Variation in cranial shape in medieval Japanese from Kamakura City

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Abstract Many medieval skulls from Kamakura, Japan were found to be characterized by dolichocephaly, although these medieval people are most likely to be the ancestors of the modern Japanese. The specificity in the metric cranial traits has been repeatedly demonstrated by archaeological findings from other medieval sites in Kamakura City. It is not known whether these specific features were shared by the descendants of the medieval Kamakura people due to a complete lack of the skeletal remains belonging to the later half of the medieval period. Fortunately, we obtained access to a new series of skeletal remains of the later half of the medieval period from the Nozoji-ato site, and examined the variation in cranio metric traits during the medieval period. The results revealed that the Nozoji-ato series were more brachycephalic than the populations within medieval Kamakura City and demonstrated the presence of secular changes within the Japanese medieval period. New data from the Nozoji-ato series thus showed that the medieval people within Kamakura City exhibited wider intra-regional variations in cranial measurements than previously anticipated. It is concluded that this contrasts with the commonly accepted theory that medieval populations were homogeneous in terms of dolichocephaly.

Key words: medieval, Japan, variation, crania, brachycephalization

Introduction

The theory of the population history of Japan, a dual-structure model, assumes an initial occupation of the Japanese archipelago from the Upper Palaeolithic of Southeast Asia, giving rise to the Neolithic Jomon people, a second wave of migration from a Northeast Asian source in the Aeneolithic Yayoi period, and the mixture between them (Hanihara, 1991). Based on the incidence of non-metric cranial traits (Dodo and Ishida, 1990, 1992), as well as genetics (Shinoda, 2007), metric cranial traits (Nakahashi, 1993; Kawakubo, 2007; Kawakubo et al., 2009), and metric and non-metric dental traits (Matsumura, 1994), there is a clear distinction between the native Jomon and the immigrant Yayoi. The Yayoi were thus one of the lineal ancestors of the modern Japanese. The medieval period of Japan spanned nearly 400 years, from 1185 AD to 1573 AD, and was a turbulent period characterized by the rise of the warrior class to political power, and the establishment of military governments. Suzuki et al. (1956) conducted the first systematic study of medieval Japanese human skeletons from the burial site at Zaimokuza in Kamakura City, the center of a military government during the medieval period. Many skull measurements from these individuals evidenced dolichocephaly, chameprosopy (low and wide face), and prognathism, thought likely to be the result of environmental factors, including dietary conditions and the effects of medical care (Suzuki et al., 1956). These characteristics are noteworthy because the medieval Kamakura people are thought to be the most likely ancestors of modern Japanese, as mentioned above. The subsequent excavation of the Gokurakuji, Yuigahama Chusei Shudan Bochi (locations no. 372 and Seika-ichiba) and Yuigahama-minami sites neighboring the Zaimokuza site confirmed the presence of dolichocephaly, low and wide face, and prognathism (Nagaoka et al., 2006, 2013). However, it is not known whether these specific features were shared by the descendants of the medieval Kamakura people due to a complete lack of any skeletal remains belonging to the later half of the medieval period. Fortunately, we obtained access to a new series of skeletal remains from the Nozoji-ato site, and examined the variation in cranio metric traits during the medieval period. The results revealed that the Nozoji-ato series were more brachycephalic than the populations within medieval Kamakura City and demonstrated the presence of secular changes within the Japanese medieval period. New data from the Nozoji-ato series thus showed that the medieval people within Kamakura City exhibited wider intra-regional variations in cranial measurements than previously anticipated. It is concluded that this contrasts with the commonly accepted theory that medieval populations were homogeneous in terms of dolichocephaly.
ations and similarities in cranial measurements among the medieval populations, and finally to confirm whether the specific features were shared by the populations over a long term from the medieval period or when and how these features began to change.

