

Cross-Cultural Estimation of the Human Generation Interval for Use in Genetics-Based Population Divergence Studies

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ABSTRACT The length of the human generation interval is a key parameter when using genetics to date population divergence events. However, no consensus exists regarding the generation interval length, and a wide variety of interval lengths have been used in recent studies. This makes comparison between studies difficult, and questions the accuracy of divergence date estimations. Recent genealogy-based research suggests that the male generation interval is substantially longer than the female interval, and that both are greater than the values commonly used in genetics studies. This study

evaluates each of these hypotheses in a broader cross-cultural context, using data from both nation states and recent hunter-gatherer societies. Both hypotheses are supported by this study; therefore, revised estimates of male, female, and overall human generation interval lengths are proposed. The nearly universal, cross-cultural nature of the evidence justifies using these proposed estimates in Y-chromosomal, mitochondrial, and autosomal DNA-based population divergence studies. *Am J Phys Anthropol* 128:415–423, 2005. © 2005 Wiley-Liss, Inc.

For more than 40 years, researchers have used molecular genetic information to detect population relationships (Wray, 2001). Researchers estimate the date at which a population diverged into two groups by counting genetic mutation differences between groups to determine the number of generations since divergence, and then multiplying this by the generation interval (which is the average number of years per human generation). Genetic information has been used to propose dates for a number of significant human species and population divergence events. These include fairly recent events such as the initial Polynesian migration (Hage and Marck, 2003) and the Mongol expansion in Asia (Zerjal et al., 2002, 2003), as well as more ancient events such as the evolution of specific genes and haplotypes within the hominid line (Wooding et al., 2002; Zietkiewicz et al., 2003).

The accuracy of a population divergence date is directly related to the accuracy of the length of the generation interval. Unfortunately, researchers currently use a wide range of generation interval estimates (Table 1), often without discussion or citation regarding the source of the estimate (e.g., Wooding et al., 2002; Bortolini et al., 2003). Therefore, the accuracy of dates computed in these analyses is uncertain, and comparison between population divergence studies using differing generation intervals is difficult.

Weiss (1973) modeled the generation interval as part of his investigation of a variety of human demographic parameters in traditional anthropological situations. His analysis predicts an average generation interval ranging from 25.9–27.9 years, depending on the female fertility rate, the survivorship rate, and the population growth rate of the population in question. As his model used only female fertility rates, the generation interval of Weiss (1973) represents the female generation interval rather than the male or overall human generation interval.

Two recent studies used large genealogy databases to determine the generation intervals of two human populations (Table 2) (Tremblay and Vézina, 2000; Helgason et al., 2003). These studies each included two results that are relevant to population divergence date research: 1) the female generation interval is substantially shorter than the male interval; and 2) the female, male, and overall human generation intervals are longer than commonly supposed. As both Helgason et al. (2003) and Tremblay and Vézina (2000) noted, if their results are applicable to ancient human societies, then population divergence date calculations should apply a shorter generation interval when using mitochondrial DNA than when using Y-chromosomal or autosomal DNA, and generation intervals (and therefore divergence dates) are often underestimated in genetics-based population divergence studies.

It is not known, however, whether genealogical data from the two recent Western capitalist societies included in these genealogical studies are broadly applicable either to other recent societies or to the many populations included in the long time frame of genetics-based research. Therefore, this study investigated whether the genealogy-based results are consistent with data from societies in two very different cultural categories: modern nation states and recent hunter-gatherer societies. It was found that in both nation states and hunter-gatherer societies, the female generation interval was less

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TABLE 1. Sample of generation intervals used in recent studies

Generation interval	Genetic data type	Reference
20	Autosome	Anagnostopoulos et al., 1999
	Autosome	Bachinski et al., 2003
	Autosome	Rogers et al., 2004
	Autosome	Verrelli et al., 2002
	Autosome	Wooding et al., 2002
	mtDNA	Excoffier and Schneider, 1999
	mtDNA	Kaestle and Horsburgh, 2002
25	Y-chromosome	Dupanloup et al., 2003
	Autosome	Labuda et al., 1997
	Autosome	Niell et al., 2003
	Autosome	Reich et al., 2002
	Autosome	Slotkin, 2004
	Autosome	Wang et al., 2002
	Autosome	Zhivotovsky et al., 2003
	Autosome	Zietkiewicz et al., 2003
	Y-chromosome	Behar et al., 2003
	Y-chromosome	Bortolini et al., 2003
	Y-chromosome	Hage and Marck, 2003
	Y-chromosome	Kittles et al., 1998
	Y-chromosome	Zhivotovsky et al., 2004
25–30	Y-chromosome	Bonné-Tamir et al., 2003
27	mtDNA	Bolnick and Smith, 2000
30	Autosome	Quintana-Murci et al., 2003
	Y-chromosome	Zerjal et al., 2002
	Y-chromosome	Zerjal et al., 2003
35	Y-chromosome	Brion et al., 2003

TABLE 2. Generation intervals as determined by genealogical data¹

	Male	Female	Male and female
Icelandic generation interval	31.9	28.7	30.3
French Canadian generation interval	34.5	28.9	31.7

¹ All interval values are in years. Sources: Icelandic data source is Helgason et al. (2003) for period 1742–2002. French Canadian data source is Tremblay and Vézina (2000) for period 1850–1990s.

than that of the male, and that both intervals were commonly underestimated. The genealogy-based results are supported, and revised generation interval estimates are proposed for use in genetics-based human population divergence date studies.

