



Conflict or congruence? Maternal and infant-centric factors associated with shorter exclusive breastfeeding durations among the Tsimane



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ABSTRACT

Six months of exclusive breastfeeding (EBF) is considered optimal for infant health, though globally most infants begin complementary feeding (CF) earlier—including among populations that practice prolonged breastfeeding. Two frameworks for understanding patterns of early CF emerge in the literature. In the first, maternal and infant needs trade-off, as “maternal-centric” factors—related to time and energy demands, reproductive investment, cultural influences, and structural barriers—favor supplanting breastfeeding with earlier and increased CF. A second framework considers that “infant-centric” factors—related to infant energetic needs—favor CF before six months to supplement breastfeeding.

We apply these two frameworks in examining early CF among the Tsimane—a high-fertility, high-mortality, forager-horticulturalist population residing in the Bolivian Amazon. Data were collected from a mixed-longitudinal sample of 161 Tsimane mother-infant pairs from August 2012–April 2013. Tsimane mothers generally reported introducing CF because of perceived infant needs. However, CF is introduced with continued intensive breastfeeding, and generally coupled with premastication. Risks of earlier CF relative to the minimum hazard (estimated at 5 births) were elevated for lower and higher parity mothers, but were significantly greater only after 9 births. Seventeen percent of mothers reported introducing CF because of low milk supply. Introducing CF because of low milk was most common from 0 to 3 months of age and among higher parity mothers, which may reflect physiological constraints. Maternal reproductive trade-offs and perceived infant needs may help explain the low prevalence of EBF to six months among other populations in which breastfeeding is not structurally or culturally constrained.

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1. Introduction

Six months of exclusive breastfeeding (EBF) reduces infant morbidity and mortality in a wide range of environments (Black et al., 2008; Hop et al., 2000; Kalanda et al., 2006; Kramer and Kakuma, 2002) and is sufficient to support growth under optimal conditions (Dewey, 1998; Dewey et al., 1991). EBF as compared to predominant breastfeeding is associated with longer lactational amenorrhea, while longer durations of breastfeeding reduce maternal risks of reproductive cancers and other non-communicable diseases (Chowdhury et al., 2015; Victora et al.,

2016). The onset of several developmental features between four and seven months of age further suggests that EBF for six months is biologically appropriate for our species (Hendricks and Badruddin, 1992; Humphrey, 2010; Sellen, 2009).

Globally, however, only about 40% of infants are EBF to 6 months (Lutter and Morrow, 2013; Victora et al., 2016). In many populations, the barriers to EBF are rooted in a suite of interrelated factors that have prompted declines in breastfeeding since the 20th century—e.g. lack of structural, familial, and community support for breastfeeding, availability of breast milk substitutes, maternal employment, scheduled infant feedings, and other limitations on maternal-infant interactions (Balogun et al., 2015; Harrell, 1981; Huffman, 1984; King and Ashworth, 1987; Wright, 2001). Risks associated with introduction of complementary feeding (CF) before six months of age (hereafter: “early CF”) may also be minimized when coupled with low infectious disease exposure and high-quality medical care and complementary foods.

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Yet early CF is also readily evident in the ethnographic record and among contemporary small-scale populations in which breastfeeding is universal, prolonged, and on-demand (Sellen, 2001; Veile et al., 2014). Since EBF in these higher infectious disease risk populations would presumably be feasible for mothers and maximally beneficial to infants, we hypothesize that in such populations (a) EBF may be costly to mothers, or (b) mothers perceive that infants benefit from earlier CF.

Evolutionary researchers have proposed that optimal durations of EBF vary according to the costs and benefits of EBF for mothers and infants (McDade and Worthman, 1998; Tully and Ball, 2013). For example, while EBF may benefit the health of mothers and infants, maternal time devoted to nursing cannot be spent on other fitness-enhancing activities, including wage and household labor or care of existing dependents (Hurtado et al., 1992; Panter-Brick, 1993a). From an evolutionary perspective, EBF also limits opportunities for future reproduction, as high suckling frequency and the metabolic costs of lactation combine to suppress ovulatory function (McNeilly, 1997; Veggia and Ellison, 2009). In populations in which exogenous mortality is high and extra-somatic capital is not readily accrued or transmitted, surplus maternal energy tends to favor higher fertility over investments in health, longevity, or improving conditions of individual offspring (Gibson and Mace, 2006; McAllister et al., 2012; Strassmann and Gillespie, 2002). Under such “maternal-centric” circumstances affecting residual fertility, younger, lower parity mothers may use early CF as a sub-conscious strategy to reduce lactational costs, leading to earlier resumption of postpartum ovulation and subsequent pregnancy.

