

# Ontogeny of Limb Proportions in Late Through Final Jomon Period Foragers

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**ABSTRACT** This study reports on developmental patterning in the intralimb indices of Late/Final Jomon period (4000–2300 BP) people. Jomon foragers represent the descendants of migrants from Northeast Asia, who arrived in the Japanese Islands around 20,000 BP. Among adults, Jomon brachial indices are elevated and similar to warm adapted, low latitude people, while crural indices are intermediate and similar to people from moderate latitudes. Two hypotheses regarding the development of intralimb indices among Jomon period foragers are tested: (1) intralimb indices of Jomon people maintain predicted ecogeographic relationships over ontogeny; (2) greater evolvability will be observed in the brachial index, while greater developmental constraint will be observed in the crural index. Changes in intralimb proportions in a Jomon skeletal growth series are compared to those in two contrasting samples: Inuit

from Point Hope (cold adapted) and Nubians from Kulubnarti (warm adapted). A quadratic equation best describes the ontogeny of brachial and crural indices, with high indices in infancy followed by a decline in childhood and an increase in adolescence. Despite these shifts, ecogeographically predicted differences and similarities in the indices are maintained between samples throughout ontogeny. In addition, radial relative to humeral length is significantly less correlated than tibial relative to femoral length. These results suggest genetic conservation of intralimb indices over the course of development. However, radial and humeral lengths are less correlated than tibial and femoral lengths among Jomon subadults and adults, potentially suggesting greater evolvability of the brachial index and more developmental constraint on the crural index. *Am J Phys Anthropol* 145:415–425, 2011. © 2011 Wiley-Liss, Inc.

Allen's rule was penned more than 100 years ago to explain the morphological response of birds and mammals to climate, with a particular emphasis on limb length (Allen, 1877). Allen's rule, in part, states that organisms from warmer climates have elongated limbs compared with conspecifics from colder climates (Allen, 1877). Reduction of appendage length reduces surface area for heat loss in cold climates, while greater appendage length increases surface area for heat dissipation in warmer climates (Feldhamer et al., 2007). Clinal distributions of these traits in geographically diverse species suggest that natural selection is indeed responsible for the spread of these features (Mayr, 1963; Futuyma, 1998). In humans, increased distal relative to proximal limb segment lengths were observed among groups from low latitude, warmer climates, while reduced distal relative to proximal limb segment lengths were observed in groups from high latitude, colder climates; these indices change only after long-term exposure to new environments (Trinkaus, 1981; Yamaguchi, 1989; Ruff, 1994; Holliday, 1997a,b, 1999; Weinstein, 2005; Auerbach, 2007; Temple et al., 2008). Differences in the rate of change between the indices were also reported: the brachial index appears to shift at an earlier temporal point than the crural index following exposure to new climates (Trinkaus, 1981; Holliday, 1997a, 1999).

Intralimb indices among samples of fetuses from varying ancestral, and presumably, ecogeographic backgrounds significantly differ (Schultz, 1923, 1926; Warren, 1998; Ruff et al., 2002; Warren et al., 2002). Ecogeographically predicted differences and similarities in limb

proportions were observed in diverse samples between 2.5 and 9 years of age (Ruff et al., 2002). No reference to limb proportions before or after this age range is, however, reported as the study focused on the intralimb indices of the Lagar Velho child, aged five years (Ruff et al., 2002). Shifts in intralimb indices were reported over ontogeny in some juvenile specimens, particularly those between 10 and 15 years of age, indicating that intralimb indices shift over ontogeny, but likely maintain ecogeographically appropriate relationships (Ruff and Walker, 1993; Ruff, 2007). Differences in limb proportions were implied at an early point in development between Inuit and European-Americans, though the study focused on raw limb length (Y'Ednak, 1976). Taken together, these findings suggest that ecogeographic patterning in intralimb indices may be set at an early age.

This study identifies ontogenetic patterning in the intralimb indices of Jomon people and interprets the results within developmental and ecogeographic contexts. Prehistoric foragers from the Jomon period

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occupied the Japanese Islands from ~13,000 through 2300 BP (Imamura, 1996; Kobayashi, 2005). These prehistoric people are the hypothesized descendants of a Paleolithic "microblade" culture. The "microblade" culture expresses similarity to the Paleolithic Yubetsu industry of Siberia, appeared in the Japanese Islands around 20,000 BP, and transitioned into Jomon around 13,000 BP (Imamura, 1996; Kobayashi, 2005). Modern descendants of Jomon foragers are represented by Ainu people (Hanihara, 1991; Turner, 1992; Pietrusewsky, 1999; Hammer et al., 2006), though admixture between Ainu, modern Japanese, and in Northeastern Hokkaido, nomads from Sakhalin Island is noted (Shigematsu et al., 2004; Sato et al., 2007; Komesu et al., 2008). Morphological and genetic studies of Jomon and contemporary Ainu people indicate similarity with Northeast Asian groups and the possibility of earlier migratory origins in Altai (Omoto and Saitou, 1997; Pietrusewsky, 1999, 2005; Hammer et al., 2006; Adachi et al., 2009; Hanihara and Ishida, 2009). Indigenous Paleolithic and Jomon cultures of the Japanese Islands existed in relative isolation for ~20,000 years (Hammer et al., 2006; Adachi et al., 2009).

Foragers from the Late through Final Jomon period (4000 through 2500 BP) had subsistence economies that varied between regions (Akazawa, 1999). Groups from eastern Japan lived in environments that provided year-round access to nutrient rich foods, while those from western/inland Japan relied on seasonally available resources (Akazawa, 1999). These contrasting subsistence economies were associated with a greater prevalence of enamel hypoplasia among western/inland compared to eastern Jomon foragers (Shigehara, 1994; Temple, 2007a). Little difference in leg length was noted between the eastern and western Jomon suggesting that the minimal caloric requirements for longitudinal growth were met in both groups (Temple, 2008).