**Materials and Methods**

The samples used in this study were the adult human remains from the Nozoji-ato site in Kamakura, Japan. The Nozoji-ato site is adjacent to the archaeological sites of Zaimokuza, Yuigahama Chusei Shudan Bochi (no. 372 and Seika-ichiba locations), Yuigahama-minami, and Gokuraku-ji (Figure 1). The Nozoji-ato was an old temple site of Nozoji, which was established in 1194, dedicated to the soul of a warrior, Yoshiaki Miura, and was destroyed by fire in 1872. It seems that the Miura and his descendants were buried in the temple, but there is no information on the relationship of the excavated human skeletons to the Miura family. The excavation of human remains was undertaken in 2006 by the Kamakura Board of Education. Most of the human skeletons were found in articulated positions, but dried clay adhering to the bones led to post-excavation cracking of fragile parts of bones before they were cleaned in our laboratory. The Nozoji-ato site has been dated to the chronological age between 1500 AD and 1600 AD based on the known sequence of coins and vessels: two individuals buried with Kaneitsuho coins definitely dated to 1636 AD or later, while most of the human remains (associated with Eiraku-tsuho coins and vessels) belonged to the medieval period (between 1500 AD and 1600 AD) (Tamagawa-bunkazai-kenkyusho, unpublished). The specimens used in this study all belonged to the chronological age between 1500 AD and 1600 AD, which is later than all other adjacent sites in Kamakura; the adjacent sites date to the earlier half of the medieval period (1200–1500 AD). The sample sex ratio of 4 males and 31 females indicated a sexual bias in the population, although the reasons underlying the bias remain unclear (Nagaoka et al., 2018). Since the sample size of Nozoji-ato is small due to poor preservation of the skeletal remain, the comparison among populations was conducted on well-preserved female crania alone.

Comparative samples for this study were the female human remains from the archaeological sites of Yuigahama Chusei Shudan Bochi (Seika-ichiba location) \( n = 7 \) individuals, Yuigahama-minami \( n = 43 \) individuals, Gokurakuji \( n = 23 \) individuals, Marunouchi \( n = 7 \) individuals, Kajibashi \( n = 5 \) individuals, Hitotsubashi \( n = 22 \) individuals, Ikenohata-shichikencho \( n = 35 \) individuals, and Shiokawa \( n = 17 \) individuals. Yuigahama Chusei Shudan Bochi (Seika-ichiba location), Yuigahama-minami, and Gokurakuji are medieval sites in Kamakura belonging to the earlier half of the medieval period (1200–1500 AD); Marunouchi and Kajibashi are medieval sites in Tokyo belonging to the later half of the medieval period (1500–1600 AD). The crania from Yuigahama Chusei Shudan Bochi (no. 372 location) from the earlier medieval period were not available in this study, apart from a photograph that compared the superior view of the crania between the present and precedent materials (Figure 2). Hitotsubashi, Ikenohata-
shichikencho, and Shiokawa are Edo period (1603–1867 AD) sites in Tokyo and Yamanashi, but the chronological age of Hitotsubashi is 1657–1683 AD, which is older than the two other Edo populations. The specimens from Yuigahama Chusei Shudan Bochi (Seika-ichiba location), Yuigahama-minami, Hitotsubashi, and Shiokawa are housed in the St. Marianna University School of Medicine (Kawasaki, Japan), and those from Gokurakuji, Marunouchi, Kajibashi, and Ikenohata-shichikencho are housed in the National Museum of Nature and Science (Tsukuba, Japan). Hereinafter, Yuigahama Chusei Shudan Bochi (Seika-ichiba location) and Ikenohata-shichikencho are abbreviated as Yuigahama Chusei Shudan Bochi and Ikenohata, respectively.

