

Original Research Article

What Can Variation in Stature Reveal About Environmental Differences Between Prehistoric Jomon Foragers? Understanding the Impact of Systemic Stress on Developmental Stability

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ABSTRACT This study reconstructs patterns of stress and phenotypic variation in prehistoric Japan. Greater evidence for stress is indicated by elevated enamel hypoplasia frequency among Jomon foragers from western compared to eastern Japan. Geographic variation in stress between Jomon people is related to plant-based diets and resource scarcity in western Japan. The hypothesis that Jomon people from western Japan had shorter stature than those from the east is, therefore, tested. Relationships between individual stature, geographic location, and enamel hypoplasia presence/absence are also explored. In addition, increased population density and reliance on plant foods are observed during the Late/Final Jomon period in western Japan. A second hypothesis proposing shorter stature for Late/Final Jomon people compared to those from the Middle Jomon period is tested. Statistically significant differences in stature between males and females from eastern and western Japan were not observed. Individual relationships between enamel hypoplasia and stature were rejected. Stature decreased significantly over time in western Japan. It is possible that stature between the eastern and western Jomon did not differ because the western Jomon experienced catch up growth after childhood stress episodes. It is also likely that variation in stress between the two groups was not severe enough to warrant stature reduction. Decreases in stature through time in western Japan are related to increased exposure to chronic infection and dietary stress. Overall, these results indicate that enamel hypoplasia frequencies provide an adequate index of general stress but may fail to predict the impact of stress on the human phenotype. *Am. J. Hum. Biol.* 20:431–439, 2008. © 2008 Wiley-Liss, Inc.

This study documents and interprets variation in stress as expressed through enamel hypoplasia prevalence and adult stature among Middle to Final Jomon period (5000 through 2300 BP) foragers from Japan. Adult stature is sensitive to disruptions of biological homeostasis during growth and development (Silventoinen, 2003). Reconstructions of living stature are, therefore, used to understand biological adjustment to the environment by past humans (Cook, 1984; Floyd and Littleton, 2006; Larsen et al., 2002; Sciulli and Giesen, 1993; Sciulli et al., 1990; Steckel, 1994, 1995; and others). Stature is also used by human biologists as an indicator of phenotypic plasticity in modern people (Bogin, 1995; Crooks, 1999; Dittmar, 1998; Eveleth and Tanner, 1991; Hermanussen, 1997; Loesch et al., 2000; and others).

Enamel hypoplasia is a pathological condition observed on the human dentition that is associated with disrupted enamel production during the secretory phase of amelogenesis (Hillson, 1996). These disruptions are related to a variety of systemic stressors that include malnutrition and infectious disease (Goodman and Rose, 1990). Bioarchaeological research uses enamel hypoplasia frequencies to understand the biocultural impacts of “adaptive transitions” such as the origins of food production (see reviews: Larsen, 1987, 1995) or environmental variability among foragers (Stodder, 1997; Temple, 2007a,b; Walker and Lambert, 1989). Stress levels among living people (Goodman et al., 1991; Lukacs et al., 2001; Zhou and Corruccini, 1998) and deceased primates (Guatelli-Steinberg, 2001; Guatelli-Steinberg and Skinner, 2000; Lukacs, 1999; Skinner and Newell, 2003) are also evaluated using enamel hypoplasia frequencies. These studies overwhelmingly indicate that enamel hypoplasia prevalence corresponds to levels of systemic stress.

Jomon foragers are the hypothesized descendants of Pleistocene nomads who entered the Japanese islands ~35,000 years before present (Imamura, 1996). Variation in cranial and dental size and shape suggest that Jomon foragers are biologically related to populations from Southeast Asia (Hanihara, 1991; Turner, 1987; and others), specifically indigenous people of Melanesia, or Australia (Hanihara and Ishida, 2005; Matsumura and Hudson, 2005). Y-chromosome DNA studies, however, suggest that the prehistoric Jomon were the descendants of people from Central Asia, specifically the Tibet/Altai Mountain area (Hammer et al., 2006). Similar findings are reported by studies of variability across classic genetic loci that suggest a Northeast Asian origin for Jomon people (Omoto and Saitou, 1997). Isolation from continental gene pools (Hammer et al., 2006) and similar within and between group biological variability among Jomon foragers from Honshu (Kondo, 1994; Matsumura, 1989, 2007) suggest that differences in stature between Jomon people were associated with environmental interactions.

Greater frequencies of enamel hypoplasia are observed among Jomon people from western compared to eastern Japan (Temple, 2007a). Jomon people from western Japan relied heavily on seasonally available plant foods

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Fig. 1. Map illustrating the districts of Japan and sites from which data were collected: (1) Ota; (2) Tsukumo; (3) Yoshigo; (4) Hobi; (5) Inariyama. This map was drawn by Jules Angel, Department of Anthropology, Ohio State University.

(Akazawa, 1999). This hypothesis is supported by stable isotopes extracted from human skeletal material that suggest a greater reliance on plant food among western Jomon compared to eastern Jomon (Chisholm and Koike, 1999). Human intervention in the life cycles of walnut and acorn yielding trees is associated with the domestication of these plants in many regions of Japan (Sato, 1999), while large caches of acorns and walnuts were recovered from many Jomon sites in southwestern Japan (Imamura, 1996). Western Jomon diets were also tempered with maritime resources (Minagawa, 2001). Tool kit distributions in prehistoric Japan suggest that terrestrial mammal hunting and maritime economies of the eastern compared to western Jomon were, however, more stable in nature and likely provided a year-round source of food (Akazawa, 1981, 1982, 1986, 1999).

Transitional regions such as Tokai and Kanto are classified as eastern Japan (Akazawa, 1986; Akazawa and Maeyama, 1986; Imamura, 1996; Temple, 2007a) (Fig. 1). Eastern Jomon cultures are transitional because they were located in a geographic region between northern and western Japan and Jomon people from northern Japan (i.e., Tohoku and Hokkaido) had subsistence economies that were comparatively more focused on maritime exploitation (Akazawa, 1986; Akazawa and Maeyama, 1986; A Okada, 1998; H Okada, 1998). Eastern Jomon people did, however, rely upon more sophisticated maritime exploitation and terrestrial mammal hunting systems compared with Jomon people from western Japan (Akazawa, 1981, 1982, 1986, 1999). Jomon people from eastern Japan also consumed considerable amounts of plant foods (Minagawa and Akazawa, 1992). It is, however, likely that the sophisticated fishing and terrestrial mammal hunting behavior of the eastern Jomon served to buffer periods of plant scarcity experienced by the western Jomon (Akazawa, 1986, 1999; Temple, 2007a).

This study tests the hypothesis that the greater degree of systemic stress indicated by enamel hypoplasia prevalence among western compared to eastern Jomon people will be associated with reduced stature for western Jomon foragers. Broadly speaking, this study is interested in understanding the extent to which the types of stress indicated by enamel hypoplasia frequency are associated with stature. More specifically, this study addresses how systemic stress impacted phenotypic variability between Jomon foragers from different regions of Japan.

