Breastfeeding Duration and the Social Learning of Infant Feeding Knowledge in Two Maya Communities

Luseadra J. McKerracher, Pablo Nepomnaschy, Rachel MacKay Altman, Daniel Sellen & Mark Collard

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Luseadra J. McKerracher, et al. *[full author details at the end of the article]*

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Abstract

Variation in the durations of exclusive breastfeeding (exBF) and any breastfeeding (anyBF) is associated with socioecological factors. This plasticity in breastfeeding behavior appears adaptive, but the mechanisms involved are unclear. With this concept in mind, we investigated whether durations of exBF and anyBF in a rural Maya population covary with markers of a form of socioecological change—market integration—and whether individual factors (individual learning, physiological plasticity) and/or learning from others in the community (social learning, norm adherence) mediate these changes. Using data from 419 mother-child pairs from two Guatemalan Maya villages, we fit a bivariate linear mixed model. The model compared exBF and anyBF among children from households of varying degrees of market integration whose mothers follow what we inferred to be local infant-feeding norms. It controlled for other factors expected to affect breastfeeding durations. We found evidence that exBF is associated with whether mothers follow their population's infant feeding norms, but no evidence that exBF is associated with the household's level of market integration. Conversely, anyBF is significantly associated with the household's market integration, but not with the villages' inferred norms. Because deviations from exBF norms are likely to result in infant mortality and reduced fitness, we hypothesize that the incentive to conform is relatively strong. Relatively greater individual plasticity in anyBF allows mother-child pairs to tailor it to socioecological conditions. Deviations from anyBF norms may be tolerated because they may provide later-life health/fitness payoffs, while posing few risks to infant survival.

Keywords Breastfeeding · Modernization · Market integration · Acculturation · Culture · Guatemala

This exploratory paper focuses on the possible impacts of socioecological changes and learning strategies on breastfeeding durations in Maya mothers. The socioecological factors of interest here concern changing patterns of subsistence and labor organization.

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The learning strategies under investigation include individual learning and different forms of social learning. The breastfeeding durations we examine are mothers' self-reported duration of exclusive breastfeeding (exBF) and duration of any breastfeeding (anyBF). Usually measured in days or months, exBF is the length of time during which a human infant consumes only breastmilk. Introduction of any non-breastmilk liquids, semi-solids, or solids other than medications represents the end of the period of exBF (Qureshi et al. 2011). Typically measured in months, anyBF refers to the amount of time for which an infant/young child consumes any breastmilk in any amount (Binns et al. 2016).

The extent to which exBF and anyBF are influenced by socioecological factors and learning strategies is important from both public health and evolutionary perspectives. Regarding health, there is evidence that breastfeeding duration, especially duration of anyBF, is negatively associated with maternal risk of developing numerous noncommunicable diseases, including cardiometabolic disorders, type 2 diabetes, and several reproductive cancers (Chowdhury et al. 2015; Stuebe 2015). Additionally, variation in exBF and anyBF appears to affect variation in offspring health, survivorship, and well-being during infancy and over the life course (Victora et al. 2015, 2016). Timing of exBF between 4 and 9 months of age in particular lowers infant risks of contracting potentially fatal gastrointestinal and respiratory diseases and of becoming stunted/wasted (e.g., Girma and Genebo 2002; Kramer and Kakuma 2012; Lamberti et al. 2011; Victora et al. 2016).

Regarding evolutionary demography, the relationships between exBF and anyBF and socioecological factors also have profound impacts on the fertility and fitness of both mothers and infants (e.g., Emery-Thompson 2013; McDade and Worthman 1998; Sellen 2009). Specifically, it is now well-established that on-demand, frequent breastfeeding, whether exclusive or not, impacts ovarian function and can inhibit ovulation (Labbok 2015), potentially increasing interbirth intervals. Notably, ovulatory suppression only occurs when mothers are expending more energy to support lactation and other daily activities than they are consuming through food (Valeggia and Ellison 2004, 2009; Harris and Vitzthum 2013; see also Mattison et al. 2018a). Additionally, early sexual maturity, early age at first birth, and short birth spacing (major proximate predictors of high fertility) are associated with histories of short exBF and anyBF (e.g., Nettle et al. 2011; Yermachenko and Dvornyk 2014).

Moreover, given the health and fitness consequences of breastfeeding for individuals, it is unsurprising that, among populations, durations of exBF and anyBF are associated with broad features of populations' socioecologies. Average exBF tends to be shorter in populations in which women have heavier non-domestic labor burdens and spend more time and energy working outside the home, away from their infants (Levine 1988; Meehan and Roulette 2013; Nerlove 1974). Average anyBF is related to variation in: external ecological risks, such as endemic infectious disease load (Quinlan 2007), household structure (Quinlan and Quinlan 2008), and maternal metabolic programming (Gawlik and Hochberg 2012; Gawlik et al. 2011). Both exBF and anyBF are associated with a population's subsistence economy (Sellen and Smay 2001). Generally, these associations have been proposed to be adaptive, such that the average durations of exBF and anyBF in a given population, other things being equal, are expected to be associated with the likelihood of babies surviving infancy and, later, of successfully reproducing.

It is currently not known, however, how these putatively adaptive, cross-cultural associations arose. One way of shedding light on this question is to look at variations in exBF and anyBF across families within a population as that population's socioecology changes demonstrably within the span of a human generation, such that some families/households in the population are exposed to socioecological conditions that differ markedly from those of their neighbors.

This strategy is the one we employ here. We use data from a Maya population living in two villages in the Guatemalan Central Highlands. This population is currently experiencing substantial socioecological change (Berry 2010). Most notably, the economy is shifting from predominantly subsistence agriculture to wage labor and market exchange, and this shift is associated with changes in nutrition and in fertility dynamics (McKerracher et al. 2017a). These changes seem to be driven primarily by the presence of growing numbers of people from Europe and North America visiting the area as tourists, buying and leasing property, and financing economic development (Atyeo et al. 2017; Berry 2010; McKerracher et al. 2017a).

Demographic and economic changes such as the ones affecting the study population have been found to be associated with changes in breastfeeding duration in a number of indigenous populations, including the Maya (Atyeo et al. 2017; Valeggia 2016; Veile and Kramer 2015, 2018; Veile et al. 2014; Wren et al. 2015; see also Barha et al. 2017; McKerracher et al. 2017a, 2017b). Collectively, this body of work highlights that Central American indigenous peoples are experiencing rapid changes in their nutritional, disease, and political ecologies; their access and attitudes to biomedical healthcare interventions; and their attitudes to work, parenting, and gender roles. More importantly, these studies show that each of these kinds of changes affects the ability and desire to breastfeed within these populations.

