Evolutionary biological perspectives on the public health and social issues of breastfeeding and weaning

Takumi Tsutaya[1,2,*]

[1] Department of Evolutionary Studies of Biosystems, the Graduate University for Advanced Studies, Shonan Village, Hayama, Kanagawa, 240-0193, Japan

[2] Globe Institute, Faculty of Health and Medical Sciences, University of Copenhagen, Øster Voldgade 5-7, 1350 Copenhagen, Denmark

[*] Corresponding author. E-mail: tsutaya_takumi@soken.ac.jp, tsutayatakumi@gmail.com

ABSTRACT

Breastfeeding and weaning are important topics for both biological anthropology and public health because they closely relate to infant mortality, lifetime health, and human population dynamics. Breastfeeding and weaning practices are associated with several issues that hinder the achievement of infant and mother well-being in our modern societies. By integrating the scientific knowledge which has been accumulated in biological anthropology and public health, the obtained comprehensive understanding can allow addressing these issues through effective decision making. In this review, public health and social issues pertaining to the breastfeeding and weaning of modern and historical human populations are interpreted from the viewpoint of biological anthropology, including the disciplines of evolutionary biology and bioarchaeology. These issues include the spatio-temporal constraint of breastfeeding, memes of non-breastfeeding, abuse of breast milk materiality, and mismatch in breastfeeding practices. Some issues have an evolutionary base, while others can be best

understood by considering the framework of evolutionary biology. The structure of these issues and their possible public health and social outcomes are also discussed based on the concept of trade-off. The effectiveness of the biological view in better understanding the public health and social problems in breastfeeding and weaning is lastly discussed.

KEYWORDS

breastfeeding and weaning; mismatch; trade-off; evolutionary biology; public health

INTRODUCTION

Human breastfeeding and weaning is an important area of research in biologyical anthropology, including evolutionary biology and bioarchaeology, as well as public health, by closely relating to both health and reproduction. Scientific knowledge on breastfeeding and weaning has accumulated in these disciplines under different scopes and practices. A comprehensive understanding leading to effective outcomes can be achieved by combining the knowledge obtained in biology and public health, although this type of effort was rarely performed (Fewtrell et al., 2020; Kendall et al., 2021; Sellen, 2001; Stuart-Macadam and Dettwyler, 1995; Tomori et al., 2018). This review aims to decipher the public health and social problems of breastfeeding and weaning through the lens of biological anthropology, with the aim of generating insights that may benefit public health campaigns and policy making and provide future directions of research.

Public health benefits of breastfeeding

Breastfeeding and weaning which are directly related to infant and maternal health

represent one of the most important targets of public health promotion campaigns. Breast milk contains various antimicrobial agents and bioactive substances, as well as nutrients, which promote infant health and survival and have lifelong health benefits (Ballard and Morrow, 2013; Jackson and Nazar, 2006; Section on Breastfeeding, 2012; Victora et al., 2016; WHO, 2009). Six months of exclusive breastfeeding and at least two years of continuing breastfeeding are recommended to increase infant survivorship, especially in regions with poor hygienic and nutritional environmental conditions (Kramer and Kakuma, 2012; WHO, 1998, 2009). During the first few years of life, the immune system of infants is underdeveloped making them vulnerable to pathogens. Breast milk can compensate for this infant vulnerability in the immune system (Jackson and Nazar, 2006; Section on Breastfeeding, 2012; Victora et al., 2016; WHO, 2009). When a mother encounters a pathogen, immunoglobulins, such as IgG and secretory IgA, which are specific to the pathogen, are released into the mother's breast milk (Jackson and Nazar, 2006; Victora et al., 2016). In addition to cellular immunity, which is notably mediated by macrophages and lymphocytes, breast milk is rich in nonspecific antipathogen components such as lysozyme and lactoferrin (Ballard and Morrow, 2013; Jackson and Nazar, 2006; Victora et al., 2016; WHO, 2009). These factors exert a protective effect on mucous membranes of the respiratory and gastrointestinal tracts of infants consuming breast milk (Jackson and Nazar, 2006; Victora et al., 2016).

Human breast milk contains relatively higher concentrations and great diversity of complex oligosaccharides, which play an important role in the development of the intestinal microbiota (Zivkovic et al., 2011). Oligosaccharides are the third most abundant components (i.e., 5–23 g/L), after lactose and lipids, and present over 200 different structures differing in size,

charge, and sequence (Kunz et al., 2000; Ninonuevo et al., 2006). Oligosaccharides reach the large intestine without being digested and provide nutrients for *Bifidobacterium*, which exerts a range of beneficial health effects on the host. Oligosaccharides provided by breast milk selectively fuel the intestinal microbiota of infants, a feature that has probably been acquired through the co-evolution of milk components and the intestinal microbiota (Zivkovic et al., 2011).

Breast milk also provides lifelong, long-term health benefits. Breastfed infants have a reduced risk of developing infectious diseases, obesity, and type II diabetes, not only in childhood, but also into adulthood (Binns et al., 2016; Robinson and Fall 2012; Section on Breastfeeding, 2012; Victora et al., 2016). Furthermore, the experience of breastfeeding in mothers decreases their risk of postpartum hemorrhage, breast cancer, and ovarian cancer (Section on Breastfeeding, 2012; Victora et al., 2016; WHO 2009).

Lactational amenorrhea, or temporal postnatal infertility, occurs in lactating mothers, which can be regarded as a safeguard to ensure the health and survival of both the mother and infant. Prolactin which is secreted by sucking stimuli of the nipples prevents the release of gonadotropin-releasing hormone from the hypothalamus, resulting in a suppression of ovulation (Hill et al., 1999; WHO 2009; Wood, 1994). As a consequence, the mother is less likely to have another pregnancy while breastfeeding continues. In addition to responding to suckling stimuli, this suppression system is affected by the nutritional status, making ovulation suppression less effective when the mother is well nourished (Valeggia and Ellison 2009). When nutritional conditions are adequate, it is more adaptive to have many children. However, conceiving another child while having a breastfed infant confers greater risk for the health and survival of the mother and infant under poor nutritional conditions. Lactational

amenorrhea is thus considered to have evolved to avoid such risks.