Similar to previous studies (i.e., Temple, 2007a), this research contains samples from different temporal periods. Samples from western Japan contain both a Middle and Late to Final Jomon component. Chipped stone axes and other plant processing tools appear in greater volumes among Late to Final Jomon people in western Japan indicating an increased reliance on plant foods over time (Imamura, 1996). This dietary behavior is further suggested by increased carious tooth frequencies among Late to Final compared to Middle Jomon period foragers (Temple, 2007a,b). Reliance on these plant foods is also associated with seasonal food shortages and stress related to nutritional deprivation, particularly in western Japan (Temple, 2007a). No changes in enamel hypoplasia are, however, observed between Middle and Late to Final Jomon groups (Temple, 2007a).

Climatic cooling is reported during the Middle Jomon period and dated to ~4300 BP (Tsukada, 1986). Population density in the Chubu highlands as well as the Kanto and Tokai regions decreased during this time (Koyama, 1978). In contrast, population density during the Late to Final Jomon period increased in both the Tohoku and Chugoku regions (Koyama, 1978). Increased population density represents migrations into Tohoku and Chugoku following climatic cooling (Habu, 2004). It is likely that Jomon people occupied single base camps on a yearly basis and used peripheral sites to process hunting/gathering/fishing materials (Watanabe, 1986); this pattern of behavior dates to the Initial Jomon period (9500 to 6000 BP) in western Japan (Pearson, 2006). Elevations in systemic stress and infectious diseases are associated with increased population density and sedentism in many contexts (Armstrong, 1990; Cockburn, 1971; Cohen and Armelagos, 1984; Larsen, 1997; Sattenspiel, 2000). Stunted growth is often attributed to chronic infectious disease in many contexts (Eveleigh and Tanner, 1991). This study, therefore, tests a second hypothesis that stature will be reduced among Late to Final compared to Middle Jomon period foragers-in spite of enamel hypoplasia prevalence that indicate little variation in stress levels over time.

MATERIALS

Skeletal material from which data were collected was recovered from five archaeological sites in eastern and western Japan (Fig. 1). All of these skeletal remains are curated by the Laboratory of Physical Anthropology at Kyoto University and University Museum at the University of Tokyo. All sites date from the Middle to Final Jomon period (5000 to 2300 BP). These dates are based on radiocarbon analysis of pottery. Pottery-based chronologies date the Middle Jomon from 5000 to 4000 BP, Late Jomon from 4000 to 3000 BP, and the Final Jomon from 3000 to 2500 BP in western Honshu and 2300 BP in eastern Honshu.

Data for the eastern Jomon were collected from three sites in the Tokai region (Hobi, Inariyama, and Yoshigo). Data for western Jomon sites were collected from two sites in the Chugoku district (Ota and Tsukumo). Eastern Jomon culture is classified in a variety of ways, one being associated with Kamegaoka pottery. Kamegaoka pottery originated in the Tohoku region, later spreading to Tokai, Kanto, and Hokkaido (Habu, 2004). Late to Final Jomon culture in western Japan is related to a less decorative pottery style that originated in central Kyushu (Imamura, 1996). In contrast, Jomon tool kit distributions divide various regions of Honshu, Kyushu, and Hokkaido into three separate subsistence zones (Akazawa, 1986, 1999; Akazawa and Maeyama, 1986).

Discriminant function analysis of tool types from 94 Middle to Final Jomon sites separated settlement systems into three resource groups: two settlement types that best fit marine and hunting economies with peripheral plant cultivation/gathering and one settlement type consistent with plant exploitation and a lesser focus on marine foraging and hunting (Akazawa, 1986). The first type of settlement is characterized by stemmed scrapers, stone awls, and flake scrapers with a negative correlation with chipped stone axes (Akazawa and Maeyama, 1986). This group is concentrated above 38°N latitude in northern Japan (i.e., Tohoku and Hokkaido). The second group was discriminated by grooved stone net sinkers, chipped projectile points, and polished stone axes and located in central Honshu between 137°N longitude and south of 38°N latitude (i.e., Kanto and Tokai). This region is categorized as eastern Japan. Chipped stone axes, grinding querns, notched stone net sinkers, grinding stones, and grinding slabs characterize the third group. These sites are all located in western/inland Japan. Stable isotope studies suggest a similar dietary pattern among Jomon people as those predicted by tool kit distributions (Chisholm and Koike, 1999; Minagawa, 2001; Minagawa and Akazawa, 1992). Overall, eastern Jomon sites reflect a transitional area between economies with heavy maritime foci in northern Honshu and Hokkaido and those with less sophisticated tools for maritime exploitation in western Japan (Akazawa, 1999).

METHODS

Enamel hypoplasias were recorded as deficiencies in enamel thickness appearing as horizontal grooves on tooth surfaces. Approximately 50% or more of the crown height was present on all examined teeth. The identification of enamel hypoplasia follow Skinner et al. (1995) and Guatelli-Steinberg (2003), where adjacent perikymata were compared to possible enamel defects to prevent confusing normal variation in tooth morphology with enamel hypoplasia.

Antimeric enamel hypoplasia frequencies were calculated as the total number of incisor and canine antimeres that both exhibit enamel hypoplasia divided by the total number of observed incisor and canine antimeres. Overall enamel hypoplasia frequencies were calculated by dividing the total number of anterior teeth with enamel hypoplasia by the total number of anterior teeth observed. Individual based enamel hypoplasia prevalence was determined by dividing the total number of individuals with at least one anterior tooth expressing enamel hypoplasia by the total number of individuals with at least one observ-

able anterior tooth. Differences in overall enamel hypoplasia frequency were compared using 95% confidence intervals; if the intervals do not overlap, the frequencies are considered different. Enamel hypoplasia frequencies reported by antimeric teeth and individual were compared using a *G*-statistic. Differences in enamel hypoplasia prevalence were compared between the eastern and western Jomon. For a more detailed description on enamel hypoplasia data collection methods, see Temple (2007a,b).

Stature in once living people is estimated by placing individual long bone measurements into predictive equations derived from individuals of known height and similar ancestry (Krogman and Iscan, 1986). Jomon stature is most accurately estimated by applying regression equations derived from living Japanese people (i.e., Fuji, 1960) to long bone measurements (Kouchi, 1987). Living Japanese do not have similar body proportions to Jomon people (Kato and Ogata, 1989; Yamaguchi, 1989). Applying stature equations produced from populations with disparate body proportions routinely over or underestimates living height (Holliday and Ruff, 1997). Equations derived from modern Japanese do, however, express the lowest variance of all stature estimation formulae applied to the long bones of Jomon people (Kouchi, 1987).

