bering Sea Eskimo*. Smithsonian Institution Press.
- Friesen, T. M., & Mason, O. K. (Eds.). (2016). *The Oxford handbook of the prehistoric Arctic*. Oxford University Press.
- Frost, H. M. (1973). *Remodeling and its relationship to metabolic bone disease*. Charles C. Thomas.
- Geller, P. M. (2008). Conceiving sex: Fomenting a feminist bioarchaeology. *Journal of Social Archaeology*, 8(1), 113–138.
- Geller, P. M. (2017). *The bioarchaeology of socio-sexual lives: Queering common sense about sex, gender, and sexuality*. Springer.
- Gerlach, C., & Mason, O. K. (1992). Calibrated radiocarbon dates and cultural interaction in the Western Arctic. *Arctic Anthropology*, 29(1), 54–81.
- Giddings, G. L. (1964). *The archaeology of Cape Denbigh*. Brown University Bicentennial Publications.
- Gillispie, T. E. (2018). *An overview of Alaska's prehistoric cultures*. Alaska Department of Natural Resources.
- Halfman, C., Saddler, R., & Clark, J. (2014). *Bone collagen stable isotope analysis of three prehistoric humans from the Upper Kuskokwim village of McGrath, western interior Alaska*, Fairbanks, Alaska: Annual Meeting of the Alaska Anthropological Association.
- Hawkey, D. E., & Merbs, C. F. (1995). Activity induced musculoskeletal stress markers (MSM) and subsistence strategy changes among ancient Hudson Bay Eskimos. *International Journal of Osteoarchaeology*, 5, 324–338.
- Hawkey, D. E., & Street, S. R. (1992). Activity induced stress markers from the Eastern Aleutian Islands. *American Journal of Physical Anthropology Supplement*, 14, 89.
- Hill, E. C., Pearson, O. M., Durband, A. C., Walshe, K., Carlson, K. J., & Grine, F. E. (2020). An examination of long bone diaphysis of Holocene foragers from Roonka, South Australia. *American Journal of Physical Anthropology*, 172(4), 682–697.
- Hollinger, R. E., Eubanks, E., & Ousley, S. (2004). *Inventory and assessment of human remains and funerary objects from the Point Barrow region, Alaska, in the National Museum of Natural History, Smithsonian Institution*. Office of Repatriation, National Museum of Natural History, Smithsonian Institution.
- Holt, B., Whittey, E., Niskanen, M., Sládek, V., Berner, M., & Ruff, C. B. (2018). Temporal and geographic variation in robusticity. In *Skeletal variation and adaptation in Europeans* (pp. 91–132). Wiley.
- Hrdlička, A. (1930a). *An anthropological survey of Alaska* (p. 46). American Bureau of Ethnology, Annual Reports, Smithsonian Institution.
- Hrdlička, A. (1930b). The ancient and modern inhabitants of the Yukon. In W. P. True (Ed.), *Explorations and fieldwork of the Smithsonian Institution 1929* (pp. 137–146). The Lord Baltimore Press.
- Hrdlička, A. (1945). *The Aleutian and Comander Islands and their inhabitants*. The Wistar Institute of Anatomy and Biology.
- Ingold, T. (1998). From complementarity to obviation: On dissolving the boundaries between social and biological anthropology, archaeology and psychology. *Zeitschrift für Ethnologie*, 123(1), 21–52.
- Jarvenpa, R., & Brumbach, H. J. (2006). Gender, subsistence, and ethnography. In R. Jarvenpa & H. J. Brumbach (Eds.), *Circumpolar lives and livelihoods: A comparative ethnoarchaeology of gender and subsistence* (pp. 1–23). University of Nebraska.
- Jenness, D. (1957). *Dawn in arctic Alaska*. University of Chicago Press.
- Jensen, A. M. (2014). The archaeology of north Alaska: Point Hope in context. In C. E. Hilton, B. M. Auerbach, & L. W. Cowgill (Eds.), *The foragers of Point Hope: The biology and archaeology of humans on the edge of the Alaskan Arctic* (pp. 11–34). Cambridge University Press.
