Estimation of skeletal adult age distribution of Okhotsk people in northern Japan

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Abstract The demographic structure of prehistoric hunter-gatherer societies has contributed to our understanding of the life history patterns of past human populations. The purposes of this study are to examine the human skeletal remains associated with the Okhotsk culture, to estimate age-at-death distribution using the Buckberry–Chamberlain system of auricular surface aging and the Bayesian approach, and to discuss whether paleodemographic estimates can yield an appropriate mortality profile of prehistoric hunter-gatherers in Japan. The application of the Bayesian theorem to the age-at-death estimation was based on the modern Japanese and Spitalfields known-age collections, assuming uniform, reference, and model prior probabilities. The age distributions of the Okhotsk had low proportions of young adults and high proportions of elderly adults. The results indicated that 24.4–51.3% of individuals were above the age of 55 years. The newly employed technique of the Bayesian estimation yielded the age distributions with significant numbers of elderly individuals, which are contrary to usual paleodemographic estimates. The results of this study suggest direct and plausible evidence of demographic traits in the Okhotsk people and allow us to reveal the mortality schedules of the prehistoric hunter-gatherers that otherwise could not be reconstructed from historical or ethnological records.

Key words: age-at-death, auricular surface, hunter-gatherer, Okhotsk, Bayesian theorem

Introduction

The demographic structure of prehistoric hunter-gatherer societies has contributed to our understanding of the life history patterns of past human populations. “Human life history traits evolved hundreds of thousands of years ago when all members of our species pursued a foraging lifestyle, so it is logical to regard the world’s few surviving hunter-gatherer communities as potentially rich sources of information about ancestral human demographic patterns and processes” (Chamberlain, 2006: 58). Although ethnological records of living populations provide clues to demographic estimates of prehistoric societies (Howell, 1979), the ethnological data do not suggest direct evidence of demographic traits.

The reconstruction of age-at-death distribution of human skeletal remains reveals the paleodemographic traits from past human people themselves, but suffers from the persistent problem of the validity of adult age estimation techniques (Bocquet-Appel and Masset, 1982, 1985, 1996; Buikstra and Konigsberg, 1985; Horowitz et al., 1988;

Mensforth, 1990; Konigsberg and Frankenberg, 1992). Age estimation is fairly accurate for subadults, but not for adults (Murray and Murray, 1991; Bocquet-Appel and Bacro, 1997; Milner et al., 2000). Analyses of archeological samples from different places and times have generally reported a concentration of deaths between 25 and 45 years and a lack of elderly individuals over the age of 60 years. Some studies have interpreted that the lack of elderly individuals in archeological samples is related to severe living conditions (e.g. Kobayashi, 1967; Lovejoy et al., 1977; Alesan et al., 1999; Nagaoka et al., 2006). However, skeletal age distribution differs from the distribution recorded in historical documents or model life tables in that the age distributions of skeletal samples have high proportions of young adults and low proportions of elderly adults (Weiss, 1973; Howell, 1982; Chamberlain, 2006; Storey, 2007).

Paleodemographers have sought solutions to overcome the difficult problem of age-at-death estimation (Bocquet-Appel and Masset, 1982, 1996; Konigsberg and Frankenberg, 1992; Chamberlain, 2000, 2006; Buckberry and Chamberlain, 2002; Hoppa, 2002; Storey, 2007). A consensus on procedures for estimating age-at-death from a skeletal sample, the “Rostock Manifesto,” advocated the Bayesian theorem to provide the methodological basis of adult aging techniques (Hoppa, 2002). The pioneering work of Konigsberg and Frankenberg (1992) expressed the Bayesian theorem as:

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$$p_{ai} = \frac{p_{ia}\tilde{d}_a}{\sum_{a=1}^w p_{ia}\tilde{d}_a}, \quad (1)$$

where p_{ai} is the posterior probability of being a particular age a conditional on being a particular state of an age indicator i , and p_{ia} is the probability of being a particular state of an age indicator i conditional on being a particular age a . $\tilde{d}_a$ represents the prior probability of age a . a is a discontinuous age interval indexed from 1 to w ($1 \leq a \leq w$), while i is a discontinuous age indicator state indexed from 1 to n ($1 \leq i \leq n$). The calculation of equation (1) is based on skeletal collections in which the ages of the individuals are known. For a given archeological sample, when the frequency of individuals in age indicator state i is expressed as f_i , the age distribution for this sample $\hat{d}_a$ is expressed as:

$$\hat{d}_a = \sum_{i=1}^n f_i p_{ai}. \quad (2)$$

The calculation of the posterior probability from known-age human skeletal collections and an appropriate prior probability is fundamental information to obtain the age distribution of human skeletal remains from an archeological site according to equation (2).