Stature estimation from long bone length using the equations of Pearson (1899) show close similarity with Jomon stature estimated from anatomical measurements that incorporate the entire skeleton and include a soft-tissue correction factor (Saeki, 2006). Individual stature was, therefore, recorded as the mean estimated living height derived from the regression equations of Fuji (1960) and Pearson (1899). Maximum femoral length was used as the primary indicator of stature. Where maximum femoral length was not possible to measure, stature was estimated from tibial or maximum radial length. Humeral length is not used by this study because it significantly underestimates Jomon stature (Kouchi, 1987). Separate equations for the estimation of stature from long bone length were used for males and females.

The impact of enamel hypoplasia presence on individual height was tested using multiple correspondence analysis ($n = 45$). Correspondence analysis plots the rows and columns of multivariate BURT tables in low-dimensional space and superimposes different classes of data to provide a joint display of their relationships (Greenacre, 1981). This procedure is used to evaluate the association between several qualitative variables in multidimensional space (i.e., MDS) by defining an area of points in MDS, the metric structure of MDS, and the fit of this area into low dimensional subspace where the points are projected. Here, males and females from eastern and western Japan were classified as "tall" and "short" based on height that is, respectively, above or below the mean height for each region. Correspondence analysis was then used to produce a graph showing the association between geographic location (east v. west), height classes (tall v. short), and enamel hypoplasia presence or absence. A relationship between enamel hypoplasia and height is expected if the stressors related to enamel hypoplasia presence influenced adult stature. This procedure was only performed on eastern and western Jomon people because the temporal groups from western Japan yielded considerably small sample sizes.

Stature was compared between the Jomon from eastern and western Japan for males and females separately

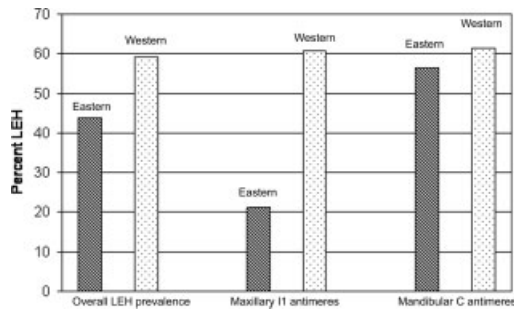


Fig. 2. Prevalence of enamel hypoplasia between eastern and western Jomon people.

TABLE 1. Enamel hypoplasia prevalence by individual

Location	N Individuals	% LEH	N Adults	% LEH	N Subadults	% LEH
Eastern	164	48.2	106	48.1	34	52.9
Western	122	64.8	90	64.4	22	68.2

TABLE 2. Confidence intervals for overall enamel hypoplasia prevalence between eastern and western Jomon

Group	% LEH	N Teeth	95% CI
Eastern Jomon	36.8	559	0.328–0.409
Western Jomon	56.7	495	0.530–0.611

using a pooled *t*-test with one tail of distribution. Use of a pooled *t*-statistic assumes that the data are univariate normal and have equal variances (Gotelli and Ellison, 2004). A folded *F*-statistic was produced to test equality of variances; data were also tested for univariate normality. These tests were also performed separately for males and females from the Ota and Tsukumo sites, both from western Japan. Ota is dated to the Middle Jomon period (5000 to 4000 BP), while the Tsukumo site is dated to the Late/Final Jomon period (4000 to 2300 BP). All statistical tests were performed using the SAS 9.1 computer program.

RESULTS

Geographic distributions of enamel hypoplasia prevalence are reported in Figure 2 and Tables 1 and 2. Antimeric maxillary incisor enamel hypoplasia prevalence ($G = 11.8$; $P \leq 0.001$) and overall ($G = 7.8$; $P \leq 0.01$) as well as adult ($G = 7.8$; $P \leq 0.01$) based individual enamel hypoplasia frequencies were statistically significantly more prevalent in the western compared to eastern Jomon (Fig. 2; Table 1). The 95% confidence intervals for antimeric incisor and overall enamel hypoplasia frequencies do not overlap between eastern and western Jomon indicating a significant difference (Table 2). No statistically significant difference in enamel hypoplasia frequency was observed between eastern and western Jomon mandibular canines (Fig. 2; Table 2). This lack of difference is likely attributable to a sampling bias, where Jomon mandibular canines were extracted in association with achieved identities (Temple and Sciulli, 2005) or differences in age-of-stress experienced by the two groups.

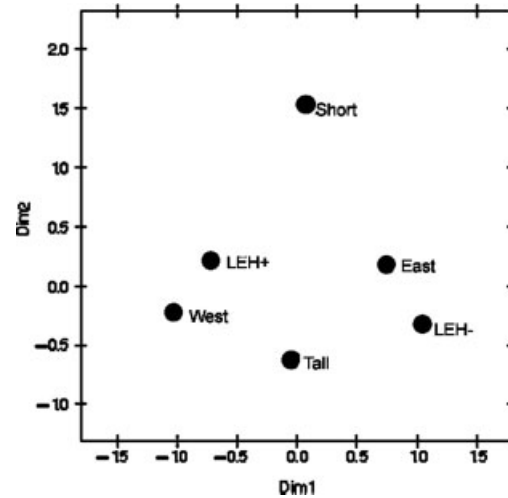


Fig. 3. Correspondence analysis of individual height class, enamel hypoplasia presence/absence, and geographic location.

TABLE 3. Geographic variation in Jomon stature^a

Group	Mean stature ^b	N	$P \leq (t)$
Eastern Jomon males	157.5	50	
Western Jomon males	158.9	27	0.389 (–0.087)
Eastern Jomon females	149.0	45	
Western Jomon females	150.2	14	0.092 (–1.71)

^aStature was estimated using separate equations for males and females.

^bStature is reported in centimeters.

Figure 3 shows the results of multiple correspondence analysis performed on stature class (tall or short), enamel hypoplasia presence or absence, and geographic location (eastern or western). Figure 3 explains 85.9% of the total variation associated with these variables. Dimension one accounts for 50.5% of this variation, while dimension two explains 35.4%. The χ^2 value produced for these relationships is 162.07 ($df = 25$; $P \leq 0.001$). A relationship between eastern Jomon people and enamel hypoplasia absence are observed in the upper quadrant of dimension one and lower quadrant of dimension two (Fig. 3). An association between western Jomon people and enamel hypoplasia presence is observed in the lower quadrants of both dimensions one and two (Fig. 3). Short and tall statures are, however, found toward the center of dimension one and not in association with any other variables (Fig. 3). These results indicate that enamel hypoplasia presence or absence is not related to adult stature.

Stature distributions for the Jomon samples were univariate normal. Geographic means in stature for Jomon males and females are listed in Table 3. Folded *F* statistics produced to test the variance in stature among males ($F = 1.77$; $P \leq 0.120$) and females ($F = 1.27$; $P \leq 0.658$) from eastern and western Japan were not significant. Pooled *t*-statistics were employed to explain if the mean statures reported for these groups were significantly different. No differences were observed in mean stature between Jomon males ($t = -0.87$; $P \leq 0.389$) and females ($t = -1.71$; $P \leq 0.091$) from eastern and western Japan.