- Jensen, A. M. (2016). Archaeology of the Late Western Thule/Iñupiat in North Alaska (A.D. 1300–1750). In T. M. Friesen & O. K. Mason (Eds.), *The Oxford handbook of the prehistoric Arctic* (pp. 513–535). Oxford University Press.
- Jolles, C. Z. (2006). Inupiaq society and gender relations. In R. Jarvenpa & H. J. Brumbach (Eds.), *Circumpolar lives and livelihood: A comparative ethnoarchaeology of gender and subsistence* (pp. 238–262). University of Nebraska Press.
- Jones, H. H., Priest, J. D., Hayes, W. C., Tichenor, C. C., & Nagel, D. A. (1977). Humeral hypertrophy in response to exercise. *Journal Bone and Joint Surgery*, 59(2), 204–208.
- Kelly, R. L. (1998). *The foraging spectrum: Diversity in hunter-gatherer life-ways*. Smithsonian Institution Press.
- King, J. W., Brelsford, H. J., & Tullos, H. S. (1969). 17 analysis of the pitching arm of the professional baseball pitcher. *Clinical Orthopaedics and Related Research*, 67, 116–123.
- Knobbe, S. (2010). *Reconstructing activity patterns in prehistoric Jomon people using long bone cross-sectional geometry* (MA thesis). Department of Anthropology, University of Missouri, Columbia.
- Kofinas, G. P., Chapin, F. S., BurnSilver, S., Schmidt, J., Fresco, N. L. F. L., Kielland, K., Martin, S., Springsteen, A., & Rupp, S. T. (2010). Resilience of Athabaskan subsistence systems to interior Alaska's changing climate. *Canadian Journal of Forest Research*, 40(7), 1347–1359.
- Kramer, J., & Wilson, D. J. (2016). Imaging of rowing, canoeing, and kayaking injuries. In A. Guermazi, F. A. Roemer, & M. D. Crema (Eds.), *Imaging in sports-specific musculoskeletal injury* (pp. 449–465). Springer.
- Lantis, M. (1947). *Alaskan Eskimo ceremonialism*. JJ Augustin Publisher.
- Lantis, M. (1984). Aleut. In D. Damas (Ed.), *Handbook of North American Indians Arctic* (Vol. 5, pp. 161–184). Smithsonian Institution Press.
- Larsen, H., & Rainey, F. G. (1948). *Ipiutak and the arctic whale hunting culture* (Vol. 42). Anthropological Papers of the American Museum of Natural History.
- Laughlin, W. S. (1968). Hunting: An integrated biobehavioral system and its evolutionary implications. In R. B. Lee & I. DeVore (Eds.), *Man the hunter*. Aldine Publishers.
- Laughlin, W. S., Laughlin, S. B., & Beman, S. B. (1991). Aleut kayak hunter's hypertrophic humerus. *Current Research in the Pleistocene*, 8, 55–57.
- Laugrand, F., & Oosten, J. (2015). *Hunters, predators, and prey: Inuit perceptions of animals*. Berghahn.
- Lieverse, A. R., Bazaliiskii, V. I., Goriunova, O. I., & Weber, A. W. (2009). Upper limb musculoskeletal stress markers among Middle Holocene foragers of Siberia's Cis-Baikal. *American Journal of Physical Anthropology*, 138(4), 458–472.
- Lippert, D., & Dudar, J. C. (2021). *Inventory and assessment of human remains and funerary objects requested by Holy Cross Village, Alaska, in the collections of the National Museum of Natural History, Smithsonian*

- Institution. Office of Repatriation, National Museum of Natural History, Smithsonian Institution.
- Macintosh, A. A., Pinhasi, R., & Stock, J. T. (2017). Prehistoric women's manual labor exceeded that of athletes through the first 5500 years of farming in Central Europe. *Science Advances*, 3(11), ea03893.