Elevated brachial indices were identified in adult Jomon remains by studies carried out over the last century (Kiyono and Hirai, 1928; Ishiwa, 1931; Ohba, 1935; Suzuki et al., 1957; Suzuki and Hojo, 1966; Ogata et al., 1971; Dodo, 1980; Yamaguchi, 1981, 1989; Baba, 1988; Kato and Ogata, 1989; Takigawa, 2006; Temple et al., 2008). Mean adult brachial indices were similar to and even greater than groups from low latitude, warm climates (Sub-Saharan Africa), while mean adult crural indices were similar to groups from higher latitude, temperate climates (Europe) (Yamaguchi, 1989; Temple, 2007b). Earlier studies concluded that brachial and crural indices of Jomon people were attributable to energetic adaptation (Yamaguchi, 1981; Kato and Ogata, 1989), though global patterning in human limb proportions rule out such relationships (Holliday and Falsetti, 1995; Holliday, 1999). This patterning may also be related to changes in intralimb indices experienced in response to the warmer Japanese climate (Temple et al., 2008). It, therefore, remains possible that the elevated brachial indices were associated with a more immediate response to the climate of the early Holocene, while the crural index reflects an ancestral morphotype. Such interpretations imply that Jomon brachial indices had a greater degree of evolvability than crural indices in response to ambient temperature during the early Holocene in Japan.

At this point, it is unknown if the limb proportions of Jomon people represent a developmental response to environmental stimuli (i.e., ambient temperature) or if

these morphological features are genetically conserved. Moreover, it is not understood if differences in evolvability and developmental constraint are associated with the elevated brachial index and intermediate crural index observed in Jomon people. Developmental constraint references limits on the amount of variant phenotypes in response to the structure, character, composition, or dynamics of the developmental system (Maynard-Smith et al., 1985). Evolvability reflects the capacity of an organism to produce heritable phenotypic variation (Kirschner and Gerhart 1998). More specifically, reduced correlation between traits is observed in those that express a greater degree of evolvability, while developmental constraint may be associated with significantly greater correlation between traits (Futuyma, 1998; Young et al., 2010). This study will explore the question of conservation and plasticity as well as developmental constraint and evolvability in the intralimb indices of Jomon people by testing two hypotheses on the intralimb indices of subadults.

### Research hypotheses

Two primary hypotheses associated with the ontogeny of brachial and crural indices among prehistoric Jomon people are tested. The first hypothesis evaluates the general responsiveness of the indices to climate in comparative context. If intralimb indices are more conserved in response to ambient temperature, then Jomon people will maintain ecogeographically appropriate similarities and differences with comparative samples over the course of ontogeny. The brachial index of Jomon people should remain similar to warm-adapted samples across age groups, while the crural index of Jomon people should remain similar to cold-adapted samples regardless of age group.

The second hypothesis addresses differences in developmental constraint and evolvability in the brachial and crural indices. It is expected that the Jomon crural index will express a greater degree of developmental constraint, while the Jomon brachial index will express a greater degree of evolvability. Significantly lower correlations between radial and humeral length compared to tibial relative to femoral length will be observed.

### MATERIALS AND METHODS

Data were collected from subadult and adult skeletal remains dated to the Late/Final Jomon period (4000–2300 BP). Table 1 lists the age-specific sample sizes for the Late/Final Jomon group (see below for discussion on age groups). Skeletal remains were derived from 18 archaeological sites on Honshu and Hokkaido Islands (see Fig. 1). All sites were dated using pottery chronology and/or radiocarbon methods. Site chronologies obtained from radiocarbon methods suggest that dates based on pottery typologies are appropriate in the absence of absolute dating (Imamura, 1996). The average northern latitude of these sites is 35.7° and the average annual high temperature is ~27.1°C, while the average annual low temperature is 5.8°C (Fukui, 1977). Middle Holocene temperatures were predicted to have been ~3°C warmer than the current environment (Tsukada, 1986).

Table 1 also lists the number of individuals from Hokkaido relative to the number of individuals from Honshu in each age and sex grouping. Using Jomon foragers from Honshu and Hokkaido may be problematic due to

TABLE 1. Sample composition for the jomon, medieval nubian, and tigara groups

Age group 1 <sup>a</sup>	N radius/humerus	N tibia/femur
Jomon	5 (0:5) <sup>b</sup>	9 (0:9)
Nubians	18	18
Tigara	5	4
Age Group 2 <sup>c</sup>		
Jomon	25 (3:22)	32 (6:26)
Nubians	52	52
Tigara	13	21
Age Group 3 <sup>d</sup>		
Jomon	5 (1:5)	7 (2:5)
Nubians	13	13
Tigara	12	23
Age Group 4 <sup>e</sup> ♂		
Jomon	42 (4:38)	51 (9:42)
Nubians	7	7
Tigara	33	32
Age Group 4 <sup>e</sup> ♀		
Jomon	37 (3:34)	33 (10:23)
Nubians	7	7
Tigara	33	36

<sup>a</sup> Age Group 1 includes individuals between zero (0) and two (2) years of age.

<sup>b</sup> Number of individuals from Hokkaido relative to the number of individuals from Honshu.

<sup>c</sup> Age Group 2 includes individuals between three (3) and 10 years of age.

<sup>d</sup> Age Group 3 includes individuals between 11 years of age through epiphyseal fusion of both long bones in either the brachial or crural index.

