

# THE EVOLUTIONARY ECOLOGY OF HUMAN LACTATION: CORRELATES OF DURATION OF BREASTFEEDING

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by  
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## Ethics Statement



The author, whose name appears on the title page of this work, has obtained, for the research described in this work, either:

- a. human research ethics approval from the Simon Fraser University Office of Research Ethics

or

- b. advance approval of the animal care protocol from the University Animal Care Committee of Simon Fraser University

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## Abstract

Humans breastfeed our infants for less time than expected for primates of our size. Additionally, human breastfeeding duration appears more variable than in nonhuman species. This early and flexible weaning pattern affects maternal fertility as well as infant health and survivorship, from both within- and across- species perspectives. So, understanding what factors enabled humans to wean relatively early and flexibly is an important goal for human evolutionary demography. Yet, what these factors are and how they influence breastfeeding behaviour remain unclear.

To address this gap, I present a series of three papers that each tests several hypotheses regarding influences on breastfeeding duration. The first paper reports a study that uses secondary data from small-scale human societies to investigate the effects of energetic factors on among-population variation in breastfeeding duration. The second has similar aims to the first, but uses within-population field data from indigenous Maya women from Guatemala to evaluate the energetic hypotheses. The third study, again using field data from Maya women, assesses a different set of hypotheses: that socio-ecological change and sources of socially-transmitted information about how to feed infants influence duration of breastfeeding.

The first study shows that, across populations, breastfeeding duration associates negatively with maternal body mass, positively with maternal height, and negatively with dietary quality of weaning foods. The second indicates that within-population variation in breastfeeding duration associates negatively with maternal height, negatively with maternal access to help with infant

care, and positively with parity. The last study suggests that duration of exclusive breastfeeding associates negatively with conservativeness of the source from which mothers learn about infant feeding behaviour. It also indicates that full duration of breastfeeding associates positively with household modernization.

Taken together, these results suggest two things. One is that reduced duration of breastfeeding relates to greater maternal access to energy. The second is that socio-cultural factors influence variation in duration of breastfeeding in humans. These findings are consistent with previous claims that increases in energy availability and/or the development of complex cultural systems for information transmission contributed to the evolution of short, flexible breastfeeding and high fertility in humans.

## **Dedication**

To Kate Addison, Erin Addison, Elijah Brosseau, Luke Brosseau, Mira Friedman-Lindquist, Calli Friedman-Lindquist, and the other children of earlier parts of my life: Your curiosity, your fastidiousness about food in early childhood, your growth, and your development inspired this project.

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# 1 Introduction

## 1.1 Breastfeeding and human evolutionary studies

Infant mammals rely on mother's milk for energy, nutrients, and immunity to pathogens. Weaning represents the process through which infant mammals transition from reliance on mother's milk to reliance on solid foods for nutrition and immune support. Compared to other primates, humans both begin and end this process much earlier than predicted for our infants' body size, for our infants' brain size (Emery Thompson 2013; Hawkes and Paine 2006; Kaplan et al. 2000; Kennedy 2005; Robson and Wood 2008; Shaoul et al. 2014), and for when our infant's first molars erupt (Humphrey 2010; Robson and Wood 2008). That is, humans end exclusive breastfeeding earlier than expected. We also completely cease all breastfeeding (breastfeeding supplemented by non-milk liquids, semi-solids, and/or solids) earlier than predicted for our size. Additionally, it appears that humans are exceptionally flexible in when we end exclusive and all breastfeeding (Sellen 2007; 2009). The duration of exclusive breastfeeding and the duration of all breastfeeding vary substantially among human populations, among mothers within a population, and even among children of the same mother. The absolute size of the human range of variation for duration of all breastfeeding is nearly as great as the range of variation in duration of all lactation observed across all other primates, irrespective of body size (see Barrickman et al. 2008 for wild primate range; see Sellen 2001b for natural fertility human range).

Attempting to understand the factors that enable us to end exclusive and all breastfeeding relatively early and to time these events very flexibly has become an important focus for research in human ecological and evolutionary studies over the last two decades (Gray 1995; 1996; Jay 2009; Humphrey 2010; Quinlan 2007; Quinlan and Quinlan 2008; Sellen 2001a; 2007; 2009; Sellen and Smay 2001; Zollikofer and Ponce de León 2010). There are two main reasons for the increased interest in this topic. The first concerns demography. The duration of exclusive breastfeeding and the duration of all breastfeeding impact the length of intervals between births (Deaner et al. 2003; Marlowe 2005; McDade 2001; Valeggia and Ellison 2004; 2009; Vitzthum 1994). Extended periods of intense breastfeeding are often associated with relatively long inter-birth intervals (IBIs). Short periods of sporadic breastfeeding are often associated with relatively short IBIs (Howie and McNeilly 1982). All else equal, when fertility is not regulated by reliable contraceptive methods, mothers with relatively shorter IBIs are likely to have larger completed family sizes than mothers with longer ones (Howie and McNeilly 1982). Scaled up to the population level, larger families result in population growth and possibly the need for migration when population size outstrips local availability of resources. So, understanding the mechanisms that drive variation in the duration of exclusive breastfeeding and the duration of all breastfeeding can offer insights into past and present human fertility and migration. Given its possible demographic implications, understanding the mechanisms that enabled relatively early and flexible weaning to evolve may shed light on why human populations are larger and have colonized far more diverse territories than populations of other primates (Hamilton et al. 2009; Sear and Coall 2011; Wells and Stock 2007).

The second reason that the duration of exclusive breastfeeding and the duration of all breastfeeding interest evolutionary anthropologists is that they appear to affect health outcomes throughout infancy, childhood, and adulthood (Hurtado et al. 2006; McDade 2001; McDade 2003; Sellen 2009; Sellen 2007; Vitzthum 2008; Wells 2011; 2012a; Wells 2010). In contemporary humans, early introduction of foods other than breastmilk is associated with increased infant morbidity and mortality risks (Kramer and Kakuma 2004; 2007; 2012; Labbok et al. 2004; McDade 2001; 2003). Early termination of exclusive breastfeeding and/or of all breastfeeding appears also to be associated with increased risks of developing metabolic disorders later in life. These disorders include heart disease, type 2 diabetes, and polycystic ovarian syndrome (Godfrey et al. 2010; Lanigan and Singhal 2009; Martin-Gronert and Ozanne 2005; Owen et al. 2005a; 2005b). As such, identifying the ecological and evolutionary factors that contribute to variation in the duration of exclusive breastfeeding and the duration of all breastfeeding may improve public health recommendations regarding infant and young child feeding (Hoi and McKerracher 2015; Sellen 2007; 2009).

Since variation in the durations of both exclusive breastfeeding and all breastfeeding correlates with variation in infant and later life morbidity and mortality, it is reasonable to assume that weaning behaviours are subject to natural selection (Brown et al. 2013). Mother-infant pairs who time the end of exclusive breastfeeding and the end of all breastfeeding well enough to allow infant survival and reduce risks of infant illness are relatively likely to pass on their genes to subsequent generations than mother-infant pairs who mistime these feeding transitions (Humphrey 2010; Shaoul et al. 2014). Significantly, the strength of selection declines with an organism's age (Hughes and Reynolds 2005; Medawar 1952; Ricklefs 1998). As such,

behaviours that affect infant survivorship such as those associated with breastfeeding and weaning are likely subject to particularly strong selection. But, as suggested by the high levels of observed variation in the duration of exclusive breastfeeding and the duration of all breastfeeding in humans (again, see Sellen 2001b), this presumed selection has not resulted in a canalized, universal infant and young child feeding strategy for our species. Rather, it appears that, if genetic selection has taken place (e.g. Jonas et al. 2013), it has favoured high levels of plasticity in the genes that influence infant and young child feeding behaviours. It remains an open question as to what factors enable and/or constrain this ontogenetic and behavioural plasticity (Emery Thompson 2013).

In light of the centrality of variation in breastfeeding behaviours to understanding both past human demography and contemporary public health, identifying the correlates and, ideally, the causes of this variation is imperative. This dissertation uses a comparative approach (Harvey and Pagel 1991) – that is, it compares observations of durations of exclusive and all breastfeeding among contemporary individuals and populations – to shed new light on what ecological factors may have enabled the evolution of relatively early and flexible weaning in humans.