- Maschner, H. D. G. (2016). Archaeology of the Eastern Aleut region. In T. M. Friesen & O. K. Mason (Eds.), *The Oxford handbook of the prehistoric Arctic* (pp. 323–348). Oxford University Press.
- Mason, O. K. (1998). The contest between the Ipiutak, Old Bering Sea, and Birnirk polities and the origin of whaling during the first millennium A.D. along Bering Strait. *Journal of Anthropological Archaeology*, 17(3), 240–325.
- Mason, O. K., & Gerlach, S. C. (1995). Chukchi hot spots, paleo-polynyas, and caribou crashes: Climatic and ecological dimensions of North Alaska prehistory. *Arctic Anthropology*, 32(1), 101–130.
- McCartney, A. P., & Veltre, D. W. (1999). Aleutian Island prehistory: Living in insular extremes. *World Archaeology*, 30(3), 503–515.
- Mihesuah, D. A. (2003). *Indigenous American women: Decolonization, activism, empowerment*. University of Nebraska Press.
- Mongle, C. S., Wallace, I. J., & Grine, F. E. (2015). Cross-sectional structural variation relative to midshaft along hominin diaphyses. I. The forelimb. *American Journal of Physical Anthropology*, 158(3), 386–397.
- Murdoch, J. (1892). *Results of the Point Barrow expedition* (Vol. 9). Annual Report of the Bureau of Ethnology to the Secretary of the Smithsonian Institution.
- Murray, S. O. (2002). *Pacific homosexualities*. Writers Club Press.
- Nagurka, M. L., & Hayes, W. C. (1980). An interactive graphics package for calculating cross-sectional properties of complex shapes. *Journal of Biomechanics*, 13, 59–64.
- Nansen, F. (1893). *Eskimo life*. Longmans, Green, and Company.
- Nelson, W. E. (1900). *Eskimo about the Bering Strait*. Government Printing Office.
- O'Neill, M. C., & Ruff, C. B. (2004). Estimating human long bone cross-sectional geometric properties: A comparison of noninvasive methods. *Journal of Human Evolution*, 47(4), 221–235.
- Osborn, K. (1990). *The peoples of the Arctic*. Chelsea House Publishing.
- Pearson, O. M., & Lieberman, D. E. (2004). The aging of Wolff's "law": Ontogeny and responses to mechanical loading in cortical bone. *Yearbook of Physical Anthropology*, 125(S39), 63–99.
- Pelham, T. W., Robinson, M. G., & Holt, L. E. (2020). Injuries in spring canoers and kayakers: Etiology, mechanisms of injury, treatment options, and practical applications. *Strength and Conditioning Journal*, 42(3), 22–29.
- Pinart, A. (1873). Voyage à la côte nord-ouest d'Amérique d'Ounalashka à Kadiak (îles Aléoutiennes et péninsule d'Alaska). *Bulletin de la Société de Géographie, Paris*, 6, 561–581.
- Pratt, K. L. (1984). Classifications of Eskimo groupings in the Yukon-Kuskowkwim region: A critical analysis. *Études Inuit/Studies*, 8, 45–71.
- Pullar, G. L. (1995). The Qikertarmut and the scientist: Fifty years of flashing world views. In T. L. Bray & T. W. Killion (Eds.), *Reckoning with the dead: The Larsen Bay repatriation and the Smithsonian Institution* (pp. 15–25). Smithsonian Institution Press.
- Rainey, F. G. (1947). *The whale hunters of Tigara* (Vol. 41). Anthropological Papers of the American Museum of Natural History.
- Ray, D. J. (1964). Nineteenth century settlement and subsistence patterns in Bering Strait. *Arctic Anthropology*, 2(2), 61–94.
- Ray, P. H. (1885). *Ethnographical sketches of the natives of Point Barrow*. Report of the International Polar Expedition to Point Barrow, Alaska, in response to the resolution of the House of Representatives, December 11, 1884. 48th Congress, 2nd Session, House Executive Document 44, part 3. Washington: Government Printing Office.