Because of these health benefits, breastfeeding has been promoted worldwide during the last several decades, especially in regions with poor nutritional and hygienic environmental conditions (Pérez-Escamilla, 2020; Rollins etal., 2016; WHO, 1998). The public health benefit of breastfeeding is evident even in modern developed countries (Chen and Rogan 2004).

Breastfeeding in biological anthropology

Breastfeeding and weaning are important research topics in biological anthropology, including the disciplines of evolutionary biology and bioarchaeology, because they directly relate to inclusive fitness, reproduction, and population dynamics. Breast milk has evolved in the ancestors of mammals approximately 310 million years ago, then became the primary nutrient source for infants approximately 210-170 million years ago (Oftedal, 2012). Breastfeeding is a form of maternal investment in infants which results in a conflict between mother and infant, where the mother tries to optimize investment to the current offspring and her future reproductive opportunity, while the infant tries to draw maximum investment from the mother (Fewtrell et al., 2020; Trivers, 1974). The maternal-infant conflict, as well as species-specific life history, ecology, and sociality, have resulted in diverse patterns of breastfeeding and weaning in mammals (Fewtrell et al., 2020; Sellen, 2007). Studying the variations of weaning patterns among species and individuals can inform on the diversity of reproductive strategies and environmental adaptations (Hinde and Milligan, 2011; Lee, 1996). Additionally, the age at the end of weaning is considered the strongest proximate determinant of interbirth intervals (Bongaarts, 1978, 2015), due to the effect of lactational amenorrhea.

Therefore, measures of breastfeeding and weaning practices, such as breastfeeding duration and weaning ages, have been used in anthropological and bioarchaeological studies to understand past and current population dynamics as well as their outcomes on health (Helle et al., 2014; Humphrey, 2010; Katzenberg and Herring, 1996; Konner and Worthman, 1980; Tsutaya and Yoneda, 2013, 2015; Wood et al., 1985).

The objective of this review

In this review, current and past public health and social issues pertaining to breastfeeding and weaning are interpreted from the viewpoint of biological anthropology with the aim to investigate the underlying mechanisms and provide better understanding of the problems. Four aspects of public health and social issues in breastfeeding and weaning are discussed: spatio-temporal constraint of breastfeeding, memes of non-breastfeeding, abuse of breast milk materiality, and mismatch in breastfeeding practices. Lastly, more effective public health practices will be proposed by considering the concept of trade-offs.

SPATIO-TEMPORAL CONSTRAINT OF BREASTFEEDING

Frequent breastfeeding and milk with low energy density

Humans and human ancestors lived as nomadic foragers in their evolutionary time until the very recent Holocene, which resulted in frequent breastfeeding and production of milk with low energy output in humans. Forager mothers typically carried their offspring with them during foraging activities for the first few years of the offspring life (Draper and Cashden, 1988; Blurton Jones and Sibly, 1978; Blurton Jones et al., 1989), as many other non-human primate species (Nakamichi and Yamada, 2009). Forager mothers thus spent a lot of time with

their offspring and breastfed frequently (Konner and Worthman, 1980; Konner, 2016).

Such a forager lifestyle led to the evolution of feedback systems in breast milk production resulting in milk with low energy density. Prolactin which stimulates milk production in the mammary gland is secreted by the pituitary gland upon stimulation of sucking on the mother's nipple (Hill et al., 1999). Milk production continues as long as prolactin levels in the blood remain high, but in fact, prolactin levels decline very quickly: the half-life of prolactin in the blood system is approximately 30 minutes (Nunley et al., 1991). Therefore, pproximately two hours after the last sucking stimulus to the nipple, blood prolactin levels are generally reduced to basal levels (Howie et al., 1980; Glasier et al., 1984). In the foraging lifestyle, when mother and infant spent a lot of time together, frequent breastfeeding kept the prolactin levels high, allowing breastfeeding to continue for several years (Konner and Worthman, 1980; Sellen, 2001; Sellen and Smay, 2001).

Humans, like many other non-human primates, secrete dilute milk that is rich in sugars (i.e., lactose) but relatively low in fat and proteins, and has a low energy density (Hinde and Milligan, 2011). The average human milk has lactose, fat, and protein concentrations of about 7.3%, 3.7%, and 1.3%, respectively (Hinde and Milligan, 2011). By contrast, mammals in which mothers leave the infants in the nest to forage for food over several days (e.g., rabbits and Echidna) have a high energy density in their milk to prevent starvation of the infants even if breastfeeding bouts have an interval of several days (Hinde and Milligan, 2011). For example, the hooded seals (*Cystophora cristata*) secrete thick milk (1% lactose, 61% fat, 5% protein) almost continuously for the first four days of life, thus transferring a total of 7 kg of fat to their young to enable them to survive in the cold ocean (Oftedal and Iverson, 1995; Oftedal, 2000). Compared to these other mammals, the composition of human milk is more

characteristic of a species in which mothers forage together with the infants and frequently breastfeed.

Work-life balance in breastfeeding

Contrary to the foraging mothers during the evolutionary timeframe, employed mothers in modern industrialized countries typically do not bring their infants to the workplace, which hinders the continuation of breastfeeding. The need to resume work is one of the most frequently cited reasons for mothers to stop breastfeeding in modern industrialized countries (Rollins et al., 2016). The separation of mother and infant resulting in the absence of suckling stimuli over a whole day promotes a cessation of breast milk production because of the feedback system in milk production (Hill et al., 1999). If a time and suitable environment for breast pumping or breastfeeding the infant are not provided, it will be difficult for employed mothers to continue breastfeeding after returning to work (Heymann et al., 2013; Steurer, 2017). Also, the absence or lower availability of paid maternity leave leads to an earlier cessation of breastfeeding (Chai et al., 2018; Heymann et al., 2013; Navarro-Rosenblatt and Garmendia, 2018; Steurer, 2017).