The anthropological diagnoses of the adult human remains were conducted based on the standard methods of aging described by Lovejoy (1985), Brooks and Suchey (1990), Buckberry and Chamberlain (2002), and Sakaue (2006), and of sex determination following Phenice (1969), Bruzek (2002), and Walker (2008). Measurements of the maximum cranial length, cranial basal length, maximum cranial breadth, least frontal breadth, basion–bregma height, middle facial breadth, facial height, orbital breadth, orbital height, nasal breadth, and nasal height were based on the method described by Martin and Knussmann (1988) and Baba (1991), and upper facial heights were measured following the method in Howells (1973). There was no significant intra- and inter-observer error in the cranial measurement parameters, except in the orbital breadth and height (Sakura and Mizoguchi, 1983).

Line charts of standardized measurements were plotted to capture the differences in measurements between the present and comparative data. The means and standard deviations of 43 individuals from Yuigahama-minami were used for standardization of the measurements. One-way analysis of variance with post-hoc Tukey honest significant difference test was calculated for differences among populations. After the comparative specimens were divided into the earlier half of the medieval and Edo groups, a discriminant analysis was performed for Yuigahama-minami and Ikenohata on the maximum cranial length and breadth. The obtained discriminant function was then applied to the individuals from Nozoji-ato and comparative samples to classify them into two groups. The statistical analyses were computed by the statistical package IBM SPSS Statistics 22.

Cranial measurements of the Nozoji-ato series were conducted by the first and second authors, and measurements of comparative data and analyses were done by the first author alone.

Results and Discussion

The measurements of the cranial vaults indicated the presence of significant differences in the maximum cranial length and breadth, and length–breadth index among populations (Table 1; Appendix 1). Figure 2 shows the superior view of the cranium from Nozoji-ato (a), which has a more brachycephalic shape than that from an adjacent medieval site (b). Figure 3 shows the scatter diagram of the maximum cranial length and breadth; the results indicate that the crania from Nozoji-ato had larger cranial breadth than those of counterparts from Gokurakuji, Yuigahama Chusei Shudan Bochi, and Yuigahama-minami. In Figure 4a and b, the Nozoji-ato series shows a larger cranial breadth and length–breadth index than those of the earlier half of the medieval period (Figure 4a), while the length–breadth index of the cranium of Nozoji-ato did not show any difference compared to those from the later half of the medieval and Edo periods (Figure 4b). The measurements of the female faces showed no significant difference between Nozoji-ato and comparative samples (Appendix 2) but had a larger middle facial breadth and orbital breadth than of those from the later half of the medieval and Edo periods (Figure 4c, d).

Figure 2. Superior view of crania from the Nozoji-ato (specimen no. 62-2) (a) and an adjacent medieval site (Yuigahama Chusei Shudan Bochi no. 372 location) (specimen no. 145) (b).
Table 1. Comparison of the maximum cranial length and breadth among the Nozoji-ato and comparative samples