Alternatively and despite additional risks of pathogen exposure, early CF may promote infant growth and immune maturation, or compensate for insufficient milk quantity or quality. Six months of EBF may not universally meet the needs of all infants given variation in birth size, growth velocity, milk volume, iron and other available nutrients in milk (Fewtrell et al., 2007; Kramer and Kakuma, 2002; Nielsen et al., 2011; Reilly and Wells, 2005; Waterlow, 1981). EBF infants are also not immune from infection, and infants who experience repeated energy losses from pathogen exposure may require supplementation (Waterlow, 1981; Wilson et al., 2006). Turkana, Aka, and Ngandu mothers have reported the belief that infants should be supplemented shortly after birth to buffer against disease risks (Gray, 1998; Meehan and Roulette, 2013). More recent evidence suggests that introducing small amounts of common allergenic foods between 4 and 6 months may promote immunotolerance (Koplin et al., 2010; Prescott et al., 2008; Wennergren, 2009). Finally, perceived low milk supply is often emblematic of modernized infant care practices that interrupt the positive feedback loop between suckling frequency and milk production (e.g. scheduled nursing bouts, bottle feeding, decreased maternal-infant contact) (Greiner et al., 1981; Gussler and Briesemeister, 1980). However, in populations in which such practices are rare, low milk supply is still reported, often in connection with perceived infant satiety, maternal dietary sufficiency, and labor conflicts (Levine, 1988; Moffat, 2002).

We examine evidence of both maternal- and infant-centric factors influencing CF practices among the Tsimane, a natural-fertility forager-horticulturalist population residing in the Bolivian Amazon. Tsimane reproductive investment appears directed towards higher fertility despite potential costs to offspring: contraceptive use is rare while high fertility is socially and economically desirable; higher parity-for-age is associated with earlier weaning; child growth begins to falter around the time of weaning; and shorter interbirth intervals are associated with higher rates of infant mortality (Gurven et al., 2012; McAllister et al., 2012). The Tsimane are well-nourished and relatively unburdened by non-communicable diseases, including obesity, diabetes, and

reproductive cancers (Gurven et al., 2013). We propose that Tsimane mothers are therefore unlikely to consciously vary EBF durations to benefit their own health, but maternal-centric factors, indicative of surplus energy budgets or greater reproductive potential, may be associated with shorter EBF durations.

Conversely, there are few structural or cultural constraints impeding longer breastfeeding durations. Mothers give birth at home, generally begin breastfeeding shortly after birth, and do not ritually discard colostrum (Veile et al., 2014). Though CF is introduced on average at four months, infants are more likely to be observed breastfeeding than they are CF up to 13 months of age (Veile et al., 2014), which suggests early CF may not supplant breastfeeding. Tsimane mothers carry infants in slings throughout the day and “breastsleep” (McKenna and Gettler, 2016) at night. Mothers are rarely absent from infants; subsistence activities are largely domestic (Gurven et al., 2009) and families generally travel together on longer excursions (Ellis, 1996; Miner et al., 2014). As such, early CF may be motivated by infant-centric factors.

The research presented in this paper is organized into three sections. For comparative purposes, we first assess Tsimane breastfeeding and CF practices according to population indicators of age-appropriate infant and young child feeding practices (World Health Organization, 2007). We complement this with ethnographic description of CF practices, and examine Tsimane mothers' reported reasons for introducing CF. Lastly, we evaluate maternal and infant factors in predicting age of CF introduction as reported in ethnographic interviews and in a statistical model.

2. Methods

2.1. Study population and data collection

The Tsimane are an indigenous forager-horticulturalist population residing in the Beni Department of Bolivia. The population is estimated at 15,000, distributed over 90 villages of varying size (~80–500), ecology (riverine floodplain, terra firme forest), and access to market towns (Miner et al., 2014; Reyes-García et al., 2014). Infant mortality rates vary between 10 and 20% (Gurven et al., 2007; Gurven, 2012) and the total fertility rate is 9.1 births (McAllister et al., 2012). Parasitism is endemic (Blackwell et al., 2013; Martin et al., 2013), while access to medical care and family planning services is limited (McAllister et al., 2012).

A mixed-longitudinal study was conducted across nine Tsimane villages from September 2012–April 2013. The villages vary with respect to river access and distance to the market town of San Borja (pop. ~24,000) (Supplementary Table 1). All families with children aged 0–35 months were asked to participate. One family declined, and interviews were not successfully coordinated with another 13 families who agreed to participate (random with respect to village and infant age). The final sample included 161 families from 150 households, representing 92% of all eligible families present.

Ethnographic interviews, dietary recall, and anthropometric measures were collected during in-home visits. To examine longitudinal changes in feeding practices, a follow-up study was conducted with a subset of 48 infants from six villages who were less than 12 months old at initial interviews. Monthly dietary recalls and anthropometric measures were collected from these subjects over the next 4–6 months. The number of follow-up visits per subject varied due to date of initial interview and family absence during visits to communities (2–6 visits per subject, mean \pm SD = 3.2 \pm 1.4). Descriptive statistics for subjects by study group are given in Table 1.

At every visit, 24-h dietary recalls were first conducted to establish infant feeding status. Following WHO (2007) guidelines (Supplementary Table 2), EBF was defined as consumption of breast

Table 1
Subject characteristics for sample and by study group.