- Reeves, N. M., Auerbach, B. M., & Sylvester, A. D. (2016). Fluctuating and directional asymmetry in the long bones of captive cotton-top tamarins (*Saguinus oedipus*). *American Journal of Physical Anthropology*, 160(1), 41–51.
- Rhodes, J. A., & Knüsel, C. J. (2005). Activity-related skeletal change in medieval humeri: Cross-sectional and architectural alterations. *American Journal of Physical Anthropology*, 128(3), 536–546.
- Rogers, J. J. (2020). *Maize, mobility, and migration: Variation in long bone functional adaptation in the pre- and proto-historic American southwest* (MA thesis), Department of Sociology and Anthropology, George Mason University, Fairfax, Virginia.
- Rosa, E. R. (2019). *Adapting in the Arctic: Comparing functional adaptation in the long bone diaphyses of Alaskan hunter-gatherers* (MA thesis), Department of Sociology and Anthropology, George Mason University, Fairfax.
- Ruff, C. B. (2002). Long bone articular and diaphyseal structure in Old World monkeys and apes, I: Locomotor effects. *American Journal of Physical Anthropology*, 119(4), 242–305.
- Ruff, C. B. (2016). *Calculating moments*. <http://www.hopkinsmedicine.org/fae/mmacro.html>
- Ruff, C. B. (2019). Biomechanical analysis of human skeletons. In M. A. Katzenberg & A. Grauer (Eds.), *Biological anthropology of the human skeleton* (pp. 189–224). Wiley.
- Ruff, C. B., Burgess, M. L., Squyres, N., Junno, J.-A., & Trinkaus, E. (2018). Lower limb articular scaling and body mass estimation in Pliocene and Pleistocene hominins. *Journal of Human Evolution*, 115, 85–111.
- Ruff, C. B., Garafalo, E., & Holmes, M. E. (2013). Interpreting skeletal growth in the past from a functional and physiological perspective. *American Journal of Physical Anthropology*, 150(1), 29–37.
- Ruff, C. B., & Holt, B. (2018). The Balkans. In C. B. Ruff (Ed.), *Skeletal variation and adaptation in Europeans* (pp. 397–418). Wiley.
- Ruff, C. B., Holt, B., Niskanen, M., Sladek, V., Berner, M., Garofalo, E., Garvin, H. M., Hora, M., Junno, J.-A., Schuplerova, E., Vilkkama, R., & Whittey, E. (2015). Gradual decline in mobility with the adoption of food production in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, 112(23), 7147–7152.
- Ruff, C. B., Holt, B., & Trinkaus, E. (2006). Who's afraid of the big bad Wolff?: "Wolff's law" and bone functional adaptation. *American Journal of Physical Anthropology*, 129(4), 484–498.
- Ruff, C. B., & Larsen, C. S. (1990). Postcranial biomechanical adaptations to subsistence strategy on the Georgia Coast. In C. S. Larsen (Ed.), *The archaeology of Mission Santa Catalina de Guale: 2. Biocultural interpretations of an economy in transition* (pp. 121–131). Anthropological Papers of the American Museum of Natural History.
- Ruff, C. B., & Larsen, C. S. (2001). Reconstructing behavior in Spanish Florida: The biomechanical evidence. In C. S. Larsen (Ed.), *Bioarchaeology of Spanish Florida: The impact of colonialism* (pp. 181–206). University Press of Florida.
- Ruff, C. B., Sylvester, A. D., Rahmawati, N. T., Suriyanto, R. A., Storm, P., Aubert, M., Joannes-Boyau, R., Berghuis, H., Pop, E., Batenburg, K. J., Coban, S. B., Kostenko, A., Noerwidi, S., Renema, W., Adhityatama, S., & Joordens, J. C. (2022). Two Late Pleistocene human femora from Trinil, Indonesia: Implications for body size and behavior in Southeast Asia. *Journal of Human Evolution*, 172(103), 252.
- Ruff, C. B., Walker, A., & Trinkaus, E. (1994). Postcranial robusticity in Homo III: Ontogeny. *American Journal of Physical Anthropology*, 93(1), 35–54.