<sup>e</sup> Adults include individuals with epiphyseal fusion of both long bones in the index under consideration (brachial or crural).

temperature differences between the two regions. The northern latitudinal range of Hokkaido is approximately 41.4–45.5° and is classified as a continental microthermal environment. Hokkaido Island experiences temperatures ranging from -10 to 25°C with accumulations of sea ice during winter months (Fukui, 1977). Comparatively warmer temperatures were, however, reported for the mid-Holocene, ca. 7250 through 3240 BP (Kawahata et al., 2003). Mann-Whitney *U* tests and Folded *F* tests suggest that brachial indices do not significantly differ in average value or variance between adult males (Mann Whitney:  $P < 0.83$ ;  $F = 1.71$ ,  $P < 0.5194$ ) or females (Mann Whitney:  $P < 0.213$ ;  $F = 2.83$ ,  $P < 0.32$ ) from Hokkaido and Honshu. The same tests indicate that crural indices do not significantly differ in average value or variance between adult males (Mann Whitney:  $P < 0.06$ ;  $F = 2.13$ ,  $P < 0.228$ ) or females (Mann Whitney:  $P < 0.394$ ;  $F = 1.64$ ,  $P < 0.394$ ) from Hokkaido and Honshu. Similar results were derived by Takigawa (2006) using ANOVA methods. This suggests subadults from Honshu and Hokkaido can be pooled, though there remains an unequal distribution of individuals from Hokkaido relative to Honshu in each age group.

Comparative samples were derived from Point Hope, Alaska and Kulubnarti, Nubia. Sample sizes for these groups are listed in Table 1. The Point Hope site consists of two separate occupations (Larsen and Rainley, 1948). One earlier group utilized this cemetery between 2100 and 1500 BP (Ipiutak), while a second cultural group utilized the cemetery between 600 and 400 BP (Tigara). Significant differences in relative limb lengths are noted

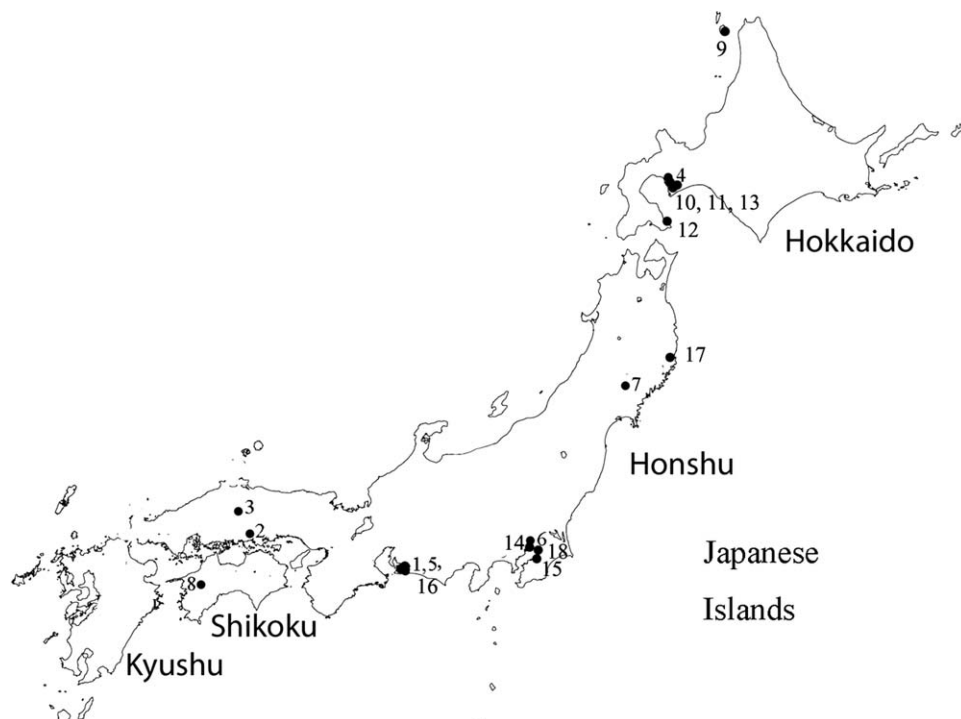


Fig. 1. Map of archaeological sites yielding Late-Final Jomon period skeletal remains utilized by this study. 1: Yoshigo, 2: Tsukumo, 3: Yosekura, 4: Takasago, 5: Hobi, 6: Ubayama, 7: Ebishima, 8: Kamikuroiwa, 9: Funadomori, 10: Irie, 11: Takasago, 12: Usujiri, 13: Usu-Moshiri, 14: Kainohana, 15: Kasori, 16: Inariyama, 17: Tagara, 18: Nakabyo.

between the Ipiutak and Tigara adult samples (Holliday and Hilton, 2010). As a result, this study includes measurements from only the Tigara cultural occupation of the Point Hope site. Point Hope is located at  $\sim 68^\circ$  northern latitude and experiences average annual high temperatures of  $10^\circ\text{C}$  and average annual low temperatures of  $-22^\circ\text{C}$ . Limb proportions of adults in the Tigara collection are comparatively low among modern human samples from diverse environments (Holliday and Hilton, 2010), and therefore, represent an appropriate high latitude, cold adapted comparative sample.

The medieval Nubian sample was recovered from the Kulubnarti Island in Northern Sudan  $\sim 130$  km south of Wadi Halfa (Van Gerven et al., 1995). The sample is comprised of individuals who occupied the site from  $\sim 1500$  through 600 BP. The site is located at  $21^\circ$  northern latitude and experiences average annual high temperatures of  $41^\circ\text{C}$  and average annual low temperatures of  $15^\circ\text{C}$ . Limb proportions among adults in the medieval Nubian sample are comparatively elevated among modern human samples from diverse environments (Holliday, 1997a,b; Ruff et al., 2002), and therefore, represent an appropriate low latitude, warm adapted comparative sample. C. Ruff measured adults from the Kulubnarti

sample and shared these measurements with the authors (Ruff et al., 2002; Ruff, pers. comm.).