Descriptor (Range, mean \pm SD)	All subjects surveyed		Initial interview only		Prospective follow-up	
	N	%	N	%	N	%
Infant sex	161		117		44	
Male	92	57.1	62	53.0	30	68.1
Female	69	42.8	55	47.0	14	31.8
Infant age (mos.)	(0–35, 13.8 \pm 9.8)		(0–35, 17.4 \pm 9.0)		(0–10, 4.3 \pm 10.5)	
0–5	46	28.5	17	14.5	29	65.9
6–11	27	16.8	12	10.3	15	34.1
12–23	61	37.9	61	52.1	–	–
24–35	27	16.8	27	23.1	–	–
Maternal age (yrs.)	(14–49, 26.9 \pm 8.5)		(14–49, 26.7 \pm 8.3)		(14–45, 27.6 \pm 9.1)	
<20	33	20.4	24	20.5	9	20.5
20 to 29	71	44.1	52	44.4	19	43.1
30 to 39	38	23.6	29	24.8	9	20.5
40 and over	19	11.8	12	10.3	7	15.9
Number of births	(1–13, 5 \pm 3)		(1–13, 4 \pm 3)		(1–12, 5 \pm 3)	
No previous birth	27	16.8	20	17.1	7	15.9
2 to 8 births	115	71.4	82	70.1	33	75.0
9 or more	19	11.8	15	12.8	4	9.1
Spanish fluency						
None	72	45.9	50	44.2	22	50.0
Conversational	72	45.9	52	46.0	20	45.5
Fluent	13	8.2	11	9.9	2	4.5
Region						
Near Town	88	54.7	78	66.7	10	22.7
Remote	73	45.3	39	33.3	34	77.2

milk only, and CF as breastfeeding with any other solids or liquids (including water and formula). Weaning was defined as the full cessation of breastfeeding. At initial interviews, 30 infants were EBF, 106 had already begun CF, and 25 were already weaned. Among the infants sampled prospectively, 20 were EBF and 24 were CF when first interviewed. Over the course of the prospective study, 15 of these EBF infants transitioned to CF, and all infants were still breastfeeding at the end of the study.

Interviews were conducted in the Tsimane language by a trained assistant, with MM or GG present. MM conducted interviews in Spanish with ten mothers of mixed ethnicity who spoke Spanish as their primary language. The initial interview consisted of short-answer questions about the focal child's birth, breastfeeding, complementary feeding, and pre-mastication practices. Mothers of non-EBF infants were asked what the first foods and liquids they gave to their infants were, the age at which they gave them, and why they started CF. The earlier age of first food or liquid was recorded as age at CF. For EBF infants in the follow-up study, age at CF was recorded from subsequent dietary recalls. Maternal height was measured to the nearest 0.1 cm using a portable stadiometer (Seca 217).

2.2. Maternal and infant factors examined in conjunction with EBF duration

In statistical analysis, we consider three proxies of maternal condition expected to favor future over current reproductive investment, and therefore earlier CF: greater maternal height, lower parity, and a greater number of household females over the age of 7. Though maternal height is an indication of health and nutrition during childhood, these conditions may reflect access to family support and other resources that persist into adulthood. As an indicator of relatively improved condition and access to resources that can be invested in higher fertility, we predict that greater height will be associated with earlier CF. Younger mothers at lower

parity are also expected to introduce CF earlier, as these mothers are presumed to subconsciously favor future reproductive investment. Finally, Tsimane females over the age of 7 (who include maternal offspring, siblings, and other relatives) make significant contributions to child care (Winking et al., 2009). Mothers may divert more infant care to these all mothers, and thus begin CF earlier.

Infant-centric factors considered included sex and birth season. Milk composition in humans and other animals has been observed to vary by infant sex (Fujita et al., 2012; Hinde, 2009; Hinde et al., 2014; Powe et al., 2010; but see Quinn, 2013), which may differently affect EBF durations. Rainy season births among the Tsimane have been associated with lower maternal BMI and greater morbidity risks for infants (Curven, 2012), which may negatively influence maternal lactation or infant birth size.

We also considered the influence of village location, as a previous study showed that EBF durations in remote Tsimane villages were shorter than in villages closer to market (Veile et al., 2014). Perceptions of low milk and infant size at CF introduction are evaluated in limited analyses, as these were reported only in conjunction with reasons for CF introduction in initial interviews. In our mixed-longitudinal design, infant age relative to current feeding status and age at CF introduction varied widely across subjects. As such, age at CF was not evaluated in terms of time-varying factors such as maternal weight, % body fat, BMI, infant weight, length, or illness bouts.

Ethical approval

All study protocols were approved by the University of California Santa Barbara Institutional Research Board Human Subjects. Permission to conduct research was granted to the Tsimane Life History Project (THLHP) and affiliates. The THLHP maintains formal agreements with the local municipal government of San Borja and the Tsimane governing body (*Gran Consejo Tsimane*). Research permission was also granted independently to MM by the Estación Biológica de Beni.

The purpose of the study was explained to each of the study villages in community meetings held prior to beginning data collection. Subjects gave informed consent orally before each interview and follow-up visit. Subjects were compensated for their time with small care packages that included household goods (e.g. yarn, thread, combs) and over-the-counter medicines (e.g. paracetamol, salve).

