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Evolutionary biological perspectives on current social issues of breastfeeding and weaning

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Abstract

Breastfeeding and weaning are actively studied from evolutionary, medical, and social research perspectives because of their close association with infant mortality, lifetime health, and human population dynamics. Each discipline benefits from an interdisciplinary exchange of knowledge regarding the bases, processes, and consequences of these phenomena. However, current social issues related to breastfeeding and weaning have received little attention from an evolutionary biology perspective. We address this gap by reviewing current social issues related to human breastfeeding and weaning in an evolutionary framework. This approach helps build a conceptual framework with the goal of better understanding ultimate causes of or influences on these current social issues. The six social issues reviewed here fall into three categories: the spatiotemporal constraints of breastfeeding, abuse of breast milk as valuable material, and mismatch in breastfeeding practices. Some of these issues have an evolutionary basis. We analyze the structure of these social issues and discuss their possible solutions in terms of extension of the trade-off theory in evolutionary biology. Our discussion on the current social issues in breastfeeding and weaning highlights the effectiveness of an approach rooted in evolutionary theory and biological anthropology.

KEYWORDS
breastfeeding and weaning, evolutionary biology, mismatch, social issues, trade-off

1 | INTRODUCTION

1.1 | Medical, evolutionary, and social foundations of breastfeeding and weaning

Human breastfeeding and weaning (HBW) is the focus of medical, evolutionary, and social studies. HBW is a set of behaviors shaped by evolution and is also affected by cultural factors. HBW, being closely related to health and reproduction, has profound medical and social consequences. In this review, we discuss current social issues (CSIs) associated with HBW. We use a biological anthropology approach that relies on evolutionary principles to investigate human behaviors. Our aim is to provide insights that may help in resolving the CSIs and in providing direction for future research on HBW.

HBW that directly improves infant and maternal health represents one of the most important targets of public health promotion campaigns (Pérez-Escamilla, 2020; Rollins et al., 2016; WHO, 1998). Breast milk contains various antimicrobial agents and bioactive substances, as well as nutrients, which promote infant health and survival and has lifelong health benefits (Ballard & Morrow, 2013; Jackson & Nazar, 2006; Section on Breastfeeding, 2012; Victora et al., 2016; WHO, 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 immune system

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vulnerability (Jackson & Nazar, 2006; Section on Breastfeeding, 2012; Victora et al., 2016; WHO, 2009). Immunoglobulins, cellular immunity, and nonspecific antipathogen components exert a protective effect on mucous membranes of the respiratory and gastrointestinal tracts of infants consuming breast milk (Jackson & Nazar, 2006; Victora et al., 2016). Human breast milk contains relatively higher concentrations and greater diversity of complex oligosaccharides among mammals (Tao et al., 2011; Warren et al., 2001), which play an important role in the development of the intestinal microbiota by providing nutrients for *Bifidobacterium* (Kunz et al., 2008; Ninonuevo et al., 2006; Zivkovic et al., 2011) and preventing binding of pathogens to epithelial cells of infant's intestine (Newburg et al., 2005). Breast milk also provides lifelong, long-term health benefits by reducing the risk of developing infectious diseases, obesity, and type II diabetes, not only in childhood, but also into adulthood (Binns et al., 2016; Robinson & 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 not to conceive another child under poor nutritional conditions and 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 mother's nutritional status, making ovulation suppression less effective when the mother is well nourished (Valeggia & Ellison, 2009).

Breastfeeding and weaning are important research topics in evolutionary studies, including biological anthropology, because they directly relate to inclusive fitness, reproduction, and population dynamics. Breast milk evolved in the ancestors of mammals ~310 million years ago, and then became the primary nutrient source for infants ~210–170 million years ago (Oftedal, 2012). Breastfeeding is a form of maternal investment in infants that results in a conflict between mother and infant, where the mother optimizes investment in current offspring and her future reproductive opportunity, while the infant draws maximum investment from the mother (Fewtrell et al., 2020; Trivers, 1974). This 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 variation in weaning patterns among species and individuals can in turn illuminate a diversity of reproductive strategies and environmental adaptations (Hinde & Milligan, 2011; Lee, 1996). For example, Hadza, a population of foragers in northern Tanzania, wean their children at 2.5 years of age, which is 6–9 months earlier than !Kung, a population of foragers in northwestern Botswana and northeastern Namibia (Blurton Jones et al., 1989). This difference relates to females' foraging efficiency (distance traveled, how old the offspring is carried until, and contribution from children's foraging) and contributes to Hadza's higher fertility (Blurton Jones et al., 1989, 1992). Additionally, the duration of breastfeeding 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 et al., 1996; Konner & Worthman, 1980; Tsutaya & Yoneda, 2013, 2015; Wood et al., 1985).