METHODS AND DATA

The human generation interval (sometimes referred to as the generation length; Weiss, 1973) is the mean number of years between successive generations. In mitochondrial DNA (mtDNA) studies (in which the genetic information of interest is passed only along the maternal lineage), the relevant interval is the female generation interval, which in this study is designated as I_f . Within a population, I_f is equal to the mean maternal age at reproduction (Weiss, 1973). Note that this is not the mean age of first parturition, but the mean age of all parturitions by all women within a population history. Similarly, the male generation interval (I_m) is the parameter of interest for Y-chromosome studies, and equals the mean paternal age over all childbirths within a population history. The overall human generation interval (I_h) is the generation interval of interest in studies

using autosomal (and X-linked) data, and is the combined male and female mean age at reproduction. These three generation intervals are only dependent on the behavior of reproducing adults; people who do not have children cannot affect the time between births. Therefore, childhood mortality, adult sterility, and postreproductive mortality do not affect the generation interval of a population (except to the extent that they might modify the behavior of reproducing adults).

Relative male and female reproductive age difference

The female generation interval (I_f) will be estimated using maternity data, and (as described below) I_m and I_h will be estimated using I_f and the mean difference in male and female reproductive ages. In this paper, a population's mean male/female age difference at first marriage will be used as a proxy for the mean male/female reproductive age differential. That is, the mean age differential at which men and women enter the culturally defined normal reproductive unit will be used as a measure of the true differential of the mean paternal and maternal ages over all childbirths. Similarly, both Helgason et al. (2003) and Tremblay and Vézina (2000) used the marriage unit as a proxy for the reproductive unit. In this study, it is not necessary to assume that all reproduction occurs within marriage. Instead, it is only assumed that the age differential of first marriage approximately equals the age differential of reproduction. Nevertheless, the appropriateness of using first marriage age differential as a proxy for reproductive age differential must be considered; infidelity is to be expected in all human societies,¹ and the cultural response to infidelity varies widely (Broude, 1994; Jankowiak et al., 2002). However, it also appears that infidelity is universally condemned by spouses (of both sexes) in most situations (Betzig, 1989; Jankowiak et al., 2002). More importantly for the current analysis, sex outside of marriage does not necessarily affect the relevant age differentials. Note that premarital sex between future marriage partners, postreproductive marriage practices, and extramarital sex practices that either do not result in offspring or that average to reproductive age ratios equal to marriage age ratios cannot alter the reproductive age differential, and therefore may be disregarded. In the absence of data on the age differential of extramarital reproductive activity, marriage age differential data will be used, and the effects of hypothetical levels of false paternity (or remarriage) and age changes on generation interval estimates will be evaluated.

Two sets of marriage age data are used to test the hypothesis that the mean female generation interval is shorter than that of males. The United Nations (2000) published mean-age-at-first-marriage data for 199 countries, using information from national censuses and surveys taken between 1970–1998. Eight countries did not report male ages, and therefore were eliminated from the sample. The remaining 191 countries represent 84% of the world's countries, and over 97% of the world's population, and include both very small and very large nations.

¹ Helgason et al. (2003) reported that genetic analyses indicate a false paternity rate of less than 1.5% in modern Iceland. However, this value cannot be assumed to be applicable to other societies.

TABLE 3. Hunter-gatherer male/female age differential at first marriage¹

Hunter-gatherer society	C.U.	Age diff.	Hunter-gatherer society	C.U.	Age diff.	Hunter-gatherer society	C.U.	Age diff.
Africa			North America			Lake Yokuts		
Hadza	39	4.0	Attawapiskat Cree	2	2.5	North Foothill Yokuts	57	1.5
=kade	40	7.5	Mistassini Cree (1828)	2	3.0	Bella-Coola	58	-1.5
G/Wi	40	7.0	Naskapi	2	7.0	Cowichan	59	2.0
Hai//om	40	5.0	Nipigon	2	8.5	Stalo	59	3.0
Nharo	40	2.0	North Sauteaux	2	8.0	Lummi	61	4.0
!Kung Dobe Area	41	8.0	Plains Cree	2	7.5	Puyallup	62	6.0
!Kung Nyae Nyae	41	6.0	Rainy River (Emo)	2	5.0	Comox	63	3.0
!Kung Southern Auen	41	2.5	Round Lake Ojibwa	2	5.0	Lillooet	63	9.0
/Auni (Khomani)	42	4.0	Rupert House Cree	2	7.0	Shuswap	63	5.5
Baka Pygmies	49	2.0	Micmac	3	9.0	Thompson	63	4.0
Aka (Mbuti)	50	3.0	Arapaho	4	12.0	Flathead	64	4.0
Efe	50	3.0	Blackfoot (1875)	4	22.0	Sanpoil	64	3.0
Mbuti	50	2.5	Gros-Ventre	4	9.5	Sinkaietk	64	0.0
Dorobo	51	8.0	Yurok	5	3.5	Assiniboine	65	9.0
Asia			Quileute	27	5.0	Crow	66	11.0
Ainu (Hokkaido)	1	2.0	Aleut	31	5.0	Antarianunt S. Paiute	69	3.0
Gilyak	3	11.0	Nunivak	33	8.0	Cattail Paiute	69	2.0
Andaman Islands	6	2.0	Digueno	36	3.0	Comanche	69	9.0
Semang	23	4.5	Kiliwa	36	4.0	Death Valley Shoshoni	69	2.0
Agta (Cagayan)	24	2.0	Walapai	36	2.5	Deep Springs Paiute	69	3.0
Agta (Casiguran)	24	3.3	Yavapai	36	2.5	Kaibab Southern Paiute	69	3.5
Shompen	24	3.0	Eastern Pomo	37	2.0	Kidutokado	69	6.5
Ayta (Pinatubo)	26	2.0	Northern Pomo	37	12.0	Monache	69	2.0
Batek (Palawan)	26	4.8	Washo	38	1.5	Owens Valley Paiute	69	3.0
Hill Pandaram	30	6.0	Kiowa (1800s)	43	2.0	Wadadokado Paiute	69	2.5
Kadar	30	11.0	Kutenai	44	4.0	Cahuilla	70	5.0
Paliyans	30	14.0	Beaver (1880)	47	3.0	Cupeno	70	4.0
Yukaghir	34	6.0	Carrier	47	3.5	Tubatulabal	71	4.0
Australia			Chilcotin	47	1.0	Nootka	72	4.0
Anbarra	7	11.5	Chippewyan	47	14.0	Wappo	75	3.0
Gidjingali	7	12.0	Chiricahua Apache	47	2.5	Yuki (Poper)	76	3.0
Mulluk	8	15.0	Dogrib (1807)	47	6.0	Polar		
Groote Eylandt	9	24.0	Han	47	5.0	Aivilingmiut Inuit	32	5.5
Gunwinggu	10	19.0	Hare	47	3.0	Caribou Inuit (1922)	32	4.5
Southern Arenda	11	16.0	Holikachuk	47	9.5	Copper Inuit	32	12.0
Badjatang	12	7.5	Hupa	47	1.5	Kobuk Inuit	32	9.0
Ngatjan	13	14.0	Ingalik	47	9.0	Labrador Inuit	32	11.0
Dieri	14	12.0	Kaska	47	2.0	Netsilik Inuit	32	6.0
Ualaria	15	14.5	Koyukon	47	5.0	Noatak Inuit	32	3.0
Warunggu	15	19.5	Kutchin	47	1.0	Nunamiut Inuit	32	13.0
Karuna	16	13.0	Mattole	47	3.0	Polar Inuit	32	11.0
Yintjingga	16	13.0	Sarsi	47	2.5	Tareumiut Inuit (1852)	32	2.5
Yir-Yoront	16	17.0	Satudene-Bear Lake	47	14.0	South America		
Djaru	17	8.0	Slave	47	7.5	Ona	28	2.0
Jankundjara	17	14.0	Tahltan	47	4.0	Tehuelche	29	5.0
Mineng	17	8.5	Tanaina	47	13.2	Guahibo	35	4.0
Pintubi	17	13.0	Tutchone	47	9.0	Guato	45	2.0
Walbiri	17	13.0	Chinook	52	4.0	Nukak	46	5.5
Kaiadilt	18	16.0	Maidu	53	2.0	Nambikwara	48	1.5
Murngin	19	18.0	Nisenan Southern	54	0.0	Guayaki (Ache)	67	9.0
Tiwi	20	26.0	Maidu			Northern Ache	67	5.0
Worora	21	20.0	Modoc	55	3.0	Siriono	68	2.5
Jeidji	22	11.5	Nez Perce	56	2.0	Yahgan	73	2.5
Lungga	25	10.0	Tenino	56	3.5			

