

Reports

Fertility and Agriculture Accentuate Sex Differences in Dental Caries Rates

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The transition from foraging to farming is associated with a widespread and well-documented decline in oral health, wherein women experience a more rapid and dramatic decline than men. Historically, anthropologists have attributed this difference to behavioral factors such as sexual division of labor and gender-based dietary preferences. However, the clinical and epidemiological literature on caries prevalence reveals a ubiquitous pattern of worse oral health among women than men. Research on cariogenesis shows that women's higher caries rates are influenced by changes in female sex hormones, the biochemical composition and flow rate of saliva, and food cravings and aversions during pregnancy. Significantly, the adoption of agriculture is associated with increased sedentism and fertility. I argue that the impact of dietary change on women's oral health was intensified by the increased demands on women's reproductive systems, including the increase in fertility, that accompanied the rise of agriculture and that these factors contribute to the observed gender differential in dental caries.

The health profile of modern humans is directly influenced by evolutionary and cultural transitions that occurred over the course of human history. For example, the origin and intensification of farming reduced dietary breadth and diversity (Barker 2006; Rindos 1984) and allowed dense, sedentary settlements on regionally variable timetables (Bellwood 2005; Cohen 1977; Kennett and Winterhalder 2006). Though the stimulus for agricultural origins is controversial and demographic pressure (Cohen 1977), environmental change (Childe 1951), and socioeconomic competition (Hayden 1990, 1995) have been proposed, many agree that this transition increased the prevalence of nutritional deficiencies and infectious diseases and altered demographic parameters, including fertility (Cohen 1989; Cohen and Armelagos 1984; Larsen 1995). As oral health declined with the shift from

foraging to agriculture, women were affected more severely than men in both the Old World and the New World (Larsen 1998; Lukacs 1996). Diet change and sexual division of labor have traditionally been implicated in this differential decline in health; however, new research requires the adoption of a more complex explanatory model (Lukacs and Largaespada 2006).

I show that women's reproductive biology and changes in fertility across the Neolithic demographic transition (Ndt) contributed to the decline in oral health among women. As farming and sedentism intensified, fertility increased, inter-birth intervals decreased, and total fertility escalated in comparison with that of foragers (Bentley 1996; Bentley, Paine, and Boldsen 2001). The increase in fertility accompanying the Ndt is now established for Old and New World cemetery samples (Bocquet-Appel and Naji 2006). I posit that this increase in fertility makes an indirect yet significant contribution to the increase in dental caries rates by intensifying female reproductive function and concomitant physiological effects. Specifically, higher fertility heightens the negative consequences of hormonal fluctuations (e.g., changes in dietary preferences and immunological competence during pregnancy) and variations in saliva composition over the life course (Lukacs and Largaespada 2006).

This article challenges the consensus view that the decline in women's oral health with the origin and rise of agriculture is due solely to changes in diet and sexual division of labor. It does so by demonstrating the inadequacy of current analytical paradigms for the study of dental health and by questioning the validity of two widely accepted axioms regarding oral health: (1) women's oral health is significantly worse than men's due only to differences in behavior and (2) the decline in oral health with the shift to agriculture is due solely to dietary change. It begins by reviewing meta-analyses of dental caries prevalence in living and prehistoric human populations to demonstrate the ubiquity and consistency of the pattern and the degree to which women's oral health status is significantly worse than men's. This is followed by a discussion of female-specific hormonal patterns that influence female oral health and then a review of changes in demography and women's reproductive ecology that accompany the transition to agriculture. The paper concludes with a call for a more comprehensive evolutionary and ecological model of cariogenesis.

In this analysis, dental caries is used as a proxy indicator of women's oral health. Dental caries is a disease process involving progressive, focal demineralization of dental hard tissues by organic acids derived from bacterial fermentation of dietary carbohydrates, especially refined sugars (Featherstone 1987, 2000; Mandel 1979). In clinical research on oral health in living populations, dental caries is diagnosed by the presence of a "white spot," an area of subsurface demineralization. In bioarchaeology, dental caries lesions are routinely diagnosed as focal areas of necrotic cavitation of enamel and

dentine (Hillson 2001; Tayles, Domett, and Nelsen 2000). This difference in caries diagnosis makes comparison of caries rates in past and present populations problematic. However, in this analysis, gender differences in caries rates in living populations and, independently, sex differences in prehistoric samples are considered internally consistent and reliable data for comparative analysis.

Repositioning Oral Health in an Evolutionary Ecological Framework

Significant methodological and theoretical issues influence the analysis of oral health in living and prehistoric populations. Rigorous analysis of oral pathology requires attention to interobserver variance in methods, response to critiques of the osteological paradox, and the need for firmer theoretical grounding within an evolutionary and behavioral ecological framework. These issues are addressed in CA+ online supplement A.

Meta-Analyses Reveal a Consistent Pattern in Caries Prevalence by Sex

Meta-analyses of dental caries rates in living and prehistoric populations exhibit two significant patterns: (1) females tend to have higher caries rates than males and (2) the increase in caries with age is greater in females than in males. Two extensive meta-analyses of caries prevalence, based on studies completed prior to widespread fluoridation of community drinking water, demonstrate these patterns clearly. In the mid-twentieth century, a national survey of the literature on dental

Table 1. Sex Differences in Dental Caries Experience in Two African Groups

Age (years)	Caries Prevalence (%; n)		DMFT (SD)	
	Female	Male	Female	Male
Burkina-Faso: ^a				
12	30.7 (238)	26.6 (267)	.8	.6
18	60.6 (264)*	46.2 (228)	2.2**	1.5
35-44	81.7 (257)*	63.1 (236)	8.0*	4.4
Guinea-Bissau: ^b				
12	2.8 (2.6)	2.4 (2.5)
30-39	10.5 (7.2)*	6.3 (6.7)
50-50	16.4 (7.7)*	9.5 (7.1)

Note: DMFT = decayed, missing, and filled teeth.

^aVarenne, Petersen, and Ouattara 2004.

^bMatthesen et al. 1990.