2.3. Statistical analysis

All statistical analyses were performed using R (ver. 3.2.1). EBF and breastfeeding durations were estimated using multiple methods. First, the proportion of infants EBF at 0–5 months was estimated following WHO (2007) guidelines (Supplementary Table 2), using current feeding status of infants aged 0–5 months only. Second, mean \pm SE age of CF introduction for all children surveyed was estimated by Kaplan-Meier survival analysis, with EBF infants censored at age of interview. Ages of CF introduction reported during initial interviews and in follow up dietary recalls did not significantly differ (mean \pm SE = 130 \pm 5 vs. 135 \pm 8 days, log rank test p = 0.72), and were combined in subsequent analyses. All weaning ages were reported from maternal recall in initial interviews. Mean \pm SE age at weaning was also estimated by Kaplan-Meier survival analysis for all children aged 12–35 months (no children were weaned before one year of age). For all non-EBF children, mean \pm SD age at CF introduction and weaning as reported in initial interviews were calculated by village, infant sex, age group, and maternal parity group.

Age of CF in association with perceptions of infant growth and milk supply at time of CF introduction was examined by chi-square. Variance in premastication was assessed in a generalized mixed-effects model using the *lme4* package (Bates et al., 2014). The model included maternal ID as a random effect and infant age and meat and fish consumption the day prior as controls. We included maternal age, maternal Spanish fluency (“none” vs. “conversational to fluent”) and village location (remote vs. near market) as proxies of a more traditional lifestyle, predicting that younger and more acculturated mothers would be less likely to report premastication.

A Cox proportional hazards model was used to assess variation in EBF duration in association with maternal- and infant-centric factors. We first constructed a baseline Cox model that included the five maternal and infant factors discussed above, along with village location, and the time elapse since the reported age at CF introduction (to control for recall bias). A penalized spline term for parity was used upon further examination of the data. We determined the best fit Cox model using backwards stepwise selection with AICc, and evaluated the model for proportional hazards assumptions, influential observations, and nonlinearity of continuous variables. The final model was fit using the *smoothHR* package (Meira-Machado et al., 2013), which computes optimal degrees of freedom as specified by AICc, and estimates log hazard ratios and corresponding confidence intervals for nonlinear continuous variables.

The relationship between perceived low milk and age at CF introduction was assessed via linear regression. This analysis was limited to responses from non-EBF mothers in initial interviews ($n = 127$). The model included the same covariates from the final Cox model, substituting a parity group category in place of the non-linear spline, and adding a binary term for whether or not CF was introduced owing to perceived low milk supply. The model was checked for interactions among covariates and assumptions of normality.

3. Results

3.1. Tsimane infant feeding practices

According to population estimates based on 24-h dietary recall and WHO specified age groups (Supplementary Table 2), all Tsimane infants have been breastfed. Only 53% of mothers breastfed within 1 h of birth (Table 2), though these times are approximate since Tsimane women do not typically wear watches. All infants are estimated to begin CF by 6–8 months, and all children are estimated to breastfeed for at least one year, with 87% still breast-feeding at two years of age (Table 2).

As estimated by Kaplan-Meier survival analysis ($n = 161$, n events = 146), mean \pm SE time to CF introduction was 132.6 ± 4.9 days (approximately 4.4 months) and mean age at weaning ($n = 100$, events = 21) was 824.1 ± 36.5 days (approximately 27 months). Although according to WHO indicators 64% of infants are estimated to be EBF at 0–5 months (Table 2), only 25% of children

with known age at CF (38/146) reportedly began CF at the recommended ages of 6–8 months—75% began CF at 0–5 months. Among non-EBF children at initial interviews ($n = 130$), reported mean \pm SD age of CF was 3.8 ± 2.0 months, with 41% reporting CF before four months of age; mean \pm SD age at weaning was 19.1 ± 5.9 months, with only 13% of children weaned before two years of age. (Supplementary Table 3).

Food costs and preparation time for the most common Tsimane complementary foods appear to be minimal. Mothers do not prepare special foods for infants, though the diet is generally soft and bland, and conducive to infant consumption. Most meals are “*jo’na*”, referring to any rice, plantain, or pasta-based stew mixed with meat or fish. Family members generally eat seated on the ground, consuming individual bowls and additional helpings as desired. Mothers are primarily responsible for feeding infants and young children, though other family members may share snacks and drinks. Before age one, infants sit in their mothers’ laps and are spoon- or finger-fed from their mothers’ plates. By age two, most children are eating from their own plates, and by age three may be serving themselves liquids, meals, and snacks.

Introduction of liquids and solids is not rigidly imposed. Among non-EBF mothers ($n = 131$), 38% introduced liquids first, 23% introduced solids first, and 39% introduced both at the same age. However, solid foods in early months frequently referred to “*chinsi*”, the clear broth portion of *jo’na*. Chicha (a fermented beverage made from manioc, corn, or plantain), water, and juice were the most common first liquids introduced. Liquids were served in *erepas* (hollowed out *Crescentia cujete* gourds), plastic cups, and occasionally bottles. Though 11% of infants aged 0–23 months in initial dietary recalls were reportedly bottle-fed the day prior with non-maternal milk liquids (Table 2), none were given liquids exclusively by bottle. Infants in near market villages were no more likely to have been bottle-fed than infants in more remote villages (14% vs. 7%, chi-square = 0.95, $p = 0.33$).