¹ C.U., culture unit; those societies sharing same three top levels in SIL International (2004) language phylogeny were grouped into a single culture unit. This consolidates 157 hunter-gatherer societies into 76 independent culture units. Age diff., age differential computed as mean male age at first marriage – mean female age at first marriage. Computed from data in Binford (2001, p 281–286), except =kade and Aka from Kelly (1995, p246) and Northern Ache from Hill and Hurtado (1996).

The second set of marriage-age data (Table 3) shows the age differential at first marriage for 157 recent hunter-gatherer societies. Table 3 is based on data collected by ethnographers during the 19th and 20th centuries, as reported in Binford (2001) and elsewhere.

These two data sets each contain numerous societies that may have historical or social commonalities, and

therefore statistical calculations using these data sets may suffer from a lack of independence. This circumstance, often termed Galton's problem, is common in cross-cultural studies (Mace and Pagel, 1994; Ember and Ember, 2000; Korotayev and de Munck, 2003). However, Galton's problem can usually be avoided by random sampling of a large data set (Ember and Ember, 2000). The

TABLE 4. *Hunter-gatherer birth ages*

Hunter-gatherer society	Mean maternal age at first birth	Mean maternal age at last birth	Source
Africa			
Dobe Ju/'hoansi (1963–1973)	21.4	34.4	Howell (1979)
Australia			
Anbarra	15.9	35.0	Kelly (1995)
Arnhem Land (polygamous)	19.2	34.3	Kelly (1995)
Arnhem Land (monogamous)	19.3	34.1	Kelly (1995)
Asia			
Batek (Palawan)	18.0	26.3	Kelly (1995)
North America			
Mistassini Cree (1828)	21.9	39.0	Kelly (1995)
Kutchin (pre-1900)	22.8	35.0	Kelly (1995)
Kutchin (post-1900)	19.8	39.0	Kelly (1995)
South America			
Northern Ache (born before 1959)	19.5	42.1	Hill and Hurtado (1996)
Northern Ache (reservation period)	17.7	38.5	Hill and Hurtado (1996)
Yanomama (Mucajai)	16.8	39.9	Early and Peters (1990)

nation-state data include almost all of the countries and population in the world, and therefore must be representative of the total world sample. To evaluate the impact of Galton's problem on this large data set, a subset of 25 nations will be randomly selected (with replacement) and the age differential mean will be computed, and this process will be repeated 1,000 times. The resulting standard deviation and range of the means will be evaluated to assess subcluster structure within the data set.

While the data in Table 3 include a large sample of hunter-gatherer societies, it nevertheless reflects only a fairly small subset of hunter-gatherer societies that exist or have existed in the recent past, and many of the societies in the sample share common historical roots. Therefore, to avoid Galton's problem, the hunter-gatherer data were aggregated into culture units that share a common language ancestry, so that any historical relationships between these aggregated culture units are unlikely to be recent (Foster, 1996; Ember and Ember, 2000; Korotayev and de Munck, 2003). For the sample of 157 hunter-gatherer cultures, this results in 76 culture units, with membership as shown in Table 3.

Estimation of generation interval values

The average female generation interval is known for a group of European developed nation states (Council of Europe, 2002), and may be estimated for less-developed countries and hunter-gatherer societies. These estimates are computed using mean maternal ages at first and last childbirth, assuming linear or symmetric birth patterns during reproductive years on a population-wide basis (Lutz, 1989; Hill and Hurtado, 1996). Maternal birth age figures are available for 40 less-developed countries included in the World Fertility Survey conducted between 1974–1978 (Durch, 1980; Lutz, 1989), and for a small number of hunter-gatherer societies (Table 4). As with age differential data, historical relationship concerns relating to Galton's problem were considered. The World Fertility Survey data may contain a sufficiently large and diverse sample as to avoid serious relationship problems; as with age differential data, this will be evaluated by repeated random subsampling. To minimize historical relationship concerns with hunter-gatherer society data, the societies in Table 4 are aggregated by continent when computing generation interval estimates.