**p* < 0.001.

***p* < 0.05.

caries reviewed 24 independent reports of caries prevalence in the permanent dentition by sex (National Research Council and Committee on Dental Health 1952). The majority (*n* = 21; 87.5%) found that females had higher caries rates than males. By contrast, two studies (8.3%) reported no intersex difference, and one study (4.2%) found that males had higher caries rates than females. Published reports evaluated in this meta-analysis were conducted in the 1930s and 1940s and varied in how caries prevalence was reported and whether statistical tests were applied. In conclusion, the study found that “both the caries attack rate and the total accumulated caries experience in the permanent teeth have been reported to be greater in females than in males of comparable age” (p. 153). In support of the second general pattern, the positive correlation between age and caries rates, the national survey found that “the caries experience appears to be higher in males in the younger ages and higher in females in the older age groups” (p. 158).

A second meta-analysis investigated the role of fluorides in the recent decline of dental caries in industrialized countries. In this study, Haugejorden (1996) provided extensive data on decayed, missing, and filled teeth (DMFT) by gender in European and American children from 12 to 17 years of age. Data from two separate meta-analyses are presented, one in the prefluoride era, including studies conducted between 1946 and 1959, and another completed in the postfluoride era (1983-93). Figure 1 was created from data presented in Haugejorden’s (1996, 370) table 1. Values on the X-axis (the weighted mean D(M)FT¹) were calculated from data reported for between four and six independent studies of dental caries rates by age group and by sex. The Y-axis is calibrated by age at the time caries experience was assessed. The number of

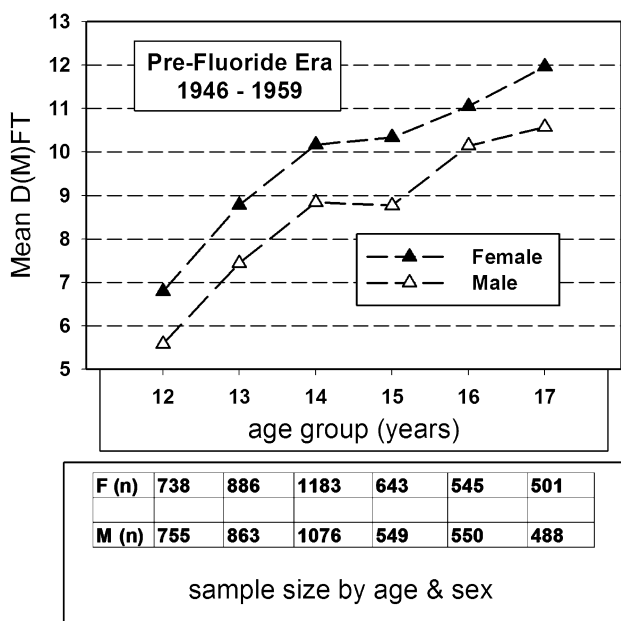


Figure 1. Sex differences in caries rates by age (mean decayed, missing, and filled teeth [DMFT]), Euro-American clinical samples (data from Haugejorden 1996).

1. The acronym D(M)FT signifies the mean number of decayed and filled teeth; no missing (M) teeth were observed in these samples of juvenile and young adults.

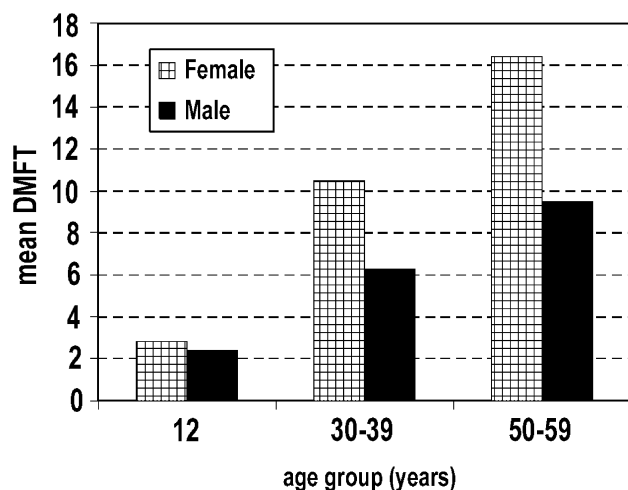


Figure 2. Sex differences in caries rates by age (mean decayed, missing, and filled teeth [DMFT]), Guinea-Bissau, Africa (data from Matthesen et al. 1990).

studies and sex-pooled sample sizes differ across age groups: 12 years cohort (studies = 4, $n = 1,493$), 13 years (5, 1,749), 14 years (6, 2,259), 15 years (4, 1,192), 16 years (5, 1,095), and 17 years (5, 989). Two clear patterns can be discerned in figure 1: (a) dental caries experience, as indicated by weighted mean D(M)FT, increases with age from 12 to 17 years in both sexes, and (b) at every age, females exhibit significantly greater mean D(M)FT than males.

Extensive evidence in support of a steeper increase in caries prevalence during ontogeny in females than in males comes from epidemiological studies of oral health in geographically widespread populations. Representative examples are reviewed from four continents: Africa, Asia, Europe, and North America. In Burkina Faso and Guinea-Bissau, West Africa, three age groups were analyzed, and no significant sex differences were found in caries prevalence or mean DMFT among 12-year-olds (table 1). However, in older age groups, females were found to have higher caries prevalence and mean DMFT. In the Burkina Faso study, caries prevalence and DMFT were significantly higher among 18-year-old females ($p < 0.05$) and were highly significantly greater ($p < 0.001$) for women in the 34–44 age group (Varenne, Petersen, and Ouattara 2004). Similarly, in Guinea-Bissau, sex differences in caries rates diverge significantly in the 30–39 and 50–59 age groups (fig. 2; Matthesen et al. 1990). This pattern persists in samples from Madagascar and Niger (table 2), where a significantly higher mean DMFT was reported for women in the 35–44 age group in both studies. However, sex differences in mean DMFT were nonsignificant in 6-, 12-, and 18-year-old age groups (Petersen and Kaka 1999; Petersen and Razanamihaja 1996). This trend in caries experience by age for Burkina Faso and Niger is readily discernible graphically in figures B1 and B2 in CA+ online supplement B.