Buckberry and Chamberlain (2002) examined the Spitalfields known-age sample, and applied the Bayesian theorem to their auricular surface aging technique. They calculated the posterior probability of age, given auricular surface stage, assuming uniform prior probability. Storey (2007) estimated the adult age distribution for a Pre-Columbian Maya skeletal population based on Buckberry and Chamberlain's (2002) posterior probability of age by auricular surface stage, and found an age distribution with a significant number of older adults, contrary to usual paleodemographic estimates. The preliminary works conducted by the first author and colleagues (Nagaoka and Hirata, 2008; Nagaoka et al., 2008) employed Buckberry and Chamberlain's (2002) auricular surface system for estimating the adult age distributions of the human skeletal remains from archeological sites in Japan. The calculation of the posterior probability was based on the Spitalfields known-age collection, assuming uniform prior probability. The results confirmed that the new technique yielded realistic age distributions with significant numbers of elderly individuals. It is reasonable to consider that the new technique provides important information to afford new perspectives on the age-at-death distribution of skeletal populations. However, no other study has employed this new technique or reconstructed paleodemographic features of skeletal populations. Applying the new method to skeletal populations under various assumptions of known-age samples and prior probability strengthens the basis of new paleodemographic estimates.

The purposes of this study are to examine the human skeletal remains of prehistoric hunter-gatherers in Japan; to reconstruct adult age distributions using the Bayesian approach for auricular surfaces; and to compare the skeletal age distributions obtained from different age estimation assumptions (i.e. those by different known-age collections and

different prior probabilities). The object of this study are the human skeletal remains associated with the Okhotsk culture, which flourished in Hokkaido, Kurile Islands, and Sakhalin Island of Northeast Asia during the 5th–13th centuries AD (Amano, 2003). The application of the new method to the Okhotsk people allows us to document and interpret the mortality schedules of the prehistoric hunter-gatherers that otherwise could not be reconstructed from historical or ethnological records.

Materials

The target sample is defined as groups of individuals whose age-at-death is unknown, while the reference sample is defined as groups of individuals whose age-at-death is known and provides information on the age-at-death of the target sample (Konigsberg and Frankenberg, 1992).

The target sample consisted of 91 human skeletal remains from the Hamanaka, Kabukai, Omisaki, Tomiiso, Utoro, Oniwaki, and Moyoro sites in Hokkaido, which were housed in Hokkaido University (Sapporo, Japan) and Sapporo Medical University (Sapporo, Japan) (Figure 1; Table 1). These

Figure 1. Map of Japan showing geographical locations of archeological sites of Okhotsk culture.

Table 1. Okhotsk sample

Site	Location	Number of individuals				Source
		Male	Female	Unknown	Total	
Hamanaka	Rebun	2	4	0	6	Sapporo Medical University
Kabukai	Rebun	0	1	0	1	Sapporo Medical University
Omisaki	Wakkanai	11	7	2	20	Sapporo Medical University
Tomiiso	Wakkanai	0	1	0	1	Sapporo Medical University
Utoro	Shari	1	2	0	3	Sapporo Medical University
Oniwaki	Rishiri	2	3	0	5	Hokkaido University
Moyoro	Abashiri	35	19	1	55	Hokkaido University
Total		51	37	3	91	

archeological sites belonged to the Okhotsk culture, which spread from southern Sakhalin Island to northeastern Hokkaido and the Kurile Islands during the 5th–13th centuries AD (Yamaura and Ushiro, 1999; Amano, 2003). The regions occupied by the Okhotsk people were surrounded by a harsh environment with subzero winter temperatures (Hudson, 2004). Archeological and stable isotopic evidence has revealed that the subsistence of the Okhotsk people depended on sea-mammal hunting, shallow- and deep-water fishing, and land animal hunting (Yamaura and Ushiro, 1999; Yoneda, 2002; Naito et al., 2010). Biodistance studies of craniofacial and odontological morphology and ancient DNA have strongly indicated affinities among the Okhotsk, Amur, and Neolithic Baikalian (Yamaguchi, 1981, 1991; Ishida, 1988, 1996; Hanihara et al., 2008; Komesu et al., 2008; Sato et al., 2009). Oxenham and Matsumura (2008) compared the oral and physiological well-being of the Okhotsk people with other hunter-gatherer populations in Arctic regions and found that oral health profiles are sensitive to subsistence strategies among cold-adapted populations. Shimoda et al. (2012) examined degenerative changes of the spine in the Okhotsk people and found that severe osteophytes on the body of the lumbar vertebrae were more frequently detected in the Okhotsk males. They concluded that, because they developed a considerable maritime infrastructure, the lifestyle required for sea-mammal hunting and fishing seems to have particularly affected the incidence of severe degenerative changes of the lumbar vertebrae.