That being said, at least three important unknowns about the associations between breastfeeding behavior and rapidly changing socioecological conditions in indigenous populations remain. Most obviously, it is currently unclear whether these kinds of economic and demographic changes generally result in shorter or in longer periods of exBF and anyBF. Generally, the prediction has been that we should expect increased market integration to be associated with declines in rates of breastfeeding initiation and in length and intensity of exBF and anyBF (e.g., Hoke 2017; Veile et al. 2014). There are a number of complementary reasons for this prediction. One is that a population's integration into the wage labor market means that mothers are more likely to engage in the kinds of work where they cannot easily bring their babies with them. This separation between mothers and infants reduces the opportunities for on-demand breastfeeding and also means that infants spend more time in the care of others who provide babies with non-breastmilk foods, interrupting the breastmilk supply-and-demand cycle (e.g., Levine 1998; Moffat 2002; Nerlove 1974). Another reason for the prediction is that increased market integration allows easy access to energy-dense foods, such that mothers more quickly resume ovulation and become pregnant again after giving birth, even while breastfeeding (Valeggia and Ellison 2004, 2009). A new pregnancy can lead to termination of lactational investment in the previous child (e.g., Jakobsen et al. 2003). A third reason is that the increased stress associated with inequality and competition introduced by market integration may drive accelerated life history strategies in mothers (McKerracher et al. 2017a), including truncated exBF and anyBF. Lastly, it has also been reasoned that market integration substantially increases

exposure to the infant feeding norms of relatively wealthy, prestigious urbanites and/or immigrants from the Global North, and these norms favor brief or nonexistent periods of exBF and anyBF. It may be that exposure to these norms reduces the normative breastfeeding durations in indigenous populations undergoing demographic and economic transitions (Huffman 1984). Despite these expectations, however, previous work suggests that the direction of the effects of increased market integration on length of breastfeeding varies. Length of exBF in particular may increase, decrease, or remain unchanged in relation to market integration (e.g., Gonzales de Cassio et al. 2013; Veile and Kramer 2015, 2018; Veile et al. 2014).

The second unknown is that we have little understanding of whether exBF and anyBF respond to socioecological changes in similar ways, or if physiological or cultural differences affect how they each respond to socioecological changes. To date, the few studies directly relevant to this question have produced conflicting results, with both durations increasing in some populations, decreasing in other populations, and responding in opposite ways in still others (e.g., Gonzales de Cassio et al. 2013; Veile and Kramer 2015; Veile et al. 2014). We suggest that this variability in how exBF and anyBF respond to rapid shifts in socioecological conditions may be connected to how these behaviors are learned.

This brings us to the third unknown, which is that, as suggested above, we have a very limited understanding of the proximate biological and cultural mechanisms determining the ways exBF and anyBF are adapted (or not) to socioecology. In principle, mother-infant dyads may adjust breastfeeding behavior to socioecological conditions through individual mechanisms (e.g., physiology, individual learning). Indeed, many mothers from a variety of different contexts report breastfeeding and weaning in ways that are responsive to their babies' cues (e.g., Cameron et al. 2012; Martin et al. 2016), to their own bodies' cues (e.g., Fujita et al. 2012), to cues from their household environments (e.g., Sellen 2001), or through self-teaching (e.g., Redshaw and Henderson 2012) rather than learning about what to do from other adults. Mothers may also learn their infant feeding strategies culturally—that is, from other members of their population, who perhaps model behaviors or offer advice, instruction, and explanation. In support of the latter hypothesis, which emphasizes the role of cultural learning, we know from previous work that mothers from a wide range of populations acquire information about how to feed infants through cultural transmission (Balsamo et al. 1992; Dettwyler 2004:720–21; Fouts et al. 2012; Hadley et al. 2010; Meehan and Roulette 2013; Newson 2013; Schafer et al. 2015; Snopkowski and Kaplan 2014; Stewart et al. 2013; Wehr et al. 2014; Wells 2006). Furthermore, adhering to cultural norms around infant feeding is often constructed as "good parenting," whereas deviations from them are viewed negatively (Knaak 2010; Meehan and Roulette 2013; Murphy 1999; see also Creighton 1992; Gray 1996). Thus, learning culturally may be a key mechanism underpinning previously observed cross-cultural variation in associations between average breastfeeding durations and socioecological factors.

Although we know that aspects of infant feeding are learned culturally in many—if not all—human populations, theory from evolutionary norm psychology (reviewed in Gelfald and Jackson 2016) predicts that different infant feeding behaviors may be more or less likely to represent foci for cultural learning and attention, depending on the ecological context. In particular, deviations from central tendencies in some behaviors have high and immediate fitness costs (i.e., increased morbidity, mortality). We should

expect such behaviors to be more likely to be transmitted culturally and for the norms around those behaviors to be relatively tightly policed (e.g., Henrich and Henrich 2010). Fitness stakeholders such as grandmothers have a vested interest in making sure their grandchildren are fed appropriately so as to survive infancy, and they may be especially likely to offer and reinforce recommendations when the consequences of not doing so decrease the survivorship chances of their grandchildren (Euler et al. 2001; Newson et al. 2007). Similarly, mothers may be particularly likely to solicit and to make use of recommendations and may be especially attuned to norms related to behaviors where deviations are likely to result in serious illness for their babies (Olander et al. 2016). Furthermore, the visibility of a given behavior might matter, with behaviors in public or semi-public spaces (e.g., giving of supplementary foods during family meals, bottle-feeding outside of the home) subject to more cultural control than those in private (e.g., comfort feeding from the breast at night). In contrast, we might expect infant and young child feeding behaviors for which any fitness consequences are likely to be relatively minor and/or delayed in realization until adult life (i.e., duration of anyBF) to be less carefully monitored and thus more sensitive to dynamics of individual mother-child dyads and their immediate, household-level socioecological cues.

With the foregoing ideas in mind, we have three objectives in this paper. The first is to describe the self-reported breastfeeding behaviors in the focal population and to frame these reported breastfeeding durations in terms of cultural norms or tendencies. The inhabitants of the two villages (designated here as "A" and "B") are, as mentioned above, becoming more reliant on participation in the market economy, which is precipitating a variety of other social and demographic changes (Berry 2010). We will call these changes "modernization" to be consistent with studies carried out in other populations (e.g., Veile and Kramer 2018; Veile et al. 2014; see also Mattison and Sear 2016 for a thoughtful, general definition of modernization). At the time of data collection, modernization had affected village B much more than village A (McKerracher et al. 2017a). Our second aim is to assess the extent to which modernization impacts exBF and anyBF. In this assessment, we pay attention to possible differences between the two breastfeeding milestones, both in terms of their physiology and in terms of the cultural emphasis placed on them. Our third and final objective is to investigate the effect of different learning strategies—individual versus social—on reported breastfeeding durations. We include this last aim to explore the mechanisms through which variation in exBF and anyBF respond to variation and changes in socioecological conditions.

Materials and Methods

Study Population

This study is based on data concerning 82 women and their 419 fully weaned children from two rural villages in the Sololá region of the Guatemalan Central Highlands. Situated at ~1500 m above sea level in rugged terrain and with a warm, biseasonal (wet and dry) climate, the villages are each home to between one and two thousand Maya people (Nepomnaschy 2005; see also Wren et al. 2015). Both villages are mainly

accessed by boat, although B has a fairly reliable road access as well (Atyeo et al. 2017; Berry 2010; Nepomnaschy 2005).