Representative evidence for Asia comes from three sources. The first is a national survey of oral health in China, based

on extraordinarily large samples from diverse ethnic groups and geographic regions (Wang et al. 2002). Females tend to exhibit higher DMFT and caries prevalence at all ages, but the differences were found to be significantly greater among adults aged 35–44 years (fig. 3; table 3). Among the Yami aboriginals of Lanyu Island, China, mean DMFT was greater among males 4–6 years of age, while in each age group from 7 to 12 years of age, females were found to consistently exhibit greater mean DMFT than males (table 4; Lin and Chu 1997). Likewise, caries prevalence and mean DMFT were greater among 5-year-old male school children of Pondicherry, India, but by 12 years of age, females exhibited greater values for both measures of dental morbidity (Saravanan, Anuradha, and Bhaskar 2003).

Representative evidence for Europe comes from Spain and Denmark. Alvarez-Arenal et al. (1996) found that females in two age groups (35–44 and 44–64) in Oviedo, Spain, exhibited significantly higher caries rates than men (table 5; fig. C1 in CA+ online supplement C). A study of Danish female identical twin pairs found a direct correlation between the number of teeth lost and the number of children a woman had (total fertility): the twin with more offspring exhibited higher rates of tooth loss (Christensen et al. 1998). Because dental caries is frequently a precursor to antemortem tooth loss, this result indirectly suggests that higher caries rates are associated with increased fertility. The authors conclude that “the long-term costs of childbearing on women’s health may have been substantial and they may still be significant” (Christensen et al. 1998, 204). Through the use of robust regression techniques and pathway analysis, parity was recently found to be strongly associated with tooth loss in a large sample of white and non-Hispanic black American women ($n = 2,635$; Russell, Ickovics, and Yaffee 2008). The relationship between parity and tooth loss was examined by age and by socioeconomic position, yet the mechanisms of the association remained undefined.

In a study of low-income African Americans in Nashville, Seibert et al. (2004) found little difference in mean DMFT between females (7.52) and males (7.93) in the 9–19 age

Table 2. Sex Differences in Mean Decayed, Missing, and Filled Teeth in Madagascar and Niger

Age (years)	Madagascar ^a			Niger ^b	
	Female	<i>n</i> ^c	Male	Female (<i>n</i>)	Male (<i>n</i>)
6	4.7	1,866	5.1	2.09 (184)	2.16 (189)
12	3.3	1,992	2.8	1.24 (204)	1.36 (196)
15	5.8	1,130	5.1
18	7.3	792	6.1	2.38 (159)	2.72 (141)
35–44	14.5	1,809	10.9	6.34 (233)*	4.71 (167)

^aPetersen and Razanamihaja 1996.

^bPetersen and Kaka 1999.

^cText indicates that *n* is “balanced by sex.”

* $p < 0.001$.

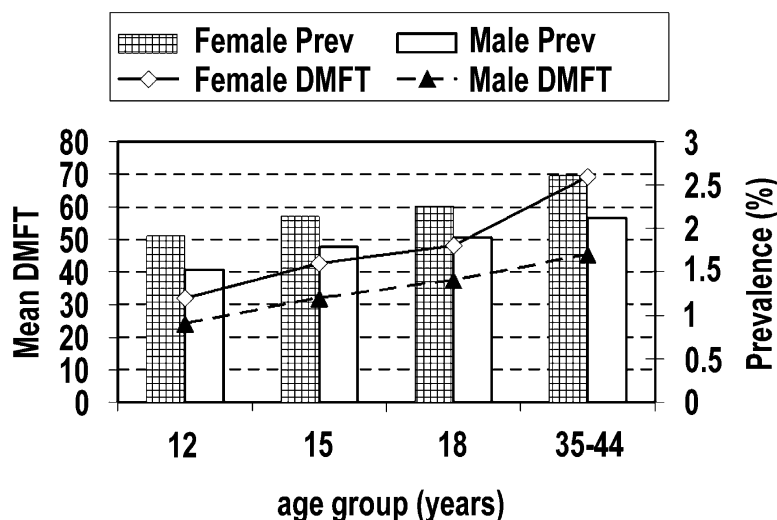


Figure 3. Sex differences in caries rates (mean decayed, missing, and filled teeth [DMFT] = line graph, left Y-axis; prevalence = bar graph, right Y-axis), China national survey (data from Wang et al. 2002).

group. By contrast, in the adult group (20–39 years), females had a mean DMFT of 15.18, double that for males (7.22). The authors conclude that “dental caries increased more rapidly in females as they reached adulthood,” and while no explanation is provided, they state that “this observation deserves further study” (Seibert et al. 2004, 27). Finally, when mature adults 35–44 years of age from Africa ($n = 3$), Asia ($n = 3$), and Europe ($n = 3$) are compared, females consistently exhibit higher DMFT scores (table 6).

A recent global meta-analysis of dental caries prevalence by sex in prehistory included 147 skeletal samples with diverse chronological contexts and wide-ranging cultural affiliations and subsistence patterns (Lukacs and Thompson 2007). When dental caries experience was reported by sex for large samples, the mean tooth count caries rate was significantly greater in females than in males in three continents (Asia, North America, and Central and South America) and tended to be greater in females than in males in two continents (Africa and Europe). The continental pattern translated into an average tooth count caries rate 3.6% greater among women than among men. A categorical approach revealed that females had significantly higher caries rates than males in 73.6% of comparisons (106/144). Despite analytical complications inherent to paleodemographic and bioarchaeological research (Boldsen 1997; Paine and Boldsen 2002) and issues such as the small size, representativeness of samples, and identification of sex in skeletons, the prevailing pattern of dental health in prehistory is consistent and clear: females typically experience significantly greater dental caries rates than males. This sex difference in dental caries is discernible in all age groups and attains higher levels of significance with increasing age.