The comparative data for the target sample are those of the Jomon collections from the middle to final stages (BP 4700–2100). The Jomon sample consisted of 86 individuals from the Ebishima, Kikumatenaga, Gionbara, Saihiro, Torihorigome, Kowashimizu, Kosaku, Kitagawa, and Ikawazu sites in mainland Japan (Nagaoka et al., 2008). Archeological evidence suggested that the Jomon people had a pottery-using culture, and depended on gathering, fishing, and hunting, and exploited an extremely wide range of animals, fish, plants, etc. (Kobayashi, 1994). The Jomon people are one of the important components of the modern Japanese (Hanihara, 1991), and an analysis of mitochondrial DNA has suggested that they originated from over a wide range of the Asian continent (Shinoda, 2007).

In order to estimate the age of the target sample, two known-age collections of modern Japanese and Spitalfields were utilized as the reference sample (Table 2). The former comprises collections of modern Japanese individuals of known age whose birth years were between 1851 and 1923

Table 2. Two reference skeletal collections of known age and sex

Age in years	Japanese			Spitalfields		
	Male	Female	Total	Male	Female	Total
15–24	12	5	17	4	4	8
25–34	26	7	33	10	6	16
35–44	30	8	38	9	10	19
45–54	30	4	34	14	19	33
55–64	13	8	21	21	18	39
65–74	11	12	23	19	19	38
75–84	6	5	11	6	13	19
85–94	0	0	0	3	5	8
Total	128	49	177	86	94	180

and who represented low socioeconomic groups. The skeletal remains consist of 177 individuals over the age of 15, and are housed in Chiba University (Chiba, Japan). The Spitalfields collection is from London, UK, and the data from this were adapted from Buckberry and Chamberlain (2002). Buckberry and Chamberlain (2002) examined 180 individuals from the Spitalfields known-age collection from the 18th and 19th centuries as reference sample. Figure 2 and Table 2 show age distributions of two reference skeletal collections. The Spitalfields sample has a significantly older distribution than the Japanese (U -test, $P < 0.001$).

In this study, the exclusion of skeletons of the individuals aged 14 years and under circumvents the unavoidable problems of infant under-representation in skeletal populations (Kobayashi, 1967).

Methods

Demographic assumption

Demographic estimates of samples always require the uniformitarian assumption that the biological processes related to aging and sexual dimorphism were the same in the past as in the present (Weiss, 1973; Howell, 1976; Hoppa, 2002; Chamberlain, 2006).

Sex determination

The sex determination of individuals 15 years of age and older was carried out based on macroscopic assessment of pelvic features: preauricular sulcus, greater sciatic notch, composite arch, inferior pelvis, and ischiopubic proportion (Bruzek, 2002), ventral arc, subpubic concavity, and medial aspect of the ischiopubic ramus (Phenice, 1969). However, the sexes were pooled in the analyses, as sexual differences

Figure 2. Age distribution of two reference skeletal collections of known age and sex. There is a significant difference between Japanese and Spitalfields (U -test, $P < 0.001$).

were not observed in auricular surface aging (Lovejoy et al., 1985; Murray and Murray, 1991; Buckberry and Chamberlain, 2002; Mulhern and Jones, 2005).

Adult age estimation

The reliable estimation of age-at-death distribution of the target sample requires a good osteological age indicator, the use of the Bayesian theorem, good known-age skeletal collections, and the selection of an appropriate prior probability of age distribution in the target sample (Hoppa, 2002).

The auricular surface is an useful age indicator (Kobayashi, 1967; Lovejoy et al., 1985; Buckberry and Chamberlain, 2002; Osborne et al., 2004; Igarashi et al., 2005), as its decay is persistent in forensic and archeological contexts and it seems to cover wide ranges of ages up to elderly individuals (Storey, 2007). This study analyzed iliac auricular surfaces of adult individuals 15 years of age and above using two techniques: the original method of Lovejoy et al. (1985) and the revised method of Buckberry and Chamberlain (2002). Here, the term 'adult' includes individuals aged 15–19 years. This study classified individuals into three age categories: 15–34, 35–54, and ≥ 55 years.