Difficulties of breastfeeding in public

Because of the evolutionary characteristics of frequent breastfeeding associated with breast milk of lower energy ouput, lactating mothers need to breastfeed their infants even when they are outside the home. However, the social environments of modern industrialized societies typically prevent mothers from breastfeeding outside their homes. Despite laws in many countries prohibiting the exclusion of nursing mothers from public places, many mothers feel

uncomfortable breastfeeding in public (Boyer, 2012; Leeming et al., 2013; Stearns, 1999), and this discomfort is one of the reasons for stopping breastfeeding (Boyer, 2018). The female breast has long been sexualized in Western societies, which is a norm that inhibits breastfeeding in public (Bartlett, 2005; Saha, 2002; Stearns, 1999; Yalom, 1997). The affective connotation created by these norms, both directly and indirectly, often discourages breastfeeding, by making the mother concerned that others may feel discomfort because she is breastfeeding in public spaces (Boyer, 2012, 2018; Leeming et al., 2013).

The potential discomfort of others with mothers breastfeeding in public may be interpreted in terms of human learning. In primates, learning is necessary for the acquisition of parenting behaviors (Abello and Colell, 2006). However, most people in modern industrialized societies grow up with little or no experience of seeing females breastfeeding their infants in their daily contexts, due to the low fertility rates and norms that sexualize female breasts. In such a social context, the tendency to sexualize female breasts is exaggerated, because people hardly observe breasts that feed infants, contrary to the sexualized views ubiquitous in modern society (Acker, 2009). Removing the practice of breastfeeding from people's perceptions further reinforces the idea that breastfeeding should be hidden from the public (Boyer, 2012). In terms of learning and attitude toward breastfeeding in public, it would be important to target non-adults across sexes for breastfeeding promotion campaigns in public health (Acker, 2009).

Maternal discomfort of breastfeeding in public might be reinforced by the cognitive change related to pregnancy and childbirth. Pregnancy and childbirth are associated with the largest changes in sex hormone levels and brain structures across life, thus modifying cognition in females who have experienced pregnancy and childbirth (Anderson and Rutherford, 2012;

208 Barba-Müller et al., 2019; Hoekzema et al., 2017; Pearson et al., 2009). Although there are
209 fewer studies conducted in humans compared to other animals, pregnant mothers are more
210 sensitive to social cognition, especially to potential threats and negative emotions of others
211 (Anderson and Rutherford, 2012; Pearson et al., 2009), and such changes in social cognition
212 partly last at least two years postpartum (Hoekzema et al., 2017). These pieces of evidence
213 suggest that postpartum mothers are biologically sensitive to the negative feelings of others,
214 which reinforces the maternal concern that others may feel discomfort when breastfeeding in
215 public (Boyer, 2012, 2018; Leeming et al., 2013). Cognitive changes during the pregnancy
216 and postpartum period, which originally evolved as a possible risk-avoidance mechanism for
217 vulnerable mothers and infants (Anderson and Rutherford, 2012), may exaggerate the stress
218 that mothers experience when breastfeeding in public in the modern social environment.
219

220 **MEMES OF NON-BREASTFEEDING**

221 **Flexible weaning**

222 Compared to non-human primates, humans have greater flexibility in determining weaning
223 ages (Sellen, 2007). In human populations with traditional lifestyles, the typical age at the end
224 of weaning is 2–3 years, but wide variation exists between populations (Sellen, 2001, Sellen
225 and Smay, 2001; Tsutaya and Yoneda, 2013). Breastfeeding periods in various human
226 populations range from a few hours to over six years, which is equivalent to the combined
227 breastfeeding periods of all the non-human mammals (Sellen, 2009). Great apes do not have
228 such flexibility with weaning ages. In wild chimpanzees, for example, typical breastfeeding
229 periods are 4–5 years and infants who cannot consume breast milk due to maternal death
230 before the age of three years rarely survive (Matsumoto, 2017).

231 The typical age at the end of weaning in humans is earlier than in great apes (Hawkes et al.
232 1998; Humphrey, 2010; Figure 1). Humans exhibit unique behaviors of cooperative breeding,
233 in which individuals other than the mother are deeply involved in child-rearing and active
234 food provisioning to immature individuals (Hawkes et al., 1998; Kramer, 2005; Kramer and
235 Veile, 2018). In humans, infants are weaned relatively early, while other individuals such as
236 the father, grandmothers, older sisters, and other kins contribute to providing food for the
237 immature children, which allows the mother to invest her energy in the next pregnancy. These
238 evolutionary features have allowed humans to successfully shorten interbirth intervals without
239 increasing infant and child mortality (Kaplan et al., 2000; Kramer and Ellison, 2010; Reiches
240 et al., 2009; Figure 1). Humans have consequently evolved to simultaneously raise multiple
241 dependent children of different ages (Jones, 2011).
242
243 **Historical practices of non-breastfeeding**
244 In premodern human societies, the evolutionary characteristics of flexible weaning are
245 sometimes exaggerated due to cultural reasons, which prevents the benefits of breastfeeding.
246 Many such cases in premodern Europe have been reported (Fildes, 1986; Obermeyer and
247 Castle, 1996; Thorvaldsen, 2008). For example, in a study of three 19th century Finnish
248 parishes, the infant mortality rate in the two parishes where breastfeeding was not practiced
249 was 2–3 times higher than in the parish where it was practiced, with a mortality rate of 1–6
250 months after birth reaching 18% and 29%, respectively (Lithell, 1981). A study investigating
251 the relationship between breastfeeding rates and infant mortality in Germany from the end of
252 the 19th to the beginning of the 20th century found that the infant mortality rate measured one
253 year after birth was 29% in an area where 46% of infants were never breastfed and 19%

where they were breastfed for over 6 months, compared to 18% in an area where 19% of infants were never breastfed and 43% where they were breastfed for over 6 months (Knodel and van de Walle 1967).