The pattern documented here raises the question of what factors contribute to this prevalent discrepancy. If the decline

in oral health that accompanies the Ndt is due exclusively to changes in diet and methods of food preparation, why does agricultural intensification impact women’s oral health more than men’s?

Female Sex Hormones and Physiological Changes Associated with Pregnancy Impact Caries Prevalence and Accentuate Sex Differences in Oral Health

Anthropologists frequently report higher caries prevalence in females than in males and attribute this finding to cultural and, less often, physiological factors. Cultural factors include sex-based differences in dietary behavior—specifically, sexual division of labor in which women prepare and serve food, have easier access to stored food supplies, and eat more frequently during the day than males. Evidence comes from diverse settings, including central Africa (Walker and Hewlett

Table 3. Sex Differences in Dental Caries Prevalence in China (Wang et al. 2002)

Age (years)	Caries Prevalence (%)		DMFT (SD)	
	Female	Male	Female	Male
5	76.7	76.4	4.5 (4.2)	4.5 (4.2)
12	51.0	40.6	1.2 (1.6)	.9 (1.4)
15	57.1	47.7	1.6 (2.0)	1.2 (1.8)
18	60.1	50.5	1.8 (2.2)	1.4 (1.9)
35–44	69.6	56.5	2.6 (3.1)	1.7 (2.4)
65–74	67.7	61.8	13.0 (18.2)	11.6 (15.1)

Note: $n = 23,452$ per age group; total $n = 140,712$. Sample size by sex not indicated. DMFT = decayed, missing, and filled teeth.

Table 4. Sex Differences in Dental Caries (Mean Decayed, Missing, and Filled Teeth) among Yami Aboriginal Children of Lanyu Island, Taiwan (Lin and Chu 1997)

Age (years)	Female (SD) <i>n</i>	Male (SD) <i>n</i>
7	.81 (1.29) 21	.39 (1.12) 13
8	1.73 (1.71) 15	1.22 (1.73) 18
9	2.35 (1.63) 20	1.59 (1.46) 17
10*	2.04 (1.43) 24	1.18 (1.36) 28
11	3.11 (2.15) 9	2.41 (2.08) 29
12	4.20 (4.31) 25	3.11 (2.79) 27
Total	1.99 (2.59) 114	1.59 (2.04) 132

* $p < 0.05$.

1990), North America (Larsen 1983), East Asia (Temple and Larsen 2007), South Asia (Lukacs 1996), and Southeast Asia (Oxenham and Tayles 2006).

Physiological factors include sex differences in development, physiology, and hormones. For example, the earlier eruption of teeth in females and the effects of pregnancy are among the factors considered in caries etiology, yet the influence of these agents on caries rates is either grouped with cultural factors or discounted (Kelley, Levesque, and Weidl 1991; Larsen 1998). A case in point is Temple and Larsen's (2007) study of Yayoi Period Japanese, in which caries experience in the older subsample (>23 years) was found to be significantly greater in females than in males. Though female reproductive physiology was considered as a factor contributing to this pattern, it was discounted in favor of exclusively dietary explanations for differences between the sexes. The authors contend that a more universal trend of elevated caries rates would be evident among females if reproductive and hormonal factors were involved.

Earlier eruption of teeth in women as a primary cause of sex differences in caries rates is frequently cited in anthropological (Larsen 1997) and clinical (Antunes et al. 2003; Fédération Dentaire Internationale 1988) literature. However, an early and infrequently cited investigation of sex differences in caries prevalence specifically addressed the relationship between dental development and caries prevalence in girls and boys of the same age (Mansbridge 1959). Results of this carefully designed study "do not support the commonly accepted view that sex differences in caries are explained by earlier eruption of permanent teeth in girls" (p. 308). The study concludes that part of the difference in dental caries between the sexes is "constitutional" in origin. "Constitutional" connotes genetic causation, yet Mansbridge provides no examples of how "constitutional" factors impact differences in caries by sex.

A recent survey of biomedical and clinical research suggests an answer to this question. Lukacs and Largaespada (2006) revealed that female sex hormones and associated physiological factors can have a significant impact on cariogenesis. Five factors appear to be especially relevant. (1) Experimental re-

search on animals in controlled laboratory settings reveal that estrogens are positively correlated with increased caries rates while androgens are not (Muhler and Shafer 1954). (2) Saliva flow rate is lower in women than in men, reducing clearance of food residue from teeth and the oral cavity (Dodds, Johnson, and Yeh 2005; Dowd 1999; Tabak 2006). (3) The biochemical composition of saliva during pregnancy is altered in ways that significantly reduce its antimicrobial function and buffering capacity (Laine et al. 1988; Salvolini et al. 1998; Streckfus et al. 1998). (4) Suppression of women's immune response system during pregnancy may contribute to a reduction in antimicrobial activity in the oral cavity (Cheyney 2007; Fessler 2002). (5) During pregnancy, food cravings (e.g., for high-energy, sweet foods during the third trimester) and aversions (e.g., to meat, potentially high in teratogens in the first trimester) are evolutionary adaptations to insure fetal health and nourishment yet may also enhance the cariogenic nature of the mother's oral environment (Flaxman and Sherman 2000; Vallianatos 2007).

Higher estrogen levels in women over their life span have a cumulative and incremental effect that predisposes pre-adolescent girls to higher caries rates than boys during childhood. With the onset of puberty, estrogen levels fluctuate regularly, further enhancing hormonal predisposition to cariogenesis. During pregnancy, estrogen levels attain maximal levels and trigger other important physiological effects that promote cariogenesis, including dietary change (aversions and cravings that change throughout pregnancy; Vallianatos 2007), changes in salivary flow rate and biochemical composition (Salvolini et al. 1998), and a compromised immune response system (Cheyney 2007). The mechanistic synergism of these forces in contributing to higher caries risk among females throughout their life span is not fully documented or understood; however, if hormonal and physiological factors work in an independent or additive manner, their impact on women's oral health could be significant. The fact that women's caries experience increases with age at a greater rate than men's in diverse ethnic groups from different ecological and cultural settings supports this interpretation.