Lovejoy et al. (1985) established eight modal age phases according to the chronological metamorphosis related to transverse organization, density, apical change, retroauricular area, and porosity. The method of Lovejoy et al. (1985) has been one of the most widely used criteria of adult age estimation (e.g. Murray and Murray, 1991; Saunders et al., 1992; Bedford et al., 1993; White and Folkens, 2000; Osborne et al., 2004; Schmitt, 2004). The eight stages correspond to the age groups 20–24, 25–29, 30–34, 35–39, 40–44, 45–49, 50–59, and ≥ 60 years. To compensate for this, the individuals 15–19 years which were previously estimated based on the criteria of dental development (Ubelaker, 1989), the degree of development and closure of the occipital synchondrosis (Wakebe, 1990), and the degree of ossification and epiphyseal union of the pelvis and long bones (Flecker, 1942; Webb and Suchey, 1985) were added to the age-at-death distribution derived from the method of

Lovejoy et al. (1985). Furthermore, the number of individuals in the stage corresponding to 50–59 years was divided into two, which were then assigned to age categories of 35–54 and ≥ 55 years.

However, the method of Lovejoy et al. (1985) has been criticized due to the difficulty of classifying individuals into eight stages (Buckberry and Chamberlain, 2002; Falys et al., 2006; Mulhern and Jones, 2005) and the systematic underestimation of age in older adults (Bocquet-Appel and Masset, 1982, 1985, 1996; Walker et al., 1988; Mensforth, 1990; Konigsberg and Frankenberg, 1992). Buckberry and Chamberlain (2002: 232) have stressed, "The separate features of the auricular surface described by Lovejoy et al. (1985), such as porosity, surface texture, and marginal changes, appear to develop independently of each other. The age of onset for each stage of different features of the auricular surface appears to vary, and as a consequence the 5-year age categories of Lovejoy et al. (1985) tend to overlap."

Buckberry and Chamberlain (2002) proposed a revised quantitative system of 5–19 composite scores according to five morphological traits of the auricular surface: transverse organization, surface texture, microporosity, macroporosity, and apical change. The 5–19 composite scores of the five traits are then classified into seven stages. The most important strategy of their system is the employment of the Bayesian theorem to provide posterior probability, by age and auricular surface stage. The contingency tables of age and Buckberry and Chamberlain (2002)'s auricular surface stage for two sets of reference samples (Japanese and Spitalfields) (Table 3) were used for calculating the posterior probability of being a particular age conditional on being a particular state of an age indicator. The prior probabilities used in the calculation are uniform, reference, and model ones (Table 4). In uniform priors an equal prior probability is assigned to each age category, while reference ones were calculated from the age distribution of the reference sample (Chamberlain, 2006). Model priors represent model age structure taken from model life tables of Coale and Demeny (1983) and the age structure of Level 1 ($e_0 = 20$) and Level

Table 3. Number of individuals of two reference samples according to age and Buckberry and Chamberlain's (2002) auricular surface stage

Age in years	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Stage 6	Stage 7	Total
Japanese								
15–34	1	9	21	10	8	1	0	50
35–54	0	0	8	27	32	4	1	72
≥55	0	0	1	7	19	22	6	55
Total	1	9	30	44	59	27	7	177
Spitalfields								
15–34	3	4	8	5	4	0	0	24
35–54	0	2	12	13	17	6	2	52
≥55	0	0	2	14	43	35	10	104
Total	3	6	22	32	64	41	12	180

Table 4. Prior probabilities of age by assuming five mortality schedules

Age in years	Uniform priors	Reference priors of Japanese collection	Reference priors of Spitalfields collection	Model priors, $e_0 = 20$	Model priors, $e_0 = 50$
15–34	0.33	0.28	0.14	0.33	0.12
35–54	0.33	0.41	0.29	0.31	0.18
≥55	0.33	0.31	0.59	0.36	0.71

13 ($e_0 = 50$) in West model life tables were used.

The first author observed auricular surfaces twice in the interval of two weeks. Skeletal individuals recorded with discrepancies between the two observations were observed a third time. There is no significant difference for the Okhotsk sample between the two observations by the methods of Lovejoy et al. (1985) (U -test, $P > 0.05$) and Buckberry and Chamberlain (2002) (U -test, $P > 0.05$). To avoid inter-observer error, the first author alone recorded the age markers. According to Buckberry and Chamberlain (2002), color photographs of auricular surfaces were taken and sequenced for each feature in order to check the consistency of the recording.