Age was estimated in subadults on the basis of tooth development and emergence. Tooth emergence was recorded according to standard osteological protocols and compared with reference standards (Buikstra and Ubelaker, 1994). Tooth development was recorded on the basis of radiographic images of the deciduous and permanent dentition and compared to previously published standards (Liversedge and Molleson, 2004; Smith, 1991). Detailed descriptions of these criteria are available in Cowgill (2008), Okazaki (2007), and Temple (2007b) and were recorded consistently between observers. Subadults were divided into three age groups: Age Group 1 (AG 1: 0.0 - 2.0 years), Age Group 2 (AG 2: 2.1 - 10.9 years), and Age Group 3 (AG 3: 11.0 years through epiphyseal union). Adults (Age Group 4) are also included to provide a developmental endpoint. Subadult age groups were defined on the basis of modern human life cycles including infancy (0 through 2.0 years), childhood/juvenility (2.1 through 10.9 years), and adolescence (11.0+ years) (Bogin, 1998). Adults are defined as follows: all individuals with fully fused humerus and radius or any individual with fully fused femur and tibia.

All subadult samples are composed of individuals of unknown sex. However, it is well established that adult males have greater brachial indices compared to adult females (Trinkaus, 1981; Aiello and Dean, 1990; Ruff, 1994). This problem is not possible to overcome due to the inaccuracies of determining sex in subadult skeletal remains and represents a potential source of error. Sex in adults was determined using morphological features of the Os pubis and greater sciatic notch. These features were scored on a qualitative scale according to standard osteological protocols (Buikstra and Ubelaker, 1994). Methods used to determine sex in the Kulubnarti adult series are consistent with those employed for the Jomon and Point Hope series (Ruff, pers. comm.).

Maximum diaphyseal lengths were recorded from all subadults to the nearest millimeter using a sliding osteometric board. These measurements were collected from the humerus (HL), radius (RL), femur (FL), and tibia (TL) following standard osteological protocols (Buikstra and Ubelaker, 1994). Adult limbs were also measured

TABLE 2. Line-fitting methods used to characterize the ontogeny of jomon brachial and crural indices

Brachial	Jomon
t Linear	0.794 <sup>a</sup> (.433 <sup>b</sup> )
t Quadratic	3.168 (.003)
t Cubic	0.868 (.392)
t Quartic	—
Crural	Jomon
t Linear	0.515 (0.476)
t Quadratic	2.896 (0.006)
t Cubic	0.267 (0.791)
t Quartic	—

<sup>a</sup> *T* statistic calculated for the specified regression method.

<sup>b</sup> *P*-value of the *t*-statistic calculated for the specified regression method.

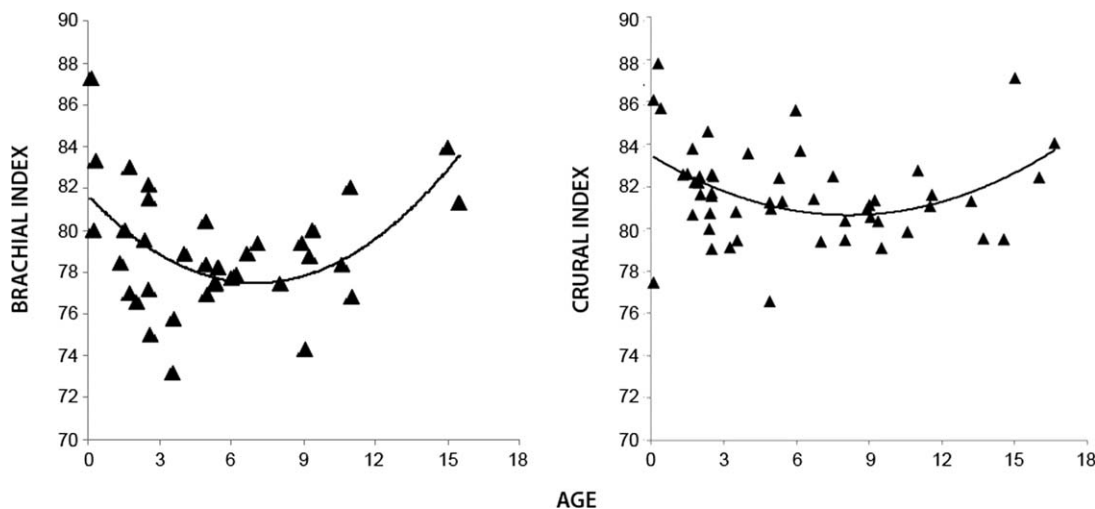


Fig. 2. Quadratic curves describing the ontogeny of Jomon intralimb indices. (a) Brachial index relative to age. (b) Crural index relative to age.

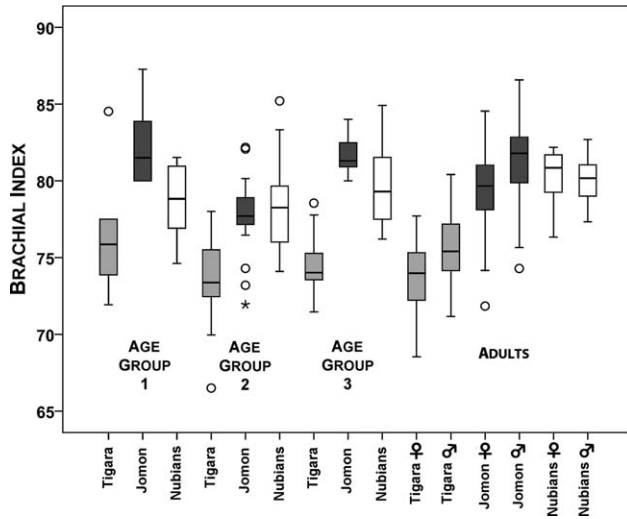


Fig. 3. Box plots of brachial indices for each age and geographic group.