Powder infant formula (a ~400 g cereal box) is available in market kiosks, but costs about 40 b (~\$US 6), equivalent to more than a half-day’s wage labor. Through a government program, infants at least 6 months old were eligible to receive one 30-serving bag of formula per month. These could be obtained in San Borja and were sporadically given out by visiting health promoters. When received, formula was given to infants but also consumed in powder form by other family members.

Tsimane mothers frequently premasticate foods deemed too hot, too dry, too tough, or a choking hazard (most commonly *jo’na*, roasted plantains, smoked or dried meats, and fish). Mothers reported occasionally orally transferring liquids mouth-to-mouth, generally when they were traveling and didn’t have a drinking vessel handy, or when they wanted infants to drink “a lot” (perhaps in cases of illness or dehydration). In initial interviews, 84% and 51% of non-EBF mothers ($n = 132$), respectively, reported having ever premasticated solids or orally transferring liquids. Premastication and orally transferring liquids were reported in 54% and 9%,

Table 2

Estimates of age-appropriate infant and young child feeding practices in Tsimane children aged 0–23 months. Sample sizes for each indicator reflect WHO-specified age groups (in parentheses).

Indicator (WHO, 2007)	n	%	95% CI
Initiation of breastfeeding within 1 h (0–23 months)	70/131	53%	(44.5; 62.1)
Ever breastfed (0–23 months)	133/133	100%	(96.5; 1.00)
EBF under 6 months (0–5 months)	29/45	64%	(48.7; 77.7)
CF by 6–8 months (6–8 months)	13/13	100%	(71.7; 100.0)
Breastfeeding at 1 year (12–15 months)	18/18	100%	(78.1; 100.0)
Breastfeeding at 2 years (19–23 months)	13/15	87%	(58.4; 97.7)
Predominant breastfeeding (0–6 months)	5/45	11%	(4.2; 24.9)
Bottle-feeding (0–23 months)	14/133	11%	(6.1; 17.3)

respectively, of all 24-h dietary recalls, declining in frequency by infant age (Fig. 1). In a mixed-effects logistic regression adjusting for infant age, the likelihood of pre-mastication the day prior was greater with consumption of fish, but did not vary with consumption of meat, village region, maternal age, or maternal Spanish fluency (Supplementary Table 4).

3.2. Tsimane mothers' self-reported reasons for introducing CF

In open-ended questions, 88% of mothers (121/137) cited specific reasons for introducing CF, with the remaining 12% reporting “no reason/just because”. Responses were grouped into nine categories (Fig. 2). Overall, 64% of mothers followed infant cues in introducing CF—either perceiving that their infants were hungry, big, or developmentally ready for food, or sick, small and in need of supplementation. Higher proportions of mothers who introduced CF at recommended ages (6–7 months) vs. earlier (0–5 months) reported doing so because infants were hungry, grabbing at food, big/growing well, or “just because” (Supplementary Table 5). All mothers who reported that their infants were small or sick, or that they themselves were sick or had no/low milk, introduced CF before 6 months of age. Sixty-five percent of mothers who reported no/low milk (15/23) introduced CF within the first month of life.

Responses that infants were crying or hungry may represent the same perception. Mothers used several terms to describe infant crying (*shavnaqui*, *shavñye*, *tari*, *váti*, *vara'shaqui*), which translate to wailing, crying with tears, and loud or incessant crying. Across 188 h of daytime focal follows, infants aged 0–16 months were observed crying in less than 1% of 5-min observational intervals (Martin, 2015). The onset of persistent crying may therefore be an honest signal of energetic needs or interest in food.

Mothers reporting that their infants were small at birth relative to other Tsimane newborns were no more likely to introduce CF before 4 months of age than mothers who perceived their infants as the same size or larger than other newborns (42% vs 38%, chi-square = 0.05, $p = 0.814$). However, mothers who reported their infants as small at the time of CF introduction were more likely to have introduced CF at 0–3 months as compared to mothers who reported their infants as similar to or larger than other same-aged infants (59% vs. 31%, chi-square = 8.05, $p = 0.004$).

Seventeen percent of mothers cited low milk supply as a reason for introducing CF. In their own words they had “no breast milk” (*itšij tashin*) or were “dry” (*chañej*). These mothers were no more

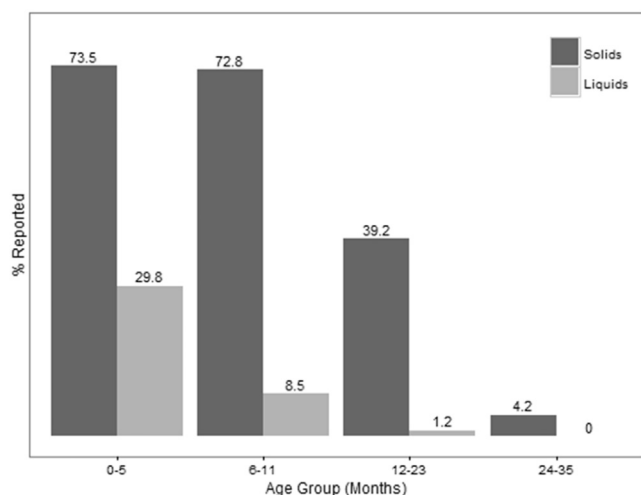


Fig. 1. Prevalence by age group of pre-mastication (solids) and oral transfer (liquids) reported in all 24-h dietary recalls with non-EBF children ($n = 236$).

