Chapter 10: Mixed-Feeding in Humans: Evolution and Current Implications

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Abstract:

Current age-based breastfeeding recommendations are supported by ample evidence and improve maternal and infant health. However, mixed-feeding trajectories—from complementary feeding introduction to full weaning—vary widely across populations. While numerous sociocultural factors influence this variation, comparative primate and human biological and cultural evidence also suggests that flexible mixed-feeding may be a human evolutionary norm. Durations of exclusive and total breastfeeding are expected to vary with infant energetic needs and maternal time, physical, and reproductive constraints. This perspective does not challenge current recommendations, but advocates for parallel dialogs about individually optimal mixed-feeding trajectories among families and health care providers.

Introduction:

Lactation is a defining mammalian trait, selected over evolutionary time to protect and nourish offspring, optimize maternal reproductive investment, and regulate postpartum offspring development (Blackburn et al., 1989; Oftedal, 2012; Pond, 1977; Power and Schulkin, 2016). Humans, however, are also distinguished by the simultaneous use of infant feeding alternatives,

with practices such as wet-nursing and vessel feeding with milks from other species documented to at least 7000 BC (Hastrup, 1992; Hrdy, 1992; Hewlett and Winn, 2014; Maher, 1992; Power and Schulkin, 2016). The 19th-20th centuries saw unprecedented global declines in breastfeeding initiation and duration, owing to numerous sociocultural influences (see Chapter 1). These declines were definitively linked to increased infant mortality, giving rise to the origins of pediatric medicine (Piovanetti, 2001) and debates over what infant feeding practices should be recommended (Feachem and Koblinsky, 1984).

In 2002, the World Health Organization (WHO) began recommending **exclusive breastfeeding** (**EBF**) for the first six months of life, followed by continued breastfeeding and **complementary feeding** (**CF**) with other liquids and solids for at least two years of age (WHO, 2002). Longer exclusive and total breastfeeding durations reduce risks of infectious morbidity and mortality in infants (Kramer and Kakuma, 2012; Lamberti et al., 2011; Victora et al., 2016). "Suboptimal" breastfeeding practices (non-initiation of breastfeeding, CF before six months, and weaning before 2 years) may also increase risks of chronic diseases by altering infant immune and metabolic development, which evolved expecting continuous input from the numerous bioactive factors in maternal milk (Martin and Sela, 2013; Power and Schulkin, 2016; Schack-Nielsen and Michaelsen, 2007; see also Miller, Chpt x, Quinn, Chpt X).

Since the 1990s, breastfeeding promotion has improved initiation rates in many countries, but has had more limited effect on EBF and total breastfeeding durations (Lutter and Morrow, 2013). Lack of structural and social support (Hough, Chpt X, Tomori Chpt X), maternal work, health issues, attitudes, and accessibility and aggressive marketing of infant formula undermine breastfeeding in many populations (Balogun et al., 2015; Piwoz and Huffman, 2015). However, the growing social value and opportunity costs of breastfeeding may be shifting practices in

some contexts, with higher socioeconomic status increasingly associated with improved breastfeeding duration *within* higher-income countries (Grummer-Strawn et al., 2008; Jessri et al., 2013). Yet while socioeconomic and cultural factors unquestionably influence breastfeeding patterns, widespread variance in durations of exclusive and total breastfeeding may also have deeper evolutionary origins, which are further illuminated through comparative primate analysis and life history theory (see Veile).

Species-typical **lactational strategies**—including milk composition and yield, the frequency and duration of nursing bouts, and the total duration of lactation—vary by phylogenetic history, ecology, and patterns of growth and development (Hinde and Milligan, 2011). One derived feature of human lactation may be pronounced flexible **mixed-feeding** (Box 1), which is unique among other primates (Sellen, 2009, 2007) and likely co-evolved with other features of human biology, ecology, culture, and social organization (McDade and Worthman, 1998).

This chapter reviews the evolutionary origins of mixed-feeding in humans, first examining differences in human and non-human primate offspring provisioning, and then variability in human lactation, infant development, and maternal reproductive interests that may have favored flexible CF and weaning. In closing, I consider the relevance of evolved flexible mixed-feeding for public health and individual breastfeeding decisions. Current breastfeeding recommendations have helped increase breastfeeding rates and reduce maternal and infant morbidity worldwide, and it is not the position of this author to question or disfavor them. Instead, this review may help foster parallel dialogs about the costs and benefits of different mixed-feeding options or norms that individual families will confront across their own breastfeeding trajectories. These individual optima would consider not only epidemiological

evidence from population studies, but expected variation in individual infant energy demands, lactational performance, and maternal time, energy, and reproductive trade-offs.