TABLE 3. Mann-Whitney *U* test results for brachial indices

Brachial index	<i>U</i>	<i>P</i> ≤
AG 1: Jomon V. Tigara	20	0.014
AG 1: Jomon V. Nubians	69	0.126
AG 2: Jomon V. Tigara	272	0.0002
AG 2: Jomon V. Nubians	656	0.75
AG 3: Jomon V. Tigara	65	0.001
AG 3: Jomon V. Nubians	63	0.377
AG 4♂: Jomon V. Tigara	196	0.0004
AG 4♂: Jomon V. Nubians	1311	0.162
AG 4♀: Jomon V. Tigara	1263	0.0002
AG 4♀: Jomon V. Nubians	275	0.643

according to standard osteological protocols and include the following measurements: maximum femoral length, tibial length (lateral condyle to medial malleolus), maximum humeral length, and maximum radial length. These measurements were converted to maximum diaphyseal lengths to maintain consistency with the subadult samples, using equations provided by Ruff (2007: 702). Brachial indices were calculated as  $RL/HL \cdot 100$ . Crural indices were calculated as  $TL/FL \cdot 100$ .

This study is first interested in characterizing the pattern of ontogeny in brachial and crural indices among Jomon people. Previous studies applied polynomial expansions on relative measurements of the postcranial skeleton with the underlying goal of explaining age-dependent changes in long bone lengths, cortical bone density, and some postcranial proportions (Pinhasi et al., 2005, 2006; Mays et al., 2009). Several similar line fitting methods are attempted here to help explain changes in Jomon intra-limb indices over the course of ontogeny. Polynomial curve fitting follows the methods of “forward selection” described by Zar (2010). Simple linear models are first fit to the data. These are followed by second, third, and fourth degree polynomial expressions as necessary. Following the addition of new polynomial expressions the hypothesis  $H_0: \beta_j = 0$  is tested to understand if the new equation provides significantly better explanatory power, with significance based on a *t*-statistic. Once a statistically insignificant result is reached, the previous equation is selected as a best fit. The expansion is carried over one additional term to ensure that further equations are inappropriate for the data (Zar, 2010: 461–462).

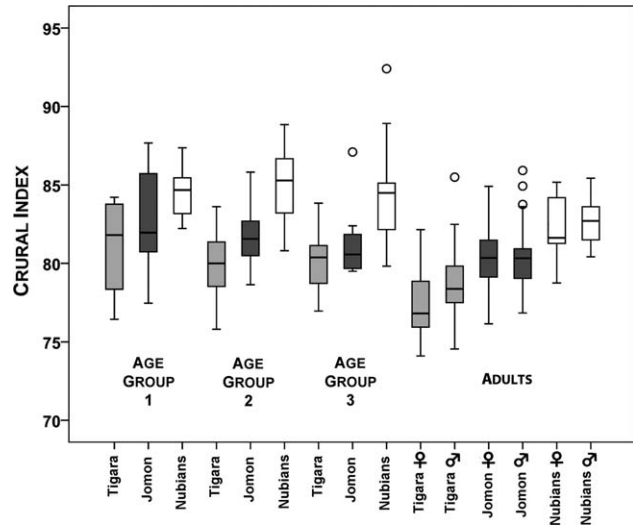


Fig. 4. Box plots of crural indices for each age and geographic group.

TABLE 4. Mann-Whitney *U* test results for Jomon crural indices

Crural Index	<i>U</i>	<i>P</i> ≤
AG 1: Jomon V. Tigara	24	0.571
AG 1: Jomon V. Nubians	134	0.077
AG 2: Jomon V. Tigara	456	0.003
AG 2: Jomon V. Nubians	1399	0.0001
AG 3: Jomon V. Tigara	93	0.414
AG 3: Jomon V. Nubians	94	0.02
AG 4♂: Jomon V. Tigara	1014	0.0014
AG 4♂: Jomon V. Nubians	253	0.0041
AG 4♀: Jomon V. Tigara	1113	0.0005
AG 4♀: Jomon V. Nubians	213	0.029

Box plots of brachial and crural indices were derived for each geographic sample and age group. Interquartile ranges of brachial and crural indices for Jomon people in each age group were then compared to the medieval Nubian and Tigara samples in the same age group to determine if these indices differed in association with geography (climate) over the course of ontogeny.

Mann-Whitney *U* statistics were calculated to test the null hypothesis that the samples would have equivalently ranked brachial and crural indices within each age group (Sokal and Rohlf, 1995). Mann-Whitney *U* tests utilized by this study include multiple comparisons of data. Many biological researchers apply the Bonferroni correction method to such comparisons to reduce the probability of a Type I error (Sokal and Rohlf, 1995). Bonferroni corrections were, however, not applied to minimize the probability of committing a Type II error and due to questions regarding standardization of application (Moran, 2003). Furthermore, recent morphological studies argue that careful evaluation of significance patterning is preferred, particularly when clear biological processes are observed (Cowgill, 2010).

RMA regression analysis combined with the “Quick-Test” method was applied to help explain age-specific differences in the bivariate distribution of RL relative to HL and TL relative to FL between the Jomon and comparative groups of the same age class. RMA regression was chosen because the samples were measured with error, and more importantly, do not include a dependent

variable (Smith, 2009). RMA regression was performed on all three geographic samples for a given age cohort (Age Groups 1, 2, 3, and 4). "Quick-Test" methods were then applied to test the null hypothesis that the groups do not significantly differ in the number of individuals distributed above or below the RMA line of best fit for the samples (Tsutakawa and Hewett, 1977).

Finally, this study predicts greater evolvability in the brachial index and greater developmental constraint acting to limit variability in the crural index. Correlation analysis was carried out between RL relative to HL and TL relative to FL. Fisher-*z* transformations of correlation coefficients were compared using two-sample *t* tests (Zar, 2010). This procedure was performed independently for the subadult and adult Jomon samples. In the adult sample, males and females are compared separately due to differences in the brachial index between the sexes (Trinkaus, 1981; Yamaguchi, 1989) that may influence covariation between limb elements.

## RESULTS

Table 2 and Figure 2 show the results of the line fitting methods used to characterize the ontogeny of intralimb indices among Jomon subadults. Linear equations do not fit the Jomon brachial or crural indices. Results suggest that the quadratic equation was a significantly better fit to the ontogeny of Jomon brachial and crural indices, with higher order polynomials falling below significance. Both indices have higher values in infancy, decline during childhood, and increase again in adolescents.