| Population                  | Period       | Chronology | Region      | Maximum cranial length | Maximum cranial breadth | Length–breadth index | Bagion–bregma height | Length–height index | Breadth–height index |
|-----------------------------|--------------|------------|-------------|-------------------------|-------------------------|----------------------|----------------------|---------------------|----------------------|
|                             |              |            |             | (n) M (SD)              | (n) M (SD)              | (n) M (SD)           | (n) M (SD)           | (n) M (SD)           | (n) M (SD)           |
| Nozoji-ato                  | Medieval     | AD 1500–1600 | Kamakura    | 15 177.6 4.1            | 14 138.4 4.6            | 14 78.2 3.8         | 4 133.3 2.6         | 4 75.5 3.1          | 4 96.6 2.6           |
| Yuigahama Chusei Shudan Bochi | Medieval     | AD 1300–1500 | Kamakura    | 6 182.3 8.2            | 7 134.4 4.8            | 6 74.3 4.2          | 2 122.5 0.7         | 1 71.1              | 2 92.5 2.9           |
| Yuigahama-minami            | Medieval     | AD 1200–1400 | Kamakura    | 41 177.8 5.8           | 40 133.7 4.5           | 39 75.4 2.9         | 31 131.6 4.7        | 31 74.1 2.4         | 30 98.4 3.8           |
| Gokurakuji                  | Medieval     | AD 1200–1400 | Kamakura    | 23 177.5 4.7           | 21 135.5 4.6           | 21 75.2 3.1         | 7 131.0 6.2         | 7 74.1 3.3          | 6 99.8 6.6           |
| Marunouchi                  | Medieval     | AD 1500–1600 | Tokyo       | 7 171.7 2.6            | 7 135.0 2.3            | 7 78.6 2.2          | 7 128.7 2.4         | 7 75.0 1.6          | 7 95.4 2.4           |
| Kajibashi                   | Medieval     | AD 1500–1600 | Tokyo       | 5 172.2 8.3            | 5 135.8 4.1            | 5 79.1 6.0          | 4 131.8 1.5         | 4 76.3 4.4          | 4 97.5 2.6           |
| Hitotsubashi                | Edo          | AD 1657–1683 | Tokyo       | 22 175.4 5.0           | 22 136.8 4.8           | 22 78.1 3.6         | 20 131.2 4.1        | 20 74.9 3.0         | 20 96.1 2.7           |
| Ikenohata                   | Edo          | AD 1603–1867 | Tokyo       | 35 171.3 5.8           | 35 135.3 4.9           | 35 79.1 3.5         | 35 132.1 7.0        | 35 77.2 4.5         | 35 97.8 6.4           |
| Shiokawa                    | Edo          | AD 1603–1867 | Yanamashi   | 17 175.1 8.5           | 17 137.8 5.5           | 17 78.8 3.4         | 14 132.0 6.0        | 14 74.8 3.4         | 14 95.7 5.4           |

Analysis of variance

| Degree of freedom | F-value | Probability | Significant difference by Tukey’s honest significant difference test |
|-------------------|---------|-------------|---------------------------------------------------------------------|
|                   | 8       | 5.388**     | Nozoji-ato > Ikenohata*; Yukigahama Chusei Shudan Bochi > Marunouchi*; Yukigahama Chusei Shudan Bochi >> Ikenohata**; Yukigahama-minami >> Ikenohata**; Gokurakuji >> Ikenohata**; Gokurakuji >> Shiokawa*; |
|                   | 8       | 2.580       | None                                                                |
|                   | 8       | 5.177**     | None                                                                |
|                   | 8       | 1.067       | None                                                                |
|                   | 7       | 2.373       | Ikenohata > Yukigahama-minami*                                       |
|                   | 8       | 1.180       | None                                                                |

n, number of individuals; M, mean; SD, standard deviation; *P < 0.05; **P < 0.01.
Discriminant analysis was conducted on the maximum cranial length and maximum cranial breadth, and the discriminant function with Wilks’ lambda (0.701), eigenvalue (0.427), canonical correlation (0.547), and percentage of correct classification (70.3%) were obtained: discriminant function = 0.174 × (maximum cranial length) – 0.110 × (maximum cranial breadth) – 15.591. Discriminant scores of the present and comparative samples calculated from this discriminant function are shown in Figure 5. Individuals from Nozoji-ato and comparative samples were classified into the medieval and Edo groups with a cutoff value of −0.035. Results indicated that 57.1% (8/14) of Nozoji-ato belonged to the Edo group, while 42.9% (6/14) belonged to the medieval group (Table 2). More than half the individuals from Yuigahama Chusei Shudan Bochi (66.7%, 4/6), Yuigahama-minami (76.9%, 30/39), Gokurakuji (71.4%, 15/21), and Hitotsubashi (54.5%, 12/22) belonged to the medieval group, while those from Marunouchi (85.7%, 6/7), Kajibashi (60%, 3/5), Ikenohata (62.9%, 22/35), and Shiokawa (58.8%, 10/17) belonged to the Edo group (Figure 5; Table 2). Therefore, more individuals from Nozoji-ato were classified into the Edo group than were the individuals from Yuigahama Chusei Shudan Bochi, Yuigahama-minami, and Gokurakuji in the earlier half of the medieval period (Figure 5). It is possible that the low percentage of correct classification of the discriminant function (70.3%) is related to the composition of materials that encompassed the transition period between the later half of the medieval and the Edo and the small number of variables for calculation.