Box 1. Researchers have long grappled with the "meanings of weaning" to define infant feeding transitions in humans and other species (Lee et al., 1991; Lee, 1996). Clinical and epidemiological researchers typically describe breastfeeding trajectories in terms of current feeding status or EBF and total breastfeeding duration. Anthropologists, however, stress weaning as a gradual process (e.g. Martin, 1984, McDade and Worthman, 1998; Dettwyler, 2004; Sellen, 2007) and note that discrete feeding events may have little impact on maternal energy or offspring nutritional independence, which are more relevant in comparing lactational trajectories across species (Lee, 1996; Humphrey, 2010). For example, offspring may remain primarily dependent on maternal milk for some time after being introduced to other foods, and conversely be almost entirely dependent on other foods by the time of full weaning.

In this chapter, *mixed-feeding* **refers to breastfeeding combined with complementary foods**—the latter defined according to the World Health Organization (WHO, 2008) as anything other than human milk, including other liquids and formula. In this usage, *mixed-feeding* denotes any period of lactation that is not EBF, but deviates from the WHO term *complementary feeding*, which ideally is reserved to describe "appropriate" feeding in breastfed children at least 6 months old (WHO, 2008). *Weaning* in this chapter denotes the complete cessation of breastfeeding.

Weaning trajectories in primates

Across mammalian groups, higher-quality (i.e. more energy-rich and easy to digest) weaning foods are associated with shorter EBF but not shorter mixed-feeding durations; instead, prolonged mixed-feeding may facilitate learning and immunocompetence (Langer, 2003). Within mammals, primates exhibit relatively long EBF and mixed-feeding durations (Langer, 2003). This prolonged primate "transitional feeding" period is marked by gradual additions of independently foraged or shared foods to the diet (Sellen, 2009). However, adults share food with offspring in only about half of primate species: some prosimians and Old World monkeys, most New World monkeys, and all of the great apes (Brown et al., 2004; Jaeggi and van Schaik, 2011). Most of this sharing is **passive transfer**, with mothers passively allowing infants to take food from them (Brown et al., 2004; Jaeggi and van Schaik, 2011). Transfers generally occur with foods that are difficult to acquire or process, but are infrequent and of minimal nutritional consequence, and may largely facilitate offspring foraging knowledge and skill acquisition (Brown et al., 2004; Jaeggi et al., 2008; Jaeggi and van Schaik, 2011; Jaeggi and Gurven, 2013). **Direct provisioning** with foods of high nutritional quality has only been observed in humans and callitrichids (marmosets and tamarins)—two primate groups distinguished by long-term monogamous pair bonds, substantial cooperative breeding, direct paternal care, and relatively short interbirth intervals (Burkart et al., 2009; Kaplan et al., 2000; Kappeler and van Schaik, 2002).

As compared to other great apes, humans introduce CF about six months earlier and wean 1-3 years earlier than projected, even though they have larger brains, higher energy needs, and remain dependent on direct provisioning from caregivers well into the juvenile period (Sellen, 2007). However, humans also consume more protein and fat-rich diets, exhibit more intense and

systematic **allomaternal care** (i.e. direct care provided by any individual other than the mother), and provide substantial energy to infants and juveniles through direct food provisioning. While primates have relatively long lactation periods, it is in the reproductive interests of mothers to reduce their energetic loads through mixed-feeding as early as possible (Langer, 2003). Enhanced dietary quality and availability in humans may have buffered infants against the risks of decreasing human milk consumption while reducing maternal energetic costs—in turn leading to relatively earlier resumption of postpartum ovulation, shorter interbirth intervals, and higher fertility (Galdikas and Wood, 1990; Robson and Wood, 2008; Short, 1994; van Noordwijk et al., 2013).