This should ensure that the aggregated culture units had little historical contact with or influence on each other. Note that only eight separate cultures are represented by the 11 entries in Table 4. This fairly low sample size could affect the accuracy of hunter-gatherer generation interval estimates.

The maternal ages at last birth in the World Fertility Survey nation states were weighted by Lutz (1989), using detailed parity data to account for mortality during reproductive years, so for nation states, $I_f = (F_f + F_l)/2$, where I_f is the female generation interval for a particular society, and F_f and F_l are the maternal ages of first and mortality-weighted last birth for that society, respectively. However, the hunter-gatherer data in Table 4 are not weighted; the age-at-last-birth data are based on the last parturition of women who survived to the end of the reproductive lifespan, rather than on all women in a population history. Using the above equation for hunter-gatherer populations would fail to account for mortality during reproductive years, and would produce an artificially high I_f value. Therefore, a mortality factor was applied to account for accumulating mortality when computing the hunter-gatherer generation interval:

$$I_f \approx \frac{\sum_{i=F_f}^{F_l} (1 - M_f(i - F_f))}{F_l - F_f + 1}$$

where I_f is the female generation interval, F_f and F_l are the female ages at first and last birth, respectively, and M_f is the percentage of the female hunter-gatherer reproductive population that dies annually.² For Ache hunter-gatherers, M_f was nearly linear during reproductive years, with a value of about 0.6% per year (Hill and Hurtado, 1996). Similarly, Dobe Ju/'hoansi reproductive-age adults of both sexes born before 1950 had a nearly linear mortality rate of 0.6% annually (Howell, 1979).

²The value inside the summation computes a mortality-weighted age. These ages are then averaged. The calculation assumes a linear or symmetric number of childbearing around the average for the population (Lutz, 1989; Hill and Hurtado, 1996). Because F_f and F_l are not necessarily integers, the equation is only approximate. Both female and male generation intervals were computed using algebraic expressions for the summation of i and i^2 .

An M_f value of 0.6% will be used for maternal generation interval calculations for all hunter-gatherer societies.

Unfortunately, paternal birth ages are seldom reported for either nation states or hunter-gatherer societies. However, paternal ages at first and last childbirth may be computed by adding the male/female reproductive age differential to the female ages of first and last childbirth. As noted previously, age differential at first marriage is used in this report as a proxy for the reproductive age differential. Thus, the male generation interval for nation states may be computed as $I_m = ((F_f + D_{ns}) + (F_l + D_{ns}))/2 = I_f + D_{ns}$, where I_m , F_f , F_l , and I_f are the relevant nation-state figures as above, and D_{ns} is the marriage age differential in nation states. Once again, because the hunter-gatherer data are not weighted for mortality, the hunter-gatherer generation interval calculation is more complicated:

$$I_m \approx \frac{\sum_{i=F_f+D_{hg}}^{F_l+D_{hg}} i(1 - M_m(i - (F_f + D_{hg})))}{F_l - F_f + 1}$$

where I_m , F_f , and F_l are the relevant hunter-gatherer society figures as above, D_{hg} is the marriage age differential for hunter-gatherer societies, and M_m is the percentage of the male hunter-gatherer reproductive population that dies annually. For the Ache, M_m was approximately linear during reproductive years at 0.9% (Hill and Hurtado, 1996), and this value will be used for paternal generation interval calculations for hunter-gatherer societies. Use of an M_m value that is greater than M_f is consistent with modern societies, although the root causes of the mortality differential are not well understood (Hemström, 1999; Salomon and Murray, 2002). Due to this uncertainty, generation intervals are also calculated using $M_m = M_f = 0.6\%$.

Because males and females contribute equally to autosomal generation intervals, the overall human generation interval is the simple average $I_h = (I_f + I_m)/2$.

The marriage and childbirth age data used in this analysis are population statistics that were collected at different times by different researchers, and therefore are subject to temporal and methodological inconsistencies. This could reduce the accuracy of generation interval calculations. However, it does not seem likely that such inconsistencies would be consistently biased in either direction, and therefore should not significantly affect the computed values.

RESULTS

Reproductive age differential

Of the 191 nation states included in the sample, only one³ has a mean female age at first marriage that is greater than the mean male age at first marriage. The mean male/female age difference at first marriage for the 191 nation states is $D_{ns} = 3.5 \pm 1.7$ years. This is

TABLE 5. False-paternity effect on reproductive age differential¹

Assumed false-paternity rate (percentage)	Assumed mean false-paternity age change (years)	Reproductive age differential (years)
Less-developed nation states		
0	N/A	3.5
10	-1.7	3.4
10	-3.4	3.2
20	-1.7	3.2
20	-3.4	2.9
Hunter-gatherer societies		
0	N/A	7.0
10	-4.8	6.5
10	-9.6	6.0
20	-4.8	6.0
20	-9.6	5.1

¹ Mean false paternity age change is mean number of years that male – female age differential of false paternities differs from that of true paternities. It is set to one or two times the standard deviation of D_{ns} or D_{hg} , which is the age at first marriage differential assuming no false paternities for nation states or hunter-gatherer societies, respectively. It is negative because only the case in which false paternities have a lower age differential than true paternities is of current interest. Positive reproductive age differential indicates that male reproductive age is larger than that of female. N/A, not applicable.

significantly different from a null hypothesis of zero difference in ages ($t = 28.9$; $df = 190$; $P < 0.001$). Random sampling of 25-nation subgroups produced a mean of the age differential means equal to 3.5 ± 0.3 years, with a range of 2.7–4.6 years. Fifty-nation subgroups produced very similar results. This small standard deviation and range suggest that the marriage age differential data are not strongly influenced by historical or social sub-clusters within the sample.