The mechanisms by which these non-breastfeeding practices prevailed are often explained by ideological reasons, such as coercion from others and popular beliefs (Obermeyer and Castle, 1996), although they remain unknown in some cases. As discussed earlier, the struggle between returning to work and continuing breastfeeding is not limited to the contemporary mothers. In post-industrial historical cities, the home and workplace were separated, making continued breastfeeding incompatible with the earning of income for mothers (Fildes, 1995, but see Nitsch et al., 2011). In addition, as discussed later in the next section, the practice of hiring a wet nurse instead of breastfeeding one's infant became popular among European aristocrats during the 16th–19th centuries (Fildes, 1986), possibly because breastfeeding posed time constraints and reduced opportunities for postpartum mothers to continue maintaining social relationships and fulfilling courtly ambitions (Yalom, 1997). In addition, several other explanations have been given for the non-practice of breastfeeding in historical periods. Hrdy (1999) explained that mothers were forced by relatives not to breastfeed to shorten the period of lactational amenorrhea and produce more male offsprings who could become heirs. Some researchers explained that the practice of non-breastfeeding was also associated with a strong taboo on sexual relations during the entire breastfeeding period imposed by the Church, where males wanting to resume intercourse with their wives encouraged or forced them to stop breastfeeding (Matthews Grieco, 1991; Thorvaldsen, 2008). In any case, regardless of the initial reason, humans imitate, continue, and develop the habits displayed in the environment where they were raised (Boyd et al., 2011). The practice

of not breastfeeding may not have been adaptive in the long run, but in the short run, was passed down from generation to generation.

ABUSE OF BREAST MILK MATERIALITY

Flexible relationship between infants and providers of breast milk

Humans are a species in which females other than the mother (allomothers) can routinely breastfeed the infants, while allomaternal breastfeeding is relatively rare among non-human primates (Packer and Pusey, 1992). In some gregarious non-primate animals such as sheep, to avoid mistaking their offspring, females imprint the scent of their offspring within a few minutes of birth and thereafter refuse to suckle any individuals without that scent (Kendrick et al., 1992). Primates do not develop such a strong discrimination system and learn to distinguish their offspring from those of other mothers (Hrdy, 1999). The maternal program in primates is generally more permissive than in sheep and other species, where allomaternal childcare is sometimes observed in some species. However, primate species that practice routine allomaternal breastfeeding in wild settings are limited to humans and some monkey species, including some Malagasy primates, capuchin monkeys in South America, and golden snub-nosed monkeys (*Rhinopithecus roxellana*, Colobinae) in China (Baldovino and Di Bitetti, 2008; Eberle and Kappeler, 2006; Tecot et al. 2013; Sargeant et al., 2015; Xiang et al., 2019).

In human foragers, Hewlett and Winn (2014) examined the prevalence and frequency of allomaternal breastfeeding in depth. According to these authors, an investigation of the Human Relations Area Files (HRAF), a database of documents describing the societies and cultures of various peoples around the world, found that 97 of the 208 societies studied had

300 practiced allomaternal breastfeeding. In only six cultures was allomaternal breastfeeding
301 routinely practiced, and in most of the remaining cultures, allomaternal breastfeeding was
302 practiced in emergency situations, such as the death of the mother or the mother's inability to
303 produce milk. In addition, behavioral observations of hunter-gatherers in the Congo basin,
304 Africa, showed that 60–80% of infants up to approximately four months of age experienced
305 allomaternal breastfeeding, while allomaternal breastfeeding accounted for 15–28% of total
306 time breastfed during the day, with the main providers of allomaternal milk being female kins
307 such as grandmothers and aunts (Hewlett and Winn, 2014).
308 The flexibility of human lactation behavior that allows for allomaternal breastfeeding may
309 have been an adaptive trait in the past, when maternal mortality from childbirth and in infancy
310 was relatively high. A historical study of breastfeeding in Japan during the premodern period
311 (1603–1868) showed that breastfeeding over several years was essential for infant survival in
312 environments where high calory and nutrition food was not readily available while mothers
313 often died during childbirth and were often unable to produce breast milk due to illness or
314 hard work (Sawayama, 2017). The study showed that public systems and private networks
315 were developed in premodern Japan to connect orphaned infants needing breast milk with
316 lactating females having lost their infants (Sawayama, 2017). Allomaternal breastfeeding in
317 humans might have evolved in the framework of kin selection and/or socially transmitted
318 norms about infant breastfeeding (Hewlett and Winn, 2014). Allomaternal breastfeeding has
319 social benefits for infants, in addition to providing nutritional and immunological advantages,
320 because it allows for social bonding with other mothers in the context of highly socialized
321 cooperative human breeding (Tomasello, 2020).
322 These pieces of evidence suggest that human breast milk has relatively strong materiality