HBW has been used to maintain or shape social relationships between people, other than the one between infant and mother, driven by both conscious and unconscious intent of others. One of the best known examples of the use of HBW in social contexts is milk kinship, where breastfeeding creates enduring social ties among the breast feeder, nurslings, and their kin (Altorki, 1980; Parkes, 2005). In turn, the social meaning and power of milk kinship have sometimes intently and tactically been used in historical and modern times to construct or deconstruct social relationships (Clarke, 2007). For example, milk kinship was sometimes used to prevent an unwanted marriage because a marriage taboo emerges between people who were breastfed by the same female (Altorki, 1980). In addition, the concept of milk kinship has been acknowledged as a means of modifying the domestic status of children in relation to modern assisted reproductive technologies and surrogacy (Clarke, 2007). Since HBW has a powerful impact on health and reproduction, its practice is the subject of intent and control by others who have different interests (Bartlett, 2002). Such a ruling power relation is called "biopower"; it makes HBW and the female body a battleground of parties with different interests (Wells, 2006). Furthermore, the social meaning of HBW-related practices can be redefined in rapidly-changing current cultural contexts and emerges as novel interpretations and human behaviors. The consistency between institutionalized human milk bank practices and the rules of Islamic milk kinship is one such example, and there are debates on whether the consumption of pooled breast milk provided by human milk banks generates a milk kinship and thereby marriage taboo between the recipient infant and a number of anonymous donors' offsprings (El-Khuffash & Unger, 2012; Ghaly, 2012; Hsu et al., 2012).

1.2 | The objective of this review

In this review, we interpret CSIs pertaining to HBW from biological anthropology viewpoints to investigate the underlying mechanisms and provide a better understanding of the issues. Combined knowledge of and insights on HBW obtained from medical, evolutionary, or social research provide a better understanding of the bases, processes, and consequences of HBW-related phenomena (Tomori et al., 2018) (Figure 1). Understanding the interaction between medical and evolutionary aspects of HBW is an active research area (Fewtrell et al., 2020). A large number of published studies in this area are based on the investigation of the

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evolutionary basis of medical issues related to HBW (Fewtrell et al., 2020; Sellen, 2001; Wells, 2006). In the opposite direction, current medical knowledge is applied for evolutionary studies (Kendall et al., 2021; Stuart-Macadam & Dettwyler, 1995). Research in this field covers past social issues in HBW, such as non-breastfeeding practices in medieval/premodern Europe (Fildes, 1986; Hrdy, 1999; Obermeyer & Castle, 1996; Thorvaldsen, 2008) and deprivation of breastfeeding practices by companies marketing artificial formula (Palmer, 2009). However, there are several novel social issues of HBW that are currently emerging in modern industrialized societies, such as peer-to-peer milk sharing (Palmquist et al., 2019) and online marketing of breast milk substitutes (Becker et al., 2022; Han et al., 2022; van Tulleken et al., 2020). While these issues have been actively studied for their public health risks by medical experts, evolutionary basis and implications of such issues are rarely discussed. Biological anthropology may provide the ultimate explanation of why, rather than how, such social issues emerge, from the longer timespan of human evolution. Such insights can be useful in alleviating or solving these problems.

We have reviewed the recent literature on the six CSIs of HBW, that can be grouped into three categories as spatiotemporal constraints on breastfeeding, abuse of breast milk as valuable material, and mismatch in breastfeeding practices. We have integrated these categories in a conceptual framework by considering their evolutionary roots (Figure 2). First, we show species-specific behavioral flexibility in HBW. Second, we highlight the existence of biological constraints and discuss the CSIs of HBW that originate from biological constraints. Finally, we adopt the trade-off theory of evolutionary biology to derive a better understanding of CSIs and suggest solutions for the issues.