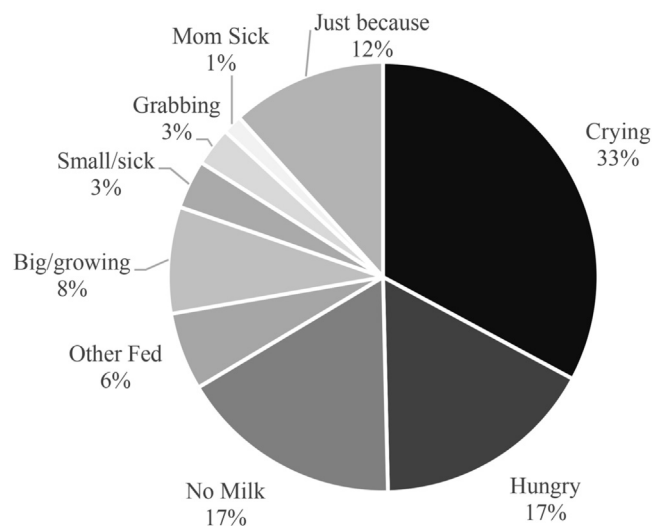


Fig. 2. Tsimane mothers' self-reported reasons for introducing CF ($n = 137$).

likely to initiate breastfeeding 24 h after birth than were mothers who introduced CF for other reasons (chi-square = 0.71, $p = 0.39$). However, 95% of these mothers introduced CF at 0–3 months of age, compared to just 32% of mothers who reported introducing CF for other reasons (chi-square = 30.41, $p < 0.001$). These mothers were also more likely to report their infants as small for their age at the time of CF introduction, as compared to mothers who introduced CF for other reasons (71% vs. 28%, chi-square = 15.24, $p < 0.001$). We did not ascertain whether mothers blamed perceived low milk for small infant size or if mothers gauged low milk from perceived poor infant growth or other cues. However, some mothers reported taking active steps to increase milk supply, such as drinking more liquids and massaging breasts with salt or warm papaya skins, and others reported that problems self-resolved and subsequently began EBF. All mothers who reported low milk continued breastfeeding.

In a separate line of questioning, 40% (49/125) of mothers reported receiving advice to introduce CF. Of these, 46% were advised to begin CF by their own mothers or mothers-in-law, 31% by other kin, 8% by other Tsimane, and 14% by a *napo* (a non-Tsimane Bolivian national). Advice to begin CF generally echoed the same reasons cited by mothers—because of crying or hunger (59%), so that infants would grow well and be healthy (13%), because the infant was small or sick (11%), or because the mother had no milk (9%). Primiparous mothers did not report receiving advice any more frequently than did multiparous mothers (40% vs. 43%, chi-square = 0.0005, $p = 0.98$).

In initial interviews 41% of mothers (60/146, including those still EBF) reported ever getting professional advice from a doctor, nurse, or other health care worker about when to feed their infants. However, only 53% of those mothers were told to introduce CF at 6 months: 25% were told to begin later than 6 months, 17% earlier, and the remaining 5% did not recall any specific age. Of those who received professional advice, 69% (37/54) introduced CF earlier than they had been recommended.

3.3. What predicts timing of CF introduction?

The best fit Cox model for time to CF included maternal height, parity, and the time elapse since CF introduction (Table 3). Contrary to our prediction, taller mothers were more likely to initiate CF later: each additional centimeter of height was associated with a 5%

lower CF risk. The penalized spline for parity resulted in a U-shaped hazard curve with the minimum hazard (i.e. longest EBF duration) at five births, and women at lower and higher parity more likely to introduce CF earlier (Fig. 3). Log hazard ratios of CF were not significantly greater than the minimum at 1–3 births—including for primiparous mothers (LnHR = 0.37, 95% CI = -0.07–0.81)—but were significantly greater after nine births (LnHR = 0.45, 95% CI = 0.01–0.89). The number of household females over age seven, village region, infant sex, and birth season were eliminated during model selection based on AICc. A model substituting a nonlinear term for maternal age instead of parity resulted in a poorer fit, though the resulting hazard curve was similar to that observed for parity (Supplementary Fig. 1).

In a linear regression adjusting for covariates, mothers who reported introducing CF because of perceived low milk began CF on average 3.4 months earlier than those who introduced CF because of other reasons (Table 4). As in the survival analysis, greater maternal height was associated with later CF introduction, and primiparity with earlier CF introduction. The association between higher parity and earlier CF introduction appears mediated by perceived low milk, as is evident when low milk is excluded or included in the model (Table 4). Forty-seven percent of high parity (>8 births) mothers (8/17) reported introducing CF because of perceived low milk, as compared to only 13% of mothers with 2–8 births (13/84) and 13% of primiparous mothers (3/20). There were no significant interactions between parity group and low milk or height.