A power calculation was performed to explain the probability of committing a Type II error in failing to reject the null hypothesis that height between eastern and western

TABLE 4. Temporal variation in stature^a

Group	Mean Stature ^b	N	P ≤ (t)
Middle Jomon males	160.8	11	
Late/Final Jomon males	156.3	16	0.0008 (−3.84)
Middle Jomon females	151.99	5	
Late/Final Jomon females	149.24	11	0.0088 (−3.04)

^aStature was estimated using separate equations for males and females.

^bStature is reported in centimeters.

Jomon people was not significantly different. This statistic (i.e., ϕ) was calculated using the equation reported in Zarr (1999: 136–137). Probabilities for committing a Type II error in rejecting the null hypothesis regarding height differences between Jomon males ($\phi = 3.17$; $P \leq 0.99$) and females ($\phi = 0.09$; $P \leq 0.43$) from eastern and western Japan were not significant.

Temporal means for Jomon stature are listed in Table 4. Folded F statistics produced to test the variance in stature among males ($F = 1.93$; $P \leq 0.298$) and females ($F = 1.95$; $P \leq 0.358$) were not statistically significant. Pooled t -statistics were used to test the hypothesis that there were significant differences in stature between Jomon people from different time periods. Results from the pooled t -statistic indicate significantly greater stature among Middle compared to Late to Final Jomon period males ($t = -3.84$; $P \leq 0.008$) and females ($t = -3.04$; $P \leq 0.0088$) (Table 4).

DISCUSSION

Geographic variation in stature

Statistically significant differences in stature between Jomon people from eastern and western Japan and individual relationships between enamel hypoplasia and stature suggest were not observed. This suggests that variation in childhood stress as expressed through enamel hypoplasia prevalence did not alter adult height. Similar observations are reported in the prehistoric Georgia Bight region, where precontact preagricultural groups had significantly greater frequencies of enamel hypoplasia than precontact agriculturalists, but did not differ in stature (Larsen et al., 2002). Enamel hypoplasia and porotic hyperostosis presence was associated with growth stunted subadults from prehistoric Illinois; adult stature is not, however, reduced in groups with greater prevalence of enamel hypoplasia and porotic hyperostosis (Cook, 1984). Enamel hypoplasia presence was related to reduced stature in some but not all samples of living school children from India (Lukacs et al., 2001). These trends are common in physical anthropology: Cumulative stress experiences of a population as indicated by enamel hypoplasia frequency are not associated with stature variation (Boldsen, 1998; Floyd and Littleton, 2006; Lukacs and Pals, 1993). It is likely that variation in stature is associated with more severe exposure to systemic stress, not necessarily prevalence of teeth with enamel defects (Lukacs et al., 2001).

Here, “severity” refers to stress experienced over an extended duration because stature reduction is associated with chronic systemic disruption (Bogin, 1998; Eveleth and Tanner, 1991). Australian Aborigines with repeated evidence of systemic stress experienced at early ages were less likely to achieve phenotypically normal stature than those who experienced singular stress episodes at later ages (Floyd and Littleton, 2006). Simple enamel hypoplasia prevalence does not reflect this information (Hillson,

1996; Hillson and Bond, 1997). Several possibilities for the lack of stature variation between groups with different enamel hypoplasia frequencies must, therefore, be considered in the absence of data that reveals stress duration/severity.

Canalization of stature and equal severity in stress experiences between the eastern and western Jomon encompass two important possibilities regarding the lack of variation in height between these groups. Canalization refers to the concept that the development of physical traits become more difficult for external stimuli to disturb as an organism matures (Waddington, 1957). Stature heritability among the modern people of Japan ranges from ~ 0.72 in monozygotic twins at birth to 0.94 in monozygotic twins at 11 years of age (Ooki and Asaka, 1993). These values represent the upper range of heritability reported among modern people. Greater exposure to stress is, however, associated with increased environmental influences on stature, particularly stressors of a chronic nature (Silventoinen, 2003).

One way individuals with stunted development achieve normal stature is through catch up growth. Catch up growth is an increase in growth duration or velocity following a period of developmental perturbation (Stinson, 2000). Catch up growth allows the human phenotype to recover from periods of developmental perturbation by reestablishing the original growth trajectory. Catch up growth is reported among contemporary populations (Adair, 1999; Cameron, 2002; Hermanussen, 1997; Stinson, 2000). It is, however, noted that catch up growth is rare when individuals are not removed from the environment initially associated with developmental disruption (Stinson, 2000). This possibility is supported by studies of enslaved Africans from South Carolina. Growth stopped in men at 21 years of age and 19 years of age in women. Individuals who were in the first or second percentiles for stature before 11 years of age achieved final heights in the 25th to 30th percentiles as adults (Steckel, 1989). Rations of meat were provided to enslaved Africans after 12 years of age as compensation for work and likely represented an improved diet compared to younger children (Steckel, 1987).

Changes in the nutritional environment of prehistoric Jomon foragers after a certain age are possible to test on human skeletal remains. For example, isotopic ratios derived from human skeletal remains across age categories explain the types of foods consumed at specific ages. Given the fact that social identity in Jomon society was based on age-related achievements (Habu, 2004; Mizoguchi, 2002; Temple and Sciuilli, 2005), it is possible that foods with greater nutritional quality were introduced into the Jomon diet at certain ages. Further research into this possibility using stable isotope analysis of Jomon diet and age is necessary to more adequately address this question.

A second possibility for the lack of variation in stature between eastern and western Jomon people is also associated with the canalization of growth, age of stress experiences, and catch-up growth. Patterns of growth stunting associated with stress during infancy were rectified by catch up growth in South Africa: Individuals who experienced developmental disturbances between 0 and 2 years of age underwent catch up growth between 4 and 5 years of age (Cameron et al., 1998). It is, however, important to note that growth also has significant plasticity during

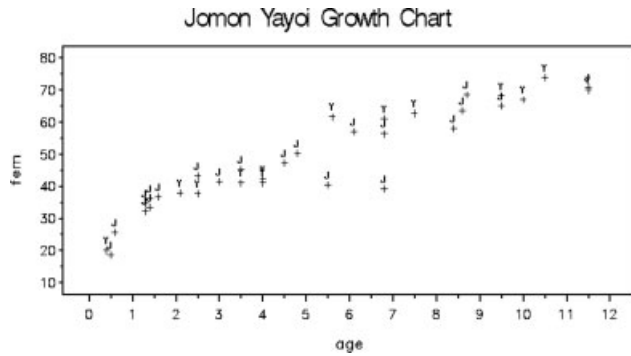


Fig. 4. Percentages of achieved femoral growth by age between Jomon (J) and Yayoi (Y) subadults.

adolescent years and catch up growth among stunted adolescents is reported (Cameron, 2002; Hermanussen, 1997). Thus, perturbations of height occurring early in development are possible to correct through either of these growth spurts.