2 | FLEXIBILITY IN HBW PATTERNS

The typical age at the end of weaning in humans is earlier than it is in great apes (Hawkes et al., 1998; Humphrey, 2010; Figure 3). Humans exhibit unique behaviors of cooperative breeding, in which individuals other than the mother are deeply involved in child-rearing and active food provisioning to immature individuals (Hawkes et al., 1998; Kramer, 2005; Kramer & Veile, 2018). In humans, infants are weaned relatively early, while other individuals such as the father, grandmothers, older sisters, and other kins contribute to providing food for immature children, which allows the mother to invest her energy in the next pregnancy. These evolutionary features have allowed humans to successfully shorten interbirth intervals without increasing infant and child mortality (Kaplan et al., 2000; Kramer & Ellison, 2010; Reiches et al., 2009; Figure 3). Humans have consequently evolved to simultaneously raise multiple dependent children of different ages (Jones, 2011).

Furthermore, compared to nonhuman primates, humans have greater flexibility in determining weaning ages (Sellen, 2007). In human populations with traditional lifestyles, the typical age at the end of weaning is 2–3 years, but wide variation exists between populations (Sellen, 2001; Sellen & Smay, 2001; Tsutaya & Yoneda, 2013). Breastfeeding periods in various human populations range from a few hours to over 6 years, which is equivalent to the range of breastfeeding periods of all non-human mammals (Sellen, 2009). Great apes do not have such flexibility with weaning ages. In wild chimpanzees, for example, typical breastfeeding periods are 4–5 years and infants who cannot consume breast milk due to maternal death before the age of 3 years rarely survive (Matsumoto, 2017).

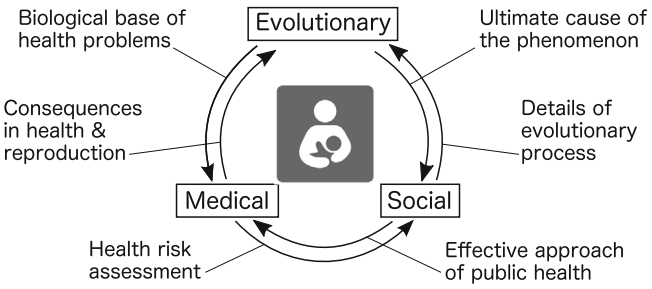

FIGURE 1 Three research domains (medical, evolutionary, or social) focusing on human breastfeeding and weaning (HBW), and the exchange of ideas and knowledge among these domains.

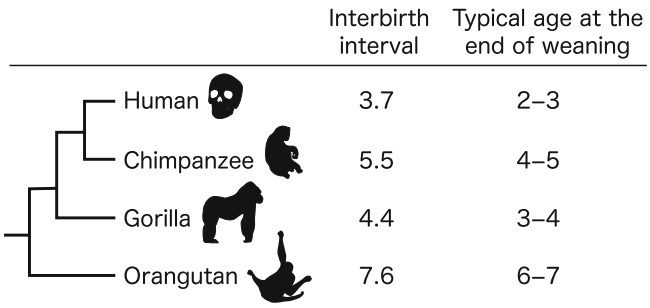

FIGURE 3 Typical interbirth intervals and age at the end of weaning in humans and great apes (Hawkes et al., 1998; Humphrey, 2010; Robson et al., 2006; van Noordwijk et al., 2018).

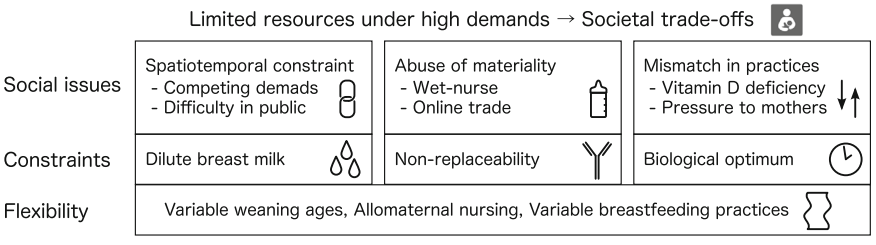

FIGURE 2 A conceptual framework of the causes behind the social issues pertaining to human breastfeeding and weaning (HBW).

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Because of this flexibility, humans could often culturally modify the age of weaning. Moreover, human breast milk is highly exchangeable, as shown later, allowing the breast milk provider for a specific infant to be different from the mother (Palmquist, 2020). The flexibility in HBW practices has been further increased with the aid of current medical technologies, such as breast pumps, milk banks, and chestfeeding by transmasculine individuals (MacDonald et al., 2016). This flexibility and the persisting constraints discussed in the next section are the cause of the social issues pertinent to HBW.