In 1996, a civil war that had raged in Guatemala for more than 30 years and had impacted the highland communities both directly and indirectly officially ended. From 1996 onward, Europeans and North Americans began to visit and buy properties in and around the communities. This growing presence of relatively affluent outsiders has been associated with a number of socioecological changes to the villages, particularly village B. Chief among these, as mentioned, was a switch from an almost entirely agrarian economy, largely for subsistence, to heavier reliance on cash cropping alongside considerable participation in other forms of wage labor, particularly in service and construction. Additionally, a regularly staffed health post and a small vocational school were established in the 2000s in village B. These shifts have been accompanied by an increase in the numbers of female earners and in woman-headed households (Berry 2010). Further, a small but steadily increasing number of women in the villages are beginning to manage their fertility biomedically (McKerracher et al. 2017a). Further details on the communities are available in Berry (2010) and Nepomnaschy (2005).

Data Collection

The data used in this study were collected between January and April 2013, following approval by the Simon Fraser University Research Ethics Board, SFU-REB protocol 2012so668. Each participant was informed of the study's goals and the protocols in her native language, Kakchiquel, by local, female, Kakchiquel-speaking field assistants. Each learned that participation was completely voluntary, that she could withhold any information she did not want to share, and that she could withdraw from the study at any time with no negative consequences for her. Those who agreed to participate and were literate printed and signed their names on consent forms containing said information. Illiterate participants had the documents read to them in Kakchiquel, and they signed with an X, a thumbprint, an initial, or a signature, depending on personal preference.

The dataset comprises information on reported exBF, anyBF, household demographic factors, maternal anthropometry, maternal control of a share of family resources, sources from which mothers obtained cultural knowledge regarding infant and young child feeding strategies, and weaning food choices. With the exception of the anthropometric measures, the data were collected via two sets of recall-based, structured interviews with mothers, none of whom were pregnant at the time of the study. The interviews were carried out by five local research assistants, who were trained through two 4-h workshops led by a Guatemalan psychological measurement expert. The research assistants administered the interviews in the local Kakchiquel Mayan dialect (of which they and participants were native speakers), and then hand-recorded mothers' responses in Spanish on the bilingual (Kakchiquel-Spanish) interview-guide forms they were following. During the workshops, they had been trained to probe/prompt from the interview guides and to translate as they recorded. The recording was done in Spanish because none of the research assistants could write in Kakchiquel, but all had received multiple years of formal education in Spanish and could write it fluently. Subsequently, the responses were translated from Spanish to English by the research team in preparation for coding and analysis. The Spanish-English translations were verified by back-

translating a subsample of approximately 10%. No mistranslations, with the exception of some locally specific food names, were identified. Six unexpectedly high values for breastfeeding durations were recorded; in these instances, research assistants were asked to confirm these values in a short follow-up interview. All were confirmed. We note here that some of the recalled values for selection of weaning foods and for breastfeeding durations, especially the ones pertaining to exBF (Burnham et al. 2014), are likely subject to recall bias since in most cases the interviews were carried out years after even the youngest child in a family was weaned. This bias might be problematic if our main aim in this study was to accurately and precisely describe actual breastfeeding lengths in the population, but instead our main aim with these post hoc analyses is to understand how women *think* they behaved.

Anthropometric data were collected over a period of four days in which study participants gathered at their village's health post and were measured by members of our team, following the guidelines outlined by Antón, Snodgrass et al. (2009). The measurements were height (cm), taken with a portable stadiometer; mass (kg), assessed with a portable digital scale; and upper-arm skinfold thickness (mm), taken with manual-read outside skinfold calipers. Each measurement was taken at least three times, with additional measurements taken as needed until intra-observer error for the observation was less than 10%.

Data Management

The raw data generated through the interviews and anthropometric measurements were used to create the following independent and dependent variables:

exBF (Dependent) To quantify exBF, we used mothers' reported number of months for which each child consumed only breastmilk. Interviewees were instructed that introduction of any liquids or solids, including formula, animal milk, or water, would indicate the end of exBF. Women generally reported these values in months, but a few reported exBF in fractions/compound fractions of years. In such cases, we converted reported values into months. These raw values were positively skewed, so we applied $\log_{10}$ transformations to each observation (all observations were non-zero), which resulted in a better approximation of a normal distribution. This and all other transformations as well as the calculation of all descriptive statistics and preliminary analyses were carried out in R's *stat* package (R Development Core Team 2014).

anyBF (Dependent) AnyBF was quantified using recalled number of months for which each child was breastfed, including occasional feeds and comfort feeds. Again, any values reported in years/compound fractions of years were converted into months. The distribution of these values was also positively skewed, so we again applied a $\log_{10}$ transform.

Mod Score (Independent) A composite, index variable, Mod score was devised to characterize the extent to which each woman and her family had been influenced by increased market integration. Mod score encompasses nine variables pertaining to demography (whether the mother first gave birth after the arrival of the first Europeans and North Americans; whether she reported a below-population-average percentage of

infant or child deaths; whether she reported using contraception), anthropometry (whether she had a body mass index >25; whether she had upper-arm skinfold thickness more than a standard deviation above the population average), weanling diet (whether she reported feeding her youngest child weaning foods recommended by public health officials, whether she reported feeding her young child a fortified infant cereal, whether she reported avoiding weaning items contraindicated by public health guidelines such as coffee, tea, cola, or untreated water), and the woman's control of a share of household resources (whether or not she earned money in the cash economy through wage labor and/or through sale of consumables). Each of these sub-variables represents a coarse proxy of lifestyle changes associated with modernization and increased market integration (e.g., Olszowy et al. 2015; Snopkowski and Kaplan 2014; Wells 2010). The contributing variables were converted into dummy values of one or zero. Descriptions of the variable scorings are presented in Table 1, with further details available in the data supplement (ESM S1). To derive the Mod score used as a predictor in the models we reported in the main text, we summed dummy scores for each of the nine sub-variables. We used a simple summation index rather than a saved score from a correspondence analysis for ease of interpretation and visualization. Mod scores could take values between zero and nine, with zero representing the most traditional households and nine representing the most modernized ones. We report sensitivity analyses in which we evaluate the effects of varying the composition of Mod score in the supplementary materials (ESM S2).

Mode of Cultural Learning (Independent) This variable classifies the source(s) from which women learned about infant feeding. Values for mode of cultural learning were derived from women's responses to the question: "Did you learn about how to feed infants and children from anyone? If so, who? You can list as few or as many people as you would like." Women who did not report a source of infant and young child feeding knowledge were prompted by interviewers with a follow-up question: "If not, how did you learn about how to feed infants and young children?" Women who reported knowledge sources that were likely to provide culturally normative or conservative advice (i.e., female family members older than themselves, friends/neighbors/members of the community older than themselves, or from indigenous midwives who had not received any formal education) were scored as "high fidelity" cultural learners. Women who reported knowledge sources who were unlikely to provide culturally normative or conservative advice (i.e., women who reported teaching themselves, learning from their infants and young children, learning through practice, learning from Western biomedical professionals, or learning from multiple sources likely to provide conflicting information) were scored as "low fidelity" cultural learners.