## **1.2 Aims and objectives**

In a series of three studies, the project evaluates a number of hypotheses from the literature on the ecology of lactation. Several of these hypotheses derive from literature on ecological causes of variation in the duration of exclusive lactation and the duration of all/supplemented lactation in nonhuman animals. The remaining hypotheses come from the literature on ecological causes of variation in the durations of exclusive breastfeeding and all breastfeeding in humans. Tests of

the predictions of these hypotheses are carried out at multiple levels of analysis, first using a wide “lens” and then a narrower one. Specifically, the tests assess predictions regarding variation in durations of breastfeeding among human populations, among families and villages within a population, and among children within families. This nested approach was developed with a view to assessing whether the core predictions of the hypotheses of interest are general, robust, and internally consistent enough to identify plausible explanatory factors involved in the evolution of early and flexible weaning in the human lineage.

The data used in the three studies come from small-scale, predominantly natural fertility populations. There are three main reasons for focusing on such populations. One is that their infant and young child feeding strategies are less likely to have become decoupled from fecundity and fertility than those of Western, industrialized populations. In industrialized populations, use of reliable forms of contraception is widespread, with far-reaching effects on fertility patterns (Hirschman 1994). Another reason is that the behaviours of people from such populations are more likely to fall near the middle of ranges of human behavioural variation (Henrich et al. 2010). That is, Western, industrialized populations, often studied to make generalizations about human behaviour, tend to have unusual, extreme values for many behavioural and psychological metrics (e.g. attitudes towards cooperation, perception of self, composition of diet) relative to other human populations. This is not the case for small-scale populations (Henrich et al. 2010). The third reason to focus on small-scale populations is that they are relatively genetically and culturally homogenous, thus limiting potential sources of

random error/noise and improving the chances of detecting effects of interest (Binford 2001; Cavalli-Sforza et al. 1994).

### **1.3 Life history theory and parent-offspring conflict theory**

The core issue investigated in this dissertation – the factors that contribute to variation in the duration of exclusive breastfeeding and/or in the duration of all breastfeeding – is grounded in life history theory (Stearns 1976; 1992) and parent-offspring conflict theory (Trivers 1974).

Life history theory was developed to account for biological variation in how organisms grow, develop, and reproduce. The theory holds that the amount of time and energy available to each organism over its lifetime is finite and that time and energy allocated to one purpose cannot be allocated to other purposes. It further holds that organisms have evolved such that they allocate energy in ways that maximize the number of descendants they leave, given that energy budgets are finite (Stearns 1976; 1992). Time and energy can be used in three main ways: 1) growth of new body tissues, 2) maintenance of those tissues, and 3) reproduction. Because time and energy are both limited, increasing energetic or time investment in tissue growth or maintenance requires decreasing investment in reproduction and vice versa.

In sexually reproducing organisms, reproduction requires a tradeoff between “mating effort” and “parenting effort” (Stearns 1992). Mating effort refers to the time and energy an organism invests in finding, attracting, and copulating with a mate. Parenting effort refers to the time and energy an organism invests in producing and maintaining sex cells and transferring energy to offspring to support their growth and development.

In mammals, the bulk of maternal parenting effort comprises the gestation of embryos/fetuses and the feeding of young postnatally through lactation. Mothers also transfer energy to their offspring through food processing and sharing, through infant carrying, and through other forms of infant and juvenile care (Alonso-Alvarez and Velando 2012). Allocating time and energy to any of these activities requires reducing the amount of time and energy that can be allocated to other activities. For example, continuing to allocate energy to one offspring through lactation and food provisioning may prevent a mother from conceiving additional offspring because she cannot afford the total rate of energy transfer necessary for simultaneous gestation and lactation/infant feeding (Valeggia and Ellison 2004; 2009; Vitzthum 2008; Vitzthum 1994).

How mothers divide parenting effort affects both maternal and offspring fitness and sometimes these effects on fitness differ between mothers and offspring. This brings us to the other key theory that has informed my work—parent-offspring conflict theory (Trivers 1974). Parent-offspring conflict theory is based on the observation that, in sexually reproducing organisms, a mother and an offspring share only ~50% of their genes (the other ~50% of an offspring's genes are inherited from its father). This theory contends that, while offspring and maternal fitness interests often align, there are also many instances in which they differ. Offspring fitness generally benefits from increases in maternal investment. A mother, however, may lose opportunities to have additional descendants and thus pay overall fitness costs if she invests too heavily in any given offspring. As such, offspring can be expected to seek to secure more maternal time and energy investment than mothers are willing to provide, resulting in conflict between mothers and infants over the allocation of parenting effort.

The extent to which maternal and offspring fitness interests diverge hinges on ecological factors, most notably offspring quality, offspring sex, and maternal condition (Trivers 1974; Trivers and Willard 1973). Specifically, parent-offspring conflict theory suggests that offspring of relatively high quality and of the sex most likely to convert maternal investment into relatively high reproductive success are relatively likely to secure more time and energy resources from mothers than other offspring. Additionally, maternal condition is expected to influence investment decisions. Most importantly, mothers nearing the end of their reproductive careers should be willing to invest heavily in their later-born offspring, because doing so does not come at the cost of lost opportunities to invest in subsequent descendants, since they would be unlikely to conceive such descendants anyhow (Pennington and Harpending 1988).

With respect to lactation, life history theory and parent-offspring conflict theory yield a number of specific insights and predictions. Namely, the duration of exclusive lactation/breastfeeding and the duration of all lactation/breastfeeding are expected to be foci of maternal-offspring conflict. We should expect the timing of these events to be sites of conflict because lactation constitutes the most energetically expensive form of parenting effort and requires steep tradeoffs (Butte and King 2005; Gittleman and Thompson 1988) and because maternal and offspring fitness interests differ (Haig 1993; Trivers 1974). As such, maternally-driven declines or termination in lactational investment are expected to be met with fussing, crying, and/or tantrums on the parts of offspring demanding further investment. In turn, mothers may respond to these offspring demands with refusals to breastfeed (Haig 2007; 2010; Wells 2003). These conflicts are predicted to occur relatively early if offspring are of poor quality and thus not as likely to convert high maternal investment into high reproductive success via extended

lactation/breastfeeding. The timing and severity of conflicts over weaning may decline as mothers age and continued lactation no longer carries heavy opportunity costs in lost opportunities to invest in future offspring (Pennington and Harpending 1988).

Moreover, the nature of conflicts and of breastfeeding strategies more generally are likely to be influenced by the broader ecological (including socio-cultural) conditions that affect overall maternal time and energy budgets. It is reasonable to assume that features of the natural and social environment (e.g. extrinsic mortality risks, food availability, residence patterns or availability of allocare providers) affect when mothers are most likely to pursue high quality versus high quantity strategies for investment in reproduction. The pursuit of offspring quality versus offspring quantity should impact weaning conflicts and vice versa (Hinde and Kilner 2007).

#### **1.4 Previous studies on variation in the timing of the ends of exclusive and all breastfeeding in small-scale human populations**

This dissertation uses insights from life history theory and parent-offspring conflict theory to investigate potential causes of variation in the duration of exclusive breastfeeding and in the duration of all breastfeeding within and among small-scale human populations. A number of previous studies have taken similar comparative approaches when examining human breastfeeding/weaning. In this section, I systematically review the among-population portion of this body of literature. Reviewing all of the within-population studies comprehensively is beyond the scope of this introductory chapter, as this literature is relatively large and features analyses

that are often exploratory rather than hypothesis-testing in nature. Nonetheless, I also provide a brief thematic overview of this latter body of work. I then highlight a number of the shortcomings of both previous cross-cultural and within-cultural studies. Then, in the last part of this section, I suggest that studies concerning the evolutionary biology of nonhuman animals and concerning the quantitative study of cultural transmission may offer new insights to the study of infant and young child feeding behaviours.

Previous cross-cultural studies have generally focused on variations of one or more of five hypotheses: 1) **the women's workload hypothesis**, 2) **the weaning food availability hypothesis**, 3) **the extrinsic risk hypothesis**, 4) **the availability of allocare hypothesis**, and 5) **the live fast-die young hypothesis**.

**The women's workload hypothesis** (Nerlove 1974; Quinlan and Quinlan 2008) holds that the amount of time women spend working outside the home impacts when women begin supplementing their infant's diets with non-breastmilk foods and thus infant's age at the end of exclusive breastfeeding; early supplementation may also precipitate early weaning/shorter duration of all breastfeeding. The rationale is that separation of mothers from infants while mothers work out of the home both reduces opportunities for infants to suckle and increases opportunities for infants to be fed alternatives to breastmilk when in the care of non-mothers. Both at a within-population level and a cross-cultural level, this hypothesis predicts that the duration of exclusive breastfeeding and the duration of all breastfeeding should be negatively associated with the amount of time women dedicate to non-domestic labour.