Jomon foragers have reduced percentages of achieved femoral growth compared to Yayoi agriculturalists, particularly between 5 and 8 years of age (Fig. 4) (Temple, 2007b). In addition, enamel hypoplasia frequencies were recorded from incisor and canine crowns. Incisor and canine crowns develop from ~0.6 to 11 years of age (Smith, 1991). Since a significant amount of the stress variation indicated by enamel hypoplasia prevalence between the eastern and western Jomon and femoral growth disruption is associated with younger age groups, it is possible that the extent to which systemic stress disrupted achieved adult height is minimal because of the corrective nature of the mid-childhood and adolescent growth spurts (Cameron, 2002).

Catch up growth is not possible to observe in skeletal collections because the growth curve after 12 years of age is not explained by the same function as those before 12 years and it is an individual phenomenon only observable in longitudinal studies (Lovejoy et al., 1990). Furthermore, subadult sample sizes for the eastern and western Jomon are not large enough to compare linear growth patterns. Catch up growth as a possible contributor to the lack of variation in stature between the Jomon from eastern and western Japan, therefore, remains a distinct, yet untestable, possibility.

Another possible reason for the observed similarity in stature between Jomon people from eastern and western Japan is the saltatory nature of human growth. Longitudinal studies of American "Caucasians" indicate that a majority (90–95%) of time during infancy is not associated with changes in body length (Lampl et al., 1992). Instead, growth in body length occurs in quick periodic spurts (Lampl, 2002). Approximate numbers of days for stress duration extrapolated from microscopic analysis of enamel hypoplasia in Point Hope Inupiaq varied between 58 and 73 days, while those observed in Neandertals varied between 29 and 37 days (Guatelli-Steinberg, 2005). Investigations of enamel microstructure reveal similar durations of stress for the people from Christ-Church, Spitalfields (King et al., 2005). Given the durations of stress associated with enamel hypoplasia, the possibility that stress experiences among the Jomon from western Japan happened during periods of normal growth stasis is unlikely.

A final explanation for the lack of variation in height between the eastern and western Jomon is selective mor-

tality: Individuals who underwent stress episodes severe enough to impact terminal height died before reaching adulthood. Increased stature is observed in populations with greater stress loads as indicated by enamel hypoplasia prevalence in prehistoric Ohio (Sciulli and Oberly, 2002). Models of survivors and non-survivors from St. Thomas' Anglican cemetery (mid 19th CE) found that individuals with reduced stature and greater stress loads were associated with younger age-at-death (Saunders and Hoppa, 1993). Mortality-based stature biases are addressed by this study through the temporal comparison of height between the Ota and Tsukumo Jomon people. These sites are separated by ~1500 years (Ota: 5000 to 4000 BP; Tsukumo: 3500 to 2500 BP). Greater stature is observed among the Ota compared to Tsukumo Jomon people indicating a negative relationship between time and height. If a mortality bias was associated with the lack of stature variation observed between the eastern and western Jomon samples, increases in height over time would be observed.

Temporal variation in stature

Significant differences in stature between the Ota and Tsukumo Jomon highlight another important finding of this study: Stature decreases in western Japan between the Middle and Late to Final Jomon period. This result is antithetical to previous studies that suggest an even distribution of stress between the two groups based on enamel hypoplasia prevalence (Temple, 2007a). Declines in stature among genetically homogenous people are associated with chronic bouts of systemic stress (Bogin, 1998; Eveleth and Tanner, 1991; Silventoinen, 2003). Population expansions are observed in western Japan during the Late to Final Jomon period (Koyama, 1978). Environments with greater population density often experience increases in infectious disease prevalence because of greater contact with and exposure to pathogens (Armstrong, 1990). Greater numbers of human hosts, for example, allow pathogenic agents to survive for greater periods of time continually infecting people (Cockburn, 1971). Many pathogens also infect people from contact with or exposure to fecal material; here, people are inadvertently exposed to human or animal feces and transmit the microorganisms found on this waste product to the oral cavity (Sattenspiel, 2000). Coastal people have a particularly elevated risk for these diseases because of decreased access to fresh water and the use of bathing facilities as latrines (Walker, 2006). Increased population density combined with coastal habitation sites likely placed Late to Final Jomon people at a greater risk for chronic infection.

Hunter-gatherers who underwent increases in social complexity or population density experienced increased levels of systemic stress (Stodder, 1997; Walker and Lambert, 1989). Coastal foragers from the Channel Islands of California, for example, experienced concomitant reductions in stature and increases in periostitis during periods of population growth (Lambert, 1993). Similarly, evidence for disruption in femoral growth is associated with an elevated prevalence of chronic infectious disease in prehistoric people from Ohio (Lovejoy et al., 1990). Late to Final Jomon period foragers had significantly greater frequencies of periostitis than those from the Middle Jomon (Temple, 2007b). These findings suggest that declines in

stature during the Late to Final Jomon period in western Japan likely reflect increased exposure to chronic infection.

Increased usage of plant processing tools and dental caries prevalence suggest a transition to an economic system with a greater reliance on plants during the Late to Final Jomon period (Imamura, 1996; Temple, 2007a). Plant-based diets are often associated with elevated levels of systemic stress because humans inefficiently synthesize the proteins, vitamins, and minerals contained in plant foods (Murphy and Allen, 2003). Nutritional status influences patterns of growth and development as well as immune system responses to invading pathogens (Shell-Duncan, 1997). Infectious disease and growth are linked because immunostimulation diverts essential nutrients that activate various cytokines, particularly IL-1, IL-6, and TNF- α , during acute-phase responses to invading pathogens (Solomons et al., 1993). In Kenya, for example, growth disruption is related to a combination of contact with infectious bacteria such as *Escherichia coli* and under-consumption of protein, vitamin-A, calcium, and zinc (Berti et al., 2000). It is further noted that greater dental caries prevalence also predisposes the human body to infectious disease susceptibility (Calcagno and Gibson, 1991). This indicates that the increased prevalence of infectious disease in later Jomon groups may reflect increased pathogen exposure combined with diminished immune function in response to dietary stress.

Pervasive plasticity and Jomon stature

Plasticity in growth is an integral component of human biological adjustment to environmentally and behaviorally induced stressors. Growth perturbations compensate for disruptions in biological homeostasis: growth stunting allows the developing organism to focus nutritional content to essential biological functions during periods of stress (Bogin, 1998). This biological function is of primary importance during perinatal through childhood development when energetic demands are considerably greater in association with brain growth (Leonard and Robertson, 1992). One cost of this biological adjustment is reflected in greater mortality rates among individuals who fail to achieve optimal body size (Bogin, 1995; Saunders and Hoppa, 1993). Growth stunting in childhood related to stress also has negative impacts on adult maximal oxygen consumption, and thus, physical work capacity (Spurr, 1984). An important benefit of growth stunting to acknowledge is survival if organisms overcome stress exposure (Bogin, 1995). Growth stunting is, therefore, an evolutionary trade-off in circumstances where individuals with reduced height associated with systemic stress survive the initial disease state.