323 that can be separated between specific pairs of infant and mother (Boyer, 2010). In other
324 words, human milk is highly exchangeable and thus sometimes can be a subject of abuse and
325 exploitation. Such problems can be seen in the marketing of infant formula, wet nursing, and
326 the online trade of breast milk. These problems related to human breast milk can be regarded
327 as an abuse of the greater flexibility in human weaning practices (Sellen, 2007), which
328 enabled a higher fertility in an evolutionary timeframe. If such an evolutionary characteristic
329 is misused under specific contexts, such as poor nutritional and hygienic conditions, slavery,
330 and online trade without a quality assuarance, tragic consequences of high infant mortality
331 rate, exploitation of the lactating maternal body, and negative health effects on the infant and
332 mother emerge.
333
334 **Breastfeeding, commercialism, and politics**
335 Flexible human breastfeeding and weaning practices have been exploited by modern
336 commercialism, resulting in a global decline of breastfeeding and an increased mortality risk
337 in infants (Palmer, 1988). From the end of the 19th century to the 1970s, formula companies in
338 the U.S., with some health workers on their side, conducted extensive marketing campaigns to
339 replace the human milk by infant formula. As a result, breastfeeding rates declined
340 dramatically. For example, only 25% of the infants born in U.S. hospitals were breastfed until
341 the time of discharge in 1967 (Palmer, 1988). Human milk contains not only nutrients but also
342 various immune mediators and oligosaccharides, and even today, the industrially produced
343 artificial milk is far behind real breast milk (Ballard and Morrow, 2013; Jackson and Nazar,
344 2006; Section on Breastfeeding, 2012; WHO, 2009). At a time when hygienic environments
345 and medical technologies were not as advanced as today, the replacement of human milk by

infant formula came at a great cost. Studies conducted in several U.S. cities in the 1910s reported that formula-fed infants had a mortality rate three times higher in the first month of life and two to three times higher during the first year of life due to diarrhea and infectious diseases compared to breastfed infants (Davis, 1913; Woodbury, 1922). Despite this reported evidence, formula companies, in pursuit of profit, expanded their sale channels beyond the U.S., then the use of infant formula spread to countries and regions where it was not originally needed. Especially in developing countries with poor hygiene, less advanced medical technologies, and lower levels of education, the mortality rate of formula-fed infants increased significantly, while social movements denouncing this fact flourished and boycotts of the products occurred in the 1970s (Palmer, 1988). The World Health Organization published the "International Code of Marketing of Breast-milk Substitutes" in 1981, as an internationally agreed voluntary code of practice to regulate the marketing of breastmilk substitutes for the protection of breastfeeding (WHO, 1981). Although this code has contributed to restoring the breastfeeding rates, violations of this code persist worldwide among modern commercial societies (Becker et a., in press; Han et al., 2021; Pérez-Escamilla, 2020). Violations of the code is more evident under the pandemic of COVID-19 (Becker et al., in press; van Tulleken et al., 2020).

Exploitation of the lactating human body

The history of wet nursing relates to the exploitation of lactating mothers' bodies and the death of some infants in some cultural and social contexts. Examples of widespread social problems of wet nursing were previously encountered in Europe. Wet nurses were popular in medieval and premodern Europe in two different contexts: higher social class and orphanages.

First, the practice of not breastfeeding one's infant and having a wet nurse feeding the infant became popular in historical European countries, especially among wealthier social classes (Fildes, 1986, 1995). In Greece and ancient Rome in the 5th–4th century B.C., wet nurses were often employed by wealthy families. This practice spread throughout Europe, and although mothers breastfed their infants for most of the general population, it was common for aristocrats, wealthy merchants and farmers, doctors, and scholars in 16th to 19th-century Europe to hire wet nurses instead of breastfeeding their infants (Fildes, 1986, 1995). Over time, the practice of wet nursing became widespread, even among people of lower social classes (Hrdy, 1999). Second, it was common in some parts of historical Europe for orphanages to hire wet nurses to breastfeed abandoned infants. In medieval and premodern Europe, the relatively short breastfeeding period with ineffective lactational amenorrhea and lack of effective contraceptive methods resulted in many children born at short intervals, which were often abandoned because of insufficient economic resources to raise them (Hrdy, 1999). Due to the poor hygienic conditions in the orphanages housing these abandoned infants, infant mortality rates were extremely high, and in the 18th century, the mortality rate for orphans exceeded 50% in most orphanages, sometimes reaching 90% (Fildes, 1986). Mothers who abandon their infants lose the effects of lactational amenorrhea, allowing them to quickly conceive again and give birth to another infant, leading to an ever-increasing number of abandoned children. To reduce the high infant mortality rate in orphanages, local females were contracted to breastfeed orphans (Fildes, 1986).

Such a practice of wet nursing in historical Europe, however, resulted in a cascading tragedy (Fildes, 1986, 1995; Hrdy, 1999). Wet nurses who were contracted to breastfeed sometimes "subcontracted" the infants to even lower-paid females to earn a margin (Hrdy,

1999). In some cases, poor women became pregnant and gave birth to acquire the ability to secrete milk, and earn money by breastfeeding orphans, while their offspring were forced to leave orphanages (Hrdy, 1999). Although wet nurses were typically welcomed into the home and carried out breastfeeding under the supervision of the family members in wealthier classes, infants were sent to rural villages to be breastfed and raised outside the reach of family supervision in less affluent classes (Fildes, 1995). This practice of sending infants to rural villages is described in novels written in the 19th century, such as Gustave Flaubert's "Sentimental Education" (published in 1869). There was no guarantee that the wet nurses taking care of the infants were truly able to produce milk and provide appropriate care (Fildes, 1986; Hrdy, 1999). In addition, the mothers who had left their babies to wet nurses could not benefit from lactational amenorrhea, threby often experiencing repeated pregnancies and deliveries. As a result, they suffered from various reproductive health problems, such as anemia, cervical lacerations, and infections, caused by these frequent pregnancies and deliveries, and often died young (Shorter, 1982).

These problems related to wet nurses, associated especially with slavery and racism, are also encountered in more recent times. In the U.S. and the colonies during the era of slavery, black females were frequently exploited and abused as wet nurses (Jones-Rogers, 2017; West and Knight, 2017). Many enslaved breastfeeding Black mothers were forced to breastfeed their owners' infants, which increased the mortality rate for wet nurses' children (Green et al., 2021; West and Knight, 2017). Black wet nurses lived with the owner's family and provided domestic services to the family, reducing the opportunity to interact with their children (Green et al., 2021; West and Knight, 2017). It has been suggested that some Black females may refuse to breastfeed their infants as breastfeeding is associated with traumatic memories of

enslaved wet nurses that passed down through the generations (Green et al., 2021; West and Knight, 2017). Even today, the exploitation of breastfeeding Black women in the context of social business has become an issue. Medolac, a for-profit company, started a business in 2014 which claimed to increase breastfeeding rates among Black women and provide them with an income from selling their breast milk to the company (Harrison, 2019; Morrissey and Kimball, 2017). However, the questionable effectiveness of Medolac's public health claims, its ignorance of the local Black community, and racist elements throughout its business structure led to harsh criticism. Medolac's business plan was canceled in 2015 (Harrison, 2019; Morrissey and Kimball, 2017).