3 | SPATIOTEMPORAL CONSTRAINT OF BREASTFEEDING

3.1 | Frequent breastfeeding and milk with low energy density

Humans and human ancestors lived as nomadic foragers until the very recent Holocene, which resulted in frequent breastfeeding and production of milk with low energy output. Forager mothers typically carried their offspring with them during foraging activities for the first few years of the offspring's life (Blurton Jones et al., 1989; Blurton Jones & Sibly, 1978; Draper & Cashdan, 1988), as do many other nonhuman primate species (Nakamichi & Yamada, 2009). Forager mothers thus spent a lot of time with their offspring and breastfed frequently (Konner, 2016; Konner & Worthman, 1980).

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 prolactin levels decline very quickly: the half-life of prolactin in the blood system is approximately 30 minutes (Nunleyt et al., 1991). Therefore, ~2 h after the last sucking stimulus to the nipple, blood prolactin levels are generally reduced to basal levels (Glasier et al., 1984; Howie et al., 1980). In the foraging lifestyle, when mother and infant spent a lot of time together, frequent breastfeeding kept prolactin levels high, allowing breastfeeding to continue for several years (Konner & Worthman, 1980; Sellen, 2001; Sellen & Smay, 2001).

Humans, like many other nonhuman 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 & Milligan, 2011). The average human milk has lactose, fat, and protein concentrations of about 7.3%, 3.7%, and 1.3%, respectively (Hinde & 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 milk with high energy density that prevents starvation of the infants even if breastfeeding bouts have an interval of several days (Hinde & Milligan, 2011). For example, hooded seals (*Cystophora cristata*) secrete rich milk (1% lactose, 61% fat, 5% protein) almost continuously for the first 4 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, 2000; Oftedal & Iverson, 1995). Compared with these other mammals, the composition of human milk is more characteristic of a species in which mothers forage together with infants and frequently breastfeed.

To summarize, humans have dilute milk, similar to that of other primates, which constraints breastfeeding behavior. Unlike hooded seals, which produce milk rich in calories, humans cannot leave their infants for long periods. HBW is not flexible enough to allow the modification of milk composition, and humans therefore must adhere to a frequent breastfeeding pattern. This constraint leads to two CSIs: competing time demands on working mothers and difficulties of breastfeeding in public.

3.2 | Competing time demand on working mothers

Contrary to foraging mothers during human evolutionary history, today's employed mothers 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). In addition, 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 & Garmendia, 2018; Steurer, 2017). Such an issue is also applicable for self-employed mothers who have difficulties earning money due to the time demands of breastfeeding.

3.3 | Difficulties of breastfeeding in public

Because of the evolutionary characteristic of frequent breastfeeding associated with breast milk of lower energy output, 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 in some countries (Boyer, 2012; Leeming et al., 2013; Stearns, 1999), and this discomfort is one of the reasons for stopping breastfeeding (Boyer, 2018). It is said that the female breast has long been sexualized especially 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). Vulnerability or feelings of

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insecurity during breastfeeding would further prevent mothers from breastfeed in public due to the fear of abuse from others. At the same time, however, breastfeeding mothers are not just passive agents but sometimes engage in social and political movements (also known as lactivism) that advocate breastfeeding and motherhood in general by intentionally bringing breastfeeding into public view, both in the real world and online (Boon & Pentney, 2015; Boyer, 2011).

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 (Abelló & Colell, 2006). However, it is possible that people in modern industrialized societies might grow up with little or no experience of seeing females breastfeeding their infants in their daily contexts (Hoddinott & Pill, 1999), due to both 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 attitudes toward breastfeeding in public (Acker, 2009; Hoddinott & Pill, 1999), it would be important to target non-adults across sexes for breastfeeding promotion campaigns in public health.

Maternal discomfort of breastfeeding in public might be reinforced by cognitive changes 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 & Rutherford, 2012; Barba-Müller et al., 2019; Hoekzema et al., 2017; Pearson et al., 2009). Although there are fewer studies conducted in humans compared to other animals, pregnant mothers are more sensitive to social stimuli, especially to potential threats and negative emotions of others (Anderson & Rutherford, 2012; Pearson et al., 2009), and such changes in social cognition partly last at least 2 years postpartum (Hoekzema et al., 2017). These pieces of evidence suggest that postpartum mothers are biologically sensitive to the negative feelings of others, which reinforces the maternal concern that others may feel discomfort when breastfeeding in public (Boyer, 2012, 2018; Leeming et al., 2013). Cognitive changes during the pregnancy and postpartum period, which originally evolved as a possible risk-avoidance mechanism for vulnerable mothers and infants (Anderson & Rutherford, 2012), may exaggerate the stress that mothers experience when breastfeeding in public in the modern social environment.