As noted previously, the rate of infidelity leading to false paternity (i.e., reproduction in which the biological father is not the mother's husband) is unknown in most societies. To investigate the potential impact of false paternity, the reproductive age differential was computed using assumptions of 10% and 20% false paternity (Table 5). Because false paternity only affects reproductive age differential on a population basis if the mean age differential of false paternities differs from that of true paternities, a false-paternity age differential must also be assumed. Values for the false-paternity age differential were set to one and two times the standard deviation of D_{ns} , the marriage age differential for nation states. Even under assumptions of 20% false paternities with an average age differential twice the standard deviation of D_{ns} , the reproductive age differential is only 0.6 years less than the previously computed D_{ns} value of 3.5 years, and the male reproductive age remains well above the female reproductive age. The existence of a greater male than female reproductive age is therefore robust to significant levels of false paternity.

Bogue (1969) provided additional age at first marriage difference data from 160 censuses of 46 (mostly European) countries over the period 1899–1961. Every one of these censuses showed a greater male age, with a mean differential of 3.2 ± 1.3 years. While not directly comparable to the data used in this study due to both a limited cultural span and a broader temporal span, the data of Bogue (1969) support the direction and magnitude of the nation-state age difference. The data also

³The tiny European nation of San Marino reported a mean male age at first marriage of 22.2 years and a mean female age at first marriage of 22.3 years (United Nations, 2000). The United Nations (2000) reported an age differential of -0.2 years for San Marino due to rounding.

suggest that the European demographic transition from high birth and death rates to low birth and death rates (Herschman, 1994) has not materially affected marriage age differential.

Of the 157 hunter-gatherer societies listed in Table 3, again only one⁴ has a mean female age at first marriage that is greater than the mean male age at first marriage. After aggregating the societies into 76 language-based culture units, the mean male/female age difference at first marriage is $D_{hg} = 7.0 \pm 4.8$ years.⁵ This is significantly different from a null hypothesis of zero difference in ages ($t = 10.6$; $df = 75$; $P < 0.001$). Oddly, the mean age differential within nation states is, after rounding, exactly one-half that of the hunter-gatherer societies. This difference in age differential between the two groups is statistically significant ($t = 7.51$; $df = 265$; $P < 0.001$).

Once again, the potential impact of false paternities was investigated by assuming false-paternity frequencies of 10% and 20%, and false-paternity age differentials one and two times the D_{hg} standard deviation (Table 5). The change in age differential (1.9 years) is not large compared to the D_{hg} value (7.0 years), so the male reproductive age remains well above the female reproductive age.

Generation interval estimation

The mean maternal age at first birth for the 40 less-developed countries in the World Fertility Survey is $F_f = 20.5 \pm 1.0$ years, while $F_l = 36.1 \pm 1.5$ years. Using the formulas discussed in Methods and Data results in estimated less-developed nation-state generation intervals of $I_f = 28.3$ years, $I_m = 31.8$ years, and $I_h = 30.1$ years (Table 6A).

One thousand random subsamples of 10 nations each resulted in a mean of the age at first birth means equal to 20.5 ± 0.31 years (range, 19.4–21.4 years), while for mean age at last birth, the overall mean was 36.1 ± 0.47 years (range, 34.3–37.45 years). This suggests that sub-clusters do not seriously affect this data set, since no 10-member group was found to differ from the entire sample mean by more than 1.8 years for either age figure.

The mean female generation interval is directly available for developed European countries; the Council of Europe (2002) published statistics showing the mean age of women at childbirth for European countries at 5-year intervals from 1960–2000 ($n = 360$). In 1960, I_f was 28.1 years. It declined slightly during the following decades, reaching a low of 26.7 years in 1980. Subsequently, it gradually increased to reach 28.0 years in 2000. The overall mean across all countries and years is 27.3 ± 1.5 years. Thus, it appears that I_f was about 1 year less in these developed countries than in the sample of less-developed countries.

After aggregating the hunter-gatherer societies listed in Table 4 by continent, the mean hunter-gatherer maternal age at first birth is $F_f = 19.4 \pm 1.9$ years, and the maternal age at last birth is $F_l = 34.6 \pm 5.2$ years. This results

in estimated hunter-gatherer generation intervals of $I_f = 25.6$ years, $I_m = 31.5$ years, and $I_h = 28.6$ years (Table 6B). When calculated using $M_m = M_f = 0.6\%$, $I_f = 25.6$ years, $I_m = 32.3$ years, and $I_h = 29.0$ years.⁶

DISCUSSION

This analysis supports a substantial male/female age at first marriage differential. The near-total lack of societies with a norm of women marrying younger men indicates that women marrying older men may be classified as a human near-universal trait, as proposed by Brown (1991). As discussed earlier, marriage age differential is being used as a proxy for reproductive age differential, so a sex-based reproductive age differential may also be a near-universal trait.

For the purpose of genetics-based population divergence dating, it is important to consider whether this near-universality is a recent phenomenon. Certainly, near-universal traits can arise quickly; tobacco and metal tool use are examples of quickly arising near-universal traits (Brown, 1991). However, a change to the marriage (or reproductive) age differential does not have the immediate tangible benefits of these other traits, and could be expected to meet more cultural resistance. While perhaps one could argue that Western hegemony may have affected the marriage age differential of other cultures, one would expect that the effect would be movement towards the norm of the hegemonic culture. In fact, the hunter-gatherers in this study have an age differential that is twice that of nation states, which suggests that the age differential not only existed in the past, but may have been larger. In sum, while it is not impossible that so many societies with such different cultures could have recently adopted similar practices, it seems more likely that these recent similarities are the result of ancient similarities. In the absence of direct data on ancient reproductive ages, it is reasonable and appropriate to assume continuity and to project a substantial sex-based age differential into the ancient past. Therefore, population divergence date calculations should incorporate an age differential, with mtDNA studies using a shorter generation interval than autosome studies, which in turn use a shorter interval than Y-chromosome studies.