**The weaning food availability hypothesis** (Sellen and Smay 2001) holds that access to safe, easily digestible, nutrient-dense foods impacts both the duration of exclusive breastfeeding and the duration of all breastfeeding. The basis of this contention is that non-maternal caregivers can offer high quality non-breastmilk foods to infants, reducing lactational demands on mothers while continuing to supply infants with energy and nutrients. This hypothesis predicts that the duration of exclusive breastfeeding and the duration of all breastfeeding should increase as access to appropriate weaning foods decreases. An additional key assumption of the weaning food availability hypothesis is that access to weaning foods probably varies systematically among populations. Specifically, it assumes that populations that rely primarily on farming and/or herding for subsistence have relatively greater access to appropriate weaning foods than populations that rely primarily on hunting, gathering, and/ or fishing (Sellen and Smay 2001). As such, this hypothesis further predicts that the duration of exclusive breastfeeding and the duration of all breastfeeding are likely to be shorter in farming/herding populations than in foraging populations (Bentley et al. 1994; Sellen and Smay 2001).

**The extrinsic risk hypothesis** (Pennington and Harpending 1988; Quinlan 2007; Winterhalder and Leslie 2002) holds that the extrinsic riskiness of the environment in which an infant is raised impacts whether mothers invest in offspring quantity or in offspring quality. It suggests that when large amounts of maternal investment can substantially increase infant survivorship, mothers should invest heavily in each of their infants by extending the duration of exclusive breastfeeding and the duration of all breastfeeding. However, when the quality of the environment is such that increasing maternal investment cannot substantially reduce infant morbidity and mortality – i.e. when extrinsic risks to infant mortality are high – mothers should

instead focus on shortening intervals between births by reducing investment through lactation and having a larger number of infants. This high quantity strategy ensures at least some infants survive to adulthood by chance. The risk hypothesis predicts that mothers should invest relatively little in infants born into very low risk conditions because such infants are likely to survive and to succeed irrespective of investment. For infants to which extrinsic mortality risks are moderate, mothers are likely to invest heavily in them, so as to increase infant survivorship in the face of otherwise challenging circumstances. When extrinsic mortality risks reach levels so high that increased maternal investment cannot improve infant survivorship, mothers are expected to invest relatively little in individual infants in favour of having many children. Thus, the duration of exclusive breastfeeding and the duration of all breastfeeding are predicted to increase and then decrease as level of risk increases from low to moderate to high levels (McKerracher et al. 2012a; Quinlan 2007).

**The allocare hypothesis** (Hrdy 2009; Quinlan and Quinlan 2008) proposes that the number of people that a woman may turn to for assistance with childcare and the amount of assistance with childcare those people provide affects the duration of breastfeeding. Although the hypothesis was conceived as an explanation for variation in the timing of the end of all breastfeeding (Hrdy 2009; Quinlan and Quinlan 2008), presumably its logic also applies to among-population variation in the duration of exclusive breastfeeding. The hypothesis predicts that, as a woman's access to other childcare providers increases, infant's age at the ends of exclusive and all breastfeeding are likely to decrease. The assumption here is that non-maternal caretakers are likely to encourage the consumption of non-breastmilk foods.

**The live fast-die young hypothesis (LFDY)** contends that extrinsic morbidity and mortality risks cue maternal growth and development trajectories, which in turn cue the pace of reproduction. Under this hypothesis, mothers that developed under relatively high extrinsic morbidity and mortality regimes are expected to have been selected to stop growing early, to begin reproducing relatively early, and to reproduce relatively fast (Gawlik and Hochberg 2012; Gawlik et al. 2011; 2010; Migliano et al. 2007; Walker et al. 2008). In other words, the LFDY predicts that shorter mothers (or shorter populations) and mothers with earlier ages at first birth are likely to have shorter durations of breastfeeding. The basis of these predictions is twofold. First, under high levels of extrinsic morbidity risk, the costs of growing and maintaining extra tissue are especially high because investment in growth requires sacrificing investment in immune system development and maintenance as well as in reproduction (Abrams and Miller 2011; McDade 2003; McDade and Worthman 1999). Second, under high levels of extrinsic mortality risk, delayed or slow reproduction may lead to complete loss of reproductive opportunities due to ill-health and death (Walker et al. 2006).

All five of these hypotheses have been tested previously in one or more cross-cultural studies using data from small-scale societies. Three such studies focused explicitly on the women's workload hypothesis. In the first, using data from a cross-cultural sample of 83 natural fertility, nonindustrial populations, Nerlove (1974) evaluated the prediction that mothers from societies in which women contributed a large portion of labour to the subsistence economy would be more likely to introduce non-breastmilk foods within the first month of an infant's life than mothers from populations in which women contribute relatively little labour to the subsistence economy. The results she obtained were consistent with the prediction. Notably, though, Nerlove's study

was an early and provisional one with at least two major shortcomings – she did not control for the ancestor-descendent relationships among the populations in her sample and she used an arbitrary threshold of one month to index the duration of exclusive breastfeeding. As such, it remains unclear whether phylogenetic clustering may explain the association between unusually early introduction of non-breastmilk foods and women’s workload or whether a genuine, ecologically-driven pattern exists.

Subsequently, Levine (1988) tested a prediction of the workload hypothesis, using cross-settlement data from eight Nepalese communities. Specifically, on the assumption that a family’s landholding indexes that family’s wealth, she tested the prediction that women from relatively land-rich families would have greater access to help with domestic and subsistence labour and thus would be able to dedicate more time and energy to infant care through extended exclusive and weaning-food-supplemented breastfeeding than women from relatively land-poor families. Levine found, however, that the relationship was not clear-cut. Shortened exclusive breastfeeding and shortened supplemented breastfeeding were sometimes associated with land richness and sometimes associated with land poorness. From her description of the communities, it appears that land-richness may in some instances indicate monetary wealth and thus increased access to help with labour but may in other instances indicate that a woman is responsible for maintaining more farmland. As such, Levine’s study only suggests that workload, subsistence economy, and wealth may impact infant feeding behaviours, but the nature of the relationship is complex and not yet well-understood.

In the third and most recent test of the women's workload hypothesis, Quinlan and Quinlan (2008) used a cross-cultural sample of 58 ethnohistoric and contemporary natural fertility, nonindustrial human populations (14 hunter-gatherer-fisher populations and 44 farming and/or herding populations) to test the prediction that women's contribution to subsistence affects mean age at which infants in a population completely cease breastfeeding. While there was a trend in their data that suggests an inverse relationship between age at complete cessation of breastfeeding and women's contribution to the subsistence economy of their society, it did not achieve statistical significance. As such, their study either lacked the statistical power to shed light on the relationship between the duration of all breastfeeding and women's workload or women's workload may not directly impact the duration of all breastfeeding.

Taking the results of the three tests of the workload hypothesis together, there is no clear evidence that mothers' work outside the home impacts the duration of exclusive breastfeeding and/or the duration of all breastfeeding. It remains an open question as to whether this lack of support for the workload hypothesis is related to poor data quality, low statistical power, and/or biased estimates, or if maternal workload genuinely does not affect breastfeeding duration.

The weaning food availability hypothesis has been tested in one cross-cultural study. In that analysis, Sellen and Smay (2001) used published retrospective data from 129 populations (representing 110 distinct cultural groups) to evaluate the prediction that farming and herding populations would have better access to appropriate weaning foods than hunter-gatherer-fishers and thus would likely shorten the duration of exclusive breastfeeding and/or the duration of all breastfeeding. Sellen and Smay (2001) found, however, that hunter-gatherer-fishers have ready

access to a wide variety of foods appropriate for weaning and that they do not necessarily delay introduction of non-breastmilk foods relative to farmers, although herders appear to end exclusive breastfeeding before both hunter-gatherer-fishers and farmers. Nonetheless, Sellen and Smay (2001) did find that farmers and herders generally have shorter durations of all breastfeeding than hunter-gatherer-fishers. This finding, along with the finding that pastoralists end the period of exclusive breastfeeding relatively early, suggests that subsistence behaviour may in some way influence the way in which nutrients are transferred to infants, but it appears that this is not the result of variation in availability of weaning foods. Rather, Sellen and Smay (2001) argue that there are a variety of other more basic socioecological influences on variation in the duration of exclusive breastfeeding and the duration of all breastfeeding. Specifically, they suggest that maternal health and body size, pathogen risk, and perhaps women's non-domestic workload probably affect the durations of exclusive and/or all breastfeeding in humans and that these effects may be mediated by type of subsistence economy.