4 | ABUSE OF BREAST MILK AS VALUABLE MATERIAL

4.1 | Exchangeable relationship between infants and providers of breast milk

Humans are a species in which females other than the mother (allomothers) can routinely breastfeed infants (Palmquist, 2020), while allomaternal breastfeeding is relatively rare among non-human primates (Packer et al., 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 but do learn to distinguish their offspring from those of other mothers (Hrdy, 1999). The maternal attitudes in primates, where allomaternal childcare is sometimes observed, is generally more permissive than in sheep and other species. 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*) in China (Baldovino and Di Bitetti, 2007; Eberle and Kappeler, 2006; Tecot et al., 2013; Sargeant et al., 2015; Xiang et al., 2019).

Hewlett and Winn (2014) examined the prevalence and frequency of allomaternal breastfeeding in human foragers. 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 practiced allomaternal breastfeeding. In only six cultures was allomaternal breastfeeding routinely practiced, and in most of the remaining cultures, allomaternal breastfeeding was practiced in emergency situations, such as the death of the mother or the mother's inability to produce milk. In addition, behavioral observations of hunter-gatherers in the Congo Basin, Africa, showed that 60%–80% of infants up to ~4 months of age experienced allomaternal breastfeeding, while allomaternal breastfeeding accounted for 15%–28% of total time breastfed during the day, with the main providers of allomaternal milk being female kin such as grandmothers and aunts (Hewlett & Winn, 2014).

The exchangeability of human lactation behavior that allows for allomaternal breastfeeding may have been an adaptive trait in the past, when maternal mortality from childbirth and in infancy was relatively high. A historical study of breastfeeding in Japan during the premodern period (AD 1603–1868) showed that breastfeeding over several years was essential for infant survival in environments where high calorie and nutritious food was not readily available (Sawayama, 2017). However, mothers often died during childbirth and were often unable to produce breast milk due to illness or hard work (Sawayama, 2017). Sawayama (2017) showed that public systems and private networks were developed in premodern Japan to connect orphaned infants needing breast milk with lactating females having lost their infants. Allomaternal breastfeeding in humans might have evolved in the framework of kin selection and/or socially transmitted norms about infant breastfeeding (Hewlett & Winn, 2014). Allomaternal breastfeeding has social benefits for infants, in addition to providing nutritional and immunological advantages, because it allows for social bonding with other mothers in the context of highly socialized cooperative human breeding (Tomasello, 2020).

Together, these pieces of evidence suggest that human breast milk is a material that can be shared outside specific pairs of infants

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and the mother (Boyer, 2010). On the other hand, there is a constraint from the biological fact that, if breast milk is not provided, infants lose numerous health benefits that should have been received. There is currently no artificial material that can completely replace the health benefits of breast milk. It is because of this tension between flexibility that makes human milk highly exchangeable and constraint of its non-replaceability that human milk can sometimes be a subject of abuse and exploitation. These problems are highlighted in the CSIs of wet-nursing and the online trade of breast milk. The misuse or abuse of the evolutionary characteristics of HBW under specific contexts, such as in slavery or online trade without quality assurance, leads to tragic consequences, like exploitation of the lactating maternal body and the consequent negative health effect on the infant and mother.

4.2 | 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 in the past (Fildes, 1986, 1995; Hrdy, 1999). Because the history of wet-nursing in the past has been reviewed in detail (Fildes, 1986, 1995; Hrdy, 1999), this review confines its scope to more recent times.

These problems related to wet-nurses, associated especially with slavery and racism, are also encountered in more recent times. In the United States and the colonies during the era of slavery, black females were frequently exploited and abused as wet-nurses (Jones-Rogers, 2017; West & Knight, 2017). Many enslaved breast-feeding Black mothers were forced to breastfeed their owners' infants, which increased the mortality rate for wet-nurses' children (Green et al., 2021; West & 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 & 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 & Knight, 2017; but see Sobonya, 2018). 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 & 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 & Kimball, 2017).