The results of this study demonstrated that the Nozoji-ato cranial series was different from the populations within medieval Kamakura City, in that they were more brachycephalic than the earlier half of the medieval Japanese and showed similarity to the later half of the medieval and Edo Japanese. On the other hands, four females from the Nozoji-ato series had a wider middle facial breadth and orbital breadth than the later half of the medieval and Edo periods. Discriminant scores of two (individual nos. 11-1 and 62) out of four females from the Nozoji-ato series show that they were plotted in the Edo group and had transitional values between the medieval and Edo groups (Figure 5). It is suggested that the Nozoji-ato series are characterized by brachycephaly as well as by chameprosopy, a mosaic of cranial features of the populations from the earlier half of the medieval period and the Edo period. From the discriminant analysis, the fact that more individuals from Nozoji-ato, Marunouchi, Kajibashi, and Hitotsubashi dating to the later half of the medieval and the beginning of the Edo were classified into incorrect groups than were those from other sites suggested that the maximum cranial length and breadth were subjected to secular changes during the medieval period. This finding contrasts with the commonly believed theory that medieval populations were homogenous in dolichocephaly and other features (Suzuki, 1969; Nagaoka et al., 2006). New data from the Nozoji-ato series dated to the later half of the medieval period demonstrated secular trends within the Japanese medieval period, and therefore indicate that the medieval people within Kamakura City exhibited wider variations in cranial measurements than previously anticipated. This conclusion is supported by a bioarchaeological study carried out based on samples from Nozoji-ato: the population at this site contained an old age-at-death composition and a high preva-
Figure 4. Comparison of standardized measurements of the cranial vault among Nozoji-ato and samples from the earlier half of the medieval period (a) and among Nozoji-ato and samples from the later half of the medieval period and the Edo period (b); comparison of standardized facial measurements among Nozoji-ato and samples from the earlier half of the medieval period (c), and among Nozoji-ato and samples from the later half of the medieval period and the Edo period (d).

lence of caries and antemortem tooth loss, compared with the adjacent medieval sites within Kamakura City (Nagaoka et al., 2018). With the present and earlier data, it is plausible that specific features thought to be characteristic of the medieval Japanese are not commonly found in all populations from medieval Kamakura.

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Figure 5. Discriminant scores calculated from the discriminant function on the maximum cranial length and breadth. The individuals from Nozoji-ato and comparative samples were classified into medieval and Edo groups with a cutoff value of –0.011. The discriminant scores of two individuals (specimen nos. 11-1, 62) are shown by arrows. YCSB: Yuigahama Chusei Shudan Bochi; YM: Yuigahama-minami.

Table 2. Classification of individuals into medieval and Edo groups using the discriminant function on maximum cranial length and breadth.

| Population                                      | Period      | Total n | Classified into a medieval group | Classified into a Edo group |
|-------------------------------------------------|-------------|---------|----------------------------------|----------------------------|
| Nozoji-ato                                      | Medieval    | 14      | 6                                | 42.9%                      |
|                                                 |             |         | 8                                | 57.1%                      |
| Yuigahama Chusei Shudan Bochi                  | Medieval    | 6       | 4                                | 66.7%                      |
|                                                 |             |         | 2                                | 33.3%                      |
| Yuigahama-minami                               | Medieval    | 39      | 30                               | 76.9%                      |
|                                                 |             |         | 9                                | 23.1%                      |
| Gokurakuji                                     | Medieval    | 21      | 15                               | 71.4%                      |
|                                                 |             |         | 6                                | 28.6%                      |
| Marunouchi                                     | Medieval    | 7       | 1                                | 14.3%                      |
|                                                 |             |         | 6                                | 85.7%                      |
| Kajibashi                                      | Medieval    | 5       | 2                                | 40.0%                      |
|                                                 |             |         | 3                                | 60.0%                      |
| Hitotsubashi                                   | Edo         | 22      | 12                               | 54.5%                      |
|                                                 |             |         | 10                               | 45.5%                      |
| Ikenohata                                      | Edo         | 35      | 13                               | 37.1%                      |
|                                                 |             |         | 22                               | 62.9%                      |
| Shiokawa                                        | Edo         | 17      | 7                                | 41.2%                      |
|                                                 |             |         | 10                               | 58.8%                      |