Results and Discussion

Age-at-death distribution of the Okhotsk sample

This study examined well-preserved auricular surfaces of the Okhotsk, which are individuals of 15 years of age and above. Age estimation of the auricular surfaces was performed using the original method of Lovejoy et al. (1985) and the revised one of Buckberry and Chamberlain (2002). The Okhotsk sample is comprised of 51 men, 37 women, and 3 undetermined individuals. Table 5 shows the number of adults for each of Lovejoy et al.'s (1985) eight stages of the auricular surface and three individuals aged 15–19 years. The distribution among the eight indicator stages of individuals for Okhotsk is, in order, 9, 8, 22, 21, 15, 3, 8, and 2. The peak of individuals is concentrated in stages 3–5 and there are only two individuals in stage 8. The proportion of adult individuals in the age categories 15–34, 35–54, and ≥55 years is 46.2%, 47.3%, and 6.6%, respectively (Figure 3).

Table 6 shows the number of individuals of each of Buckberry and Chamberlain's (2002) scores and the stages of the auricular surface, and the distribution among the seven indicator stages of individuals is, in order, 3, 8, 18, 33, 15, 11, and 3. Table 7 calculated the posterior probability of age, given auricular surface stage, assuming uniform, reference,

Table 5. Number of individuals of Okhotsk associated with each of the Lovejoy et al.'s (1985) eight auricular surface stages

Stage	Male	Female	Unknown	Total
15–19 years				
	0	1	2	3
≥20 years				
Stage 1	6	3	0	9
Stage 2	4	3	1	8
Stage 3	15	7	0	22
Stage 4	15	6	0	21
Stage 5	6	9	0	15
Stage 6	1	2	0	3
Stage 7	3	5	0	8
Stage 8	1	1	0	2
Total	51	37	3	91

Figure 3. Proportion of deaths of the Okhotsk in each age group estimated from Lovejoy et al.'s (1985) auricular surface stage.

or model priors, in two reference samples. Application of the posterior probabilities (two reference samples and four priors) to the auricular surface stages yielded eight age distributions of deaths. They all increased the proportion of deaths aged ≥55 years and decreased the proportion of those aged 15–34 and 35–54 years as compared with the Lovejoy et

Table 6. Number of Okhotsk individuals in each Buckberry and Chamberlain's (2002) score and stage for the auricular surface

Score	Male	Female	Unknown	Total	Stage	Male	Female	Unknown	Total
Score 5	0	2	1	3	Stage 1	0	2	1	3
Score 6	0	0	0	0	Stage 2	5	3	0	8
Score 7	3	0	0	3	Stage 3	11	6	1	18
Score 8	2	3	0	5	Stage 4	19	13	1	33
Score 9	6	4	1	11	Stage 5	10	5	0	15
Score 10	5	2	0	7	Stage 6	3	8	0	11
Score 11	12	8	1	21	Stage 7	3	0	0	3
Score 12	7	5	0	12	Total	51	37	3	91
Score 13	7	1	0	8					
Score 14	3	4	0	7					
Score 15	2	5	0	7					
Score 16	1	3	0	4					
Score 17	3	0	0	3					
Score 18	0	0	0	0					
Score 19	0	0	0	0					
Total	51	37	3	91					

Table 7. Posterior probabilities of age and Buckberry and Chamberlain's (2002) auricular surface stage for two reference collections

Age in years	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Stage 6	Stage 7
Japanese reference sample							
Uniform priors							
15–34	1.00	1.00	0.70	0.23	0.14	0.04	0.00
35–54	0.00	0.00	0.27	0.61	0.54	0.15	0.14
≥55	0.00	0.00	0.03	0.16	0.32	0.81	0.86
Reference priors							
15–34	1.00	0.67	0.36	0.16	0.06	0.00	0.00
35–54	0.00	0.33	0.55	0.41	0.27	0.15	0.17
≥55	0.00	0.00	0.09	0.44	0.67	0.85	0.83
Model priors, $e_0 = 20$							
15–34	1.00	1.00	0.77	0.29	0.17	0.04	0.00
35–54	0.00	0.00	0.19	0.51	0.44	0.10	0.10
≥55	0.00	0.00	0.04	0.20	0.39	0.86	0.90
Model priors, $e_0 = 50$							
15–34	1.00	1.00	0.60	0.13	0.05	0.01	0.00
35–54	0.00	0.00	0.24	0.37	0.23	0.03	0.03
≥55	0.00	0.00	0.16	0.50	0.72	0.96	0.97
Spitalfields reference sample							
Uniform priors							
15–34	1.00	1.00	0.76	0.28	0.17	0.04	0.00
35–54	0.00	0.00	0.20	0.53	0.47	0.12	0.11
55≤	0.00	0.00	0.03	0.18	0.36	0.84	0.89
Reference priors							
15–34	1.00	0.81	0.57	0.35	0.18	0.00	0.00
35–54	0.00	0.19	0.40	0.42	0.36	0.26	0.29
≥55	0.00	0.00	0.03	0.23	0.46	0.74	0.71
Model priors, $e_0 = 20$							
15–34	1.00	0.82	0.59	0.36	0.18	0.00	0.00
35–54	0.00	0.18	0.38	0.40	0.33	0.23	0.26
≥55	0.00	0.00	0.04	0.25	0.48	0.77	0.74
Model priors, $e_0 = 50$							
15–34	1.00	0.74	0.42	0.15	0.05	0.00	0.00
35–54	0.00	0.26	0.44	0.27	0.15	0.08	0.09
≥55	0.00	0.00	0.15	0.58	0.79	0.92	0.91