Further evidence in support of this hypothesis comes from a genomewide scan for suggestive caries loci among Filipinos from Cebu Island, Philippines (Vieira, Marazita, and Goldstein-McHenry 2008). This study identified loci influencing

Table 5. Sex Differences in Mean Decayed, Missing, and Filled Teeth in Oviedo, Spain (Alvarez-Arenal et al. 1996)

Age (years)	Female (SD) <i>n</i>	Male (SD) <i>n</i>
35–44	12.5 (6.1) 50	8.9 (5.9) 45
45–64	14.8 (6.6) 70	9.4 (6.3) 48
65–74	16.5 (8.4) 43	14.0 (8.4) 25
Total*	14.3 (8.4) 143	10.2 (6.9) 118

* $p < 0.001$.

Table 6. Sex Differences in Dental Caries (Decayed, Missing, and Filled Teeth) among Adults 35–44 Years of Age

Country	Female		Male	
	<i>n</i>	Mean (SD)	<i>n</i>	Mean (SD)
Burkina Faso ^a	257	8.0 (. . .)	236	4.4 (. . .)
China ^b	11,726	2.6 (3.1)	11,726	1.7 (2.4)
Denmark ^c	419	16.60 (.3)	343	16.70 (.3)
France ^d	513	14.90 (5.6)	487	14.40 (6.3)
Lebanon ^e	214	16.30 (6.4)	187	15.80 (7.2)
Lithuania ^f	210	20 (median)	168	15 (median)
Madagascar ^g	905	14.50 (. . .)	904	10.90 (. . .)
Niger ^h	167	6.30 (. . .)	233	4.70 (. . .)
Philippines ⁱ		14.45 (. . .)		10.96 (. . .)

^aVarenne, Petersen, and Ouattara 2004.

^bWang et al. 2002.

^cKrustrup and Petersen 2007.

^dHescot, Bourgeois, and Doury 1997.

^eDoughan, Kassak, and Bourgeois 2000.

^fSkudutyte, Aleksejuniene, and Eriksen 2000.

^gPetersen and Razanamihaja 1996.

^hPetersen and Kaka 1999.

ⁱVieira, Marazita, and Goldstein-McHenry 2008.

high and low caries susceptibility, as well as genes regulating saliva flow, estrogen-like receptors, flavor (taste and smell), and diet preferences. A protective locus for caries was found in the X chromosome, which the investigators suggest may partly explain the ubiquitous gender difference in dental caries rates (Vieira, Marazita, and Goldstein-McHenry 2008). Variation in the *amelogenin* gene, located on the X chromosome, was recently reported to contribute to higher caries susceptibility and may influence gender differences in caries prevalence (Deeley et al. 2008).

In youth, adolescence, and their reproductive years, women are affected by hormonal and physiological factors that directly and indirectly create a more cariogenic oral environment. Understanding these factors is critical to developing a more complete picture of oral health in evolutionary and ecological context.

How Significant Are Changes in Demography and Women's Reproductive Ecology at the Onset of Agriculture?

The recent shift in focus of paleodemographic research from mortality to fertility has fostered new perspectives on the relationship among critical variables such as subsistence, settlement, demography, and disease (McCaa 2002). The consensus is that the origin and intensification of agriculture are causally linked to several aspects of recent human evolution, including the decline in human skeletal robusticity (Ruff 2006) and the decline in oral health (Larsen 1995). The adoption of agricultural subsistence, reliance on less diverse and more highly processed foods, and changes in food preparation

methods all contribute to increased caries prevalence among farmers in contrast to foragers (Cohen 1989; Cohen and Armelagos 1984; Larsen 1995). The dramatic increase in caries prevalence accompanying the Ndt is graphically presented for pooled-sex skeletal samples from North America (fig. 4 [created from data in Larsen, Shavit, and Griffin 1991, 191–92]; table 3). The general relationship between subsistence and caries prevalence derived from a more eclectic global sample is evident in figure 5, created from data reported by Turner (1979, 625; table 3). Initially, the decline in health during a period of population growth accompanying the Ndt was considered paradoxical and counterintuitive (Armelagos, Goodman, and Jacobs 1991). However, if, as many contend, farming is tightly coupled with increased sedentism and changes in demography, then the disproportionate rise in caries rates among women with the onset and intensification of agriculture may be only partly explained by diet.

This section reviews recent research on changes in fertility and women's reproductive function with sedentism and the onset of agriculture. Evidence comes from two main sources, the demography of living populations engaged in different subsistence practices and archaeologically based paleodemographic research. In response to Handwerker's (1983) analysis of fertility and sedentism, Roth (1985) reported six cases of increased fertility concomitant with sedentism. He concluded that, contrary to Handwerker's findings, "fertility definitely increases with, and as a direct result of, sedentism" (p. 381; see also Roth 2004). Another early cross-cultural study of fertility in a sample of 70 foragers, horticulturalists, and farmers found no significant association between subsistence and total fertility rate (Campbell and Wood 1988). The relative cost or contribution of children to variation in fertility among groups with different subsistence systems has been evaluated by Hewlett (1991) and Kramer and Boone (2002). The latter study finds that among intensive Maya agriculturalists, children's labor appears to play a key role in subsidizing parental reproductive effort.