While it is not the intention here to identify the reasons why age differential is a near-universal phenomenon, a few comments are in order. One would expect an ancient near-universal trait to be driven by strong biological, cultural, or psychological forces, since it appears in almost all cultures despite very different ecological and social circumstances. In the present case, one could speculate that all three forces may be at work. Biological association is suggested, for example, by the fact that male chimpanzees mature sexually later than do females (Rowe, 1996) by about 16%, which corresponds to a human age difference of about 4 years. Cultural factors may include male delay in reproduction due to a need to establish a "signal" of hunting or other economic ability (Buss, 1989; Hawkes and Bird, 2002). Psychological aspects such as age-related differences in male and

⁴The Bella Coola, who live along the seaboard of British Columbia, Canada, were reported to have a mean female age at first marriage of 16 years, and a mean male age at first marriage of 14.5 years (Binford, 2001).

⁵This value is not significantly different from the mean age differential of all 157 societies taken separately, which is 6.6 ± 5.2 years ($t = 0.460$; $df = 231$; $P = 0.646$). This suggests that Galton's problem is not important for this data set, regardless of language family grouping.

⁶In general, a change of 0.1% in M_i results in a corresponding change of approximately 0.23 years in I_i and 0.11 years in I_m , while a 0.1% change in M_m causes a corresponding change of approximately 0.28 years in I_m and 0.14 years in I_h .

TABLE 6. Summary results¹

	n	Male	Female	Male and female
A. Nation states				
Age at first marriage	191	27.3	23.8	
Less-developed nations age at first birth	40		20.5	
Less-developed nations age at last birth	40		36.1	
<i>Less-developed nations generation interval</i>		31.8	28.3	30.1
<i>Developed nations generation interval</i>	360	30.8	27.3	29.1
B. Hunter-gatherer societies				
Age at first marriage	76	21.0	14.0	
Age at first birth	5		19.4	
Age at last birth	5		34.6	
<i>Hunter-Gatherer Generation Interval</i>		31.5	25.6	28.6

¹ See text for calculation procedures and data sources.

female sexual choices may also be involved (Kenrick and Keefe, 1992; Buunk et al., 2002).

The magnitude of the age differential (and of the associated generation interval values) is less securely known than is its existence. The age differentials found in hunter-gatherer societies and nation states are significantly different. Interestingly, the male generation intervals in the two groups are almost identical, at 31.5 and 31.8 years, respectively. Female generation interval differences between hunter-gatherer societies and nation states are essentially canceled out by corresponding differences in the male/female reproductive age differential.

It is instructive to compare these results to the genealogy-based generation intervals for Icelandic (Helgason et al., 2003) and French Canadian (Tremblay and Vézina, 2000) populations (Table 2). The female and overall generation intervals found in those studies are almost identical to those found for nation states in this analysis. Likewise, the Icelandic male generation interval matches the interval found in this analysis for less-developed nation states, while the corresponding interval for French Canadians is somewhat larger. The genealogical data were drawn from historical population subsets of Western nation states, so a close match to nation-state data in this analysis is not surprising. This match does, however, provide reassurance of the robustness of generation interval estimates, since two different approaches produced similar results.

For the purpose of estimating human population divergence dates using genetic data, these results indicate that projections based on Y-chromosome data should use a generation interval of 31 or 32 years, while estimates based on autosome data should use 28–30 years. The generation interval when using mtDNA may range from 25–28 years. These intervals are larger than most of those used in the current literature (cited in Table 1).

CONCLUSIONS

This study used cross-cultural data to estimate human generation intervals for use in genetics-based population divergence studies. A significant difference exists in the values of male and female generation intervals, with males almost universally having a longer generation interval than females. This difference should be accounted for when comparing analyses that utilize genetic material of more than one type (e.g., comparing

mtDNA-based divergence dates against autosome-based dates).

The human generation intervals estimated in this study are in general accordance with genealogical data (Tremblay and Vézina, 2000; Helgason et al., 2003), and are substantially larger than the values often used in population studies. The data in this study were necessarily taken from recent populations, but their near-universality across very disparate cultures, including many hunter-gatherer cultures, suggests that it is reasonable to project similar generation intervals into the past, at least until such time as direct data from ancient populations become available.

Given the uncertainty in projecting modern data into the past, as well as uncertainty related to the relationship between age differential at first marriage and reproductive age differential, it is appropriate to use the more conservative, lower values within generation interval ranges when computing population divergence dates. Therefore, absent of other information regarding ancient reproductive behavior, values of 25, 28, and 31 years should be used for the female, overall, and male generation intervals, respectively, for those studies in which a specific generation interval value (rather than a range of years) is appropriate. Researchers performing studies confined to regions where a consistent trend in generation interval is suspected (such as an uncommonly large male/female generation interval difference in portions of Aboriginal Australia; [Chisholm and Burbank, 1991; Williams, 1975]) may wish to adjust these figures to better accommodate their local circumstances.