Online trade of breast milk

Today, with the development of technology and logistics, breast milk is widely traded online. Online milk trades take many forms, including nonprofit formal milk banks, peer-to-peer communities of cross-nursing of human milk sharing, and commercial-based buying and selling, with varying potential risks and social consequences (Palmquist et al., 2019). The online human milk trade provides easier access to breast milk for infants who are unable to consume breast milk for a variety of reasons (Gribble, 2013), and sometimes functions to strengthen local and global emotional bonds between mothers and even between human beings (Boyer, 2010; Cassidy, 2012). On the other hand, there are cultural structures that disgust the provision of milk to other people's infants through informal networks of mothers (Carter et al., 2015; Shaw, 2004). Some health professionals believe that this kind of informal and unregulated human milk trade should be totally or partially banned (Eidelman, 2015; Eisenhauer,2016; Steele et al., 2015a), while others believe that research should be

conducted and information disseminated on ways to mitigate the possible risks of sharing breast milk (Gribble and Hausman, 2012; Palmquist et al., 2019).

Besides formal breast milk banks with assured testing of milk quality, the health outcomes of the use of these breast milk should carefully be evaluated. Some human milk sold online is contaminated with microorganisms (Keim et al., 2013), cow's milk (Keim et al., 2015), tobacco metabolites, and caffeine (Geraghty et al., 2015), which can be detrimental to infant health and survival. Adults, in addition to infants, may also consume or use breast milk that is traded online (Steele et al., 2015b). In online peer-to-peer human milk-sharing communities, mothers typically try to avoid such unexpected risks by meeting the providers of breast milk in person or communicating with them over the Internet (O'Sullivan et al., 2018; Palmquist and Doehler 2016; but see Keim et al., 2014). Peer-to-peer online breast milk sharing is widespread in some regions such as the U.S. (O'Sullivan et al., 2018), yet it is also clear that there is little involvement of healthcare professionals as an information source in the community (Perrin et al., 2014). Breast milk is also a signaling substance that transmits information about environmental and physiological conditions between mothers and infants for their developmental programming and immunological protection (Ganal-Vonarburg et al., 2020; Nguyen, 2020; Quinn, 2021). Regardless of the route of the trade, the signaling function of breast milk can work in a different context when another infant consumes milk that has been separated from a particular mother-infant pair. There is an urgent need to assess the potential risks of breast milk being exchanged online, whether it is sold or provided for free (Palmquist et al., 2019).

MISMATCH IN BREASTFEEDING PRACTICES

Recommendation on breastfeeding

Exclusive breastfeeding, i.e., feeding infants only breast milk, for the first six months of their life is recommended because neonates are particularly vulnerable to pathogens and significantly benefit from the antipathogen activities of breast milk (Fewtrell et al., 2012; Kramer and Kakuma, 2012; Pérez-Escamilla et al., 2019; WHO, 1998, 2009). However, supplementation of micronutrients during the period of exclusive breastfeeding is important in some recently occurring environments of the lower exposure to sunlight. In addition, public health messages about breastfeeding promotion may put unnecessary pressure on mothers. These examples can be considered as mismatches between human breastfeeding practices that have evolved over a long time and recent rapidly changing social and cultural environments.

Vitamin D deficiency in breastfed infants

The human milk is rich in most micronutrients, except vitamin D, which can be deficient even in breastfed infants (WHO, 2009). In animals, vitamin D is mainly synthesized by ultraviolet (UV) irradiation to 7-dehydrocholesterol near the skin, while most foods contain little vitamin D, except for certain types such as fatty fish, liver, egg yolk, and mushrooms (Holick, 2011; Mulligan et al., 2010). As vitamin D is involved in calcium metabolism, its deficiency causes hypocalcemia resulting in seizures, growth retardation, and in severe cases, rickets with skeletal abnormalities (Wagner et al., 2008).

In recent years, many parents have been applying sunscreen, using sunshades, and even playing indoors to protect their infants from the sun. If these infants are exclusively breastfed, their limited exposure to the sun increases the risk of developing vitamin D deficiency, which has now been reported worldwide (e.g., Gartner and Greer, 2003). The American Academy of

Pediatrics recommends vitamin D supplements for all infants, whether they are breastfed or formula-fed, because modern living environments and diets tend to be deficient in vitamin D (Wagner et al., 2008). Although vitamin D levels in human breast milk correspond to only <3% of maternal plasma (Hollis et al., 1981; Mulligan et al., 2010), adequate supplementation of vitamin D to lactating mothers increases the vitamin D levels in the infants by transfer via the breast milk (Hollis and Wagner, 2004).

Vitamin D deficiency is a phenomenon that has spread rapidly recently due to lifestyle changes, but is thought to have been rare in most of evolutionary timeline of our ancestors (Jablonski and Chaplin, 2012), although similar or more severe phenomena can also be seen in historical populations (Brickley et al., 2014). There was no need for higher levels of vitamin D to be present in human breast milk because humans could easily synthesize sufficient vitamin D through exposure to sunlight during most periods of human evolution (Brickley et al., 2014). However, due to indoor-centered lifestyles, use of sun protection, reduced UV exposure due to air pollution, and migration of people with darker skin to higher latitudes, the opportunities and intensity of UV exposure for the modern mothers and children are typically reduced compared to the past (Gartner and Greer, 2003). These changes have placed modern exclusively breastfed infants at increased risk of vitamin D deficiency.