al.'s (1985) system (Figure 4; Table 8).

In the Buckberry and Chamberlain (2002) system, the comparison of the age-at-death distributions obtained by different reference samples and priors led to the following results: the proportion of deaths above the age of 55 years in the Japanese and Spitalfields reference samples accounted for 26.3% and 27.8% in the uniform priors, 27.7% and

29.3% in the $e_0 = 20$ model priors, and 48.0% and 51.3% in the $e_0 = 50$ model priors, respectively (Figure 4; Table 8). It is reasonable to consider that in spite of the difference in the two reference samples, consistent results were obtained in each prior and that the model prior of low mortality ($e_0 = 50$) generated a higher proportion of elderly deaths than any other prior. However, the assumption of the reference priors

Figure 4. Proportion of deaths of the Okhotsk in each age group estimated from Buckberry and Chamberlain's (2002) auricular surface stage for two reference collections, based on uniform, reference, and model prior probabilities. (J) and (S) represent Japanese and Spitalfields reference samples.

Table 8. Number of individuals aged 15 years and above for Okhotsk based on the method of Buckberry and Chamberlain (2002)

Age in years	Number of individuals				Number of individuals			
	Japanese reference sample				Spitalfields reference sample			
	Uniform priors	Reference priors	Model priors, $e_0 = 20$	Model priors, $e_0 = 50$	Uniform priors	Reference priors	Model priors, $e_0 = 20$	Model priors, $e_0 = 50$
15-34	37.2	33.5	37.5	27.0	34.1	21.0	34.6	22.1
35-54	29.9	35.2	28.3	20.3	31.6	32.0	29.7	22.2
≥55	23.9	22.2	25.2	43.7	25.3	38.0	26.7	46.7

Age in years	Percentage expressions				Percentage expressions			
	Japanese reference sample				Spitalfields reference sample			
	Uniform priors	Reference priors	Model priors, $e_0 = 20$	Model priors, $e_0 = 50$	Uniform priors	Reference priors	Model priors, $e_0 = 20$	Model priors, $e_0 = 50$
15-34	40.8	36.9	41.2	29.7	37.5	23.0	38.0	24.3
35-54	32.9	38.7	31.1	22.3	34.7	35.1	32.6	24.4
≥55	26.3	24.4	27.7	48.0	27.8	41.8	29.3	51.3

yielded different age distributions between the Japanese and Spitalfields reference collections: the proportion of deaths aged ≥55 years accounted for 24.4% in the former but 41.8% in the latter (Figure 5, Figure 6). The use of reference priors yielded the age distribution of the target sample, showing a similar distribution to the reference samples (Figure 5, Figure 6).

Comparison of aging methods

The estimation of Lovejoy et al.'s (1985) original method suggested that the age distributions of skeletal samples have high proportions of young adults and low proportions of elderly adults. However, Buckberry and Chamberlain's (2002) revised estimation has older age distributions than the original method, with the majority of individuals over 55 years of age. The new technique yielded age distributions with significant numbers of elderly individuals. This result is consistent

with the results of previous studies by the first author (Nagaoka and Hirata, 2008; Nagaoka et al., 2008).

Murlhern and Jones (2005) tested the reliability of the revised method using 309 individuals from the Terry Collection and detected that the revised method improved the accuracy of age estimation for elderly adults. Falys et al. (2006) modified the combined composite scores of Buckberry and Chamberlain (2002) into new auricular surface stages based on 167 individuals from a documented archeological population, which improved the reliability in aging the individuals aged 60 years and above. Rissech et al. (2012) evaluated the methods of Lovejoy et al. (1985) and Buckberry and Chamberlain (2002) in a Spanish forensic sample and noted that the original method performed poorly compared with the revised one. The present data and the previous studies by Murlhern and Jones (2005), Falys et al. (2006), and Rissech et al. (2012) led to the conclusions that the revised method

Figure 5. Proportion of deaths of the Okhotsk and Japanese reference collection in each age group. The age distribution was estimated from Buckberry and Chamberlain's (2002) auricular surface stage, based on Japanese reference collection and uniform/reference prior probabilities.