To date, the extrinsic risk hypothesis has been tested in two cross-cultural studies. In the first, Quinlan (2007) tested the prediction that the duration of all breastfeeding increases and then decreases as extrinsic threats to infant survival increase. He used three proxies for risks: frequency of famine, frequency of warfare, and an index of pathogen load. His sample included 85 natural fertility hunter-gatherer-fishers, farmers, and herders. His analyses did not show an association between duration of all breastfeeding and frequency of famine or frequency of warfare. However, Quinlan did find that the duration of all breastfeeding was associated with pathogen load in the predicted pattern. Notably, Quinlan's analyses did not control for a number of important potential confounds and/or mitigating factors – especially variation in average

condition of reproductive-aged women. So, Quinlan's mixed results suggest that some features of local ecology can relate to the duration of all breastfeeding and/ or vice versa, but their implications regarding maternal and infant energy balance are far from clear.

Recently, my colleagues and I carried out the second cross-cultural test of the extrinsic risk hypothesis (McKerracher et al. 2012b). We extended the logic of the hypothesis to the duration of exclusive breastfeeding, on the grounds that this variable also serves as a proxy for maternal investment. Using data from 42 natural fertility, nonindustrial farming and herding populations, we regressed duration of exclusive breastfeeding on two proxies for extrinsic risk, namely, risk of facing nutritional shortfall and risk of infectious disease. We found that the duration of exclusive breastfeeding was correlated with both proxies for risk, but not according to the predicted pattern. In the sample we used, there was no evidence that the duration of all breastfeeding was associated with either form of risk. Although we improved on Quinlan's methods by controlling for phylogeny in our analyses, we, like Quinlan, failed to control for an obvious potential confound/mitigating factor, variation in maternal condition. Given this shortcoming, these results only tentatively argue for some role for extrinsic ecological risk in driving among-population variation in the duration of exclusive breastfeeding. Taking our results together with Quinlan's, there is at best only tentative evidence that the end of all breastfeeding is affected by extrinsic risk in hunter-gatherer-fishers. But, whether the relationship is causal and whether there are intermediate or deeper factors contributing to the variation remains unresolved.

The alloparental care hypothesis has been tested in one previous cross-cultural analysis. The test was carried out as part of the aforementioned study in which Quinlan and Quinlan (2008) report

on the lack of impact of women's contribution to subsistence on the mean duration of all breastfeeding. With respect to allocare, Quinlan and Quinlan evaluated the predictions that presence of stable marital unions and access to infant care by female relatives should facilitate extended duration of all breastfeeding. They found that presence of stable conjugal unions (i.e. presence of fathers) is positively associated with longer duration of all breastfeeding. Presence of other potential allocare-givers was also significantly associated with duration of all breastfeeding, but in the opposite direction from the prediction. That is, counter to Quinlan and Quinlan's (2008; Quinlan et al. 2003) hypothesis that allocare supports extended breastfeeding, their results suggest that related allocare providers may decrease rather than increase the amount of energy mothers transfer to their infants and children through lactation. While this finding did not support Quinlan and Quinlan's original expectation, it is not a surprising result. That is, other researchers have previously derived the opposite prediction from the allocare hypothesis and suggested that increased allocare should be associated with relatively early cessation of breastfeeding, consistent with the findings of Quinlan and Quinlan (2008). So, the only available cross-cultural evidence to date provides evidence consistent with at least one set of plausible predictions from the allocare hypothesis, suggesting that this hypothesis warrants further attention.

**The live fast-die young (LFDY) hypothesis** has been tested in one cross-cultural study. Conducted by Gawlik et al. (2011), this study used data from 22 small-scale populations. Gawlik and colleagues regressed inter-birth interval (IBI)—which they used as a proxy for the duration of all breastfeeding—on several adult female and male body size variables. The body size variables included height, weight, and Body Mass Index (BMI;  $\text{mass}/\text{height}^2$ ). They found that IBIs are

strongly and significantly negatively correlated with adult female and male weight and adult female BMI, but not with height for either sex or with BMI for males. However, there are a number of shortcomings of Gawlik et al.'s work. In particular, it is unclear that length of IBIs reliably measures duration of breastfeeding. Evidence from within populations suggests that how well IBIs track breastfeeding durations is contingent on energetic status of mothers (Valeggia and Ellison 2004; 2009; Worthman et al. 1993). Since proxies for energetic status of mothers constitute the predictors in Gawlik et al.'s (2011) models, using inter-birth interval as a proxy for the duration of all breastfeeding is problematic. Additionally, their analyses did not adjust for phylogeny. They also did not control other factors likely to influence maternal development and/or current energy balance such as infant/child diet, adult diet, or access to help with infant care. Accordingly, while their findings provide preliminary evidence that body size variables may influence birth spacing, further research is needed to support the claim that the live fast-die young hypothesis can account for a portion of variation in the duration of all breastfeeding.

In sum, the cross-cultural evidence suggests that the duration of exclusive breastfeeding and the duration of all breastfeeding associate with socio-ecological variables. In particular, breastfeeding durations correlate with maternal workload, subsistence economy, pathogen load, availability of alloparental care, and adult female BMI. The relationships among these socio-ecological variables are complex, as are the relationship between breastfeeding durations and the socio-ecological variables. It remains unclear the extent to which any of the relationships are causal. The hypotheses reviewed here warrant further investigation, because none of the studies to date adjusted for other likely correlates of breastfeeding variation, so previous effect estimates are probably biased.

As mentioned previously, in addition to the among-population analyses described above, a large – and still growing – number of within-population anthropological studies have investigated socio-ecological correlates of the duration of exclusive breastfeeding and/or the duration of all breastfeeding in small-scale populations. Several of these within-culture studies have yielded evidence relevant to evaluating the five hypotheses previously outlined. In particular, focusing on **the women’s workload hypothesis**, a large number of studies suggest that women from small-scale populations in a variety of contexts (e.g. foragers from Central African and Southeast Asian rainforests, pastoralists from East African plains, and horticulturalists from Central and South America) face tradeoffs between carrying out subsistence-related tasks and breastfeeding on-demand. Thus, increases in non-childcare workloads are typically associated with shorter durations of exclusive breastfeeding, less frequent breastfeeding bouts, shorter durations of all breastfeeding, or some combination of these things.

Behavioural ecological research on small-scale African herders, especially Gray’s (1996; 1998; 1994; 1995) work with the Turkana, Sellen’s (2001a) work with the Datoga, Pennington’s (1992) work with the Herero and with semi-sedentary/cattle-raising !Kung, and Wander and Mattison’s (2013) work with the Chagga, shed light on **the weaning food availability hypothesis**. With the exception of Wander and Mattison’s (2013) study (which contains serious flaws with respect to its evaluation of the effects of availability of weaning foods), all of these analyses appear to indicate that access to fresh milk affects when small-scale herders (and the foragers that interact with them) end exclusive breastfeeding and/or all breastfeeding. There appears to be little, if any, data regarding whether a similar pattern might hold for variation in breastfeeding times within populations of small-scale foragers or of horticulturalists/agriculturalists. So, further testing of

this hypothesis, both at the cross-population level and at the within-population level, is needed. In particular, new analyses pertaining to this hypothesis at the within-population level should focus on non-herders.

With respect to **the extrinsic risk hypothesis**, no within-population studies to date have explicitly tested it and no published studies have reported data that suggest an inverse quadratic relationship between the duration of exclusive breastfeeding and/or the duration of all breastfeeding and extrinsic risk of infant death, as predicted by Quinlan (2007). Given that the cross-cultural studies carried out by Quinlan (2007) and by my colleagues and myself (McKerracher et al. 2012) suggest that extrinsic risk may influence the duration of exclusive breastfeeding and the duration of all breastfeeding, direct assessment of this hypothesis at the within-population level may be warranted.