n, number of individuals.
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Appendix 1. Cranial measurements of the Nozoi-ato sample

| Measurement items               | Male             | Female          |
|---------------------------------|------------------|-----------------|
|                                 | \( n \) | M    | SD  | \( n \) | M    | SD  |
| Maximum cranial length (mm)    | 2      | 186.5 | 6.4 | 15     | 177.6 | 4.0 |
| Cranial basal length (mm)      | 4      | 102.8 | 5.2 |
| Maximum cranial breadth (mm)   | 2      | 141.0 | 15.6 | 14     | 138.4 | 4.6 |
| Length–breadth index           | 2      | 75.5  | 5.8  | 14     | 78.2  | 3.8 |
| Least frontal breadth (mm)      | 1      | 103.1 |      | 13     | 91.5  | 2.8 |
| Basion–bregma height (mm)      | 4      | 133.3 | 2.6 |
| Length–height index            | 4      | 75.5  | 3.1 |
| Breadth–height index           | 4      | 96.6  | 2.6 |
| Middle facial breadth (mm)     | 3      | 100.2 | 5.0 |
| Facial height (mm)             | 2      | 110.5 | 3.8 |
| Upper facial height (mm)       | 2      | 66.2  | 1.7 |
| Virchow’s facial index         | 2      | 108.2 | 1.7 |
| Virchow’s upper facial index   | 2      | 65.5  | 2.0 |
| Orbital breadth (right) (mm)   | 4      | 43.7  | 1.3 |
| Orbital height (right) (mm)    | 4      | 33.5  | 0.6 |
| Orbital index (right)          | 3      | 77.7  | 2.3 |
| Nasal breadth (mm)             | 4      | 25.2  | 1.3 |
| Nasal height (mm)              | 4      | 48.6  | 2.7 |
| Nasal index                    | 4      | 51.9  | 3.5 |

\( n \), number of individuals; M, mean; SD, standard deviation.
## Appendix 2. Comparison of facial measurements among the Nozoji-ato and comparative samples