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LITERATURE CITED

- Anagnostopoulos T, Green PM, Rowley G, Lewis CM, Giannelli F. 1999. DNA variation in a 5-Mb region of the X chromosome and estimates of sex-specific/type-specific mutation rates. *Am J Hum Genet* 64:508–517.
- Bachinski LL, Udd B, Meola G, Sansone V, Bassez G, Eymard B, Thornton CA, Moxley RT, Harper PS, Rogers MT, Jurkat-

- Rott K, Lehmann-Horn F, Weiser T, Gamez J, Navarro C, Bottani A, Kohler A, Shriver MD, Sallinen R, Wessman M, Zhang S, Wright FA, Krahe R. 2003. Confirmation of the type 2 myotonic dystrophy (CCTG)n expansion mutation in patients with proximal myotonic myopathy/proximal myotonic dystrophy of different European origins: a single shared haplotype indicates an ancestral founder effect. *Am J Hum Genet* 73:835–848.
- Behar DM, Thomas MG, Skorecki K, Hammer MF, Bulgina E, Rosengarten D, Jones AL, Held K, Moses V, Goldstein D, Bradman N, Weale ME. 2003. Multiple origins of Ashkenazi Levites: Y chromosome evidence for both Near Eastern and European ancestries. *Am J Hum Genet* 73:768–779.
- Betzig L. 1989. Causes of conjugal dissolution: a cross-cultural study. *Curr Anthropol* 30:654–676.
- Binford LR. 2001. Constructing frames of reference. Berkeley: University of California Press.
- Bogue DJ. 1969. Principles of demography. New York: John Wiley and Sons.
- Bolnick DAW, Smith DG. 2003. Unexpected patterns of mitochondrial DNA variation among Native Americans from the Southeastern United States. *Am J Phys Anthropol* 122:336–354.
- Bonné-Tamir B, Korostishevsky M, Redd AJ, Pel-Or Y, Kaplan ME, Hammer MF. 2003. Maternal and paternal lineages of the Samaritan isolate: mutation rates and time to most recent common male ancestor. *Ann Hum Genet* 67:153–164.
- Bortolini M-C, Salzano FM, Thomas MG, Stuart S, Nasanen SPK, Bau CHD, Hutz MH, Layrisse Z, Petzl-Erler ML, Tsuneto LT, Hill K, Hurtado AM, Castro-de-Guerra D, Torres MM, Groot H, Michalski R, Nymadawa P, Bedoya G, Bradman N, Labuda D, Ruiz-Linares A. 2003. Y-chromosome evidence for differing ancient demographic histories in the Americas. *Am J Hum Genet* 73:524–539.
- Brion M, Salas A, González-Neira A, Lareu MV, Carracedo A. 2003. Insights into Iberian population origins through the construction of highly informative Y-chromosome haplotypes using biallelic markers, STRs, and the MSY1 minisatellite. *Am J Phys Anthropol* 122:147–161.
- Broude GJ. 1994. Marriage, family, and relationships: a cross-cultural encyclopedia. Santa Barbara: ABC-CLIO.
- Brown DE. 1991. Human universals. Boston: McGraw-Hill.
- Buss DM. 1989. Sex differences in human mate preferences: evolutionary hypotheses tested in 37 cultures. *Behav Brain Sci* 12:1–49.
- Buunk BP, Dukstra P, Fetchenhauer D, Kenrick DT. 2002. Age and gender differences in mate selection criteria for various involvement levels. *Pers Relat* 9:271–278.
- Chisholm JS, Burbank VK. 1991. Monogamy and polygamy in Southeast Arnhem Land: male coercion and female choice. *Ethol Sociobiol* 12:291–313.
- Council of Europe. 2002. Recent demographic developments in Europe. Strasbourg: Council of Europe Publishing. http://www.coe.int/t/e/social_cohesion/population/d/E9mo211960EN.PDF.
- Dupanloup I, Pereira L, Bertorelle G, Calafell F, Prata MJ, Amorim A, Barbujani G. 2003. A recent shift from polygyny to monogamy in humans is suggested by the analysis of worldwide Y-chromosome diversity. *J Mol Evol* 57:85–97.
- Durch JS. 1980. Nuptiality patterns in developing countries: implications for fertility. Washington, DC: Population Reference Bureau.
- Early JD, Peters JF. 1990. The population dynamics of the Mucajai Yanomama. San Diego: Academic Press.
- Ember M, Ember CR. 1995. Worldwide cross-cultural studies and their relevance for archaeology. *J Archaeol Res* 3:87–111.
- Ember M, Ember CR. 2000. Testing theory and why the “units of analysis” problem is not a problem. *Ethnology* 39:349–363.
- Excoffier L, Schneider S. 1999. Why hunter-gatherer populations do not show signs of Pleistocene demographic expansions. *Proc Natl Acad Sci USA* 96:10597–10602.
- Foster MK. 1996. Language and the culture history of North America. In: Goddard I, editor. *Handbook of North American Indians*, Volume 17. Washington, DC: Smithsonian Institution. p 64–116.
- Hage P, Marck J. 2003. Matrilineality and the Melanesian origin of Polynesian Y chromosomes. *Curr Anthropol* 44:121–127.
- Hawkes K, Bird RB. 2002. Showing off, handicap signaling, and the evolution of men's work. *Evol Anthropol* 11:58–67.
- Helgason A, Hrafnkelsson B, Gulcher JR, Ward R, Stefánsson K. 2003. A populationwide coalescent analysis of Icelandic matrilineal and patrilineal genealogies: evidence for a faster evolutionary rate of mtDNA lineages than Y chromosomes. *Am J Hum Genet* 72:1370–1388.
- Hemström Ö. 1999. Explaining differential rates of mortality decline for Swedish men and women: a time-series analysis, 1945–1992. *Soc Sci Med* 48:1759–1777.
- Herschman C. 1994. Why fertility changes. *Annu Rev Sociol* 20:203–233.
- Hill K, Hurtado AM. 1996. *Ache life history*. New York: Aldine de Gruyter.
- Howell N. 1979. *Demography of the Dobe !Kung*. New York: Academic Press.
- Jankowiak W, Nell MD, Buckmaster A. 2002. Managing infidelity: a cross-cultural perspective. *Ethnology* 41:85–101.
- Kaestle FA, Horsburgh KA. 2002. Ancient DNA in anthropology: methods, applications, and ethics. *Yrbk Phys Anthropol* 45:92–130.
- Kelly RL. 1995. *The foraging spectrum: diversity in hunter-gatherer lifeways*. Washington, DC: Smithsonian Institution.
- Kenrick DT, Keefe RC. 1992. Age preferences in mates reflect sex differences in human reproductive strategies. *Behav Brain Sci* 15:75–133.
- Kittles RA, Perola M, Peltonen L, Bergen AW, Aragon RA, Virkunen M, Linnoila M, Goldman D, Long JC. 1998. Dual origins of Finns revealed by Y chromosome haplotype variation. *Am J Hum Genet* 62:1171–1179.
- Korotayev A, de Munck V. 2003. “Galton's asset” and “Flower's problem”: cultural networks and cultural units in cross-cultural research. *Am Anthropol* 105:353–358.
- Labuda D, Zietkiewicz E, Labuda M. 1997. The genetic clock and the age of the founder effect in growing populations: a lesson from French Canadians and Ashkenazim. *Am J Hum Genet* 61:768–771.
- Lutz W. 1989. *Distributional aspects of human fertility: a global comparative study*. London: Academic Press.
- Mace R, Pagel M. 1994. The comparative method in anthropology. *Curr Anthropol* 35:549–564.
- Niell B, Long JC, Rennert G, Gruber SB. 2003. Genetic anthropology of the colorectal cancer-susceptibility allele APC I1307K: evidence of genetic drift within the Ashkenazim. *Am J Hum Genet* 73:1250–1260.
- Quintana-Murci L, Veitia R, Fellous M, Semino O, Poloni ES. 2003. Genetic structure of Mediterranean populations revealed by Y-chromosome haplotype analysis. *Am J Phys Anthropol* 121:157–171.
- Reich DE, Schaffner SF, Daly MJ, McVean G, Mullikan JC, Higgins JM, Richter DJ, Lander ES, Altshuler D. 2002. Human genome sequence variation and the influence of gene history, mutation, and recombination. *Nat Genet* 32:135–142.
- Rogers AR, Iltis D, Wooding S. 2004. Genetic variation at the MC1R locus and the time since loss of human body hair. *Curr Anthropol* 45:105–108.
- Rowe N. 1996. *The pictorial guide to the living primates*. East Hampton, NY: Pogonias Press.
- Salomon JA, Murray CJL. 2002. The epidemiologic transition revisited: compositional models for causes of death by age and sex. *Popul Dev Rev* 28:205–228.
- SIL International. 2004. *Ethnologue*. <http://www.ethnologue.com>.
- Slatkin M. 2004. A population-genetic test of founder effects and implications for Ashkenazi Jewish diseases. *Am J Hum Genet* 75:282–293.
- Tremblay M, Vézina H. 2000. New estimates of intergenerational time intervals for the calculation of age and origin of mutations. *Am J Hum Genet* 66:651–658.
- United Nations. 2000. *World marriage patterns 2000: United Nations Population Division Department of Economic and*