As regards **the LFDY**, some previous within-culture studies have hinted that relatively more adipose women may invest less time and energy in lactation than less adipose women (e.g. Gray 1995; Tracer 2009; see also Valeggia and Ellison 2004; 2009). This pattern is consistent with the assumption that greater adiposity results from a relatively fast life history schedule during development. That said, there are no consistent associations between the duration of exclusive breastfeeding or the duration of all breastfeeding with maternal height (Sear 2010). As such, the within-culture evidence regarding the LFDY is equivocal.

As it stands then, none of the hypotheses has been unequivocally rejected. But, on the other hand, none of the hypotheses provides a comprehensive explanation for variation in the duration of exclusive breastfeeding and/or the duration of all breastfeeding. There are at least four reasons

for why our understanding of this variation remain unclear. First, to date, evolutionary anthropologists have paid surprisingly little attention to patterns of among-species variation in lengths of lactation in nonhuman animals when developing and testing hypotheses about the duration of exclusive breastfeeding and the duration of all breastfeeding in humans. The nonhuman mammal literature indicates clear and consistent relationships between lengths of lactation and both adult female body size and adult female brain size (e.g. Barton and Capellini 2011; Dubman et al. 2012; Hamilton et al. 2011; Harvey and Clutton-Brock 1985; Isler 2011). This same corpus of literature suggests that variation in lengths of lactation is associated with variation in the quality of a species' diet (Langer 2003; 2008; Psouni et al. 2012) and the extent to which a species relies on alloparental care (Isler and van Schaik 2012; Ross and MacLarnon 2000; Ross 2003). These among-species patterns of variation imply that basic energetic factors can play key roles in constraining or even driving parental investment strategies. Such basic drivers should be accounted for before seeking more complex (i.e. socioecological or cultural) explanations for variations within and across human families and populations in the duration of exclusive and of all breastfeeding.

A second problem with previous research on human breastfeeding variation concerns data quality. The cross-cultural studies carried out to date have relied on data derived predominantly from ethnographic sources with research foci unrelated to understanding lactation biology. Furthermore, these ethnographic sources rarely report raw data or details of weaning data collection methods, and the information that *is* reported differs substantially among authors in language and style. So, the data used in previous studies are extremely variable in quality and reliability. New, higher-quality field data from more than 20 different human small-scale

populations have accumulated over the last few decades, and these can and should be used to re-evaluate earlier findings.

The third major shortcoming of the existing literature concerns a neglect of systematic study of the way in which humans acquire and share information about infant and young child feeding. That is, while basic energetic factors likely explain a considerable portion of variation in the duration of exclusive breastfeeding and/or the duration of all breastfeeding and thus should certainly be accounted for (as suggested above), a great deal of human behaviour is at least to some extent guided by information acquired through social learning from other members of our social groups. The evidence available suggests that infant and young child feeding behaviours follow this general human pattern of heavy reliance on social learning (Dettwyler 2004; Van Esterik 2002; Wells 2006). Indeed, a number of studies are beginning to show that cultural understandings of infancy and of infant needs influence the duration of exclusive breastfeeding and the duration of all breastfeeding as well as other aspects of breastfeeding and weaning behaviours (e.g. Fouts et al. 2012; Hadley et al. 2010a; Hewlett 1998; Meehan and Roulette 2013; Wells 2006). This body of work suggests that how mothers and other infant caregivers learn about infant and young child feeding likely constitutes a key set of factors interacting with and/or mitigating non-cultural ecological drivers (e.g. maternal developmental conditions) of variation in infant feeding practices. However, the studies to date have generally failed to operationalize “culture” or “cultural models of infancy” into measurable variables that we can incorporate into comparative analyses, make inferences from, and possibly even use as the basis for generalizations about human evolutionary demography and the evolution of human life history.

The fourth and last shortcoming of much previous literature on the influence of environmental and cultural ecology on duration of breastfeeding concerns the relationships among the hypotheses. Many earlier studies have tacitly viewed the hypotheses reviewed here as competing with one another in terms of explanatory power rather than as interconnected and complementary (e.g. Hamilton et al. 2011; Quinlan et al. 2003; Quinlan 2007). However, there is good reason to think that each of the proposed predictor variables used to test the hypotheses of interest impacts the others (Snopkowski and Kaplan 2014). For example, the pace of life history and its effects on energy allocation presumably affects access to potential alloparents (via numbers of sibs that can help), access to high quality foods (via number of mouths to feed), and access to cultural learning models (via demographic structure). Furthermore, even if it were the case that one of the variables drives contemporary and/or past breastfeeding variation, identifying that variable requires statistically adjusting for the other variables. Many of the key earlier studies did not make such adjustments (e.g. Gawlik et al. 2011; Hamilton et al. 2011; Quinlan et al. 2003; Quinlan 2007; Quinlan and Quinlan 2008).

In this dissertation, I seek to partially address each of these four shortcomings of the literature on within- and among-population variation in the duration of exclusive breastfeeding and the duration of all breastfeeding. Specifically, I focus on re-evaluating those hypotheses from the human literature that may apply at higher (or lower) taxonomic levels, as indicated by the findings of cross-species studies on non-human animals. That is, at both the among- and the within-population level of analysis, I report new tests of the live fast-die young hypothesis (based on the cross-species finding that maternal body size influences lengths of lactation), the weanling diet quality hypothesis (based on the cross-species findings that species with higher

quality diets cease lactation earlier), and the allocare hypothesis (based on the cross-species finding that species that rely on help with infant feeding and care cease lactation earlier). At the cross-population level of analysis, I attempt to correct for previous data quality issues by applying stringent inclusion/exclusion criteria when collecting secondary data and thus restricting my sample to only those small-scale populations for which measures appear reliable. Next, I dedicate a study to using quantitative information about the ways through which infant and young child feeding knowledge is transmitted into our analyses on inter-individual variation in the duration of exclusive breastfeeding and the duration of all breastfeeding. Lastly, at all scales of analysis, I treat the energy-related hypotheses as compatible and inter-connected with one another and with the effects of culture rather than as mutually exclusive.

## **1.5 Structure of the dissertation**

This dissertation works towards the aim of shedding light on the factors that may have contributed to the evolution of early and flexible weaning in humans. It does so via a series of three original studies that constitute chapters two, three, and four of this document. Although the studies were designed to function as chapters that “hang together” as a monograph tackling a single question, they also represent a series of standalone scientific research papers. The papers appear here as they are intended to appear in academic journals, with two exceptions. The first exception is that my mentors/collaborators are not listed as co-authors. They will be co-authors when the manuscripts are submitted for publication and I use the pronoun “we” in chapters two through four in anticipation of that. The second exception pertains to the numbering and

formatting of headings, subheadings, and captions. These have been modified so that they are consistent throughout this document.

The first set of tests, reported in the chapter entitled “Duration of breastfeeding is associated with maternal body size and use of animal-based weaning foods in a sample of 21 small-scale societies”, investigates variation at an among-human-population scale. This first study focuses on maternal energetic factors, which previous research has identified as predictors of cross-species variation in length of lactation.

The second study, reported in the chapter entitled “Duration of breastfeeding and maternal energetics in a sample of indigenous Maya women from Guatemala”, uses new interview data collected via fieldwork with small-scale, subsistence farming, Guatemalan Maya women. This study investigates the effects of the same maternal energetic factors on variation in length of all breastfeeding as those investigated in the first study, but does so at a within- and among-families scale rather than an among-populations scale.

The third and last study again uses field data from Maya women, but focuses on cultural and socio-economic influences on the timing of breastfeeding decisions, rather than on energetic constraints. This third paper/chapter is called “Breastfeeding durations are associated with culture and modernization in indigenous Maya women from Guatemala”.

Supplementary materials for studies one, two, and three appear in the first, second, and third appendices of this manuscript, respectively.

**2 Duration of breastfeeding is associated with maternal body size and use of animal-based weaning foods in a sample of 21 small-scale societies**

## 2.1 Abstract

Total duration of breastfeeding varies widely among human populations. This breastfeeding variation affects variation in infant health outcomes. It also influences demographic parameters such as length of intervals between births. But, the ecological and evolutionary factors that drive breastfeeding variability are not yet fully understood.

Research on variation in length of lactation among different mammal species suggests that maternal energy balance and factors that influence maternal-to-infant energy transfers may contribute to the variation in question.