Despite purported benefits, reduced stature indicates that the cumulative stress experiences of a population is greater than groups who do not show evidence of growth stunting (Bogin, 1995; Eveleth and Tanner, 1991; Goodman, 1994; Saunders, 2000; Steckel, 1994, 1995; Stinson, 2000). This suggests that reductions in stature among the Late to Final Jomon people, while evidence of biological plasticity, are associated with greater exposure to systemic stress. The lack of variation in stature between the Jomon people from eastern and western Japan, despite varying enamel hypoplasia prevalence, provide evidence for the human ability to correct or stave off the influence of systemic stressors on physical characteristics.

CONCLUSION

Greater rates of systemic stress among the western compared to eastern Jomon people are indicated by enamel hypoplasia frequency; yet, these two groups achieved similar adult stature. Canalization of growth in length and/or catch up growth is the most likely reasons for the lack of stature variation between the eastern and western Jomon. It is possible that systemic stress experiences between the eastern and western Jomon differed in frequency, not severity. Another reason for the lack of stature differences between the eastern and western Jomon includes the possibility that growth in length was disrupted at early ages but rectified by catch up growth.

Differences in stature are reported between the Middle and Late to Final Jomon period in western Japan yet no difference in enamel hypoplasia prevalence is observed between these two groups. Increases in population density and sedentism are observed during the Late to Final Jomon period in western Japan along with rises in chronic infectious disease prevalence. Greater evidence for plant food consumption is also reported during this time. It is likely that the reduction of stature during the Late to Final Jomon period is associated with a greater prevalence of chronic infectious disease. Increased infectious disease prevalence likely reflects a combination of diminished immune function in association with dietary stressors and increased contact with infectious pathogens as a consequence of population aggregation. Taken together, these studies illustrate that enamel hypoplasia prevalence does not adequately predict the impact of stress on human phenotypic variation.

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LITERATURE CITED

- Adair L. 1999. Filipino children exhibit catch-up growth from age 2 to 12 years. *J Nutr* 129:1140–1148.
- Akazawa T. 1981. Maritime adaptation of hunter-gatherers and their transition to agriculture in Japan. In: Thomas DH, Koyama S, editors. *Affluent foragers: Pacific coasts east and west*. Osaka: National Museum of Ethnology. p 213–258. *Senri Ethnological Studies* 9.
- Akazawa T. 1982. Cultural change in prehistoric Japan: Receptivity to rice agriculture in the Japanese archipelago. In: Wendorf F, Close AE, editors. *Advances in world archaeology*, Vol. 1. New York: Academic Press. p 151–211.
- Akazawa T. 1986. Regional variation in procurement systems of Jomon hunter-gatherers. In: Aikens CM, Akazawa T, editors. *Prehistoric hunter-gatherers in Japan: new research methods*. Tokyo: University Museum, University of Tokyo. p 73–89 27. *Bulletin* no. 27.