Figure 6. Proportion of deaths of the Okhotsk and Spitalfields reference collection in each age group. The age distribution was estimated from Buckberry and Chamberlain's (2002) auricular surface stage, based on Japanese reference collection and uniform/reference prior probabilities.

improved the accuracy of age estimation for elderly adults.

This study further indicated that the revised method yielded age distributions with significant numbers of elderly individuals even if different reference samples or priors were used. However, the assumption of reference priors yielded the age distribution of the target sample showing a similar distribution to the reference sample. Bocquet-Appel and Masset (1982) criticized reference priors as systematically biasing the age-at-death of target samples, yielding a distribution similar to that of reference samples. It is recommended that reference priors are less appropriate for the Bayesian estimation than uniform or model priors.

It is evident from this study that both the Japanese and Spitalfields reference samples led to consistent estimations under the assumption of uniform or model priors. In general, however, age-related indicators exhibit too much variation across different populations to serve as a reference (Loth and İşcan, 1989; Kemkes-Grottenthaler, 1996; Galea et al., 1998; Hoppa, 2000; Jackes, 2000). According to Wittwer-

Backofen et al. (2008: 393), "the correlation of these age-related skeletal traits to chronological age has most likely changed over the centuries." In this case also, the use of the Japanese reference sample is ideal and helps us to reduce inaccuracy when estimating the age-at-death of the target sample. Fortunately, both the Japanese and Spitalfields reference samples from different times and places led to consistent results with a significant number of elderly adults, which implies that the selection of the reference sample in the paleodemographic estimation can be considered more flexible than indicated by the previous studies.

Comparison with the Jomon series

This study compared the data of Okhotsk with those of Jomon (Nagaoka et al., 2008). The distribution among the Lovejoy et al.'s (1985) eight indicator stages of individuals for Jomon is, in order, 12, 14, 15, 24, 12, 5, 4, and 0. The proportion of adult individuals in age categories 15–34, 35–54, and ≥ 55 is 47.7%, 50.0%, and 2.3%, respectively. The Okhotsk has a slightly higher proportion of elderly individuals than the Jomon.

This study further estimated the age-at-death distributions of the Jomon, by applying the posterior probabilities to the distribution among Buckberry and Chamberlain's (2002) indicator stages, and comparing with the age-at-death distribution of the Okhotsk. The distribution among Buckberry and Chamberlain's (2002) seven indicator stages of individuals is, in order, 6, 14, 17, 17, 18, 11, and 3. In the case of the Jomon sample also, the age distribution estimation based on the posterior probability from four priors and two reference samples yielded an older distribution of deaths than Lovejoy et al.'s (1985) system. The comparison of age distributions between the Okhotsk and Jomon suggested that the former had fewer individuals aged 15–34 and 35–54 years and more individuals aged ≥ 55 years than the latter (Table 9). Although the Okhotsk and Jomon showed similar mortality patterns with a high proportion of elderly adults, the former exhibited a slightly older age distribution than the latter. In spite of the difference in reference samples and priors, all the estimations suggested that the Okhotsk had a slightly older age distribution than the Jomon.

Although there is no direct relationship between longevity and oral health, the difference between the Okhotsk and Jomon is consistent between the present data and that of Oxenham and Matsumura (2008). According to Oxenham and Matsumura (2008), the rates of the linear enamel hypoplasia and dental caries in the Okhotsk are smaller than those of the Jomon. The Okhotsk depended on sea-mammal hunting, shallow- and deep-water fishing, and land animal hunting, while the subsistence of the Jomon depended on gathering, fishing, and hunting, and exploited an extremely wide range of animals, fish, and plants. The dietary reconstruction of the Okhotsk culture based on nitrogen composition of amino acids implied the dependence of multiple marine foodwebs (Naito et al., 2010). The use of marine diet in the Okhotsk contributed to an increase in fluoride levels and cariostatic conditions in mouth (Kelley et al., 1991). With the current data available, the reasons for the difference between the Okhotsk and Jomon are not known. Further studies of the physiological well-being of prehistoric hunter-

Table 9. Number of individuals aged 15 years and above for the Okhotsk and Jomon based on the method of Buckberry and Chamberlain (2002)