With this nonhuman mammal literature in mind, we here report a series of tests of energetics-related hypotheses using data from small-scale human populations. We regressed population mean duration of breastfeeding on population means of maternal body size, maternal access to nutrient-dense weaning foods for their infants, and maternal access to energetic subsidy for infant care, or “allocare”.

We found that duration of breastfeeding was negatively associated with maternal Body Mass Index (BMI). Probing of this association in a follow-up analysis suggested that the relationship is predominantly related to large mass/high adiposity rather than short height, although there was also evidence of a height effect. Duration of breastfeeding was negatively associated with availability of nutrient-dense weaning foods. The analyses provide no evidence of an association between duration of breastfeeding and access to allocare.

These findings indicate that energetic factors related to maternal development (height) and current status (weight-for-height) as well as infant dietary quality influence length of breastfeeding. These associations suggest that conceptual models of past human life history and demography should incorporate weight, height, and weanling diet quality when relevant data are available. The findings also suggest that variation in breastfeeding strategies observed in the biomedical/public health literature may be accounted for by energetic factors, as predicted by evolutionary ecological theory.

## **2.2 Introduction**

### **2.2.1 Variation in duration of breastfeeding**

This paper reports a study that investigates variation in duration of breastfeeding among small-scale human populations in relation to variation in measures of maternal energetic status and other influences on maternal energy availability. We use four such measures: maternal height, maternal weight, maternal access to help with infant care, and use of high quality versus low quality weaning foods.

Duration of breastfeeding varies substantially within and among human populations. Some mother-infant dyads do not engage in any breastfeeding, or end breastfeeding within the first days or weeks of infant life (e.g. Khan et al. 2014; Scott et al. 2014a). Others continue breastfeeding at least sporadically until the child reaches six, seven, or even eight years of age (e.g. Harner 1973; Hilger 1957; Howell 2010; Mckerracher et al. in prep.). Across non-industrialized populations, population mean of duration of breastfeeding ranges from ~four months to ~six years (Sellen 2001b). Both this cross-population range of 3.5 years and the full

human range of birth to eight years far exceed the range of variation in length of lactation documented within species of nonhuman apes (Sellen 2009).

Within and among species variation in duration of lactation are thought to influence birth spacing and fertility (Ellison 1995; Howie and McNeilly 1982; McNeilly 1997; Valeggia and Ellison 2001; Williams 1986). In particular, shorter breastfeeding durations are generally associated with shorter intervals between births and higher lifetime fertilities (Howie and McNeilly 1982). Accordingly, identifying the factors that drive variation in duration of breastfeeding in general and the factors associated with relatively short durations of breastfeeding in particular may shed light on why humans have relatively higher fertility and are more demographically successful than other apes (Emery Thompson 2013; Hamilton et al. 2009; Wells and Stock 2007).

### **2.2.2 Focus of the study, hypotheses and predictions**

Although variation in duration of breastfeeding likely reflects both maternal and infant fitness needs and ecological constraints (maternal and infant needs and constraints do not necessarily align perfectly with one another, Trivers 1974), we focus here on maternal fitness. We do so for two main reasons. First, while infants and young children may successfully manipulate parents into providing more time and energy resources than parents would prefer to provide (Fouts et al. 2005; Wells 2003), parents have far more physical and social power than offspring (Kilner and Hinde 2008). For example, when mothers want to terminate breastfeeding, they can physically move children away from the breast (e.g. Hamilton 1981) or place children in the care of grandmothers or other caregivers (e.g. Sear et al. 2002; Sear and Coall 2011). As such, breastfeeding strategies that reflect maternal needs or benefit maternal fitness at the expense of

infant fitness are far more likely to actually be expressed. Second, we focus on maternal constraints for the pragmatic reason that data on maternal energetic status and on factors that influence it are more widely available and more easily comparable than are data on infant needs.

To explore the effect of maternal energetic constraint on among-population variation in duration of breastfeeding, we test three energetics-related hypotheses from the literature. One is the “Live Fast-Die Young” (LFDY) hypothesis (Charnov and Berrigan 1993; Walker et al. 2006). The LFDY hypothesis holds that extrinsic morbidity and mortality risks cue maternal growth and development trajectories. Developmental trajectories in turn influence the pace of reproduction. Under this hypothesis, mothers who developed under relatively high extrinsic morbidity and mortality regimes are expected to stop growing early, to begin storing fat for reproduction relatively early, to begin reproducing relatively early, and to continue reproducing relatively fast (Gawlik and Hochberg 2012; Gawlik et al. 2011; Walker et al. 2006; Walker et al. 2008). In other words, the LFDY predicts that shorter, fatter-for-height mothers (or shorter, fatter-for-height populations) are likely to have shorter durations of breastfeeding. The logic of these predictions is twofold. First, under high levels of extrinsic mortality risk, delayed or slow reproduction may lead to complete loss of reproductive opportunities due to death. Second, high levels of extrinsic morbidity risk increase the costs of growing and maintaining extra tissue, since investment in linear growth requires sacrificing investment in immune system development and maintenance as well as sacrificing future investment in reproduction (Abrams and Miller 2011; McDade and Worthman 1999; McDade 2003).

The second hypothesis we evaluate is the “alloparental care” hypothesis (Hrdy 1999; 2007; 2009; Kramer 2010; Kramer and Ellison 2010). Alloparental care refers to the provision of infant care by non-mothers. The hypothesis proposes that help with infant care can partially offset the maternal energetic costs of breastfeeding, because infant energy requirements not met by mothers can be subsidized through food provision and care by helpers (Haig 2010; Hrdy 2009; Kramer 2010; Kramer and Ellison 2010). Such subsidies allow mothers to allocate their limited time and energy to other things, such as resumption of ovulatory function and support of new pregnancies. A key prediction of this hypothesis is that populations characterized by high levels of alloparental care during infancy are likely to have shorter mean durations of breastfeeding than populations characterized by lower levels of such care.

Lastly, we test the “weanling diet quality” hypothesis. This hypothesis is informed by studies of length of lactation in non-human animals. It suggests that even the underdeveloped guts and teeth of infants can make efficient use of animal foods (Krebs 2007; Langer 2003; 2008; see also Psouni et al. 2012). The idea here is that mothers can artificially expand energy budgets without necessarily increasing their own energetic intake or reducing infant energy intake by feeding infants very nutrient-dense non-breastmilk food – animal foods in particular. The core prediction of this hypothesis is that mothers from populations who commonly feed infants animal foods are more likely to shorten durations of breastfeeding and re-allocate their own somatic time and energy to other purposes earlier.

In what follows, we report a series of among-population regression analyses designed to evaluate these test predictions. We do so with a view toward shedding light on the role of maternal energetics in variation in duration of breastfeeding in the context of small-scale human societies.

## 2.3 Materials and methods

### 2.3.1 Materials

The core dataset comprises means for small-scale populations for four continuous variables and two categorical variables (Tables 2-1 and 2-2). These variables are:

1. Duration of all breastfeeding (hereafter: “duration of breastfeeding”)
2. Adult female body mass (hereafter: “mass”)
3. Adult female height (hereafter: “height”)
4. Body Mass Index (mass in Kg/[height in m]<sup>2</sup>; hereafter: “BMI”)
5. Relative amount of time infants spend held or cared for by mothers versus non-mothers (hereafter: “allocare score”)
6. Whether ethnographic or maternal reports indicate frequent use of animal-based-foods for infants and very young children (hereafter: “diet quality score”)

Unfortunately, only duration of breastfeeding, height, weight, and BMI were available for all 21 populations. Allocare score and diet quality score were each accessible only for 13 populations.

For the continuous variables, reported mean was generally used as the mean. In the few cases in which more than one eligible source yielded differing means, the average of the means was taken.

The scoring of the two categorical variables, each assigned a value of “low” or “high”, was less straightforward. With respect to allocare score, we observed that the distribution of quantitative estimates of percentage of holding by mothers relative to allocare providers was bimodal, such that there were no populations in which mothers provided 55%-65% of infant holding. So, populations with quantitative maternal care provision values of 55% or less were scored as high allocare populations. Those with quantitative maternal care provision values of 65% or more were scored as low allocare populations. For populations in which only qualitative data were available, we interpreted observations such as “infants are in constant physical contact with their mothers” as low allocare populations. There were no populations for which high levels of allocare were reported only qualitatively. With respect to food quality score, populations for which mothers reported use of animal products other than meat broth as preferred weaning foods were scored as using weaning foods of high nutritional quality. Populations for which information regarding preferred weaning foods was available but for which women did not report using animal products as preferred weaning foods were scored as “low quality weaning foods.” The raw food quality and allocare data as well as the assigned food quality and allocare scores are reported in Table 2-2.