Pressures to breastfeed

Public health messages to promote breastfeeding sometimes put pressure on mothers and can be a cause of severe discomfort, which may harm the promotion of breastfeeding. The modern human society has forced mothers to be “good mothers” who can provide the best nutrition and care for their offspring, and the failure to be a “good mother” is regarded as the

507 responsibility of the individual under the neoliberalism agenda (Hamilton, 2016; Harrison,
508 2019; Kukla, 2006; Lupton, 2000; Stearns, 1999). Although breastfeeding is promoted as the
509 best nutrition for infants, most mothers have difficulty continuing breastfeeding in modern
510 human societies (Cai et al., 2012; Pérez-Escamilla, 2020; Rollins et al., 2016). Therefore,
511 lactating mothers are in an ambivalent situation where breastfeeding is socially promoted but,
512 simultaneously, not socially supported (Lupton, 2000). In such a situation, mothers sometimes
513 feel excessive pressure toward the promotion of breastfeeding and have severe feelings of
514 guilt and failure when they cannot initiate or continue breastfeeding contrary to their
515 expectations (Diez-Sampedro et al., 2015; Inoue et al., 2012; Lagan et al., 2014; Robinson,
516 2018). Such pressure and discomfort can lead to maternal distrust of the medical authorities,
517 when mothers think they were informed about the positive side but not the negative side of
518 breastfeeding (Lagan et al., 2014; Robinson, 2018).
519 Applying an evolutionary perspective, it can be considered that there is a conflict of interest
520 between public health and mothers, as well as between offspring and mothers. There is a
521 biological and evolutionary tension between offspring and mothers over the investment in
522 breastfeeding (Fewtrell et al., 2020; Trivers, 1974). Similarly, public health authorities often
523 encourage mothers to breastfeed longer and more intensively, while mothers try to continue
524 breastfeeding for an optimal duration to ensure benefits for themselves and their infant.
525 However, there is a cultural and social tension between public health and mothers. Based on
526 such an analogy, the tension between public health and mothers is inevitable under limited
527 resources, and can be further exacerbated under certain cultural and social conditions
528 (Fewtrell et al., 2020). In modern industrialized human societies, breastfeeding is a choice
529 when raising infants but not an obligation as the child would not die without it, as was the

530 case in the human evolutionary past. This change in the meaning of breastfeeding creates
531 room for tension between public health and mothers.
532
533 **TRADE-OFF IN BREASTFEEDING**
534 The concept of trade-offs in evolutionary biology is useful to understand and effectively
535 approach these issues related to breastfeeding and weaning. Trade-offs are the fitness costs
536 that are paid in situations where, under limited resources, changes in one trait increase fitness
537 in one aspect but decrease fitness in another. The concept of trade-offs can be used as a
538 framework for theorizing how plastic traits of individuals respond to their environment
539 throughout life history (Stearns, 1989). Therefore, it is relevant for public health approaches
540 often aiming at the behavioral transformation of human individuals (Wells et al., 2017).
541 Issues related to breastfeeding and weaning have different levels of trade-offs. For mother-
542 infant pairs, prioritizing breastfeeding comes at a cost to the mother in terms of delayed return
543 to work and limited outings (Boyer, 2012, 2018; Leeming et al., 2013; Stearns, 1999).
544 However, largely prioritizing the mother's interests has other costs, such as disadvantages to
545 the infant's health (Ballard and Morrow, 2013; Jackson and Nazar, 2006; Section on
546 Breastfeeding, 2012; WHO, 2009), and is accompanied by a maternal sense of guilt (Inoue et
547 al., 2012; Lagan et al., 2014). Between mother-infant pairs, utilization of the materiality of
548 breast milk to benefit someone else's breastfeeding practice, in the form of wet nurses and
549 human milk trade, for example, imposes costs to the infant deprived of breast milk and the
550 mother who is exploited (Fildes, 1986, 1995; Green et al., 2021; Hrdy, 1999). At the public
551 health level, the benefits of campaigns promoting breastfeeding come at the cost of adding
552 pressure on the mothers (Diez-Sampedro et al., 2015; Inoue et al., 2012; Lagan et al., 2014;

553 Robinson, 2018). These trade-offs are difficult to resolve using conventional medical and
554 public health approaches. Furthermore, problems that can receive resources without imposing
555 additional costs on the mother and infant are relatively easy to solve, and these include, for
556 example, the addition of vitamin D (Gartner and Greer, 2003; Hollis and Wagner, 2004) and
557 the regulation of the marketing of breast milk substitutes (Palmer, 1988; WHO, 1981).
558 In resource-limited situations, trade-offs are more likely to occur. Regarding breastfeeding,
559 however, the demand is high and resources are limited because breastfeeding is a highly
560 physical practice, a daily routine behavior, preventing effectiveness of external interventions.
561 First, as the practice of breastfeeding is highly physical, its outcomes are highly dependent on
562 the abilities and efforts of the individual mother-infant pairs. The mother is the only potential
563 care provider who can secrete breast milk, if the mother dones not have alternative options to
564 feed the infant with breast milk (Cassidy, 2012), which means that the biological aspect of
565 breastfeeding must inevitably depend on the mother. In addition, breastfeeding can only be
566 achieved as a physical practice. These characteristics make the mother's body the only
567 biological resource in breastfeeding in most cases, with an availability severely limited in
568 both time and space. Second, breastfeeding is a daily routine behavior whose requirements on
569 frequency and duration are too high to be ignored. Breastfeeding cannot be done intensively
570 on a specific day or time, and it continually imposes constant and frequent costs on the
571 mother. Third, there are few effective means of external intervention in breastfeeding that can
572 reduce the demand or expand the resource. Generally, there is no surgical or medication cure
573 for breastfeeding, except for some cases such as the administration of dopamine antagonist to
574 increase milk secreteion (Aono et al., 1982; Kauppila et al., 1982; Ylikorkala et al., 1982).
575 Thus, only coping strategies exist, such as reducing the risk of vitamin D deficiency in

breastfed infants by supplementing with vitamin D and circumventing the spatio-temporal constraints of breastfeeding using breast pumping. For these three reasons, resources are limited in breastfeeding and trade-offs are more likely to occur.