A Box plot depicting the ontogeny of brachial indices for the Jomon as well as comparative samples is shown in Figure 3. Results from the Mann-Whitney *U* test for differences in brachial indices between the Jomon and comparative samples are listed in Table 3. Differences between Jomon and medieval Nubian brachial indices do not attain significance in any age group. In contrast, the brachial indices of the Jomon samples are significantly higher than those reported for the Tigara in each age group.

A Box plot depicting the ontogeny of crural indices for the Jomon as well as comparative samples is shown in Figure 4. Results from the Mann-Whitney *U* test for differences in crural indices between the Jomon and comparative samples are listed in Table 4. Jomon crural indices are significantly lower than the medieval Nubian sample in Age Group 2, Age Group 3, and Age Group 4 (adult males and females). The Jomon crural index is significantly higher than the Tigara sample in Age Group 2 and Age Group 4 (adult males and females).

RMA regression analyses for the bivariate relationship of RL relative to HL are illustrated in Figure 5 for all age and geographic groups. "Quick-Test" results are listed in Table 5. There is no statistically significant difference in the number of individuals distributed above or below the RMA line between the Jomon and medieval Nubian samples in any age group. The Jomon have significantly greater numbers of individuals above the RMA line compared with the Tigara sample in all age groups.

RMA regression analyses of the bivariate relationship for TL relative to FL are illustrated in Figure 6 for all age and geographic groups. "Quick-Test" results are listed in Table 5. Significantly greater numbers of Jomon compared with Kulubnarti individuals were found below the RMA regression line for the following age groups:

TABLE 5. Results of the "quick-test" performed on the Jomon and comparative samples

AG 1	RL V. HL <sup>a</sup>	TL V. FL <sup>b</sup>
Jomon V. Tigara	$P \leq 0.05$	$P \leq 0.99$
Jomon V. Nubians	$P \leq .13$	$P \leq 0.24$
AG 2		
Jomon V. Tigara	$P \leq 0.02$	$P \leq 0.145$
Jomon V. Nubians	$P \leq .99$	$P \leq 0.001$
AG 3		
Jomon V. Tigara	$P \leq 0.003$	$P \leq 0.244$
Jomon V. Nubians	$P \leq 0.99$	$P \leq 0.054$
AG 4 Males		
Jomon V. Tigara	$P \leq 0.0001$	$P \leq 0.361$
Jomon V. Nubians	$P \leq 0.99$	$P \leq 0.01$
AG 4 Females		
Jomon V. Tigara	$P \leq 0.0001$	$P \leq 0.439$
Jomon V. Nubians	$P \leq 0.99$	$P \leq 0.308$

<sup>a</sup> Radius relative to humerus.

<sup>b</sup> Tibia relative to femur.

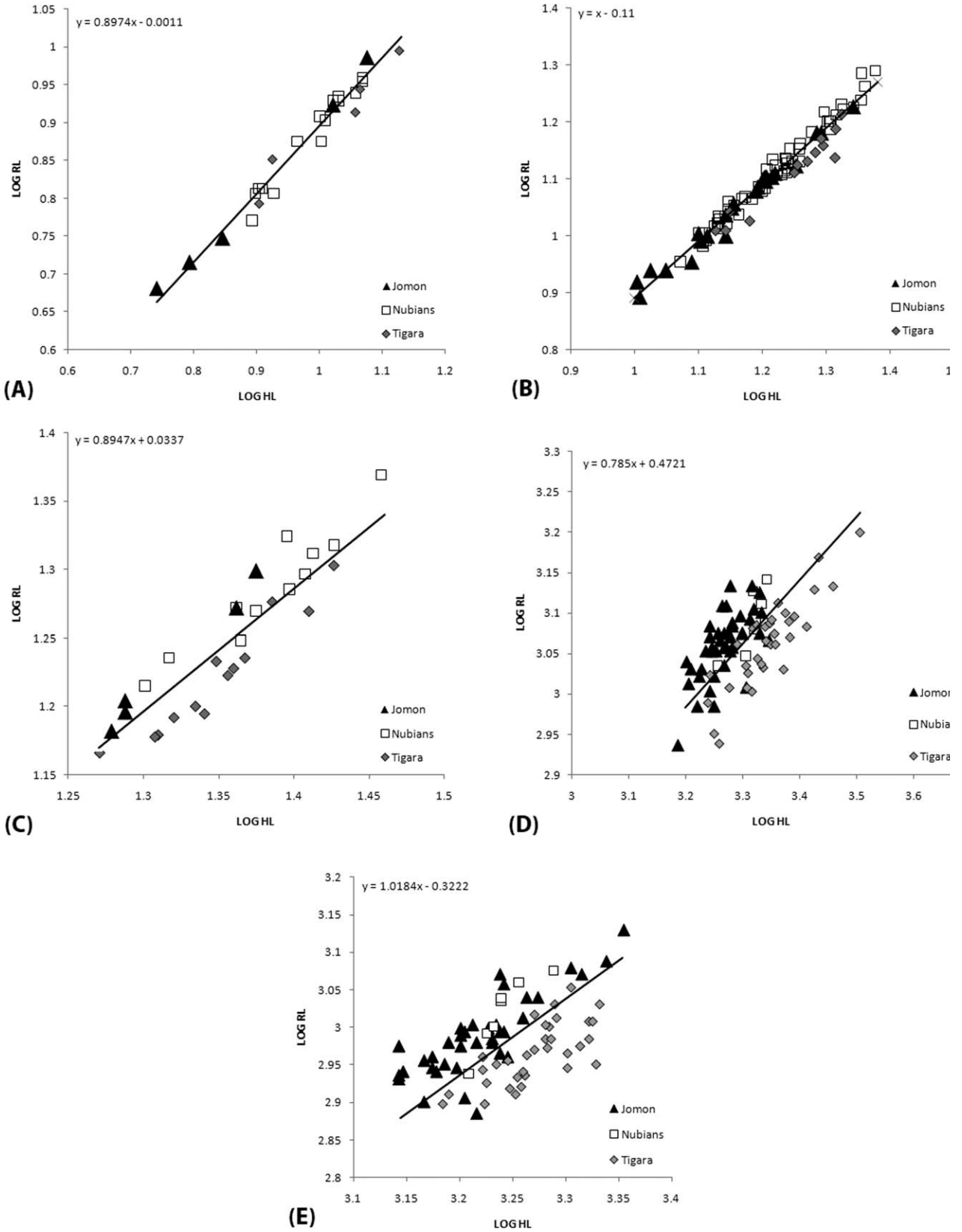
Age Group 2, Age Group 3, and Age Group 4 (adult males). Significant differences in the number of individuals found above or below the RMA regression line between the Jomon and Tigara samples were not observed for any age group.