In addition to the two independent and two dependent variables, we also included four control variables in the analyses—village, birth order, access to help with infant feeding, and infant sex. We included the control variable "village" because there are differences between the two villages in the physical and built environments that we reasoned could influence exBF and anyBF. Village was scored as a dummy variable—0 or 1, to represent A and B, respectively. Birth order and access to help with infant feeding were revealed to impact anyBF by our previous work in this population (McKerracher et al. 2017b). Access to help with infant feeding derived from a question in which women were asked if they received "no help," "a little help," or "a lot of help"

Table 1 Subsidiary variables used in calculating Mod score

Type	Variable	Scoring (+1 per variable if more traditional, 0 if more modernized)
Demography	Reported/inferred contraceptive use	1 if contraception reported and all IBIs less than 2x̄ IBIs (2*3.14 yrs. = 6.28 yrs) during fertile years (15–45), 0 if no contraception reported and/or if one or more IBIs exceed 6.28 years.
	Adulthood before or after the end of the Guatemalan civil war in 1996	1 if a woman began her reproductive career (first gave birth) after 1996, 0 if reproductive career began prior to or during 1996.
	Under five mortality	1 if number of reported infant and child deaths/number of births <0.2, 0 if number of reported infant and child deaths/number of births ≥0.2[†]
Anthropometry	Body Mass Index (BMI)	1 if above standard overweight threshold of 25, 0 if below this threshold
	Upper arm skinfold thickness	1 if ≥ x̄ (10.15 mm), 0 if < x̄ (10.15 mm)
Weanling diet	Use of protein and micronutrient supplement porridge (Incaparina) in infant diet	1 if supplement, recommended by Guatemalan government representatives, used; 0 if not used.
	Use of naturally occurring protein- and micronutrient-dense foods in infant diet	1 if biomedically recommended but expensive foods such as beans, eggs, fish, meat used; 0 if not used.
	Use of stimulants in infant diet	1 if coffee, tea, cola not used, consistent with biomedical recommendations, as weaning food; 0 if used as preferred weaning food
Participation in market economy	Woman's participation in sale of products or labor	1 if woman reports regularly doing paid work or in selling products at market; 0 if she does not.

[†] Early (1970) reports under 5 mortality for the Lago Atitlan Region for the late 1960s as ~0.285. We took a conservative approach and rounded this estimate down to 0.2 rather than up to 0.3

with providing, preparing, or giving food or drinks to infants. It was scored as 0 for women who reported no help with any infants, 1 for women who reported a little help with some infants, and 2 for women who reported a lot of help for most infants. Infant sex was also included because it is a known correlate of breastfeeding variations in many small-scale societies (e.g., Fujita et al. 2012). All data used in the analyses are available in the ESM.

Analyses

We began by visually inspecting histograms of exBF and anyBF durations (Fig. 1; this and all other figures were made using the ggplot2 package in R; Wickham 2009), calculating basic descriptive statistics, and tabulating counts of convergence on a single reported value of exBF and anyBF. These tabulations enabled us to describe reported breastfeeding durations in this population. We assumed that the most frequently

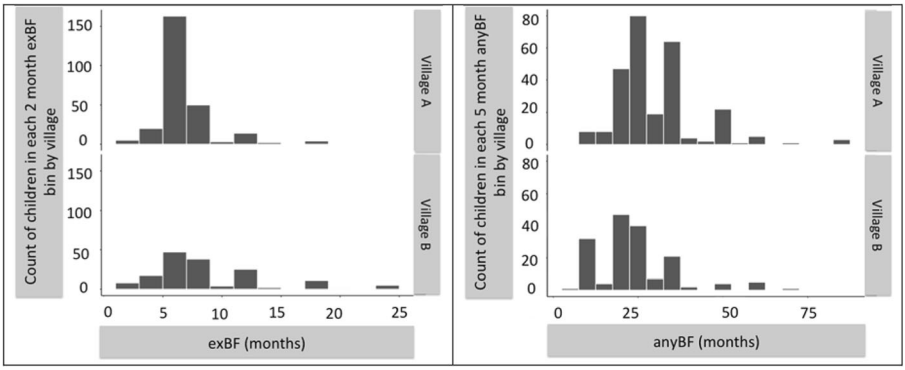

Fig. 1 Variation in length of exclusive breastfeeding (exBF) and any breastfeeding (anyBF), grouped by village. (**left**) Histogram of duration of exBF by village, binned into 2-month intervals (binwidth = 2). The overwhelming majority of women from village A report ending exBF at 6 months for most of their children. The majority of women from village B report ending exBF between 6 and 12 months. (**right**) Histogram of duration of anyBF, binned into 5-month intervals (binwidth = 5). The majority of women from village A cease anyBF when their children are between 21 and 36 months of age. The majority of village B women cease anyBF when children are between 18 and 24 months of age

reported value for each breastfeeding variable represents the cultural norm for the variable, with these modal values generally according to our (admittedly anecdotal) observations and discussions with our local research assistants about breastfeeding norms in the communities.

Next, we investigated links between breastfeeding behaviors and socioeconomic change and mode of cultural learning. To this end, we fit a bivariate linear mixed effects model that allowed one level of covariance between exBF and anyBF observed on different children born to the same mother, and a different level of covariance between exBF and anyBF observed on a given child. The model controlled for the effects of village, birth order, infant sex, and access to help with infant feeding. We conducted further post hoc tests on whether the effects of Mod score on exBF and anyBF differed and whether the effects of mode of cultural learning on exBF and anyBF differed.

We then performed a sensitivity analysis using an alternative scoring of Mod score. For this analysis, we dropped those components from the index for which expectations of direction of causality were least clear or were most likely to be heavily confounded (see ESM S2). All mixed effects regression analyses were implemented in the nlme package of R (Pinheiro et al. 2015). Because there were five children whose mothers reported both initially and during a follow-up interview that they breastfed exclusively for close to two years, which is far beyond the six to nine months when infant nutritional requirements appear to outstrip what can be provided through breastmilk alone, we also ran a sensitivity analysis in which these outliers were excluded (ESM S3).

Results

Sample Characteristics

Forty-seven of the mothers who participated in the interviews and anthropometric assessments came from village A. The remaining 35 came from village B. The village

A mothers provided information on 261 children; those from village B reported on 158 children. The participating mothers ranged in age from 28 to 55 years, with a mean (± SE) of 39 (±0.63) years. Most mothers first gave birth between the ages of 18 and 20 (McKerracher et al. 2017a). Of the 82 participants, 37 were postmenopausal. Average number of children per family surviving past age five, based on postmenopausal mothers, was roughly seven in village A and six in village B (McKerracher et al. 2017a). Their fully weaned children ranged in age from 20 months to 36 years, with a mean of 14 (±0.32) years. Of these, 218 (52%) were girls and 201 (48%) were boys.

Mod score ranged from two to nine, with a median and mode of five, and a mean of 5.7 (±0.63). Thirty of the mothers reported relying on low-fidelity cultural learning sources for infant and young child feeding information. The remaining 52 relied on high-fidelity sources.