Reference sample	Prior probabilities	Populations	Number of individuals			Percentage expressions		
			Age in years			Age in years		
			15–34	35–54	≥55	15–34	35–54	≥55
Japanese	Uniform priors	Okhotsk	37.2	29.9	23.9	40.8	32.9	26.3
		Jomon	41.3	22.6	22.1	48.1	26.2	25.7
Japanese	Reference priors	Okhotsk	33.5	35.2	22.2	36.9	38.7	24.4
		Jomon	38.6	26.8	20.6	44.9	31.1	24.0
Japanese	Model priors, $e_0 = 20$	Okhotsk	37.5	28.3	25.2	41.2	31.1	27.7
		Jomon	41.6	21.3	23.1	48.4	24.7	26.9
Japanese	Model priors, $e_0 = 50$	Okhotsk	27.0	20.3	43.7	29.7	22.3	48.0
		Jomon	33.5	14.9	37.6	38.9	17.3	43.8
Spitalfields	Uniform priors	Okhotsk	34.1	31.6	25.3	37.5	34.7	27.8
		Jomon	36.4	26.7	23.0	42.3	31.0	26.7
Spitalfields	Reference priors	Okhotsk	21.0	32.0	38.0	23.0	35.1	41.8
		Jomon	25.3	27.7	33.0	29.4	32.3	38.3
Spitalfields	Model priors, $e_0 = 20$	Okhotsk	34.6	29.7	26.7	38.0	32.6	29.3
		Jomon	36.8	25.0	24.2	42.8	29.1	28.1
Spitalfields	Model priors, $e_0 = 50$	Okhotsk	22.1	22.2	46.7	24.3	24.4	51.3
		Jomon	26.9	19.5	39.6	31.3	22.7	46.0

gatherers in Japan are required in order to reveal more information on paleodemographic differences between the Okhotsk and Jomon.

Comparison with ethnographic data

Previous studies have revealed that the age-at-death distributions obtained from skeletal samples are often different from those recorded in historical census documents in that the age distributions of skeletal samples have high proportions of young adults and low proportions of elderly adults (e.g. Howell, 1982; Chamberlain, 2006; Storey, 2007). Howell (1982) interpreted the unusual features of the skeletal population structure based on two assumptions: (1) life was difficult for prehistoric hunter-gatherers; or (2) paleodemographic estimation is distorted by inaccurate ages-at-death of the skeletal population and differential preservation of skeletal remains. It is true that this could reflect the actual age-at-death distribution, but in recent decades the systematic underestimation of the ages of elderly adults has been criticized (Bocquet-Appel and Masset, 1982, 1985, 1996; Buikstra and Konigsberg, 1985; Horowitz et al., 1988; Mensforth, 1990; Konigsberg and Frankenberg, 1992). As Chamberlain (2006: 90) noted, “[t]his pattern, which is often accompanied by absent or very few individuals aged over 60 years, is seen in analyses of skeletal samples from all regions of the world, from prehistoric through to modern times, but this mortality distribution is not found in model life tables or in historical demographic data.” In the ethnographic data of modern hunter-gatherers, the probability of a 15-year-old surviving to ≥55 years is 20.8% in the Ache in Paraguay (Hill and Hurtado, 1995), 22.3% in the Agta in the Philippines (Headland, 1989), 31.3% in the Hadza in Africa (Blurton Jones et al., 1992) and 40.7% in the !Kung in Africa (Howell, 1979).

Fortunately, advances in the methodological basis for estimating the proportion of elderly adults has yielded realistic

age distributions of skeletal populations. This study and preliminary studies by the first author (Nagaoka and Hirata, 2008; Nagaoka et al., 2008) provided age distributions with significant numbers of elderly individuals. Although we do not know the real age distribution of the skeletal populations, the proportion of deaths aged ≥55 years which ranged from 24.4 to 51.3% in the Okhotsk and from 24.0 to 46.0% in the Jomon is plausible. Since the model priors of low mortality ($e_0 = 50$) generated a higher proportion of elderly deaths than the ethnographic data, the estimation based on the high mortality model priors ($e_0 = 20$) or uniform priors are appropriate in the Okhotsk and Jomon. The present data are contrary to usual paleodemographic age distributions, which are characterized by high proportions of young adults and low proportions of elderly adults (e.g. Kobayashi, 1967; Lovejoy et al., 1977; Eshed et al., 2004; Nagaoka et al., 2006). The results of this study suggest direct and plausible evidence of demographic traits of the Okhotsk people and strengthen the methodological basis for paleodemography.

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