A reassessment of fertility in traditional agricultural and nonagricultural societies found significant differences in total fertility. Employing several methodological improvements over prior studies, the study reported total fertility of 6.5 for agricultural societies and 5.5 for nonagricultural groups (foragers and horticulturalists) and concluded that "higher fertility is primarily associated with the intensification of agriculture" (Bentley, Goldberg, and Jasienska 1993, 277). Subsequent investigation of the interrelationship among sedentism, agriculture, and fertility identified multiple causes of increased fertility among sedentary agriculturalists (Bentley 1996; Bentley, Paine, and Boldsen 2001), including larger family size (i.e., larger labor pool), availability of suitable weaning foods (resulting in a decrease in weaning age and interbirth interval), increase in nutritional intake (due to availability of stored foods), and decrease in women's workloads. These influences on fertility may be highly integrated in a bioenergetics model in which reproductive success is contingent on

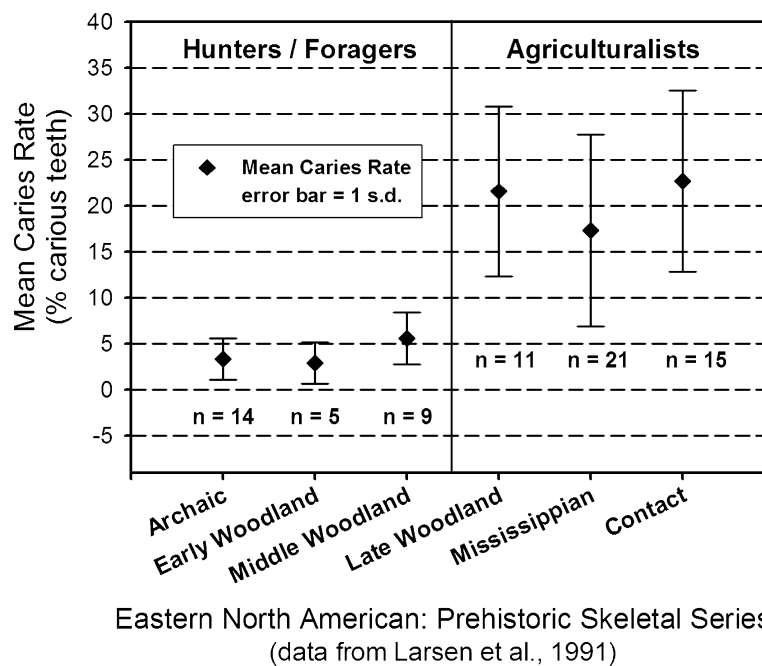


Figure 4. Dental caries and subsistence in prehistoric north America (% carious teeth).

varying local dietary and ecological conditions (Ellison 1990, 2001; Ellison et al. 1993). The higher fertility documented for sedentary women of rural Kavango District, Namibia, was greater than the fertility of nomadic foraging !Kung San women (Kirchengast and Neubert 2004). This association between fertility and subsistence in Namibia was attributed to a more stable food base, a positive energetic balance, and an increasingly sedentary lifestyle among the rural women of Kavango. The difference in fertility between groups was viewed as consistent with results reported by Bentley, Goldberg, and Jasienska (1993).

Some research questions accepted linkages among subsistence, settlement pattern, and demography. Others contend that modern forager models are inappropriate and that many accepted associations are incompletely documented or unsubstantiated (Pennington 2001). Key issues include (a) the relevance of modern hunting and foraging societies with economic links to nonforaging peoples, (b) the untested status of the “backload” model in which a four-year birth interval was adaptive in reducing the load carried by mobile women, and (c) the role of sexually transmitted diseases in lowering fertility in modern foraging groups (Pennington 2001). While these critiques represent valid concerns, the relationship between farming, sedentism, and population growth due to increased fertility is supported by a broad base of ethnographic and demographic evidence.

Paleodemographic evidence for increases in fertility comes from local, regional, and continental perspectives and provides additional support for increased fertility at the onset of

agriculture. Buikstra, Koenigsberg, and Bullington (1986) estimated fertility rates for eight Woodland and Mississippian populations from west-central Illinois. This study identified a significant increase in fertility in association with a dietary shift to high-carbohydrate seeds at a time when food processing technology was changing. Developments in ceramic technology that allowed preparation of weaning gruel may have been as important as or more important than the change in adult nutrition in influencing the increase in fertility (Buikstra, Koenigsberg, and Bullington 1986; Koenigsberg, Buikstra, and Bullington 1989).

A fertility-centered approach to paleodemography of the Americas was conducted using the Health and Nutrition in the Western Hemisphere database (McCaa 2002). One major contribution of this work was uncovering great variation in fertility in past populations and the identification of three main demographic systems. In ancient America, >1,500 years ago, fertility was surprisingly low, with a gross reproduction ratio (GRR) of 2.3. At this time, fertility, rather than mortality, was the limiting factor on population growth, a situation referred to as a low-pressure demographic system (McCaa 2002). The middle period, between 1500 and 500 BP, is characterized by high fertility and high mortality. This high-pressure system, initially associated with early horticulturalists (GRR 2.8), becomes generally associated with and intrinsic to complex agrarian systems (GRR 3.0). Although agriculture is not regarded as the innovation that triggered the rise in fertility, it is interpreted as a response to population growth and increasing density. The third and final demographic tran-

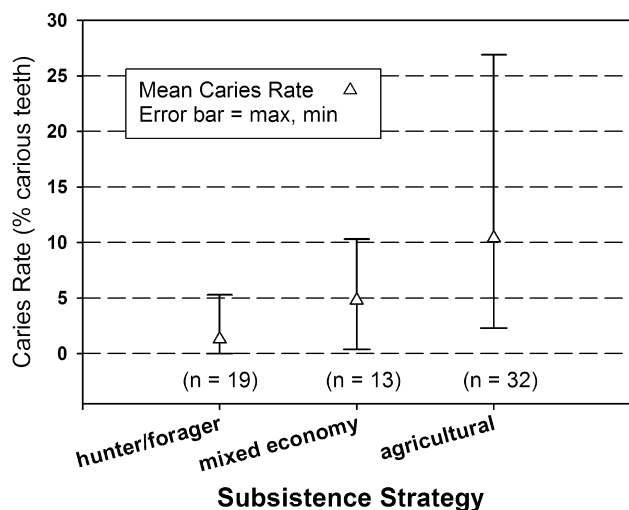


Figure 5. Dental caries rates and subsistence in a global sample of 64 groups (% carious teeth; data from Turner 1979).

sition dates to 500 BP and is associated with the arrival of Old World populations.