Variation in exBF and anyBF

Descriptive statistics for exBF and anyBF are summarized in Fig. 1 and Table 2. After excluding a substantial outlier of 60 months,[1] reported exBF in the full sample ranged from 1 to 24 months, with a mode and median of ~6 and a mean of 7.8 months. AnyBF ranged from 6 to 84 months in the full sample, with a mode and median of 24 and a mean of 27.6 (±0.61) months.

With regard to the tendency for mothers to report breastfeeding durations identical to the cultural norm—represented by the sample mode of the variable—we found that 163 of 419 (38.9%) children for which we have data were reported to have been exclusively breastfed for ~6 months. This tendency to report exBF of ~6 months was especially prevalent among village A mothers, who reported that 134 of their 260 children (53.4%) had exBF values that reflected the sample mode; only 30 of 168 children (17.8%) from village B were reported to have modal exBF values. There was lower consensus with regard to anyBF: 115 of 419 children (27.4%) were reported to have stopped breastfeeding at or near the sample mode of 24 months. The differences in consensus in anyBF between the two villages were minor relative to the exBF differences, with 77 of 260 (29.6%) mother-infant pairs from village A reported to have modal anyBF values and 38 of 159 (23.9%) mother-infant pairs from village B reported to have modal anyBF values.

Relationships between Breastfeeding Durations, Mod Score, and Mode of Cultural Learning

We present the main results regarding exBF and anyBF in relation to Mod score and mode of cultural learning in Table 3 and Fig. 2. We found mode of cultural learning to be the only significant predictor of variation in exBF (adjusting for all other predictors), with mothers who learned about infant and young child feeding from low fidelity sources reporting introduction of any complementary liquids/solids slightly later than mothers who learned from high-fidelity sources. In particular, we found no evidence of

[1] The child's mother was reinterviewed and confirmed her initial report. However, it is unlikely that a human child could survive on breastmilk alone for 60 months, so we have elected to treat the data point as an error in recall.

Table 2 Descriptive statistics for durations of exBF and anyBF. Unit for all values is months

Sample	Min	Mean	(SD)	Median	Mode	Max
Full sample exBF	3	7.8	(3.5)	6	6	24
Village A exBF	1	7.8	3.5	6	6	24
Village B exBF	1	7.0	(4.6)	6	6	19
Full sample anyBF	6	27.6	(12.3)	24	24	84
Village A anyBF	8	29.8	(11.2)	24	24	84
Village B anyBF	6	23.5	(12.2)	20	24	72

an association between exBF and Mod score, adjusting for all other predictors (see estimated "Mod score" effect in Table 3; $p = 0.566$). Our sensitivity analyses accorded with these conclusions (see ESM Tables S1 and S2).

The main results pertaining to anyBF in relation to Mod score and mode of cultural learning are presented in Table 3 and Fig. 3. We found that Mod score is a significant predictor of variation in anyBF, adjusting for all other predictors (based on the Wald test of the sum of the "Mod score.anyBF" and "Mod score" effects; $p < 0.001$), with mothers with higher Mod scores breastfeeding for shorter periods. We found no evidence that anyBF is associated with mode of cultural learning, adjusting for all other predictors (based on the Wald test of the sum of the "Mode of cultural learning (low fidelity)" and "Mode of cultural learning (low fidelity).anyBF" effects; $p = 0.444$).

Table 3 Bivariate linear mixed effects regression analysis of effects of Mod score and mode of cultural learning on both Log_{10} duration of exBF and Log_{10} duration of anyBF. Breastfeeding durations (exBF or anyBF) measured on children born to the same mother are assumed to be correlated, but the correlation between exBF and anyBF may depend on whether they are measured on the same child or different children. The exBF and anyBF durations of children born to different mothers are assumed to be uncorrelated. The variances of exBF and anyBF may differ

Fixed effect	Estimate	SE	p
Intercept	0.848	0.04	0.000***
Intercept.anyBF	0.712	0.05	0.000***
Mod score	−0.004	0.01	0.566
Mod score.anyBF	−0.020	0.01	0.004**
Mode of cultural learning (low fidelity)	0.214	0.04	0.000***
Mode of cultural learning (low fidelity).anyBF	−0.179	0.05	0.000***
Village (B)	−0.068	0.04	0.104
Village (B).anyBF	−0.008	0.05	0.858
Birth order	−0.001	0.00	0.799
Birth order.anyBF	0.007	0.01	0.189
Access to help with infant feeding	0.002	0.01	0.869
Access to help with infant feeding.anyBF	−0.030	0.01	0.030*
Infant sex (m)	−0.010	0.01	0.473
Infant sex (m).anyBF	0.026	0.02	0.273

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$

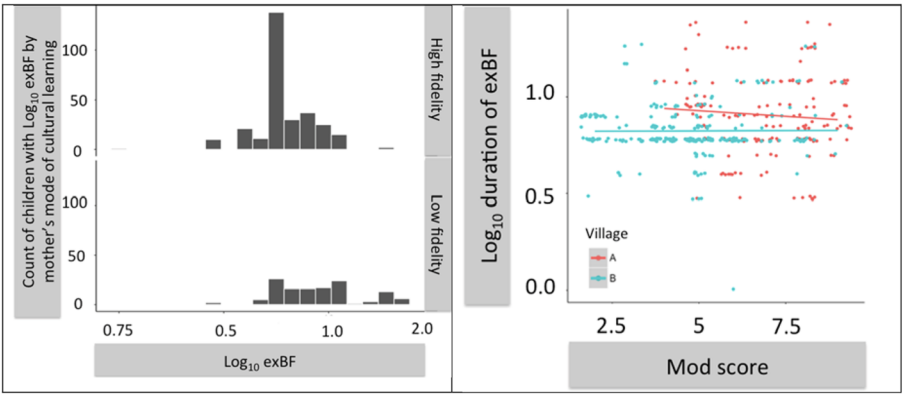

Fig. 2 Differences in exclusive breastfeeding (exBF) by mother's mode of cultural learning and her household's modernization (Mod) score. (**left**) Histogram of $\log_{10}$ duration of exBF by mode of cultural learning. Children of women who learned about infant and young child feeding from culturally conservative, high fidelity sources were more likely to have shorter durations of exBF than children of women who learned about infant and young child feeding from lower fidelity sources. (**right**) Scatterplot of $\log_{10}$ duration of exBF by Mod score. Generally, exBF appears unrelated to Mod score. This is especially clear in the case in village A, wherein most mothers report introducing complementary foods at ~6 months for most children, regardless of Mod score

Our sensitivity analyses generally accorded with these findings (ESM, Tables S1 and S2).

In addition, we found that the effects of Mod score on exBF and anyBF differ significantly (see estimated "Mod score.anyBF" effect in Table 3; $p = 0.004$). Likewise, the effects of mode of cultural learning on exBF and anyBF differ significantly (see estimated "Mode of cultural learning (low fidelity).anyBF" effect in Table 3; $p < 0.001$). In other words, anyBF is more strongly associated with Mod score than is exBF, whereas exBF is more strongly associated with mode of cultural learning than is anyBF.