Biological norms for human CF introduction and weaning

Despite *H. sapiens'* greater reliance on mixed-feeding relative to other great apes, some period of EBF and breastfeeding is still typical for our species. A plausible lower biological limit of EBF duration may be the age at which infants can efficiently manipulate, process, digest, and absorb solids and other liquids outside of human milk. These abilities require the coordination of multiple physiological systems that are often not fully mature until about 4-6 months of age. For example, the two halves of the mandible do not completely fuse until about 5 months of age, deciduous dentition does not emerge until about 7 months (Humphrey 2010), and peak adiposity—that buffers against nutritional insults—is not reached until 6-7 months (Kuzawa, 1998). Renal capacity and tolerance of non-milk solute loads are limited until about 4 months of age, fat absorption and production of salivary and pancreatic amylase do not reach adult levels until around 6 months of age, and gastric capacity increases from 10 to 90 ml in the first six months (Hendricks and Badruddin, 1992).

Six months is also a reasonable upper limit at which EBF is sufficient to supply infants with all of the energy and nutrients they require. Following the onset of copious milk production at about 36-72 hours postpartum (Kulski and Hartmann, 1981; Neville and Morton, 2001), milk secretion is primarily determined by infant demand—i.e. rate of suckling and mammary-gland emptying (Wilde et al., 1995). With on-demand feeding, milk yield and macronutrient composition are relatively stable over at least the next six months (Dewey, 2001; Kent et al., 2006; Mandel et al., 2005), even under conditions of severe maternal malnutrition (Prentice and Prentice, 1995). After about six months, however, increasing infant energy demands outstrip maximum milk yield, and infant prenatal stores of iron, zinc, and vitamin D become depleted, warranting CF to sustain optimal growth and development (Butte et al., 2002; Dewey, 2001). In an ethnographic review of 42 non-industrial societies with universal and prolonged breastfeeding, the modal age of CF introduction was six months, further supporting six months of EBF as a biological norm (Sellen, 2001).

Continued breastfeeding up through at least the first two years of life also appears evolutionarily favored. For example in the same ethnographic review, the modal age of weaning across 113 populations was 30 months, with 60% of populations surveyed typically weaning after 24 months, and none weaning before 12 months (Sellen, 2001). Furthermore, infant immune function, postpartum brain growth, and the ability to efficiently process and digest non-milk foods are still maturing up to at least two years postpartum (Hendricks and Badruddin, 1992; Holt, 1995; Milligan and Bazinet, 2008). Gastric capacity is only 480 ml at one year, tongue flexibility and chewing ability do not mature until 1 year of age, pepsin secretion (necessary for protein absorption in the stomach) does not reach adult levels until 2 years of age, and manual dexterity continues to develop during the first 2 years of life (Hendricks and

Badruddin, 1992).

Human milk also remains a vital source of continued immunological protection and nutrition across later mixed-feeding stages. Milk concentrations of lactoferrin, lysozyme, and sIgA—all important antimicrobial constituents—have been shown to increase or remain stable through 1-2 years of lactation (Perrin et al., 2013). Research in the U.S. has shown that infants gradually introduced CF after 6 months do reduce breast milk intake (from a maximum of 875 ml/day at 7 months), but maintain intakes of 550 ml/day up through 11-16 months (Dewey et al., 1984). In another study, U.S. infants consumed at least 300 ml/day of milk for up to 30 months under mixed-feeding regimens (Kent, 2007). In Amele mothers from Papua New Guinea, milk production peaked at 9 months but was still at more than 50% of peak output at 24 months (Jenkins et al., 1984; Orr-Ewing et al., 1986; Worthman et al., 1993). Milk lactose and protein concentrations are largely unchanged from 4 to 20 months of lactation (Dewey et al., 1984), fat and total energy concentration are constant or increase up through 39 months (Dewey et al., 1984; Mandel et al., 2005), and percentages of specific milk fatty acids appear constant up through 24 months (Martin et al., 2012; Mitoulas et al., 2003). Across economic scales, continued breastfeeding provides children aged 11-23 months with between 30-50% of energy requirements, 19-43% of protein requirements, and 25-75% of micronutrient requirements for vitamin A, vitamin B12, calcium, and vitamin C (Dewey et al., 1984; Dewey, 2001; Onyango et al., 2002).