In addition to these six variables, we collated basic eco-geographic and demographic data pertaining to each of the study populations (country or geopolitical region, pathogen prevalence within that country or region, latitude, linguistic taxon, mean age at first birth, mean number of live births per woman, mean length of interbirth intervals, and infant mortality rate). These were not used in our main analyses but are available in the appendix (see Appendix 1, S Tables 1.1 and 1.2).

We used four main inclusion/exclusion criteria when assembling the dataset. Three of these were applied stringently to the dataset used in the main analyses but the fourth was only rigorously applied during supplementary sensitivity analyses. First, populations had to be described as predominantly natural fertility, with little or no reported use of reliable biomedical contraception methods at the time at which breastfeeding data were collected. Second, we had several requirements pertaining to subsistence economy: included populations must have, at the time of breastfeeding study, extracted or produced more than half of their own food locally, must have produced any cultivated food using simple means (no draft animals, no large-scale irrigation), and must have engaged in at least a small amount of collection or extraction of food resources (e.g. opportunistic hunting, fishing, and/or gathering). Third, we limited our sample to only very well-studied populations. In particular, we required that populations must have been studied by cultural and/or biological anthropologists for a minimum of one year between the beginning of the era of rigorous human behavioural ecological field research (1975) and the time at which we completed our survey of the literature (August 2014). Our fourth criterion pertains specifically to breastfeeding. To be included, quantitative data on duration of all breastfeeding derived from observation on and/or interviews with a minimum of 10 women had to be available.

Data for 19 of the 21 populations come from published literature, while data for the remaining two populations are from unpublished sources. With respect to the published data, we used the sample of 22 small-scale populations assembled by Walker et al. (2006) and references therein to identify well-studied, subsistence-level populations. The Walker et al. (2006) dataset yielded a sample of nine populations that met all our inclusion criteria and one population that met the first three of our inclusion criteria. We supplemented these data with a GoogleScholar search in

which the search terms were the names or ethnonyms of populations mentioned in the text and/or in the references of Walker et al. (2006) and keywords related to breastfeeding (breastfeed\*, lactation, nurs\*, or wean\*). This search yielded information on an additional nine populations, six of which met all of our inclusion criteria and three of which met the first three of our inclusion criteria. Regarding the two sets of unpublished data, information on the Kakchiquel-speaking Mayans derive from our own fieldwork in Guatemala between 2000 and 2013 (project headed by PN). Unpublished data for Yasawa Islanders come from fieldwork carried out in Fiji by Joseph Henrich between 2003 and 2009.

**Table 2-1: Duration of breastfeeding (BF), mass, height, and BMI for 21 small-scale, subsistence-level, predominantly natural fertility human populations.**

Population	Mean Duration of all BF (months)	BF <i>n</i>	Mean Adult Female Body Mass (Kg)	Mean Adult Female Height (cm)	BMI (Kg/m <sup>2</sup> )	Breastfeeding References	Body Mass References
<b>Ache</b>	24.9	86	56.7	148.3	25.79	Hill and Hurtado 1996	Hill & Hurtado 1996; Walker & Hill 2003
<b>Aeta</b>	30.5 (IBI-4.5 months)*	unknown	38.0	138.7	19.75	Gawlik & Hochberg 2012	Bernstein & Dominy 2013; Gawlik & Hochberg 2012
<b>Agta (Cagayan)</b>	29.7 (IBI – 4.5 months)*	--	36.7	141.2	18.41	Griffin & Griffin 1992	Goodman et al. 1985
<b>Agta (Casiguran)</b>	27	155	40.3	143.0	19.71	Early & Headland 1998	Early & Headland 1998
<b>Aka</b>	36	40	43.5	145.1	20.65		Rozzi et al. 2015
<b>Amele</b>	36.3	662	42.1	150.2	23.09	Worthman et al. 1993	Worthman et al. 1993
<b>Au</b>	43	472	45.3	148.1	20.65	Tracer 1996	Tracer 1991
<b>Bofi farmers</b>	22.5	21	47.0	151.0	20.60	Fouts et al. 2005; Fouts et al. 2012	Meazza et al. 2009
<b>Bofi foragers</b>	44.5	22	47.0	151.0	20.60	Fouts et al. 2005; Fouts et al. 2012	Meazza et al. 2009
<b>Burarra</b>	24**	20	55	156		Hamilton 1981	Walker et al. 2006
<b>Efe</b>	24	10	39.4	136.0	21.30	Morelli 1987	Walker et al. 2006
<b>Gainj</b>	38.6	305	41.2	142.8	20.20	Wood et al. 1985	Wood 1978; Galdikas & Wood 1990
<b>Hadza</b>	31.2	33	46.3	150.5	20.46	Marlowe 2010	Marlowe 2010
<b>Ju'/hoansi</b>	31.5	165	41.7	150.0	18.53	Howell 2010	Howell 2010
<b>Kakchiquel Mayans</b>	27.3	109	51.9	146.3	24.25	Unpublished (this study)	Unpublished (this study)
<b>Makushi</b>	20	60	54.9	151.2	24.00	Wilson et al. 2006	Wilson et al. 2011
<b>Pume</b>	33	29	50.9	150.2	22.56	Veile 2010	Veile 2010
<b>Toba</b>	30	70	61.6	155.9	25.34	Valeggia & Ellison 2004	Valeggia & Ellison 2004
<b>Tsimane</b>	24	81	53.2	149.5	23.80	Veile 2010	Veile 2010
<b>Xculoc Mayans</b>	24**	57	51.0	142.0	25.29	Kramer 2005	Walker et al. 2006
<b>Yasawa Islanders</b>	16.2	70	93.1	168.1	32.95	Unpublished (pers. comm.)	Unpublished (pers. comm.)

**Table 2-2: Weanling diet and allocare in 21 small-scale, subsistence-level, predominantly natural fertility human populations.**

Population	First non-breastmilk foods in infant diet	Weaning food quality score	Carrying/holding or feeding of infants and young children by non-mothers	Allocare Score	Weanling diet references	Alloparenting references
Ache	“armadillo fat or insect larvae”	High	Infants spend 90+% of time in “tactile contact” with either mother or father in first year, and 40% of time in second year on mother’s body	Low	Hill & Hurtado 1996	Hill & Hurtado 1996
Agta (Cagayan)	No data available	--	52% of carrying of infants/ young children by mothers, 4% by fathers, 10% by elder sisters, 8% by grandmothers, 26% by others	High	--	Goodman & Griffin 1985
Agta (Casiguran)	rice	Low	~50% infant carrying by mothers, 4% by fathers, 46% by all others	High	De Souza, 2006	Early & Headland 1998
Aka	“corn, banana, rice porridge, meat broth, and honey”	Low	~35-50% of infant carrying in camp by mothers, ~85% of infant carrying by mothers when net hunting; 8.7% of all carrying by fathers	High	Meehan & Roulette 2013	Hewlett 1989
Amele	“watery semi-solids, then mashed starchy staples”	Low	“constant physical contact” with mothers for first 6 months; after 6 months, mothers “arrange work to minimise separation”	Low	Worthman et al. 1993	Worthman et al. 1993
Au	“sago pudding”	Low	~71% of infant life in mother’s arms, 17% in arms of others, remainder not held	Low	Tracer 1996	Tracer 2009
Bofi farmers	“rice or rice gruels”	Low	No data available	--	Fouts et al. 2005	--
Bofi foragers	no “special foods for weaning-age children”  children eat adult-like diet, which is low in animal foods	Low	~55% of infants’ lives in mothers’ arms, ~22% by others, remainder not held	High	Fouts et al. 2001; Fouts et al. 2005	Fouts et al. 2001
Burarra	No data available	Low	infants “constantly in	Low	--	Hamilton