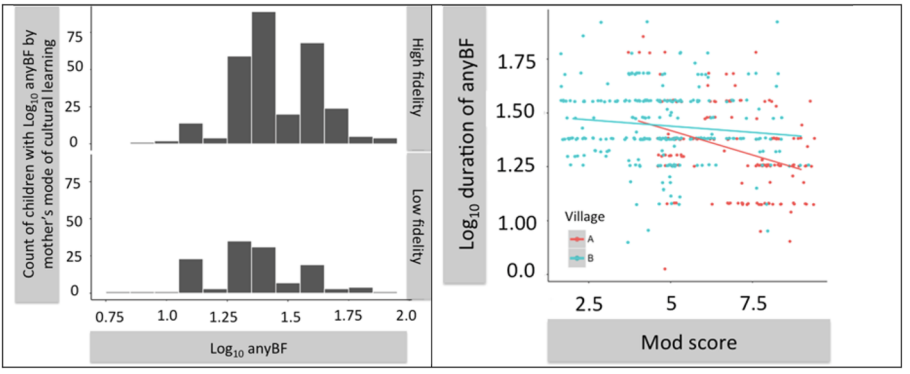

Fig. 3 Differences in any breastfeeding (anyBF) by mother's mode of cultural learning and her household's modernization (Mod) score. (**left**) Histogram of $\log_{10}$ duration of anyBF by mode of cultural learning. There are no obvious differences in duration of anyBF between children whose mothers learned about infant and young child feeding from culturally conservative, high-fidelity sources than children whose mothers learned from lower-fidelity sources. (**right**) Scatterplot of $\log_{10}$ duration of anyBF by Mod score. Duration of anyBF decreases as Mod score increases, especially among children from village A

Discussion

Summary of Main Findings

A plurality (39%) of the Maya women in this sample were most likely to report introducing complementary liquids and solids and thereby ending exclusive breastfeeding (exBF) when infants reached 6 months of age. More than one quarter (27%) of children in these villages were reported to have ceased any breastfeeding (anyBF) around 24 months of age, although a nontrivial 19%, mostly from one village (village A), continued to breastfeed until ~36 months, and an additional 11% continued beyond their third birthday. Mother-offspring pairs vary substantially within and among families in the length of these breastfeeding phases, but with an apparently reduced tendency to follow the community's cultural norms, as inferred by the village and sample modes for the two durations, in anyBF relative to exBF.

Our regression analysis suggests that sources of cultural knowledge about infant and young child feeding strategies account for some variation in exBF, with mothers who learned from lower-fidelity sources (e.g., trial-and-error learning) more likely to report exBF durations later than the normative 6 months. We found no evidence that exBF is associated with our indicator of economic and demographic modernization (Mod score), despite the fact that this index contains multiple variables expected to affect breastfeeding physiology and behavior. These findings regarding exBF are consistent with the hypothesis that exBF (or at least how mothers report it) is managed culturally rather than through tailoring individual mother-child interactions to household-level socioecological conditions. In contrast, anyBF varies not with mode of cultural learning but with Mod score, such that children from more modernized households are reported to cease anyBF earlier than children from more traditional ones. This finding accords with the hypothesis that mother-child pairs adjust the duration of anyBF to their household-level socioecological conditions rather than carefully adhering to what we infer to be cultural norms. We suggest below that differences in the fitness-relevance of the two breastfeeding duration variables may account for why they appear to differ in sensitivity to cultural norms.

Breastfeeding and Modernization

Our findings regarding both the lack of evidence of association between exBF and Mod score and the negative association between anyBF and Mod score accord with the findings of some previous studies on breastfeeding in indigenous populations undergoing economic transition, but certainly not with all.

Regarding exBF, results of earlier studies using comparable methods (i.e., interviews or surveys with individual mothers on recalled duration of exBF and anyBF for multiple children) and comparable populations (i.e., rural, indigenous, undergoing market integration at time of study) have been conflicting. Three studies, one on rural Vietnamese families, one on rural and urban Indonesian families, and one on rural Mexican families, indicate a negative relationship between exBF and modernization (Duong et al. 2005; Gonzalez de Cossio et al. 2013; Lo Bue and Priebe 2018). One—like ours—did not detect any impact (Veile and Kramer 2015): this was also with a Maya population, albeit from a different region, namely, the Yucatán, Mexico. In

contrast, both a study by Veile and colleagues on the Bolivian Tsimane people (2014) and a study by Al-Kandari and Ahmed (2018) on traditional Kuwaiti peoples detected positive relationships. It is possible that differences in research design and measurement strategies account for some of these discrepancies since measurement of modernization and length of time between cessation of exBF and data collection differed among all studies. However, given that we know breastfeeding to be ecologically sensitive and adaptively plastic (Harris and Vitzthum 2013; Sellen 2009), we suggest that the processes of socioecological change themselves and the behavioral responses to them likely vary with environmental and historical context. Variations among contexts in how transitions unfold may exert different pressures and constraints on mothers and infants (e.g., via exposures to new pathogens, introduction of new commensal microbes, incorporation of new dietary components, availability of medical care, access to a wider range of cultural models). Each unique configuration of such factors likely results in different physiological and behavioral responses (Fox et al. 2017). Consistent with this theory, some recent work indicates that local socioecology and the structure of sociocultural networks can impact the rate at which populations undergo changes in fertility in response to modernization (e.g., Colleran 2016; Mattison et al. 2018b; McKerracher et al. 2017a; Snopkowski and Kaplan 2014; Shenk et al. 2016). Given close links between fertility and breastfeeding practices (Bongaarts and Potter 2013; Labbok 2015), it is likely that similarly complex interactions influence how breastfeeding behaviors change as indigenous populations modernize. In the case of the study population, we suspect that exBF is *not* statistically associated with Mod score because the particulars of the local ecology (a recent history of civil war and high infant morality due to infectious disease; Atyeo et al. 2017) have generally necessitated tight adherence to and monitoring of exBF norms so as to buffer infants against these extreme risks.

With respect to the relationship between recalled duration of anyBF and modernization in indigenous populations, previous studies have also produced somewhat conflicting results. There is at least one case in which anyBF increases as market integration increases (Veile et al. 2014). The most common finding, however, is the pattern reported in the present study. Typically, average duration of anyBF decreases as small-scale communities begin to adopt the elements of the economic systems and other aspects of the lifeways of the dominant societies with which they interact (e.g., Gebreselassie et al. 2008; Grummer-Strawn 1996; Trussell et al. 1992); this was the case in the other Maya population for which a study on this topic has been conducted, the Xucloc Maya of the Mexican Yucatán (Veile and Kramer 2015; see also Kramer 2005).