- Akazawa T. 1999. Regional variation in Jomon hunting-fishing-gathering societies. In: Omoto K, editor. *Interdisciplinary perspectives on the origins of the Japanese*. Kyoto: International Research Center for Japanese Studies. p 223–231.
- Akazawa T, Maeyama K. 1986. Discriminant function analysis of later Jomon sites. In: Pearson RJ, Barnes GL, Hutterer KL, editors. *Windows on the Japanese past: studies in archaeology and prehistory*. Ann Arbor: Center for Japanese Studies, University of Michigan. p 279–292.
- Armstrong GJ. 1990. Health and disease in prehistoric populations in transition. In: Swedlund AC, Armstrong GJ, editors. *Disease in populations in transition*. New York: Bergin and Garvey. p 127–144.
- Berti PR, Leonard WR, Berti WJ. 2000. Stunting in an Andean community: prevalence and etiology. *Am J Hum Biol* 10:229–240.
- Bogin B. 1998. *Patterns of human growth*. Cambridge: Cambridge University Press.
- Bogin B. 1995. Plasticity in the growth of Mayan refugee children living in the United States. In: Mascie-Taylor CGN, Bogin B, editors. *Human variability and plasticity*. Cambridge: Cambridge University Press. p 46–74.
- Boldsen JL. 1998. Body proportions in a medieval village population: Effects of early childhood episodes of ill health. *Ann Hum Biol* 25:309–317.
- Calcagno JM, Gibson KR. 1991. Selective compromise: Evolutionary trends and mechanisms in hominid tooth size. In: Kelley MA, Larsen CS, editors. *Advances in dental anthropology*. New York: Wiley-Liss. p 59–76.
- Cameron N. 2002. Human growth curve, canalization, and catch-up growth. In: Cameron N, editor. *Human growth and development*. Amsterdam: Academic Press. p 1–20.
- Cameron N, De Wet T, Ellison GT, Bogin B. 1998. Growth in height and weight of South African urban infants from birth to five years: The Birth to Ten Study. *Am J Hum Biol* 10:495–504.
- Chisholm B, Koike H. 1999. Reconstructing prehistoric Japanese diet using stable isotopic analysis. In: Omoto K, editor. *Interdisciplinary perspectives on the origins of the Japanese*. Kyoto: International Research Center for Japanese Studies. p 69–73.
- Cockburn TA. 1971. Infectious diseases in ancient populations. *Curr Anthropol* 12:45–62.
- Cohen MN, Armstrong GJ. 1984. *Paleopathology at the origins of agriculture*. Orlando: Academic Press.
- Cook DC. 1984. Subsistence and health in the lower Illinois Valley. In: Cohen MN, Armstrong GJ, editors. *Paleopathology at the origins of agriculture*. Orlando: Academic Press. p 235–269.
- Crooks DL. 1999. Child growth and nutritional status in a high-poverty community in eastern Kentucky. *Am J Phys Anthropol* 109:129–142.
- Dittmar M. 1998. Secular changes in the stature and weight of Amerindian school children and adults in the Chilean Andes, 1972–1987. *Am J Hum Biol* 10:607–617.
- Eveleth PB, Tanner JM. 1991. *Worldwide variation in human growth*. Cambridge: Cambridge University Press.
- Floyd B, Littleton J. 2006. Linear enamel hypoplasia and growth in an Australian Aboriginal community: not so small, but not so healthy either. *Ann Hum Biol* 33:424–443.
- Fuji A. 1960. On the relation of limb bone length to stature. *Bull Sch Phys Educat (Juntendo University)* 3:49–61 (in Japanese).
- Goodman AH. 1994. Cartesian reductionism and vulgar adaptationism: Issues in the interpretation of nutritional status in prehistory. In: Sobolik K, editor. *Paleonutrition: the diet and health of prehistoric Americans*. Carbondale: Center for Archaeological Investigations, Southern Illinois University. p 163–177. Occasional Papers 22.
- Goodman AH, Rose JC. 1990. Assessment of physiological perturbations from dental enamel hypoplasias and associated histological structures. *Yearbk Phys Anthropol* 33:59–110.
- Goodman AH, Martinez C, Chavez A. 1991. Nutritional supplementation and the development of linear enamel hypoplasias in children from Tezontepan, Mexico. *Am J Clin Nutr* 53:773–787.
- Gotelli NJ, Ellison AM. 2004. *A primer of ecological statistics*. Sunderland: Sinauer & Associates.
- Greenacre MJ. 1981. Practical correspondence analysis. In: Barnett V, editor. *Interpreting multivariate data*. London: Wiley, UK. p 119–146.
- Guatelli-Steinberg D. 2001. What can developmental defects reveal about physiological stress in non-human primates. *Evol Anthropol* 10:138–151.
- Guatelli-Steinberg D. 2003. Macroscopic and microscopic analyses of linear enamel hypoplasia in Plio-Pleistocene South African hominins with respect to aspects of enamel development and morphology. *Am J Phys Anthropol* 120:309–322.
- Guatelli-Steinberg D. 2005. Using perikymata to estimate the growth disruption in fossil hominins. *Am J Phys Anthropol (Supp)* 40:109–110.
- Guatelli-Steinberg D, Skinner MF. 2000. Prevalence and etiology of linear enamel hypoplasia in monkeys and apes from Africa. *Folia Primatol* 71:115–132.
- Habu J. 2004. *Ancient Jomon of Japan*. Cambridge: Cambridge University Press.
- Hammer MF, Karafet TM, Park H, Harihar S, Stoneking M, Horai S. 2006. Dual origins of the Japanese: Common ground for hunter-gatherer and farmer Y chromosomes. *J Hum Genet* 51:47–58.
- Hanihara K. 1991. Dual structure model for the population history of the Japanese. *Jpn Rev* 2:1–33.
- Hanihara T, Ishida H. 2005. Metric variation of major human populations. *Am J Phys Anthropol* 128:287–298.
- Hermanussen M. 1997. Plasticity of adolescent growth in boys. *Am J Hum Biol* 9:469–480.
- Hillson SW. 1996. *Dental anthropology*. Cambridge: Cambridge University Press.
- Hillson SW, Bond S. 1997. The relationship of enamel hypoplasia to tooth crown growth: a discussion. *Am J Phys Anthropol* 104:89–103.
- Holliday TW, Ruff CB. 1997. Ecogeographical patterning and stature prediction in fossil hominids. Comment on Feltesman and Fountain. *Am J Phys Anthropol* 103:137–140.
- Imamura K. 1996. Prehistoric Japan: new perspectives on Insular East Asia. Honolulu: University of Hawaii Press.
- Kato K, Ogata T. 1989. Main long bones of limbs of the Jomon people: proportions in their lengths. *Okajimas Folia Anatomica Japonica* 66:13–22.
- King T, Humphrey LT, Hillson S. 2005. Linear enamel hypoplasias as indicators of systemic physiological stress: evidence from two known age-at-death and sex populations from postmedieval London. *Am J Phys Anthropol* 128:547–559.
- Kondo O. 1994. The skulls of the Ubayama Shell-mounds II. An analysis of intra- and inter-regional variation of the Jomon population. *Anthropol Sci* 102:59–74.
- Kouchi M. 1987. Which equations should be used to estimate the stature of ancient Japanese populations? *Bull Nat Sci Mus Tokyo*. 13:21–39.
- Koyama S. 1978. Jomon subsistence and population. *Senri Ethnol Stud* 2:1–65.
- Krogman WM, Iscan MY. 1986. *The human skeleton in forensic medicine*. Springfield: C.C. Thomas.
- Lambert PM. 1993. Health in prehistoric populations of the Santa Barbara Channel Islands. *Am Antiquity* 58:509–522.
- Lampl M. 2002. Saltation and stasis. In: Cameron N, editor. *Human growth and development*. London: Academic Press. p 251–270.
- Lampl M, Veldhuis JD, Johnson ML. 1992. Saltation and stasis: a model of human growth. *Science* 258:801–803.
- Larsen CS. 1987. Bioarchaeological interpretations of subsistence economy and behavior from human skeletal remains. In: Schiffer MB, editor. *Advances in archaeological method and theory*. New York: Academic Press. p 339–445.
- Larsen CS. 1995. Biological changes in human populations with agriculture. *Annu Rev Anthropol* 24:185–213.
- Larsen CS. 1997. *Bioarchaeology: interpreting behavior from the human skeleton*. Cambridge: Cambridge University Press.
- Larsen CS, Crosby AW, Griffin MC, Hutchinson DL, Ruff CB, Russell KF, Schoeninger MJ, Sering LE, Simpson SW, Takas JL, Teaford MF. 2002. A biohistory of health and behavior in the Georgia Bight. I. The agricultural transition and the impact of European contact. In: Steckel RH, Rose JC, editors. *The backbone of history: health and nutrition in the Western Hemisphere*. Cambridge: Cambridge University Press. p 406–439.
- Leonard WR, Robertson ML. 1992. Nutritional requirements and human evolution: A bioenergetics model. *Am J Hum Biol* 4:179–195.
- Loesch DZ, Stokes K, Huggins RM. 2000. Secular trend in body height and weight of Australian children and adolescents. *Am J Phys Anthropol* 111:545–556.
- Lovejoy CO, Russell KF, Harrison ML. 1990. Long bone growth velocity in the Libben population. *Am J Hum Biol* 2:533–541.
- Lukacs JR. 1999. Enamel hypoplasia in deciduous teeth of great apes: do differences in defect prevalence imply differential levels of physiological stress? *Am J Phys Anthropol* 110:351–363.
- Lukacs JR, Pals JN. 1993. Mesolithic subsistence in northern India: inferences from dental pathology and odontology. *Curr Anthropol* 34:745–765.
- Lukacs JR, Walimbe SR, Floyd B. 2001. Epidemiology of enamel hypoplasia in deciduous teeth: explaining variation in prevalence in western India. *Am J Hum Biol* 13:788–807.
- Matsumura H. 1989. Geographic variation of dental measurements in the Jomon population. *J Anthropol Soc Nippon* 97:493–512.
- Matsumura H. 2007. Non-metric dental trait variation among local sites and regional groups of the Neolithic Jomon period, Japan. *Anthropol Sci* 115:25–33.
- Matsumura H, Hudson MJ. 2005. Dental perspectives on the population history of southeast Asia. *Am J Phys Anthropol* 127:182–209.
- Minagawa M. 2001. Dietary patterns of prehistoric Japanese populations inferred from carbon and nitrogen isotopes in bone protein. *Bull Nat Mus Jap Prehist* 86:333–357.