Still, estimates of a species-typical weaning age for humans are imprecise. The onset of lactase nonpersistence—i.e. the down-regulation of lactase activity that occurs in individuals who do not carry the dominant alleles for adult lactase persistence—is a genetically heterogeneous trait, occurring at varying ages after the first year life (Wang et al., 1998). This

heterogeneity may represent population variation in past selection pressures on weaning ages, i.e. suggesting that different cultural environments favored earlier or later genetically regulated onset of nonpersistence. Elsewhere, various weaning threshold models have been calculated from comparative species analysis of the average ages of first permanent molar eruption (Smith et al., 1994), quadrupling of birthweight (Lee et al., 1991), or attainment of 1/3 of adult body size (Charnov and Berrigan, 1993). These models applied to humans estimate a "natural" weaning age anywhere between 2.5 and 7 years (Dettwyler, 2004; Humphrey, 2010).

Dettwyler (2004) has argued that the natural human weaning age should fall closer to 6-7 years, with earlier ages reflecting recent cultural preferences and the proliferation of breast milk alternatives. However, 6-7 years may more realistically be an upper limit for modern *Homo*. First, weaning estimates derived from the threshold models should be cautiously interpreted for great apes, and particularly humans, as they do not fit the general mammalian patterns observed for several traits (Harvey and Clutton-Brock, 1985; van Noordwijk et al., 2013, Smith et al., 2013). In no great apes do weaning ages coincide with eruption of the first molar (Humphrey, 2010). While greater body size predicts longer durations of gestation and lactation across primates (Harvey and Clutton-Brock, 1985), the energetic costs of lactation are lower than would be predicted by body size for great apes, and are lowest for humans—requiring only about a 30% increase in energy intake as compared to a 50% increase for baboons and 200-500% for most other mammals (Lee, 1996). When scaling relationships of maternal body mass are restricted to only hominoids (as opposed to all mammals or even all primates), the resulting predicted weaning age for humans is 1,078 days, or about 3 years, for female body mass of 55 kg (Martin, 2007). Finally, in an analysis of North American hunter-gatherer skeletal remains, estimated weaning ages across all specimens analyzed ranged from 1-6 years, but averaged 3.4 years

(Eerkens and Bartelink, 2013; See Chapter Halcrow). Similarly, Sellen's (2001) ethnographic review documented weaning beyond 3 years in only 14% of the populations surveyed. In sum, 6-7 years of breastfeeding is biologically feasible for humans, but comparative primate, fossil, archaeological, and ethnographic evidence suggests that weaning at 2.5-3 years is more typical for our species.

Variation due to lactational performance and infant energy needs

Though estimates for human species-typical EBF breastfeeding durations are generally congruent with current recommendations, it must be stressed that "species-typical" and epidemiological "optimal" durations are calculated from *average* measures of infant growth and development and milk volumes produced or consumed. *Individual* lactational sufficiency and infant energy demands will likely fall somewhere along a normal continuum—and may necessitate somewhat earlier or greater reliance on mixed-feeding, or where possible, allomaternal nursing or milk-sharing (see Palmquist, R-F).

Although perceived low milk supply is one of the most common reasons reported for ceasing EBF (Gatti, 2008; Li et al., 2008), researchers have long contended that only 5-10% of women experience primary lactational insufficiency owing to physiological problems (Neifert, 2001; Vahlquist, 1981). In many cases, contemporary sociocultural factors and beliefs about infant feeding separate mothers and infants and reduce suckling frequency, leading to downregulated milk production (Greiner et al., 1981; Gussler and Briesemeister, 1980). Yet, low milk supply has been reported by women across cultural and economic spectrums (Obermeyer and Castle, 1996; Tully and Dewey, 1985), including women in small-scale societies that exhibit universal and "on demand" breastfeeding (Martin et al., 2016, Hewlett and Winn 2014). It is also

increasingly recognized that low gestational age, high maternal stress, obesity, and other metabolic disorders can delay the onset of lactogenesis resulting in chronic low milk supply (Dewey, 2001; Stuebe, 2014). These latter risk factors are likely exacerbated in many populations today, and their influence on incidences of reported low milk supply in non-industrialized populations remains largely unexplored. It is nevertheless apparent that for many women globally, EBF for six months may not be feasible because of non-behaviorally induced physiological constraints.