Although breast milk is exchanged among mothers in allomaternal nursing and wet-nursing, the former is not generally regarded as exploitation. Breastfeeding of unrelated infants, when it is forced and not reciprocated (i.e., the nurse's infant receives little or no breast milk from herself or other mothers), is considered exploitation. Thus, forced wet-nursing can be seen as an institutionalized evolutionary and economic "free rider" phenomenon of the highly exchangeable nature of HBW. Due to lactational amenorrhea, the inter-birth intervals of non-lactating mothers who exploit others' breast milk would become shorter than those of lactating exploited mothers, possibly resulting in higher fertility and/or higher income by returning earlier to a better-earning job in exploiting mothers.

4.3 | 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 or human milk sharing, and commercial-based buying and selling, with varying benefits, 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 disrespect 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 to prevent any potential risks (Eidelman, 2015; Eisenhauer, 2016; Steele, Martyn, & Foell, 2015). Regardless of what some health professionals believe, however, informal and unregulated human milk trade is already widespread in some regions of the world, and research should be conducted and information should be disseminated to mitigate the possible risks of sharing breast milk (Gribble & Hausman, 2012; Palmquist et al., 2019).

Besides formal breast milk banks with assured testing of milk quality, the health outcomes of the use of breast milk traded online 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, Foell, et al., 2015). 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 & 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., 2016). 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; Miller, 2020; Nguyen, 2020; Quinn, 2021). Regardless of

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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 (Palmquist, 2018). Breast milk also facilitates the formation of a microbial community specific to the infant-mother complex (Mueller et al., 2015; Takeshita, 2017; Tamburini et al., 2016). There is an urgent need to assess the potential health consequences of breast milk being exchanged online, whether it is sold or provided for free (Palmquist et al., 2019).

5 | MISMATCH IN BREASTFEEDING PRACTICES

5.1 | Biological optimum in HBW

Although flexibility is an important characteristic of HBW, it can interfere with the biologically optimal practice that has evolved over a long period of time. The biological optimum involves exclusive breastfeeding, i.e., feeding infants only breast milk, for the first 6 months of their neonatal life (Kramer & Kakuma, 2012). It is recommended globally to maximize the health benefits of breastfeeding because neonates are particularly vulnerable to pathogens and can significantly benefit from the antipathogen activities of breast milk (Fewtrell et al., 2011; Kramer & Kakuma, 2012; Pérez-Escamilla et al., 2019; WHO, 1998, 2009). Typically, the biological optimum is empirically estimated from the vast amount of epidemiological data and supported by rigid evidence. However, the biological optimum imposes a strict constraint on breastfeeding practices and can be the cause of conflict when it clashes with the demands of current rapidly-changing living environments. Vitamin D deficiency and pressures to breastfeed are examples of CSIs arising from such clashes.

5.2 | Vitamin D deficiency in exclusively breastfed infants

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 & Greer, 2008).

In recent years, many parents have been applying sunscreen, using sunshades, and even playing indoors to protect their infants from the sun in some countries (Gartner and Greer, 2003; Mulligan et al., 2010). 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., Balasubramanian & Ganesh, 2008; Choi et al., 2013; Hatun et al., 2005; Kubota et al., 2018). 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 & Greer, 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 vitamin D levels in infants by transfer via breast milk (Hollis and Wagner, 2004).

Vitamin D deficiency can be hypothesized to have been rare over most of the evolutionary timespan of our ancestors but spread recently due to lifestyle and dietary changes. 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 modern mothers and children are typically reduced compared to the past (Gartner and Greer, 2003). It is also possible that a less diverse diet, that developed after the introduction of agriculture and domestication, may have further exacerbated vitamin D deficiency (Brickley et al., 2014). These changes have placed modern exclusively breastfed infants at increased risk of vitamin D deficiency.