- Minagawa M, Akazawa T. 1992. Dietary patterns among Jomon hunter-gatherers: Stable nitrogen and isotope analyses of human bones. In: Aikens CM, Nai Rhee S, editors. Pacific Northeast Asia in prehistory: hunter-fisher-gatherers, farmers, and sociopolitical elites. Pullman: Washington State University Press. p 69–73.
- Mizoguchi K. 2002. Archaeological history of Japan: 30,000 BCE to AD 700. Philadelphia: University of Pennsylvania Press.
- Murphy SP, Allen LH. 2003. Nutritional importance of animal source foods. *J Nutr* 133:3932S–3940S.
- Okada A. 1998. Maritime adaptations in Hokkaido. *Arctic Anthropol* 35:340–349.
- Okada H. 1998. Maritime adaptations in northern Japan. *Arctic Anthropol* 35:335–339.
- Omoto K, Saitou N. 1997. Genetic origins of the Japanese: A partial support for the dual structure hypothesis. *Am J Phys Anthropol* 102:437–446.
- Ooki S, Asaka A. 1993. Physical growth of Japanese twins. *Acta Genet Med Gemellol* 42:275–287.
- Pearson K. 1899. Mathematical contributions to the theory of evolution V. On the reconstruction of stature of the prehistoric races. *Philos Trans R Soc Lond (A)* 192:169–244.
- Pearson R. 2006. Jomon hot spot: Increasing sedentism in south-western Japan in the Incipient Jomon (14,000–9250 cal. BC) and Earliest Jomon (9250–5200 cal. BP) periods. *World Archaeol* 38:239–258.
- Saeki F. 2006. Estimation of stature and lower limb proportion of the prehistoric Jomon based on an anatomical method. *Anthropol Sci (J-Ser)* 114:17–33 (in Japanese with English summary).
- Sato Y. 1999. Origin and dissemination of cultivated rice in Eastern Asia. In: Omeoto K, editor. Interdisciplinary perspectives on the origins of the Japanese. Kyoto: International Research Center for Japanese Studies. p 143–153.
- Sattenspiel S. 2000. Epidemiology of human disease. In: Stinson S, Bogin B, Huss-Ashmore R, O'Rourke D, editors. Human biology: an evolutionary and biocultural perspective. New York: Wiley-Liss. p 225–272.
- Saunders SR. 2000. Subadult skeletons and growth-related studies. In: Katzenberg MA, Saunders SR, editors. Biological anthropology of the human skeleton. New York: Wiley-Liss. p 135–162.
- Saunders SR, Hoppa RD. 1993. Growth deficit in survivors and non-survivors: Biological mortality bias in subadult skeletal samples. *Yearbk Phys Anthropol* 36:127–152.
- Sciulli PW, Gieson MJ. 1993. An update on stature estimation in Prehistoric Native Americans of Ohio. *Am J Phys Anthropol* 92:395–399.
- Sciulli PW, Oberly J. 2002. Native Americans in Eastern North America: The southern Great Lakes and Upper Ohio Valley. In: Steckel RH, Rose JC, editors. The backbone of history: health and nutrition in the Western Hemisphere. Cambridge: Cambridge University Press. p 440–480.
- Sciulli PW, Schneider KN, Mahaney MC. 1990. Stature estimation in prehistoric Native Americans of Ohio. *Am J Phys Anthropol* 83:275–280.
- Shell-Duncan B. 1997. Evaluation of infection and nutritional status as determinants of cellular immunosuppression. *Am J Hum Biol* 9:381–390.
- Silventoinen K. 2003. Determinants of variation in adult body height. *J Biosoc Sci* 35:263–285.
- Skinner MF, Newell EA. 2003. Localized hypoplasia of the primary canine in bonobos, orangutans, and gibbons. *Am J Phys Anthropol* 120: 61–72.
- Skinner MF, Dupras TL, Moya-Sola S. 1995. Periodicity of enamel hypoplasia among Miocene *Dryopithecus* from Spain. *J Paleopathol Monogr Ser* 7:197–222.
- Smith BH. 1991. Standards of tooth formation and dental age assessment. In: Kelley MA, Larsen CS, editors. Advances in dental anthropology. New York: Wiley-Liss. p 143–168.
- Solomons NW, Mazariegos M, Brown KH, Klasing K. 1993. The underprivileged, developing country child: Environmental contamination and growth failure revisited. *Nutr Rev* 51:327–332.
- Spurr GB. 1984. Nutritional status and physical work capacity. *Yearbk Phys Anthropol* 26:1–35.
- Steckel RH. 1987. Growth depression and recovery: the remarkable case of American slaves. *Ann Hum Biol* 14:111–132.
- Steckel RH. 1989. The remarkable catch up growth of American slaves. *Growth Genetic Horm* 5:4–6.
- Steckel RH. 1994. Heights and health in the United States, 1710–1950. In: Komlos J, editor. Stature, living standards and economic development: essays in anthropometric history. Chicago: University of Chicago Press. p 153–170.
- Steckel RH. 1995. Stature and the standard of living. *J Econ Lit* 33:1903–1940.
- Stinson S. 2000. Growth variation: biological and cultural factors. In: Stinson S, Bogin B, Huss-Ashmore R, O'Rourke D, editors. Human biology: an evolutionary and biocultural perspective. New York: Wiley-Liss. p 425–464.
- Stodder ALW. 1997. Subadult stress, morbidity, and longevity in Latte Period populations on Guam, Mariana Islands. *Am J Phys Anthropol* 104:363–380.
- Temple DH. 2007a. Stress and dietary variation among prehistoric Jomon foragers from Japan. *Am J Phys Anthropol* 133:1035–1046.
- Temple DH. 2007b. Human biological variation during the agricultural transition in prehistoric Japan. Ph.D. dissertation, Department of Anthropology, The Ohio State University.
- Temple DH, Sciulli PW. 2005. Biodistance analysis of postmarital residence and social structure in Jomon period Japan: migration patterns and status determinants in a dynamic environment. *Am J Phys Anthropol Suppl* 40:205.
- Tsukada M. 1986. Vegetation in prehistoric Japan: the last 20,000 years. In: Pearson RJ, Barnes GL, Hutterer KL, editors. Windows on the Japanese past: studies in archaeology and prehistory. Ann Arbor: Center for Japanese Studies, University of Michigan. p 11–56.
- Turner CG. 1987. Late Pleistocene and Holocene population history of East Asia based on dental variation. *Am J Phys Anthropol* 73:305–321.
- Waddington CH. 1957. The strategy of genes. London: Allen and Unwin.
- Walker PL. 2006. A paleopathological perspective on coastal adaptations. *Am J Phys Anthropol (Supp)* 41:183.
- Walker PL, Lambert P. 1989. Skeletal evidence for stress during a period of culture change in prehistoric California. *J Paleopathol Mong Ser* 1: 207–212.
- Watanabe H. 1986. Community habitation and food gathering in prehistoric Japan: an ethnographic interpretation of the archaeological evidence. In: Pearson RJ, Barnes GL, Hutterer K, editors. Windows on the Japanese past: studies in archaeology and prehistory. Ann Arbor: Center for Japanese Studies, University of Michigan. pp 229–254.
- Yamaguchi B. 1989. Limb proportions in human skeletal remains of the Jomon period. *Bull Nat Sci Mus (Ser D)* 15:41–48.
- Zarr JH. 1999. Biostatistical Analysis. Englewood Cliffs: Prentice Hall.
- Zhou L, Corruccini RS. 1998. Enamel hypoplasia related to famine stress in living Chinese. *Am J Hum Biol* 10:723–733.