Correlation and Fisher-*z* transformed coefficients are listed in Table 6. A significantly higher correlation is observed between TL and FL compared with RL and HL for the subadult sample ( $t = 2.03$ ,  $P < 0.05$ ) and for adult males ( $t = 2.12$ ,  $P < 0.05$ ). No significant difference in the correlations between TL and FL, and RL and HL is observed among adult females, although there is a suggestion of a higher correlation between TL and FL ( $t = 1.36$ ,  $P < 0.10$ ).

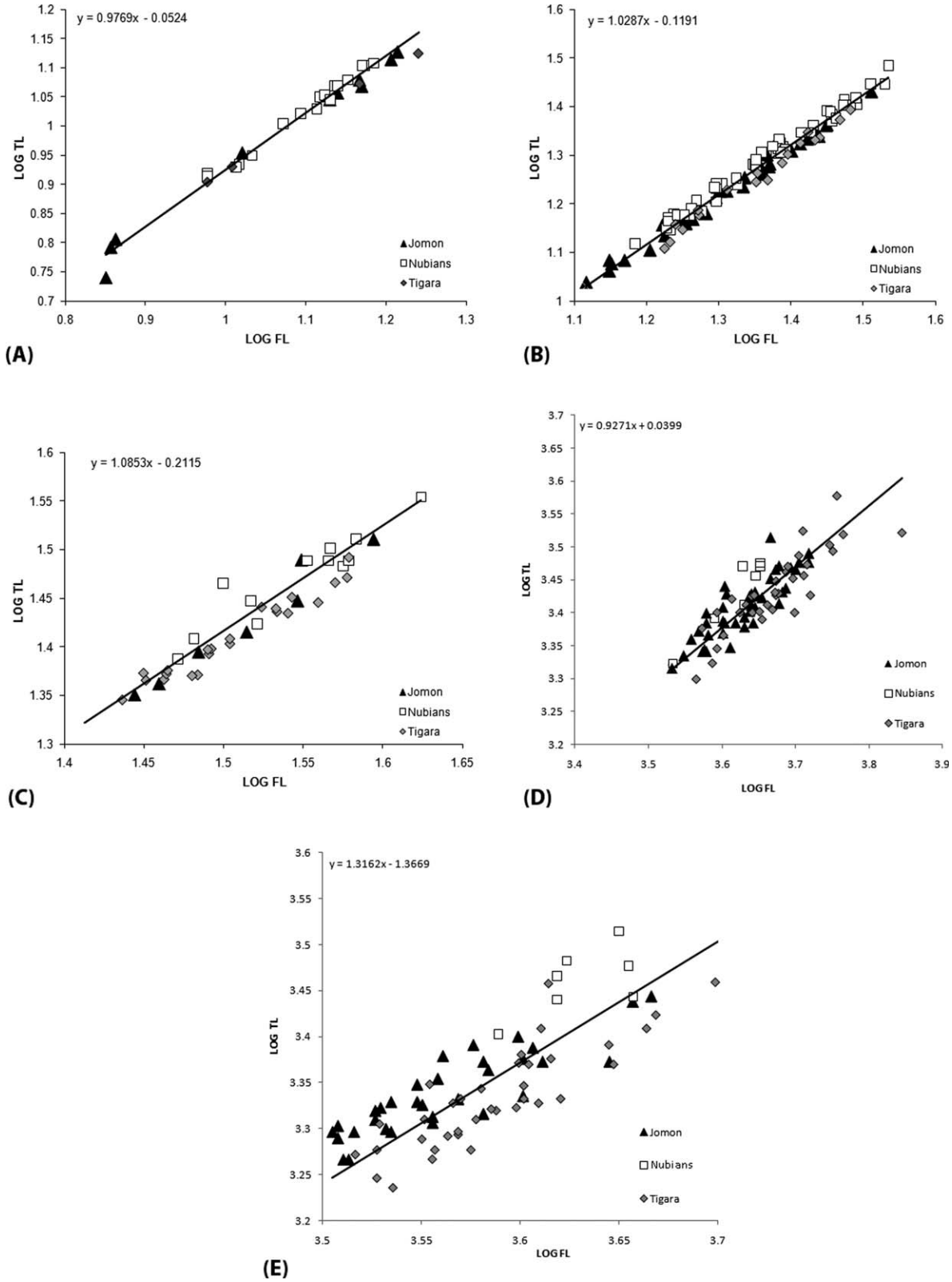
## DISCUSSION

Elevated growth coefficients are observed for the distal relative to proximal limb segments *in utero* (Moss et al., 1955) and likely carry over into infancy. Declines in both intralimb indices during childhood (3 through 10 years) and increases in the indices during adolescence (11+ years) have been reported on a large longitudinal sample of North Americans and cross-sectional sample of Native Alaskans (Ruff and Walker, 1993; Cowgill, 2006; Ruff, 2007). These results are consistent with earlier work that suggests the crural index increases at the onset of adolescence, beginning around 10 years of age, continuing to 13 years and declining thereafter (Davenport, 1933). Greater velocities of growth are observed in the proximal compared to distal segments during childhood, with greater deceleration in proximal compared to distal segments occurring at the onset of adolescence (Smith and Buschang, 2004). Earlier adolescent growth spurts are then observed in the distal compared with proximal limb segment: distal elements outpace proximal segments in terms of growth in millimeters per year between 10 and 13.5 years of age (Smith and Buschang, 2005). The quadratic functions fit to the Jomon data in the present study match these findings.