4. Discussion

Tsimane mothers' self-reported reasons for introducing CF largely reflect concern for infant needs, with very early CF (0–3 months) notably related to perceived low milk supply and poor infant growth. In general, Tsimane mothers' motivations for early CF are consistent with those of mothers in other intensive breast-feeding populations, who view early supplementation as a practice that benefits, not risks, infant health (Gray, 1998; Meehan and Roulette, 2013). Mothers who were aware of feeding recommendations largely ignored them and introduced CF earlier.

No mothers cited household, labor demands, or lack of support as reasons for introducing CF. Our prediction that factors indicative of maternal reproductive trade-offs would be associated with earlier CF was not strongly supported. Greater maternal height predicted later CF introduction, suggesting mothers in better condition or with better access to resources invest more in current offspring (via more intensive breastfeeding) than in future reproduction (via reduced lactational costs). Additional research is needed to assess if maternal height is correlated with other measures of current maternal condition—e.g. energy balance, health, or milk volume and nutritional content—which would suggest that they can better sustain the energetic costs of longer EBF.

As predicted, lower parity was associated with earlier CF, but so was very high parity. This latter finding is inconsistent with an evolutionary framework that predicts reproductive efforts will increase as opportunities for future reproduction decrease (i.e. the terminal investment hypothesis) (Williams, 1966). We propose that different mechanisms may influence EBF duration across the reproductive lifespan. At earlier ages and low parity, maternal

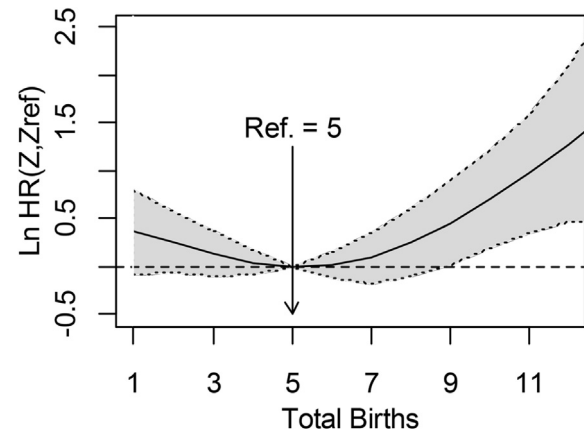


Fig. 3. Log hazard ratios of CF by parity (risk is relative to minimum hazard at 5 births).

inexperience and/or reproductive trade-offs may favor earlier CF, whereas lactational sufficiency may be constrained at advanced ages and higher parity. Higher parity Tsimane mothers more frequently reported introducing CF because of low milk, and indeed the association between high parity and early CF was no longer significant when controlling for perceived low milk (Table 4).

To our knowledge, this is the first study to explicitly link perceived low milk supply with high parity. Though behavioral mechanisms influencing milk supply among this demographic cannot be ruled out, several physiologically mediated mechanisms related to advanced age or parity could negatively impact milk synthesis. In the U.S., advanced maternal age has been linked to delayed onset of lactogenesis, which may result from age-associated increases in glucose intolerance and inflammation (Nommsen-Rivers et al., 2012). Breast milk from Gambian mothers with 10 or more births contained less endogenously synthesized fatty acids than milk from lower parity mothers (Prentice et al., 1989). Fatty acid composition could affect infant satiety or growth and be interpreted as insufficient milk supply. Finally, calcium stores become increasingly depleted with age and successive bouts of lactation (Horst et al., 1997; Nordin, 1997). Tsimane women lose relatively more bone mineral density with age as compared to American women, and bone mineral density is further reduced by relatively high parity and short interbirth intervals (Stieglitz et al., 2015). With sustained calcium secretion at high parity, homeostatic mechanisms may downregulate milk supply to conserve essential maternal function. This hypothesis may be tested in future research examining Tsimane milk composition.

In an earlier study of Tsimane infant feeding practices, Veile et al. (2014) found that EBF durations were shorter in remote forest villages as compared to near market villages. In this study, village region was eliminated as a predictive factor of CF during model selection. However, our sample did not include forest villages, while ages of CF between riverine and near market villages in the earlier study did not significantly differ. Of note, Veile et al. (2014) could not determine if longer EBF durations in near market villages resulted from relatively improved conditions, or whether public health messages influenced maternal behavior or biased maternal recall. Our results support the first interpretation, as greater maternal height and perceptions of low milk supply and poor infant growth were associated with earlier CF, but knowledge about feeding recommendations had little influence on CF decisions. At the same time, we observed marked differences in age at CF between individual villages (Supplementary Table 3), which may reflect unexplored influences of family and neighbors on individual feeding decisions.

Table 3
Best fit Cox proportional hazards model of time to CF introduction (in days).

Factor	Hazard Ratio (95% CI)	p-value
Maternal height (cm)	0.96 (0.92–0.99)	0.024
Parity	Nonlinear	0.006
Elapse time reported (days)	1.00 (1.00–1.00)	0.220

Table 4

Linear regression of age at CF introduction (months) in association with parity and perceived low milk supply (non-EBF infants, n = 127).