5.3 | Pressures to breastfeed

Public health messages to promote exclusive breastfeeding for the first 6 months (e.g., WHO, 2009) sometimes put pressure on mothers and can be a cause of severe discomfort, which may harm the promotion of breastfeeding. Some modern human societies have 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 responsibility of the individual under the neoliberalism agenda, which emphasizes market-oriented policies and individual responsibility (Hamilton, 2016; Harrison, 2019; Kukla, 2006; Lupton, 2000; Stearns, 1999). Although exclusive breastfeeding is promoted as the best nutrition for neonates for the first 6 months, most mothers have difficulty continuing breastfeeding in modern human societies (Cai et al., 2012; Pérez-Escamilla, 2020; Rollins et al., 2016). Therefore, lactating mothers are in an ambivalent situation where breastfeeding is socially promoted but, simultaneously, not socially supported (Lupton, 2000). In such a situation, mothers sometimes feel excessive pressure toward the promotion of breastfeeding and have severe feelings of guilt and failure when they cannot initiate or continue breastfeeding contrary to their expectations (Diez-Sampedro et al., 2019; Inoue et al., 2012; Lagan et al., 2014; Robinson, 2018). Such pressure and discomfort can lead to maternal distrust of medical authorities, when mothers think they were

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informed about the positive side but not the negative side of breastfeeding (Lagan et al., 2014; Robinson, 2018).

There appears to be a conflict of interest between public health and mothers, as well as between offspring and mothers. There is a biological and evolutionary tension between offspring and mothers over the investment in breastfeeding (Fewtrell et al., 2020; Trivers, 1974). Similarly, public health authorities often encourage mothers to breastfeed longer and more intensively, while mothers try to continue breastfeeding for an optimal duration to ensure benefits for themselves and their infant. It can also be discussed that public health messages represent biopower on the female body to educate and manage it (Bartlett, 2002; Wells, 2006). Therefore, there is a cultural and social tension between public health and mothers. Based on such an analogy, the tension between public health and mothers is inevitable under limited resources, and can be further exacerbated under certain cultural and social conditions (Fewtrell et al., 2020). In modern industrialized human societies, breastfeeding is a choice when raising infants but not an obligation as the child would not die without it, as was the case in the human evolutionary past. This change in the consequences of breastfeeding creates room for tension between public health and mothers. It should be noted, however, that public health is not the only agent that has a possible conflict of interest with mothers. Commercial formula industries often try to exert direct and indirect influences on mothers to discourage breastfeeding and increase their product sales (Baker et al., 2023; Rollins et al., 2023).

6 | TRADE-OFF IN BREASTFEEDING

The conceptual framework adopted in this review is summarized in Figure 2. Although HBW is characterized by flexibility, the flexibility is limited by several biological constraints. Conflicting demands arise when breastfeeding performance and benefits are sought to be achieved beyond the constraints. If the resources needed to meet the demand are limited, the necessity to manage and distribute the limited available resources gives rise to social issues. The three categories of CSIs described in this review can be understood with this framework as follows:

- Although humans can modify the age at the end of weaning, the low energy density of human breast milk constrains the maternal behaviors to frequent breastfeeding. If lactating mothers sought to achieve both continued breastfeeding and social/economic activities, CSIs such as competing time demands and difficulties of breastfeeding in public emerge.
- Although the evolutionary history of frequent allomaternal nursing results in flexible exchangeability in human breast milk, breast milk has non-replaceable biological benefits. This non-replaceability is a constraint for individuals who sought to provide more health benefits of breast milk to infants beyond their milk-producing or -obtaining capacity. The CSIs on the abuse of breast milk arise when attempts are made to compensate for the milk shortage from the resources (i.e., breast milk) of other mothers.
- Although human breastfeeding practices can vary among individuals, there is a biological optimum for breastfeeding and weaning patterns that have evolved over a long period of time. If the biological benefits of breast milk are sought to be obtained fully, it is necessary to follow the optimum. However, under current rapidly-changing living environments, following this optimum is itself a constraint in some cases, and trying to meet this demand may result in CSIs such as vitamin D deficiency and pressures to breastfeed.

We use extensions of the trade-off theory in evolutionary biology to gain a better insight into these societal phenomena. Trade-offs are the fitness costs that are paid in situations where, under limited resources, changes in one trait increase fitness in one aspect but decrease fitness in another (Garland, 2014). The concept of trade-offs can be used as a framework for theorizing how plastic traits of individuals respond to their environment throughout life history (Stearns, 1989). It is also important to consider trade-offs between competing biological functions, such as reproduction and longevity, in public health programs (Jasienska et al., 2017; Wells et al., 2017).