More recent paleodemographic research seeks to identify traces of an ancient demographic transition at the inception of agriculture by analyzing the proportion of immature skeletons in a large number of cemetery samples. Initially, a relatively abrupt increase in the proportion of immature skeletons was detected in a database composed of 38 Mesolithic-Neolithic cemeteries in Europe and North Africa (Bocquet-Appel 2002). In that analysis, the proportion of immature skeletons 5 to 19 years of age relative to the overall skeletal population of the cemetery ($_{15}P_5$) rose by 20%–30% over a span of between 500 and 700 years, reflecting a significant increase in the crude birth rate. The hypothesis of a New World “Neolithic” demographic transition was recently tested using data from 62 cemeteries in North America, between 7,755 and 350 BP (Bocquet-Appel and Naji 2006). A demographic signal accompanying the Neolithic subsistence transition in New World cemeteries occurred over a period of 600–800 years. Though agricultural origins are some 7,000–8,000 years later in North America, similarities exist in the proportion of immature skeletons in cemeteries and in the amount of change in crude birth rate and population growth rate. When North American and European data are aggregated, increases from forager to farmer in crude birth rate (forager = 42.7%; farmer = 51.5%) and in growth rate (forager = 0.6%; farmer = 1.26%) are derived. In sum, “not only did the horticultural-farming system increase the carrying capacity but the production system itself, resulting in sedentarization of society, increased individual fertility in women and raised the birthrate to an extent that is possibly unprecedented on this scale” (Bocquet-Appel and Naji 2006, 350).

Coupling Effects of Hormonal and Physiological Factors on Caries Rates in Women with the Ndt Fertility Increase Offers a New Perspective on Sex Differences in the Decline of Oral Health

If female sexual development and reproductive function are causally linked to increased caries experience in females and if adoption of a sedentary farming subsistence system increased fertility, then an integrated evolutionary and ecological model is required to understand the decline in women’s oral health. Considering the impact of hormonal and physiological sex differences on oral health does not replace existing behavioral and cultural approaches; rather, the two perspectives are complementary.

That women’s oral health tends to deteriorate more rapidly than men’s with the adoption of farming has been documented for both New World (Larsen 1998) and Old World (Lukacs 1996) populations. The evidence presented in figure 6 reveals a greater increase in caries prevalence with the adoption of maize agriculture by Native Americans of the Georgia Bight than among a composite group of South Asian skeletal samples experiencing a shift to wheat and barley. The greater increase in caries among women in both studies was attributed to dietary change and sexual division of labor. Larsen (1998, 175) considered biological factors in explaining sex difference in caries and tooth loss is a relationship not borne out by the scientific evidence.

This is simply not the case. Clinical evidence clearly supports a causal link between caries rates in women and (1) estrogen levels during development, (2) sex differences in saliva quality and quantity, and (3) the hormonal, physiological, dietary, and immunological effects of pregnancy. Ep-

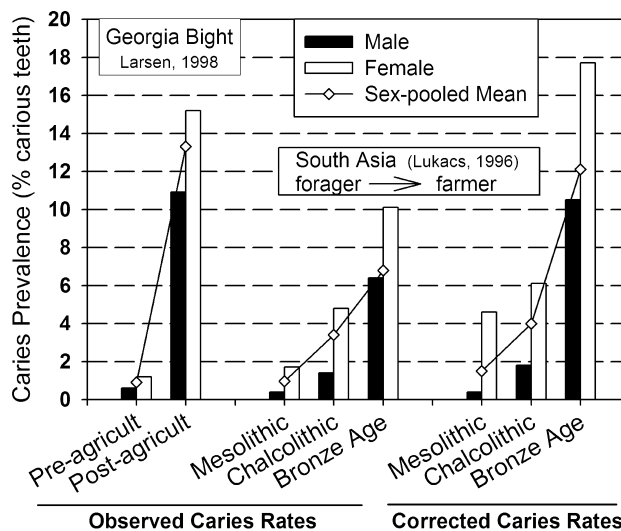


Figure 6. Sex differences in dental caries prevalence and the transition to agriculture (% carious teeth).

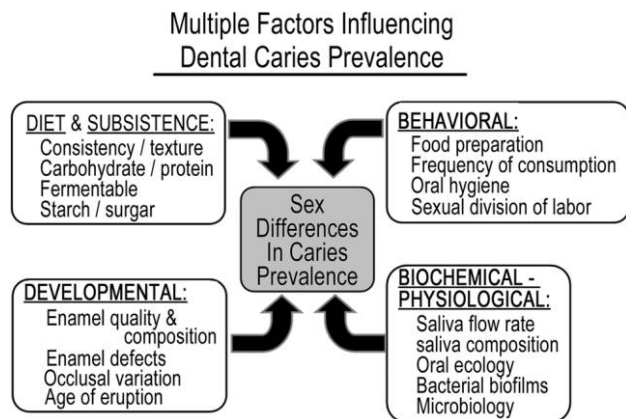


Figure 7. Multiple factors influencing dental caries prevalence.

idemiological analyses of caries prevalence must consider the amount by which women's caries rates exceeds men's, as well as the proportion of this difference that results from biological versus behavioral causes. Advances in paleodemography that permit reliable estimates of total fertility in prehistoric skeletons are essential to future success in this field of research.

Conceptually partitioning factors contributing to total caries prevalence into four additive components (diet and subsistence, behavior, development, and physiology) should help to improve our thinking about the multicausal nature of dental caries (see fig. 7). This is especially critical when considering the oral health consequences of transitioning from a foraging to a farming mode of subsistence. When a population experiences significant transformations in both diet and demography, how can major shifts in health confidently be attributed to one causal agent (e.g., diet change) and not another (e.g., increase in fertility)?

Some investigators disregard biological causation in explaining female caries experience because the pattern is not universal and because exceptions occur (Temple and Larsen 2007). This argument is surprising for several reasons: (1) primary cultigens differ regionally, (2) variations exist in dietary preferences and in nondietary uses of the dentition, (3) sex differences in the frequency of food consumption occur, and (4) a host of other relevant behavioral factors are highly variable cross-culturally (Oxenham and Tayles 2006; Steckel and Rose 2002). Ecological and behavioral variation result in occasional exceptions to the prevalent pattern of worse female oral health. Such exceptions are to be expected when cultural factors produce conditions that are unfavorable to male oral health. Such departures from expectation should be studied intensively to identify the causal factors responsible.