- Social Affairs. <http://www.un.org/esa/population/publications/worldmarriage/worldmarriage.htm>.
- Verrelli BC, McDonald JH, Argyropoulos G, Destro-Bisol G, Froment A, Drousiotou A, Lefranc G, Helal AN, Loiselet J, Tishkoff SA. 2002. Evidence for balancing selection from nucleotide sequence analyses of human G6PD. *Am J Hum Genet* 71:1112–1128.
- Wang N, Akey JM, Zhang K, Chakraborty R, Jin L. 2002. Distribution of recombination crossovers and the origin of haplotype blocks: the interplay of population history, recombination, and mutation. *Am J Hum Genet* 71:1227–1234.
- Weiss KM. 1973. Demographic models for anthropology. In: Wobst HM, editor. *Memoirs of the Society for American Archaeology*, number 27. Washington, DC: Society for American Archaeology. p 1–186.
- Williams BJ. 1975. Age differentials between spouses and Australian marriage systems. In: Swedlund AC, editor. *Population studies in archaeology and biological anthropology: a symposium, memoirs of the Society for American Archaeology*, number 30. Washington, DC: Society for American Archaeology. p 38–43.
- Wooding SP, Watkins WS, Bamshad MJ, Dunn DM, Weiss RB, Jorde LB. 2002. DNA sequence variation in a 3.7-kb noncoding sequence 5' of the CYP1A2 gene: implications for human population history and natural selection. *Am J Hum Genet* 71:528–542.
- Wray GA. 2001. Dating branches on the tree of life using DNA. *Genome Biol* 3:1–7.
- Zerjal T, Wells RS, Yuldasheva N, Ruzibakiev R, Tyler-Smith C. 2002. A genetic landscape reshaped by recent events: Y-chromosomal insights into Central Asia. *Am J Hum Genet* 71: 466–482.
- Zerjal T, Xue Y, Bertorelle G, Wells RS, Bao W, Zhu S, Qamar R, Ayub Q, Mohyuddin A, Fu S, Li P, Yuldasheva N, Ruzibakiev R, Xu J, Shu Q, Du R, Yang H, Hurles ME, Robinson E, Gerelsaikhan T, Dashnyam B, Medhi SQ, Tyler-Smith C. 2003. The genetic legacy of the Mongols. *Am J Hum Genet* 72:717–721.
- Zhivotovsky LA, Rosenberg NA, Feldman MW. 2003. Features of evolution and expansion of modern humans, inferred from genomewide microsatellite markers. *Am J Hum Genet* 72:1171–1186.
- Zhivotovsky LA, Underhill PA, Cinnioglu C, Kayser M, Morar B, Kivisild T, Scozzari R, Cruciani F, Destro-Bisol G, Spedini G, Chambers GK, Herrera RJ, Yong KK, Gresham D, Tournev I, Feldman MW, Kalaydjieva L. 2004. The effective mutation rate at Y chromosome short tandem repeats, with application to human population-divergence time. *Am J Hum Genet* 74:50–61.
- Zietkiewicz E, Yotova V, Gehl D, Wambach T, Arrieta I, Batzer M, Cole DEC, Hechtman P, Kaplan F, Modiano D, Moisan J-P, Michalsk R, Labuda D. 2003. Haplotypes in the dystrophin DNA segment point to a mosaic origin of modern human diversity. *Am J Hum Genet* 73:994–1015.