Currently, it is unclear what drives the negative association between anyBF and modernization in the Kakchiquel-speaking Maya or in most other modernizing populations. At least four obvious possible explanations are compatible with our data. One is that market integration brings with it substantial increases in energy availability via market foods and substantial decreases in energy expenditure via decreased activity and lower costs to immune function as a result of improved access to health care (e.g., Himmelgreen et al. 2014; Lieberman 2003; Veile et al. 2014). Energy surpluses enable mothers to continue breastfeeding intensively while also resuming ovarian cycling and conceiving additional children (Valeggia and Ellison 2004, 2009; Vitzthum 2009; Worthman et al. 1993). In many populations, once a new pregnancy is established

and recognized, cultural rules and/or physical and emotional discomfort encourage mothers to cease breastfeeding older sibs (e.g., Guthrie et al. 1983; Jakobsen et al. 2003; Sellen 2001). So, the shorter period between a birth and a new conception, associated with increases in energy balance resulting from modernization processes, may lead to relatively early cessation of breastfeeding.

Another plausible explanation for the negative association between anyBF and modernization in our sample is that increased market integration is associated with a tendency for women to work outside of their homes or farms (Berry 2010). Participating in wage labor or selling items at a market may separate mothers from infants. This separation inhibits frequent, on-demand breastfeeding and encourages relatively rapid replacement of breastmilk with other sources of nourishment (Dennis 2002; Jones et al. 2003; Levine 1988; McDade and Worthman 1998; Nerlove 1974; Thulier and Mercer 2009). At least one village in the study population (village A) appears to reflect this pattern (McKerracher et al. 2017b).

A third potential explanation for the negative association between anyBF and modernization concerns stress. The processes of modernization and market integration may increase inequality, competition, and conflict within populations undergoing these processes, and these undoubtedly constitute psychosocial stressors with biological consequences. Extrinsic sources of stress are known in humans to drive accelerated life history strategies featuring shorter periods of lactational investment (e.g., Gawlik et al. 2011; Migliano et al. 2007; Walker et al. 2006) and to bias people's attention toward immediate versus longer-term outcomes (Pepper and Nettle 2017). As such, it may be that the pattern of association in general, or in the study population in particular, reflects part of a response to an increasing stress load (McKerracher et al. 2017a).

The final plausible explanation concerns proximity of novel cultural models of and media about infant feeding. The modernization process may increase exposure to different norms around the acceptability or desirability of extended anyBF (Huffman 1984). However, in the Kakchiquel-Maya case, this seems unlikely because only one woman reported learning about infant feeding through direct interactions with a North American or European, and only seven said that they received information from the health post. Most of the lower-fidelity cultural learners reported self-teaching, following their babies' cues, or receiving and synthesizing information from multiple sources.

Since our measure of modernization has indicators of both energy balance and women's non-domestic labor and likely also encapsulates measures of some latent extrinsic stressors, any of the first three explanations could contribute to explaining why anyBF is associated with varying levels of market integration in this context, as in others. Further research will be required to differentiate between these three hypotheses to whatever extent that's possible since they are complementary rather than mutually exclusive.

Breastfeeding and Cultural Learning

It has been suggested that cultural norms can reinforce breastfeeding behaviors likely to improve infant survivorship when the socioecological conditions are fairly stable (Henrich and Henrich 2010; McDade and Worthman 1998; Snopkowski and Kaplan 2014). Among participants in this study, variation in anyBF did not appear to be directly influenced by cultural norms or by mode of cultural learning, but exBF did.

Specifically, Maya mothers were likely to heap their responses regarding exBF on the inferred cultural norm for this variable. Further, exBF was correlated with mode of cultural learning.

We hypothesize that such norms may mediate associations between exBF and socioecological factors such as maternal workload or endemic gastrointestinal pathogen load, which otherwise are expected to influence the length of breastfeeding exclusivity. That is, we should expect strong norms about duration of exBF to be in place, and that following these norms should, on average, reduce infant mortality so long as such factors do not change drastically within a generation. On the other hand, when key socioecological factors change within a human generation or two, strong, culturally conserved breastfeeding norms will reduce the responsiveness of real and/or reported behavior to ecological change. We expect this to be the case because mothers are likely to fear the reputational consequences of deviation from norms. This reduced responsiveness may, in turn, sometimes lead to breastfeeding maladaptations in the short term (Newson 2013; Richerson et al. 2009).

This cultural mediation hypothesis has not yet been explicitly tested, but both the biomedical and the evolutionary anthropological literatures indicate that culture, broadly construed, plays an important role in when non-breastmilk liquids, semi-solids, and solids are introduced to the infant diet (e.g., Demirtas et al. 2012; Dettwyler 2004; Hadley et al. 2010; Mueffelmann et al. 2014; Van Esterik 2002; Veile and Kramer 2015; Wilson et al. 2006; Wren et al. 2015). If supported by further inquiry, this hypothesis may account for some of the disparities among the results of different studies regarding breastfeeding and modernization. That is, some study populations may have more conservative—higher-fidelity, slower-to-change—systems for transmitting infant and young child feeding knowledge than others, perhaps with higher reputational costs for deviance from exBF norms. From this viewpoint, populations with more conservative modes of cultural learning are expected to be relatively slow to respond to changing socioecological conditions, explaining temporary mismatches between breastfeeding durations and socioecology during modernization processes.

We further hypothesize that cultural learning and social norms may have clear and detectable effects on reported exBF, but not necessarily on anyBF. Our reasoning is that the infant morbidity and mortality costs associated with timing the introduction of non-breastmilk foods incorrectly are high and immediate (Kramer and Kakuma 2012; McDade 2003; McDade and Worthman 1998; Stewart et al. 2013). This is not necessarily the case with anyBF: ending anyBF early or late impacts a child's morbidity and mortality risks, but most of these risks do not manifest until her/his postreproductive years (e.g., McDade et al. 2014; Schack-Nielsen and Michaelsen 2007; Thompson 2012). For example, McDade et al. (2014) have shown that a dose-response relationship between anyBF and a key marker of inflammation largely drops off after three months of breastfeeding, but the inflammation is perhaps more likely to affect chronic disease risk in adulthood than mortality risk in childhood. In other words, the potential *fitness* variation associated with variation in anyBF is predicted to be low. This hypothesis could account for the observations that both the Maya mothers in our sample and Western mothers (Burnham et al. 2014; see also review by Li et al. 2005) were more likely to heap their responses pertaining to exBF on the population's normative or recommended exBF than they were with their responses pertaining to anyBF. The reputational or fitness stakes may be relatively high for exBF. Further work

is needed to investigate how cultural learning shapes exBF relative to anyBF, and to directly assess the fitness consequences of deviating from the norms for each breastfeeding variable.

Limitations

There are reasons to be cautious regarding these results. Most importantly, our study was retrospective and relied on recall data, with the oldest children of the oldest mothers having been weaned more than 30 years prior to data collection; only ~50% of the children had been weaned less than a decade before data collection. Some comparisons of prospective and observational data with retrospective recall data have shown that some mothers make nontrivial errors when asked to recall anyBF years after a child's weaning (Holland 1987; Li et al. 2005; Natland et al. 2012; Promislow et al. 2005). Errors in recall may be even more common for exBF (Burnham et al. 2014; Li et al. 2005). That being said, the vast majority of mothers can accurately recall anyBF even decades after a child's weaning; most mothers can also do so with exBF (Li et al. 2005; Natland et al. 2012; Promislow et al. 2005). So, the recall data are likely sufficient to assess the ecology of breastfeeding durations in broad strokes (e.g., Veile and Kramer 2015). Importantly, behavioral recalls can be affected by the perceived social desirability of their responses. Evidence indicates that mothers who recall breastfeeding durations incorrectly tend to bias recalled durations toward what they think data collectors would like to hear (i.e., cultural norms; Burnham et al. 2014). With this in mind, assuming some recall/reporting errors were made by the participants of our study, we suggest that such errors may reflect how mothers conceive how they *should* feed infants and young children. While likely yielding inaccurate and/or imprecise information on the breastfeeding durations of individual participants, responses may actually offer unique insights into *cultural norms and values* about breastfeeding duration, which was one of our main foci in this paper.