- Sakaue, K. (1997). Bilateral asymmetry of the humerus in Jomon people and modern Japanese. *Anthropological Science*, 105(4), 231–246.
- Saladin d'Angulure, B. (1994). From foetus to shaman: The construction of the Inuit third sex. In A. Mills & R. Slobodkin (Eds.), *Amerindian rebirth: Reincarnation and belief among American Indians and Inuit* (pp. 82–106). University of Toronto Press.
- Schmitt, D., Churchill, S. E., & Hylander, W. L. (2003). Experimental evidence concerning spear use in Neandertals and early modern humans. *Journal of Archaeological Science*, 30(1), 103–114.
- Shackelford, L. L. (2005). *Regional variation in the postcranial robusticity of Late Upper Paleolithic Humans* (Ph.D. dissertation), Department of Anthropology, Washington University, St. Louis.

- Shackelford, L. L. (2007). Regional variation in postcranial robusticity of Late Upper Paleolithic humans. *American Journal of Physical Anthropology*, 133(1), 655–668.
- Shackelford, L. L. (2014). Bone strength and subsistence activities at Point Hope. In B. M. Auerbach, C. E. Hilton, & L. W. Cowgill (Eds.), *The foragers of Point Hope: The biology and archaeology of humans on the edge of the Alaskan Arctic* (pp. 181–211). Cambridge University Press.
- Shaw, C. N. (2011). Is 'hand preference' coded in the hominin skeleton? An in-vivo study of bilateral morphological variation. *Journal of Human Evolution*, 61(4), 480–487.
- Shaw, C. N., Hofmann, C. L., Petraglia, M. D., Stock, J. T., & Gottschall, J. S. (2012). Neandertal humeri may reflect adaptation to scraping tasks, but not spear thrusting. *PLoS One*, 7(7), e40349.
- Shaw, C. N., & Stock, J. T. (2009). Habitual throwing and swimming correspond with upper limb diaphyseal strength and shape in modern human athletes. *American Journal of Physical Anthropology*, 140(1), 160–172.
- Shaw, R. D. (1982). The expansion and survival of the Norton tradition on the Yukon-Kuskokwim Delta. *Arctic Anthropology*, 19(2), 59–73.
- Shaw, R. D. (1998). An archaeology of the Central Yupik: A regional overview for the Yukon-Kuskokwim Delta, Northern Bristol Bay, and Nunivak Island. *Arctic Anthropology*, 35(1), 234–246.
- Skopek, M., Bacakova, R., Bily, M., & Tunkova, K. (2009). A comparative analysis of the kayak forward stroke. *Physical Activity Review*, 7, 107–113.
- Sládek, V., Berner, M., Holt, B., Niskanen, M., & Ruff, C. B. (2018). Past human manipulative behavior in the European Holocene as assessed through upper limb asymmetry. In C. B. Ruff (Ed.), *Skeletal variation and adaptation in Europeans* (pp. 163–208). Wiley.
- Sládek, V., Ruff, C. B., Berner, M., Holt, B., Niskanen, M., Schulperova, E., & Hora, M. (2016). The impact of subsistence changes on humeral bilateral asymmetry in the Terminal Pleistocene and Holocene Europe. *Journal of Human Evolution*, 92, 37–49.
- Smith, R. W. A. (2021). Imperial terror: Toward a queer molecular ecology of colonial masculinities. *Current Anthropology*, 62(S23), S155–S168.
- Sockbeson, H. J. (1995). The Larsen Bay repatriation case and commoners of anthropologists. In T. L. Bray & T. W. Killion (Eds.), *Reckoning with the dead: The Larsen Bay repatriation and the Smithsonian Institution* (pp. 158–162). Smithsonian Institution Press.
- Sparacello, V., & Marchi, D. (2008). Mobility and subsistence economy: A diachronic comparison between two groups settled in the same geographical area (Liguria, Italy). *American Journal of Physical Anthropology*, 136(4), 485–495.