By and large, Jomon intralimb indices shift over the course of ontogeny, yet maintain similar positions relative to ecogeographically contrasting comparative samples in each age group. That is, while the intralimb indices shift over the course of ontogeny, the relative ecogeographic relationships observed in adults appear at an early point and are maintained throughout development.



**Fig. 5.** RMA regression analysis of RL relative to HL. (a) Age Group 1. (b) Age Group 2. (c) Age Group 3. (d) Age Group 4 adult males. (e) Age Group 4 adult females.



**Fig. 6.** RMA regression analysis of RL relative to HL. (a) Age Group 1. (b) Age Group 2. (c) Age Group 3. (d) Age Group 4 adult males. (e) Age Group 4 adult females.



TABLE 6. Correlation and Fisher-z coefficients for Jomon relative limb lengths

Jomon Subadults	Corr. Coefficient	Fisher-z	95% CI
RL rel. HL	0.994	2.91	0.987–0.997
TL rel. FL	0.998	3.38	0.995–0.999
Jomon Males			
RL rel. HL	0.727	0.924	0.546–0.839
TL rel. FL	0.879	1.368	0.791–0.928
Jomon Females			
RL rel. HL	0.829	1.185	0.684–0.907
TL rel. FL	0.910	1.526	0.819–0.953

Morphological differences that appear early in ontogeny and are maintained throughout development are often associated with genetic restrictions on phenotypic plasticity. Significant differences in humeral/femoral indices are observed early in ontogeny between humans and baboons and are thought to evidence genetic conservation of limb proportionality in association with locomotor patterns (Ruff, 2003). In terms of ecogeographic variability, differences in intralimb indices appear as early as fetal development (Schultz, 1923; Warren, 1998) and have been interpreted as evidence for genetic conservation of the traits in question (Holliday, 1997b: 425; Holliday, 1999: 563). Similar interpretations could be applied to the ontogeny of intralimb indices among Jomon people.

It is, however, important to point out that differences in relative appendage length have been produced in experimental contexts. Mammals exposed to colder temperatures during ontogeny express foreshortened limb length, while those exposed to warm temperatures during ontogeny express elongated limb length (Weaver and Ingram, 1969; Lee et al., 1969; Riesenfeld, 1973; Serrat et al., 2008). Relative foreshortening and elongation of limb bones in response to ambient temperature is often associated with vasoconstriction and vasodilation in growth plates (Weaver and Ingram, 1969; Lee et al., 1969; Riesenfeld, 1973; Serrat et al., 2008). This process enhances (via vasodilation) or inhibits (via vasoconstriction) chondrocyte proliferation and thereby directly mediates longitudinal growth, though endogenous factors may also play a role in these shifts (Serrat et al., 2008). Relative leg length also increases with improved nutritional environments, though these studies did not specifically address brachial and crural indices (Tanner et al., 1982; Bogin et al., 2002). More recently, activity has also been implicated in relative foreshortening and elongation of limbs via changes in solute delivery to the growth plate (Serrat et al., 2010). Evidence derived from the Jomon and other globally diverse samples does, however, suggest that human intralimb indices are directed by selection acting on fairly conserved genotypes or some pleiotropic event associated with ambient temperature.

Correlation analysis mostly supports the second hypothesis of this study. Significantly greater covariation is observed in the elements of the lower compared with upper limb in Jomon subadults and adult males; differences in correlation between the elements of the upper compared to lower limb fall just below significance in adult females, with greater correlation observed in tibial relative to femoral length. Decoupling of covariation between serially homologous elements combined with significantly greater evolvability in the upper compared with lower limb bones among anatomically modern

humans is reported (Young et al., 2010). One primary reason for differences in covariation between elements of the upper and lower limb is the functional requirements of bipedal locomotion (Young et al., 2010). In ecogeographic perspective, changes to the crural index alter muscle performance: the load arm of *quadriceps femoris* would, for example, change in relation to its power arm causing a trade-off in the ability to generate speed versus power (Trinkaus, 1983). Similar changes may occur due to shifts in the brachial index, but would not impact locomotion.

Such findings suggest that Jomon people may have responded to the ambient temperature of mid-Holocene Japan through more immediate changes in the brachial index. Current evidence suggests these changes were largely genetic as Jomon limb proportions maintain predicted differences and similarities with ecogeographically contrasting samples over the course of ontogeny. It does however appear that a greater capacity for genetic change may be found in the brachial index due to the inessential role of the upper limb in bipedal locomotion. This finding may account for the apparently more modified Jomon brachial index relative to that of putative cold-adapted ancestral populations. Excavation and description of skeletal remains from Late Pleistocene Japan, specifically those representing the ancestors of Jomon people, is necessary to further support this interpretation.

## CONCLUSIONS

This study explored the ontogeny of limb proportions among prehistoric Jomon period foragers. The ontogeny of Jomon brachial and crural indices is best described by quadratic functions due to subtle shifts in the indices over development. These shifts are attributed to normal patterns of distal/proximal limb segment growth. Both indices maintain the ecogeographic relationships observed in adults. This suggests a general pattern of genetic conservation in the intralimb indices of Jomon people, with no support for direct environmental influences over the indices during ontogeny. Correlation between radial and humeral length is significantly less than the correlation between tibial relative to femoral length in Jomon subadults and adult males. The same trend is observed in females, though marginally insignificant. While both intralimb indices are developmentally conserved, this result suggests greater latitude for genetic modification in the brachial index of Jomon people.

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