Additionally, participants were not asked to distinguish between different aspects of infant feeding behavior when they were asked where they learned about infant feeding behavior, and they were not asked expressly about their community's infant feeding norms. A stronger case about learning fidelity and infant feeding norm psychology could be made if we knew, for example, whether mothers generally learned about initiation and continuation of exBF through watching their mothers or mothers-in-law, about selection of weaning foods through childhood play and through practice as babysitters, and about anyBF through following cues from their children. Instead, we are relying on noisy data to make inferences about breastfeeding norms and attitudes. We suggest that our ability to detect a signal of a relationship between exBF and learning fidelity *in spite of this noise* hints that the real signal is strong and robust. Nonetheless, additional interviews with mothers and with people who represent sources of infant feeding knowledge in the villages should be carried out to assess the reliability of the results reported here.

Another possible limitation of the study is that the variable used to measure the relative modernization of a household was a composite one, derived from a number of variables originally collected for other purposes. We do not yet have data regarding the proxies most commonly used to measure modernization of transitioning populations, such as years of formal, state-run education or competency in a dominant/colonial

language (e.g., Hoke 2017; Snopkowski and Kaplan 2014; Veile and Kramer 2015; Veile et al. 2014). With these shortcomings of our Mod score variable in mind, we carried out a sensitivity analysis involving an alternate Mod score scoring method. Generally, the findings of this sensitivity analysis (reported in ESM S3) accorded with the findings reported in the main text, suggesting our main findings are robust. Nonetheless, caution should be exercised until standard measures of modernization become available for the study population.

Implications for Human Life History Evolution and Public Health

Our data provide evidence that variation in exBF is associated with variation in mode of cultural learning, in the context of socioecological change occurring within one or two human generations. These findings suggest that the ways mothers learn about infant feeding behaviors may mediate how socioecological change affects exBF. Indeed, modeling work indicates that socioecological variability on this one- to two-generation time scale favors reliance on culturally transmitted information to solve socioecological problems that have steep fitness consequences (Newson 2013; Richerson et al. 2009). Thus, it may be that the proposed effects of cultural transmission on the sensitivity of exBF to socioecological change has roots deep in the evolution of our species. If so, social transmission of information about when to introduce non-breastmilk foods into infant diets likely impacted the survivorship of many of our distant ancestors, perhaps via careful monitoring of exBF and lenient, ecologically contingent guidance pertaining to anyBF. In turn, the ability to pass on survival- and/or fertility-enhancing ecological knowledge, including infant feeding knowledge, may be central to our species' successful colonization of nearly every terrestrial biome on Earth (Wells and Stock 2007).

This study's findings may also be useful in developing public health interventions. Concordant with work on other populations (e.g., Atyeo et al. 2017; Brown et al. 2014; Meehan and Roulette 2013; Valeggia 2016; Veile et al. 2014; Wehr et al. 2014; Wren et al. 2015), our results suggest that integration of indigenous populations into market economies is associated with changes in reported breastfeeding behaviors, perhaps with a key mediation role for sources of cultural knowledge. This hypothesis, if supported by further analyses, suggests two sets of public health recommendations. First, if increasing market integration drives decreases in breastfeeding duration, small-scale populations in the process of integrating into market economies may warrant prioritization when allocating resources to breastfeeding promotion and institutional support. Second, if breastfeeding durations are associated with sources of cultural knowledge, recommendations, reassurance, and support should be provided not only to mothers, but also to all future parents (i.e., adolescent schoolchildren), and to the people in their communities from whom mothers learn.

Conclusions

Plasticity in exBF and in anyBF appear, at least in the sample used in this exploratory case study, to be mediated by different mechanisms. ExBF may be under relatively high-fidelity cultural control, and anyBF may be relatively individually responsive to

socioecological context. This difference implies that different events in the weaning process, while often construed as representing linked indicators of maternal-child negotiations over maternal investment, may actually be subject to quite different selection pressures and/or constraints. Treating these two events, along with other milestones in the weaning process, as independent from one another is likely to offer new insights into how these milestones shape and are shaped by our physiologies, fitness, fertility, and our (cultural) learning strategies.

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Luseadra McKerracher completed MA and PhD degrees at Simon Fraser University, following undergraduate training in anthropology at the University of Victoria. Currently she holds a postdoctoral fellowship and project management position focusing on maternal health. She is cross-appointed between the Departments of Anthropology and of Biochemistry and Biomedical Sciences at McMaster University.

Pablo Nepomnaschy is an Associate Professor at Simon Fraser University, with appointments in the Faculty of Health Sciences, the Department of Archaeology, and the Crawford Laboratory of Evolutionary Studies. He is also a Michael Smith Foundation for Health Research (MSFHR) Scholar, funded by the BC Children's Hospital Research Institute. His main research interests focus on: women's reproductive ecology, child development, and the Developmental Origins of Health and Disease (DOHaD).

Rachel Altman is an Associate Professor in the Department of Statistics and Actuarial Science at Simon Fraser University. She works primarily in the field of biostatistics, with special interests in latent variable models for longitudinal data (e.g., hidden Markov models) and methods for survival time data.

Daniel Sellen is Distinguished Professor of Anthropology and Global Health, Nutritional Sciences, and Social and Behavioral Health Sciences at the University of Toronto. He currently leads global intervention evaluations research including mobile technology innovations and has studied infant, maternal and child nutrition and reproductive health among rural foragers, herders, small farmers and vulnerable urban populations in multiple countries.

Mark Collard completed a BA in Archaeology and Prehistory at the University of Sheffield and a PhD in Hominin Palaeontology at the University of Liverpool. Currently, he is the Canada Research Chair in Human Evolutionary Studies and a professor of archaeology at Simon Fraser University.

Affiliations

Luseadra J. McKerracher[1,2] · Pablo Nepomnaschy[3] · Rachel MacKay Altman[4] · Daniel Sellen[5] · Mark Collard[2]

✉ Luseadra J. McKerracher
mckerrl@mcmaster.ca

[1] Department of Biochemistry and Biomedical Sciences and Department of Anthropology, McMaster University, Hamilton, Canada

[2] Department of Archaeology, Simon Fraser University, Burnaby, Canada

[3] Faculty of Health Sciences, Simon Fraser University, Burnaby, Canada

[4] Department of Statistics and Actuarial Science, Simon Fraser University, Burnaby, Canada

[5] Johanna and Brian Lawson Centre for Child Nutrition and Department of Anthropology, University of Toronto, Toronto, Canada