	Model 1		Model 2	
	Est. (95% CI)	p	Est. (95% CI)	p
Low milk (yes)	–	–	–3.43 (–4.15; –2.72)	<0.001
Parity group				
Prime (2 – 8 births)	–	–	–	–
Primiparous	–0.65 (–1.49; 0.20)	0.135	–0.85 (–1.56; –0.14)	0.018
High parity (9+)	–1.49 (–2.49; –0.49)	0.004	–0.32 (–1.17; 0.51)	0.437
Maternal height (cm)	0.05 (–1.51; 0.12)	0.124	0.10 (0.04; 0.15)	<0.001
Days since CF intro	0.0001 (–0.0005; 0.002)	0.214	0.0004 (–0.001; 0.001)	0.486

The age at weaning estimated by survival analysis in this study (27 months) is substantially later than mean ages (~19 months) reported from recall of already weaned infants both in this study (Supplementary Table 3) and in Veile et al. (2014). The age of CF estimated by survival analysis (4.4 months) was slightly higher than ages reported strictly from recall of non-EBF infants both here and in Veile et al. (3.8 and 4.1 months, respectively). CF and weaning ages calculated solely from recall appear biased by exclusion of infants that are still EBF and breastfeeding, respectively (i.e. right-censored). For small populations, mixed use of recall with current feeding status may best approximate typical ages of CF introduction and weaning.

The risks of earlier weaning and increased infectious disease exposure associated with early CF—as well as maternal perceptions of these risks—may vary across populations given maternal motivations, CF and breastfeeding practices, and local ecologies (Moffat, 2001). In many small-scale societies, kin support, divisions of labor, and other cultural practices are integral in maintaining intensive and prolonged breastfeeding (Meehan and Roulette, 2013; Panter-Brick, 1991; Piperataa, 2009). In populations in which early CF supplements without supplanting breastfeeding, EBF duration may be a poor indicator of breastfeeding intensity. Indeed, across lower and middle income countries, rates of EBF at 0–5 months are only weakly correlated with rates of breastfeeding at one year or more (Victora et al., 2016), with 60–90% of infants in these populations still breastfeeding at 12–15 months, despite low rates of EBF at 0–5 months (Lutter and Morrow, 2013). In other environments, the increased energy provided by early CF may paradoxically offset any additional risks posed by contaminated foods (Wilson et al., 2006), while pre-mastication may further minimize infectious exposure risks (Pelto et al., 2010). Finally, any perceived immediate benefits of early CF (e.g. weight gain, placated crying) may outweigh or be easier to discern than long-term risks, including later growth faltering, earlier weaning, and maternal health or reproductive consequences.

However, we caution that additional research is needed to fully ascertain the real or perceived costs and benefits of varying EBF durations for Tsimane mothers and infants. Our study is limited by the mixed-longitudinal design and reliance on maternal recall, which does not allow us to corroborate maternal perceptions of infant size, growth, health, or milk supply at the time of CF introduction. Subtle differences in CF practices and maternal work patterns may still influence EBF duration and weaning, but must be assessed by direct observation of breastfeeding and maternal time allocation (Panter-Brick, 1993b). Tsimane infant outcomes may vary with availability and quality of complementary foods, while early CF—even if motivated by infant needs—may still increase pathogen exposure or reduce nursing intensity enough to lead to earlier weaning. Future research with the Tsimane will consider the timing of CF introduction in association with subsequent breastfeeding behaviors, maternal energy balance, and infant growth and health outcomes.

5. Conclusion

International health organizations recommend EBF for 6 months as a universal standard of optimal infant feeding practices. Globally, however, most infants are not EBF for six months. Epidemiological and evolutionary research often frames early CF as suboptimal for infants—a consequence of structural barriers to breastfeeding, maternal energetic and time constraints, or reproductive trade-offs. However, mothers in diverse settings frequently cite concerns with infant growth, health, or milk supply as reasons for introducing CF before six months. While both maternal- and infant-centric factors likely combine to influence individual EBF durations, the contextual environment in which breastfeeding occurs may be important in predicting whether or not shorter EBF durations reflect maternal-infant conflict or congruence. Such a framework may also be useful in predicting risks of early CF in specific environments, and developing locally salient interventions to improve infant outcomes.

Though there are few if any structural barriers constraining breastfeeding among the Tsimane, we proposed that reproductive trade-offs may still favor shorter EBF durations in this well-nourished, high fertility population. Instead our results suggest that motivations for early CF are primarily infant-centric—reflecting differences in perceived infant needs that may reflect individual variation in infant growth or lactational sufficiency. In partial support of our predictions, we found a novel non-linear association between parity and earlier CF, and suggest that different behavioral and/or physiological mechanisms may constrain EBF among primiparous and high parity Tsimane mothers. Additional research on maternal and infant outcomes associated with EBF durations may better illuminate the role of reproductive trade-offs in influencing the causes and consequences of early CF in this population.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.socscimed.2016.10.003>.

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