Differences in the timing or tempo of agricultural origins and primary cultigens involved will have a direct effect, accelerating the increase in caries rates and influencing how the sexes are differentially impacted. For example, continental signatures of a worldwide Ndt are based on averages of currently available data (Bocquet-Appel and Naji 2006, 347). Bocquet-Appel and Naji contend that the tempo of the Ndt

was not the same everywhere, especially in the centers of independent agricultural invention, where a reversed causality (demographic following economic change) and much slower and gradual tempo of transition is expected. Caries data for the Levant are consistent with this interpretation, showing a small and nonsignificant increase in caries rate between Natufian (6.4%, $n = 1,160$) and Neolithic (6.7%, $n = 804$) samples in a center of agricultural development (Eshed, Gopher, and Hershkovitz 2006). By contrast, in peripheral or secondary areas where adoption of agriculture is more abrupt, dramatic, and rapid, the rise in caries should exhibit a distinct and discontinuous increase. In their study of dental pathology at the origin of agriculture in the Levant, Eshed, Gopher, and Hershkovitz (2006) did not report dental caries prevalence by sex. However, a similar pattern of sex differences in caries is hypothesized. In central or core areas, the impact of changes in fertility, diet, and division of labor should be slow and gradual; in secondary, peripheral areas, the impact of biological and cultural changes on sex differences in caries rates should be more rapid and the decline in women's oral health more precipitous and easily discerned than men's.

Concluding Remarks and Recommendations

This synthesis of clinical, evolutionary, and anthropological perspectives on differences in dental caries rates for men and women offers several important insights. (1) A broad view of clinical, epidemiological, and bioarchaeological data reveals a ubiquitous and nearly universal pattern in which dental caries rates are higher among women than among men. (2) Biological factors, such as preadolescent sex hormone levels, menstrual cycling and hormonal fluctuations, and pregnancy (hormone fluctuation, saliva composition, diet cravings and aversions, and immune suppression), have an adverse impact on women's oral health by promoting cariogenesis. (3) The relationship between subsistence and demography in modern peoples and archaeological skeletal series suggests a strong correlation between fertility and farming. The origin of ag-

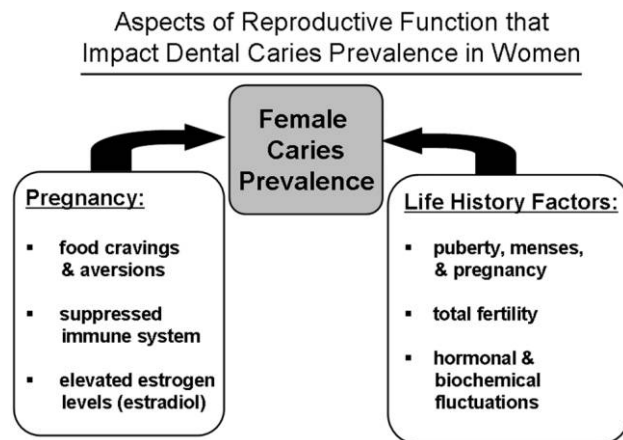


Figure 8. Aspects of reproductive function that impact dental caries prevalence in women.

riculture and associated phenomena (e.g., sedentism, need for farm labor, availability of weaning foods, decrease in inter-birth interval) are intimately tied to increased fertility. (4) Because female reproductive biology impacts oral health and because fertility increased with the advent of agriculture, some measurable amount of the Ndt increase in women's caries prevalence is attributable to the associated increase in reproductive activity.

Traditional perspectives on the impact of agriculture on women's caries rates heavily emphasize sex differences in diet and labor while discounting the impact of biological factors such as pregnancy. Early investigators who did attribute higher caries rates in women to the effects of pregnancy (Stewart 1931) argued that gestation caused nutrients, especially calcium, to leech from the teeth and bones and that a large number of births, or births spaced closely together, increased this effect (Winikoff and Castle 1987). Known as "maternal depletion syndrome," this hypothesis was refuted with respect to the hard dental tissues in the late 1930s (Lynch, Kettering, and Gies 1939).

The complex etiology and multiple mechanisms influencing sex differences in cariogenesis require broader theoretical and conceptual frameworks. A model that includes both behavioral and biological factors is essential (fig. 7). This model minimally consists of four categories, the first two of which are culturally mediated and the second two of which are biologically mediated: (a) diet and subsistence, (b) behavioral factors, (c) developmental factors, and (d) biochemical and physiological factors. Although students of dental health generally appreciate the complex etiology of caries, few embrace a broad model of cariogenesis that incorporates all four factors. The age-dependent nature of dental disease has been appreciated for many decades by clinical, epidemiological, and bioarchaeological researchers. Paradoxically, the value of a life-history approach in explaining sex differences in caries rates has been overlooked despite the significant explanatory power it offers. Although implied in the fourfold model of cariogenesis presented in figure 7, the ways in which female sexual development and reproductive function impact dental caries prevalence are explicitly highlighted in figure 8. Female life-history factors include higher estrogen levels during the full course of preadolescent development, as well as during puberty, menstrual cycling, and pregnancy. Because of its manifold significant effects, pregnancy is regarded as a primary contributor to higher caries rates in women.

Five recommendations come from this review. (1) Dental caries prevalence should be reported by sex, on the basis of both the number of teeth observed and the number of individuals studied. (2) Statistical tests for significant differences in caries experience by sex should be routinely applied. (3) All possible etiological factors should be considered when explaining sex differences in caries rates. (4) Greater caries experience in women should be an expected research finding, given the fundamental biological relationship between female sexual development, reproductive function, and oral health.

(5) Explaining the decline in women's oral health with agriculture as the exclusive result of dietary change and division of labor is short-sighted and incomplete. The increase in fertility with agriculture, in conjunction with new evidence demonstrating how female reproductive life history influences dental caries, requires that researchers acknowledge that the decline in women's dental health with agriculture results from the combined effects of fertility and agriculture.

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