| Population                 | Period     | Middle facial breadth | Upper facial height | Virchow’s upper facial index | Orbital breadth | Orbital height | Orbital index | Nasal breadth | Nasal height | Nasal index |
|----------------------------|------------|-----------------------|---------------------|-----------------------------|----------------|---------------|---------------|---------------|--------------|-------------|
|                            | n  | M  | SD | n  | M  | SD | n  | M  | SD | n  | M  | SD | n  | M  | SD | n  | M  | SD | n  | M  | SD | n  | M  | SD | n  | M  | SD | n  | M  | SD |
| Nozoji-ato Medieval         | 3  | 100.2 | 5.0 | 3  | 66.2 | 1.7 | 2  | 43.7 | 1.3 | 4  | 33.5 | 0.6 | 3  | 77.7 | 2.3 | 4  | 25.2 | 1.2 | 4  | 48.6 | 2.7 | 4  | 52.0 | 3.5 |
| Yuigahama Chusei Shudan Bochi Medieval | 6  | 96.8 | 7.3 | 12  | 60.9 | 3.1 | 5  | 64.9 | 2.3 | 16  | 40.9 | 1.6 | 16  | 32.7 | 1.8 | 15  | 80.4 | 4.8 | 16  | 24.8 | 2.0 | 16  | 46.7 | 2.3 | 16  | 53.3 | 5.3 |
| Yuigahama-minami Medieval   | 30  | 99.2 | 4.0 | 28  | 64.7 | 3.8 | 28  | 65.2 | 4.2 | 29  | 41.4 | 2.1 | 31  | 33.2 | 1.9 | 29  | 80.4 | 5.7 | 27  | 25.9 | 1.7 | 30  | 48.2 | 2.2 | 27  | 54.0 | 4.0 |
| Gokurakuji Medieval         | 2  | 101.2 | 1.3 | 3  | 62.9 | 2.8 | 2  | 60.6 | 0.0 | 3  | 43.3 | 0.2 | 2  | 33.2 | 1.9 | 2  | 76.5 | 4.8 | 3  | 25.6 | 1.3 | 3  | 47.2 | 3.7 | 2  | 55.0 | 3.4 |
| Marunouchi Medieval         | 7  | 96.8 | 3.0 | 7  | 61.3 | 3.3 | 7  | 63.4 | 4.0 | 7  | 41.0 | 1.1 | 7  | 32.7 | 1.9 | 7  | 79.9 | 6.1 | 6  | 24.9 | 2.2 | 7  | 46.1 | 1.6 | 6  | 54.2 | 5.3 |
| Kajibashi Medieval          | 4  | 94.8 | 3.8 | 5  | 62.8 | 2.1 | 4  | 66.4 | 0.9 | 5  | 42.1 | 0.5 | 5  | 33.5 | 1.5 | 5  | 79.6 | 3.1 | 4  | 24.8 | 1.9 | 5  | 47.0 | 2.2 | 4  | 52.3 | 6.3 |
| Hitotsubashi Edo            | 19  | 94.3 | 5.4 | 14  | 64.9 | 3.9 | 14  | 69.6 | 4.6 | 20  | 42.0 | 2.2 | 20  | 33.3 | 1.7 | 20  | 79.6 | 5.0 | 19  | 24.8 | 1.5 | 18  | 48.0 | 3.2 | 18  | 51.7 | 4.6 |
| Ikenohata Edo               | 30  | 94.6 | 4.0 | 25  | 65.6 | 4.0 | 22  | 69.7 | 5.3 | 34  | 41.7 | 1.8 | 34  | 34.3 | 1.9 | 34  | 82.5 | 5.0 | 33  | 26.0 | 1.7 | 32  | 49.8 | 2.7 | 32  | 52.3 | 3.5 |
| Shiokawa Edo                | 9  | 96.2 | 4.7 | 5  | 66.8 | 4.3 | 5  | 69.8 | 5.1 | 14  | 41.4 | 1.5 | 14  | 35.0 | 1.1 | 14  | 84.8 | 3.9 | 13  | 25.1 | 1.7 | 12  | 49.0 | 2.9 | 12  | 51.2 | 3.3 |

### Analysis of variance

| Population | Degree of freedom | F-value | Probability |
|------------|-------------------|---------|-------------|
|            | F                 | P        |             |
|            | 8                 | 8        | 8           |
|            | 8                 | 8        | 8           |
|            | 2.789             | 3.251   |             |
|            | 3.751             | 3.751   |             |
|            | 2.110             | 1.446   |             |
|            | 2.849             | 1.603   |             |
|            | 1.007**           | 0.002** |             |
|            | 0.001**           | 0.008** |             |
|            | 0.131             | 0.013** |             |
|            | 0.046**           | 0.040*  |             |
|            | 0.040*            | 0.040*  |             |
|            | 0.040*            | 0.040*  |             |
|            | 0.529             | 0.529   |             |

### Significant difference by Tukey’s honest significant difference test

- Yuigahama-minami >> Hitotsubashi**
- Yuigahama-Chusei Shudan Bochi* 
- Ikenohata >> Yuigahama-Chusei Shudan Bochi*
- None
- None
- None
- None
- None
- None

n, number of individuals; M, mean; SD, standard deviation; *P < 0.05; **P < 0.01.