- Stanford, D. J. (1976). *The Walakpa site, Alaska: Its place in the Birnirk and Thule cultures*. Smithsonian Contributions to Anthropology.
- Steen, S. (2003). *The interpretation of musculoskeletal stress marker data from four different Alaskan Eskimo populations* (Ph.D. dissertation), Department of Anthropology, University of Alberta.
- Stock, J., & Pfeiffer, S. (2001). Linking structural variability in long bone diaphyses to habitual behaviors: Foragers from the southern African Later Stone Age and the Andaman Islands. *American Journal of Physical Anthropology*, 115(4), 337–348.
- Stock, J. T., Bazaliiskii, V. I., Goriunova, O. I., Savel'ev, N., & Weber, A. W. (2010). Skeletal orphology, climatic adaptation, and habitual behavior among Mid-Holocene Cis-Baikal populations. In A. W. Weber, M. A. Katzenberg, & T. G. Schurr (Eds.), *Prehistoric hunter-gatherers of the Baikal region, Siberia* (pp. 193–216). University of Pennsylvania Press.
- Stock, J. T., & Pfeiffer, S. K. (2004). Long bone robusticity and subsistence behaviour among later stone age foragers of the forest and fynbos biomes of South Africa. *Journal of Archaeological Science*, 31(7), 999–1013.
- Temple, D. H., Bazaliiskii, V. I., Goriunova, O. I., & Weber, A. (2013). Skeletal growth in Early and Late Neolithic foragers from the Cis-Baikal region of Eastern Siberia. *American Journal of Physical Anthropology*, 153(3), 377–386.
- Temple, D. H., Rosa, E. R., Hunt, D. R., & Ruff, C. B. (2021). Adapting in the Arctic: Habitual activity and landscape interaction in Late Holocene hunter-gatherers from Alaska. *American Journal of Physical Anthropology*, 176(1), 3–20.
- Trinkaus, E., Churchill, S. E., & Ruff, C. B. (1994). Postcranial robusticity in Homo. II: Humeral bilateral asymmetry and bone plasticity. *American Journal of Physical Anthropology*, 93(1), 1–34.
- Trinkaus, E., Churchill, S. E., Villemeur, I., Riley, K. G., Heller, J. A., & Ruff, C. B. (1991). Robusticity versus shape: The functional interpretation of Neanderthal appendicular morphology. *Journal of the Anthropological Society of Nippon*, 99(3), 257–278.
- Turner, E. (1990). The whale decides: Eskimos' and ethnographer's shared consciousness on the ice. *Études/Inuit/Studies*, 14(1/2), 39–52.
- Turner, L. (2008). *An Aleutian ethnography*. University of Alaska Press.
- VanStone, J. W. (1979). *Ingalik contact ecology: An ethnohistory of the Lower-Middle Yukon, 1790–1935*. Anthropological Series of the Field Museum of Natural History.
- Veniaminov, I. (1984). *Notes on the islands of the Unalaska District [English Translation]*. The Limestone Press.
- Warden, S. J., Mantila Roosa, S. M., Kersh, M. E., Herd, A. L., Fleisig, G. S., Pandey, M. G., & Fuchs, R. K. (2014). Physical activity when young provides lifelong benefits to cortical bone size and strength in men. *Proceedings of the National Academy of Sciences of the United States of America*, 111(14), 5337–5342.
- Weiss, E. (2003). Effects of rowing on humeral strength. *American Journal of Physical Anthropology*, 121(4), 293–302.
- Zelazny, K. G., Sylvester, A. D., & Ruff, C. B. (2021). Bilateral asymmetry and developmental plasticity of the humerus in modern humans. *American Journal of Physical Anthropology*, 174(3), 418–433.

**How to cite this article:** Temple, D. H., Rosa, E., Hunt, D. R., & Ruff, C. B. (2023). Adapting in the Arctic II: Upper limb diaphyseal robusticity and habitual activity in Late Holocene hunter-gatherers from Alaska. *American Journal of Biological Anthropology*, 1–21. <https://doi.org/10.1002/ajpa.24734>