Support with the cost compensation is needed to resolve the issues associated with trade-offs (Tully and Ball, 2013). Unless the demand-intensive and resource-limited situation is not improved, the trade-offs cannot essentially be solved. In other words, the problems caused by the inability to breastfeed can only be solved by enabling mothers to actually breastfeed. In public health and social contexts, it can be argued that the issues related to breastfeeding may be solved by providing tailored support for the sacrificed cost which is increased by the promotion of breastfeeding, which would eliminate or mitigate the trade-off (Tully and Ball, 2013). For example, for mothers debating between continuing breastfeeding and returning to work, the trade-off cost of continued breastfeeding can be decreased by providing a social system and policymaking for paid parental leaves and an evaluation system that ensures the childcare period is not a career blank. For the trade-off between public health promotion and the pressure imposed on mothers, a public health campaign can attempt to deconstruct the image of the "perfect mother" which is reinforced in the recent neoliberal societies and serves as a basis for mothers' sense of pressure (Kukla, 2006). By focusing on the compensating factors for the trade-offs, the overall demand can be reduced, while the resources can be increased, thus creating a situation where the trade-offs are less likely to occur.

CONCLUSIONS

This review addressed four public health and social issues of breastfeeding and weaning, and interpreted them from a perspective of biological anthropology. First, our evolutionary

599 background as highly mobile hunter-gatherers has led to the evolution of milk with low
600 energy output associated with frequent periods of breastfeeding in humans, causing issues
601 related to the spatio-temporal constraints of breastfeeding. These issues include the difficulty
602 of balancing a return to work with continued breastfeeding and the difficulty of breastfeeding
603 in public. The latter problem is further exacerbated by the values of contemporary Western
604 society that sexualize female breasts. Second, the unique human evolutionary traits of
605 cooperative breeding and active food provisioning make its weaning patterns more flexible
606 than in other primates. However, the human characteristics of flexible weaning have caused
607 an epidemic of non-breastfeeding memes in the past, which increased infant mortality. Third,
608 allomaternal breastfeeding is frequently practiced in humans, and breast milk is widely
609 interchangeable, not just between specific mother-infant pairs. This characteristic has led to
610 problems related to the abuse of breast milk materiality, such as increased infant mortality due
611 to the global marketing of breast milk substitutes, exploitation of the lactating female bodies,
612 and online trade of breast milk without quality assurance. Fourth, human milk composition
613 and perceived values on human breastfeeding, which have evolved through an evolutionary
614 timeframe, have generated mismatches in recent rapidly changing socio-cultural
615 environments, creating problems of vitamin D deficiency and placing an increased pressure
616 on mothers to breastfeed. In this review, it was discussed that these problems can be best
617 understood by the concept of trade-offs in evolutionary biology. By providing support to
618 sacrificed costs of trade-offs, public health approaches that promote breastfeeding could have
619 a greater effectiveness.
620

621 **CONFLICTS OF INTEREST**

None declared.

AUTHOR CONTRIBUTIONS

TT: Conceptualization, Methodology, Validation, Investigation, Writing - Original Draft, Visualization

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FIGURE

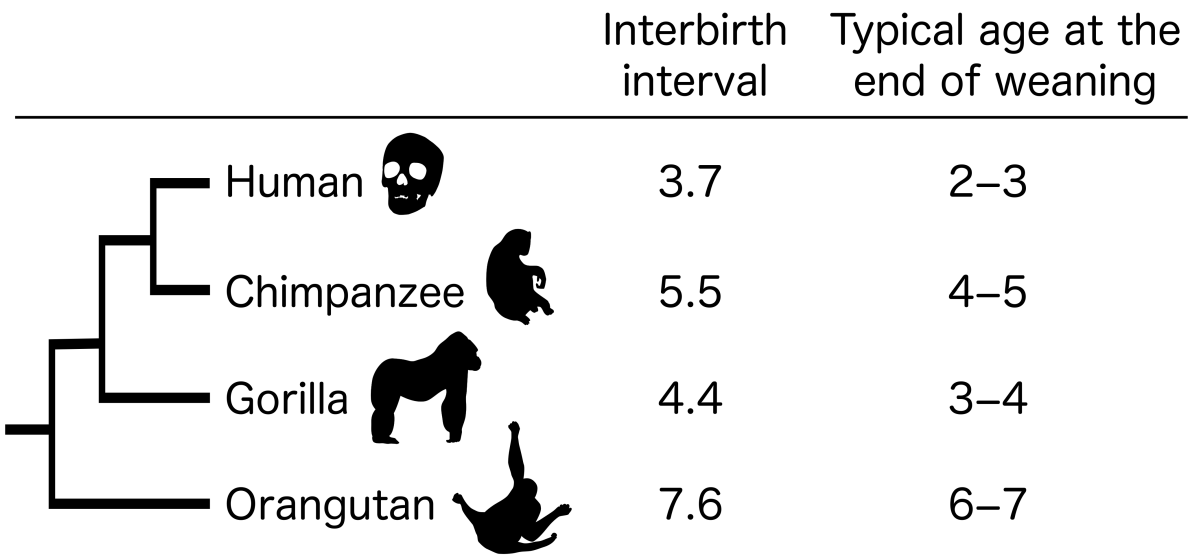

Figure 1. Typical interbirth intervals and age at the end of weaning in humans and great apes (Hawkes et al., 1998; Humphrey, 2010; Robson et al., 2006; van Noordwijk et al., 2018).