Second, maximum milk yield may be set by maternal conditions during birth and pregnancy, maternal reproductive history, infant birth weight, or early postpartum growth trajectories (Hinde and Milligan, 2011). Variation in these conditions would predict individual-specific optima for EBF duration. For example, the "weaning weight hypothesis" suggests that mammalian infant energy needs outstrip the energy supplied by EBF when infants have approximately doubled their birth weight (Lee, 1996; See also Chapter Veile). For breastfed human infants under optimal conditions, this occurs on average at 5.3 - 8.8 kg, or anywhere from 3.5 - 5 months (Humphrey, 2010). In addition, infants who experience repeated energy losses from pathogen exposure may require earlier supplementation to maintain growth (Waterlow, 1981; Wilson et al., 2006).

Third, milk composition is more sensitive to maternal nutrition from 3-12 months than at earlier lactational stages (Nommsen et al., 1991). Maternal diet substantially affects availability of milk fatty acids (Brenna et al., 2007; Martin et al., 2012; Yuhas et al., 2006, Quinn Chtr. 8) and vitamins A, B_6, and B_{12} (Butte et al., 2002; Dewey, 2001). Unmet availability of these micronutrients may be a more limiting factor on the duration of EBF than that of milk energy or protein content, particularly if infant stores are low from birth (Dewey, 2001). Finally, as

stressed by Power and Schulkin (2016), traits selected through natural selection are not necessarily "perfect". Milk is an evolved compromise that balances the needs of infants *and* the physiological capacities and reproductive interests of mothers; moreover, milk composition is constrained by species' evolutionary histories. Some important aspects of modern human environments may drastically differ from those in which our milk evolved, resulting in a mismatch between certain features of evolved milk composition and current infant environments. Human milk, for example, is naturally very low in vitamin D, as ancestrally both mothers and infants obtained sufficient vitamin D through direct sunlight exposure and subsequent storage in adipose tissues. This is no longer the case for many families today, however, and the prevalence of vitamin D deficiency is increasing, often necessitating preventive supplementation of mother or infant with vitamin D during EBF.

For many infants then, pre- or postnatal conditions affecting birth size, milk production and composition, nutrient stores, and postnatal growth and illness may warrant flexible CF introduction. Indeed, though the modal age of CF introduction in Sellen's (2001) survey was six months, supplementation with liquids before six months of age was observed in more than 70% of populations, with standard deviations of age at liquid and solid food introduction as high or higher than the mean (4.5 ± 6.0 and 5.0 ± 4.0 months, respectively). Following CF introduction, wide variability in dietary quality across populations may differently affect infant satiety, suckling intensity, and the subsequent rate of weaning. Once milk volume drops below 300-400 ml/day, protein, sodium, and lactose composition are altered (Dewey et al., 1984; Neville et al., 1991), which may affect infant demand and drive "self-led" weaning at any age. Notably, while the mean $\pm$ SD age of weaning in Sellen's (2001) survey was 29.0 ± 10.0 months, weaning ages ranged from 12 to 66 months.

The origins of flexibility: reproductive trade-offs and maternal-offspring conflict

Despite the known significance of breastfeeding for infant survival, growth, and development, lactation is energetically costly for mothers, involving the active conversion and transfer of maternal nutrients and body stores into substrate for infants (Hinde and Milligan, 2011, Veile Chtr X; Halcrow Chapter Y). In many mammals, including primates, this energy cost induces a period of postpartum infertility—termed **lactational amenorrhea** in humans—that modulates birth spacing, allowing for optimal energy allocation between current and future reproduction (Lee, 1996; McNeilly, 1997). Lactational amenorrhea is mediated by both offspring suckling intensity (signaling current infant energy demand) and the relative metabolic cost of lactation (signaling sufficient energy available for investment in future reproduction) (Ellison, 1994; Martin, 2007; Valeggia and Ellison, 2009) Relative to other mammals, primate nursing also substantially inhibits other maternal activities, and is therefore particularly costly in terms of maternal *time* constraints (Charnov and Berrigan, 1993).