Issues related to HBW have different levels of societal trade-offs. For mother-infant pairs, prioritizing breastfeeding comes at a cost to the mother in terms of delayed return to work and limited outings (Boyer, 2012, 2018; Leeming et al., 2013; Stearns, 1999). However, prioritizing the mother's interests has other costs, such as disadvantages to the infant's health (Ballard & Morrow, 2013; Jackson & Nazar, 2006; Section on Breastfeeding, 2012; WHO, 2009), and is accompanied by a maternal sense of guilt (Inoue et al., 2012; Lagan et al., 2014). Between mother-infant pairs, utilization of the materiality of breast milk to benefit someone else's breastfeeding practice, in the form of wet-nurses and human milk trade, for example, imposes costs to the infant deprived of breast milk and the mother who is exploited (Fildes, 1986, 1995; Green et al., 2021; Hrdy, 1999). At the public health level, the benefits of campaigns promoting breastfeeding come at the cost of adding pressure on the mothers (Diez-Sampedro et al., 2019; Inoue et al., 2012; Lagan et al., 2014; Robinson, 2018). Generally, these societal trade-offs are difficult to resolve. However, problems that can receive resources without imposing additional costs on the mother and infant are relatively easy to solve, and these include, for example, the addition of vitamin D (Gartner and Greer, 2003; Hollis and Wagner, 2004) and regulation of the marketing of breast milk substitutes (Lancet, 2023; Palmer, 2009; WHO, 1981).

In resource-limited situations, societal trade-offs are more likely to occur. Regarding breastfeeding, however, the demand is high and resources are limited because breastfeeding is a highly physical practice, a daily routine behavior, preventing effectiveness of external interventions. First, as the practice of breastfeeding is highly physical, its outcomes are highly dependent on the abilities and efforts of the individual mother-infant pairs. Typically, the mother is the only potential care provider who can secrete breast milk, which means that the biological aspect of breastfeeding must inevitably depend on the mother (but see Tomori et al., 2018). In addition, breastfeeding can only be achieved as a physical practice. These characteristics make

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the mother's body the only biological resource in breastfeeding in most cases, with an availability severely limited in both time and space. Second, breastfeeding is a daily routine behavior whose requirements on frequency and duration are too high to be ignored. Breastfeeding cannot be done intensively on a specific day or time, and it continually imposes constant and frequent costs on the mother. Third, there are few effective means of external intervention in breastfeeding that can reduce the demand or expand the resource. Generally, there is no surgical or medication cure for breastfeeding, except for some cases such as the administration of dopamine antagonist to increase milk secretion (Aono et al., 1982; Kauppila et al., 1981; Ylikorkala et al., 1982). 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 spatiotemporal constraints of breastfeeding using breast pumping. For these three reasons, resources are limited in breastfeeding and societal trade-offs are more likely to occur.

Support with cost compensation is needed to resolve the issues associated with trade-offs (Tully & Ball, 2013). Unless the demand-intensive and resource-limited situation is not improved, the trade-offs cannot 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 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 & 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 societal trade-off between public health promotion and the pressure imposed on mothers, a public health campaign can attempt to deconstruct the image of the "good 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 societal 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.

7 | CONCLUSIONS

This review addressed six CSIs of HBW, which can be grouped into three categories, by interpreting them from a biological anthropology perspective. The unique human evolutionary trait of cooperative breeding and active food provisioning allows for higher flexibility of weaning patterns than the other primates. However, the persistent constraints in HBW lead to the CSIs. First, our evolutionary background as highly mobile hunter-gatherers led to the evolution of human breast milk with low energy content associated with high frequency of breastfeeding, leading to CSIs related to the spatiotemporal constraints of breastfeeding. Examples of such issues include the difficulty in balancing a return to work with continued breastfeeding and in breastfeeding in public. The latter problem is further exacerbated by the contemporary attitude of sexualizing the female breast. Second, allomaternal breastfeeding is frequently practiced in humans and breast milk is interchangeable not just between specific mother-infant pairs. This characteristic has led to the abuse of breast milk as valuable material, such as exploitation of the lactating female bodies and online trade of breast milk without quality assurance. Third, the biological optimum in HBW, which evolved in our ancestors, has generated mismatches in current rapidly-changing sociocultural environments, creating problems of vitamin D deficiency and placing increased pressure on mothers to breastfeed. This review revealed that these problems can be best understood by the extension of the trade-offs theory in evolutionary biology. By providing support to sacrificed costs of societal trade-offs, public health approaches that promote breastfeeding could have greater effectiveness.

AUTHOR CONTRIBUTIONS

Takumi Tsutaya: Conceptualization; methodology; validation; investigation; writing - original draft; writing - review and editing, visualization. **Nozomi Mizushima**: Validation; investigation; writing - review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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