For human mothers then, breastfeeding decisions are paramount examples of parent-offspring conflict (Trivers, 1974). While infants benefit unilaterally from maximal breastfeeding investment, mothers may benefit more by optimally allocating energy across current infant needs, future reproduction, and other fitness-enhancing activities (McDade and Worthman, 1998; Tully and Ball, 2013; see Chapter Tully&Ball). In this vein, and even accounting for individual variation in infant growth and development, current feeding recommendations and the biologically derived estimates for species-typical EBF and breastfeeding durations are somewhat *infant-centered.* From an evolutionary perspective, maternal reproductive interests and energetic demands—including investment in older offspring and other pursuits that maintain maternal and

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household well-being—may exert equal if not greater influence on breastfeeding decisions at any age.

Breastfeeding can also benefit maternal health by reducing risks of metabolic diseases and reproductive cancers (Bartick et al., 2016) and by increasing the duration of lactational amenorrhea, leading to longer interbirth intervals and lower fertility (WHO 2005). These considerations may shift the maternal cost-benefit calculus to favor more intensive breastfeeding for many women (Tully and Ball, 2013). Ancestrally, however, breastfeeding decisions were unlikely to have been influenced by long-term maternal health risks or preferences for *lower* fertility (McAllister et al., 2016).

Variable optima: significance for public health

As is evident from the above review, human EBF and total breastfeeding durations are not rigidly physiologically constrained. Though human feeding practices are strongly culturally patterned, as in all primates our lactational trajectories are also influenced by local ecology, available resources, and maternal and infant conditions (Fairbanks and McGuire, 1995; Lee, 1996). Humans also exhibit relatively earlier and greater reliance on mixed-feeding, which likely co-evolved with a suite of other derived traits—e.g. extensive allomaternal care, overlapping generations, social foraging, proactive food sharing, enhanced dietary quality, and increased cognitive and technological capacities (Hawkes et al., 1998; Hrdy, 2007; Kaplan et al., 2000; Kramer et al., 2009). Though pathogen risk and limited nutritional availability would have selected for generally intense breastfeeding practices ancestrally, *flexible mixed-feeding is our evolutionary norm.*

Evidence of this evolved flexibility, however, is *not* evidence that the current prevalence

of non-initiation of breastfeeding or very early, rapid weaning is evolutionarily justified or minimally costly. The current age-based recommendations are generally biologically appropriate for our species, and moreover promote community and institutional support for breastfeeding, leading to improved maternal and infant health outcomes. Yet, given wide variation in individual infant growth and development, milk production, and opposing maternal constraints, are all instances of CF before six months or weaning before two years necessarily "suboptimal"?

Families, communities, and pediatricians should understand that age-based recommendations are population-based, and should not necessarily serve as strict cut-offs or automatic gauges of optimal feeding for individual mothers and infants. Indeed, some researchers have advocated emphasizing cues of "developmental readiness" between 4 and 10 months of age in making infant feeding decisions (Cattaneo et al., 2011). Without parallel dialogs acknowledging these variable needs and realities, families may ignore current recommendations altogether—and in doing so miss out on other relevant information about safe, healthy CF practices, or the nutritional and immunological benefits of prolonged mixed-feeding.

Researchers should also acknowledge that the myriad maternal factors influencing breastfeeding decisions are not just barriers to a 'one size fits all' infant optimum, but rather factors affecting the negotiated optima for mothers, their families, *and* their infants. We can continue to advocate for better structural support for breastfeeding, while also recognizing that mothers who have to or choose to work at the expense of exclusive breastfeeding still provide, through their labor, critical support for their infants and other family members. In this regard, biocultural perspectives are perhaps ideally situated to examine the embedded political economic and more immediate individual dimensions that breastfeeding decisions reflect—from historical and structural factors shaping household composition and economies, to cultural expectations

about infant feeding, growth, and behavior, to physiological variation in lactational function and infant energy needs.

Finally, research on breastfeeding and health outcomes is typically organized by comparatively narrow categories (e.g. "breastfeeding vs. formula-feeding", "EBF to six months or not"), which do not accurately reflect the diversity of mixed-feeding trajectories across families. Many research questions more relevant to these realities remain to be explored. How do different ratios of breast milk to complementary foods, breastfeeding to CF intake, and different durations of mixed-feeding affect metabolic, immune, and neurological function? Are there minimums of breast milk intake or duration that return maximum benefits? How can we better support mothers that cannot exclusively breastfeed for prolonged periods, but want to maintain breastfeeding for as long as possible? For families weighing recommendations of "optimal" breastfeeding in the context of their own individual circumstances, such research may be particularly welcome.

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