			[mothers'] lap or arms"			1981
Efe	No data available	--	~40% of holding by mothers when infant reaches 18 wks of age, 60% by others	High	--	Tronick et al. 1987
Gainj	"sweet potato, banana, and pitpit"	Low	"children under 6... rarely separated from their mothers"	Low	Wood 1978; Wood et al. 1985	Johnson 1990
Hadza	baobab paste, meat to suck on (sometimes pre-masticated)	High	68.7% of carrying by mothers, 7.1% by fathers, 24.2% by others	Low	Marlowe 2010	Marlowe 2010
Ju'hoansi	"pre-masticated meat" and "sweet vegetables"	High	~70-80% carrying by mothers, 20-30% by others	Low	Howell 2010	Howell 2010
Kakchiquel Mayans	porridges (fortified wheat, oatmeal, maize), rice, noodles, bananas, eggs, beans	Low	72% of mothers report receiving help with infant carrying and care	High	Unpublished (this study)	Unpublished (this study)
Makushi	"manioc meal, water, and sugar mix", "food from the mother's plate and fruit such as ripe bananas"	Low	No data available	--	Wilson et al. 2006	--
Pume	"pre-masticated adult food... followed by small portions of soft food such as mangoes"	High	No data available	--	Veile 2010,	--
Toba	"light broths, white breads, and mashed, starchy vegetables"	Low	50% of any infant holding by mothers, 50% by others	High	Valeggia & Ellison 2004	Valeggia 2009, p. 106
Tsimane	plantain, meat, and fish	High	Mothers provide 82.5% of care during daylight hours, ~half of which is spent in mothers' arms, the remainder in nearby hammock	Low	Veile 2010	Winking et al. 2009
Yasawa Islanders	crabs, fish, coconut milk, pawpaw, cassava, fish juice	High	No data available	--	Unpublished (pers. comm.)	--

### 2.3.2 Analyses

We carried out one set of analyses to test the predictions derived from the LFDY hypothesis and another set to test the predictions of the alloparental care hypothesis and the weanling diet quality hypothesis. In the first test of the LFDY hypothesis, we used the full dataset of 21 populations to evaluate the prediction that women from taller, leaner populations breastfeed longer than women from shorter, more adipose populations. To this end, we used Weighted Least Squares (WLS) regression to regress mean duration of breastfeeding on BMI, with observations weighted by sample size. The analysis was carried out using the stat package in R (R Development Core Team 2014).

The second analysis focused on predictions of the alloparental care and weanling diet quality hypotheses, while controlling for the effects of body size (BMI) on duration of all breastfeeding. Specifically, using the data for the 13 populations for which relevant data were available, we regressed duration of breastfeeding on allocare score, food quality score, and BMI, again weighting the regression by sample size. Duration of breastfeeding was expected to be negatively associated with all three predictors. These analyses were also carried out in R.

In addition to these analyses, we also carried out five sensitivity tests to assess the robusticity of our results, given that our sample is small and contains an influential data point. In the first of these tests, we, pseudo-replicated the full dataset 2000 times using random bootstrap sampling and then recalculated the estimates and the 95% confidence intervals for those estimates using the replicated dataset. In the second, we re-did the regressions after excluding the four populations for which the duration of breastfeeding estimates were relatively unreliable (see

asterisks in Table 2-1). In the third and fourth sensitivity tests, we attempted to control for the potential effects of phylogenetic autocorrelation in the dataset in two different ways. We first used WLS regression models in which we included continent as a covariate and then compared these models to the ones reported in the main text using the F test: in all cases, the compared models were statistically indistinguishable from one another. In the next set, we developed two linear mixed effects models (one bivariate, one multivariate) in which we allowed intercepts to vary randomly among eight clusters of populations that speak closely related languages. In the fifth and last test, we re-ran the basic analyses after excluding the influential data point.

## 2.4 Results

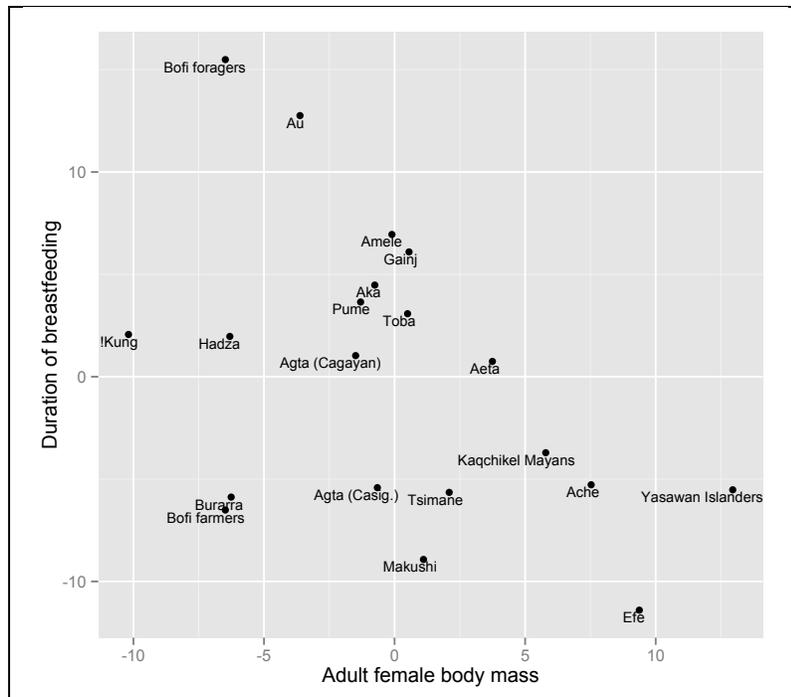
In the full sample of 21 populations, duration of breastfeeding ranges from 16.2 months in Yasawa Islanders to 44.5 months in Bofi foragers, with a mean of 29.4 and a standard error of  $\pm 1.59$ . BMI ranges from 18.41  $\text{Kg/m}^2$  in the Cagayan Agta to 32.95  $\text{Kg/m}^2$  in Yasawa Islanders, with a mean of 22.4 ( $\pm 0.72$ ).

The results from the analyses pertaining to the predictions of the LFDY hypothesis are summarized in Table 2-3 and in Figure 2-1. We found that duration of breastfeeding was negatively associated with BMI. The adjusted  $R^2$  indicates that  $\sim 49\%$  of among-population variation in duration of breastfeeding is explained by BMI. This suggests that women from high BMI populations breastfeed their infants for less time, which is consistent with the predictions of the LFDY hypothesis.

**Table 2-3: Results of bivariate linear regression analysis of effects of BMI on among-population variation in duration of breastfeeding.**

Predictor	Estimate	Standard Error	95% CI	One-tailed p
Intercept	70.393	9.354	39.5780 to 80.9107	0.0000***
BMI	-1.627	0.399	-2.2270 to -0.4589	0.0005***
Model summary	$R^2=0.536$ , adjusted $R^2: 0.494$ , two-tailed model $p=0.0010^{**}$			

**Figure 2-1**



**Fig. 2-1** Partial linear regression plot of duration of breastfeeding (months) versus adult female body mass (Kg), after controlling for adult female height (cm). Generally, duration of all breastfeeding decreases as adult female mass, adjusted for height, increases.

The model obtained with the reduced 13-population dataset in the second analysis is summarized in Table 2-4. This model explains ~75% of among-population variation in duration of breastfeeding. Duration of breastfeeding was negatively associated with both BMI ( $\beta=-0.674$ ,  $p=0.0085$ ) and food quality score ( $\beta=-0.758$ ,  $p=0.0037$ ). The slope of the relationship between duration of breastfeeding and allocare score was not significantly different from zero ( $\beta=-0.223$ ,  $p=0.4145$ ). This latter finding indicates that we cannot reject the null hypothesis that allocare does not effect duration of breastfeeding. The negative association between duration of breastfeeding and maternal BMI is again consistent with the predictions of the LFDY hypothesis. The negative association between duration of breastfeeding and food quality score is consistent with the predictions of diet quality hypothesis.

**Table 2-4: Results of multivariate linear regression analysis of effects of BMI, allocare score, and food quality score on among-population variation in duration of breastfeeding.**

Predictor	Estimate	$\beta$	Standard Error	95% CI	One-tailed p
Intercept	81.721		11.954	-0.2288 to 176.7995	0.0001 <sup>***</sup>
BMI	-1.964	-0.674	0.542	-6.4146 to 1.5068	0.0043 <sup>**</sup>
Food quality score	-11.081	-0.758	2.593	-22.1092 to 5.520	0.0019 <sup>**</sup>
Allocare score	-3.526	-0.223	4.065	-18.7137 to 6.7950	0.2072
Model summary	R <sup>2</sup> =0.823, Adjusted R <sup>2</sup> =0.746, two-tailed model p=0.0052 <sup>**</sup>				

The sensitivity analyses produced results that are consistent with those reported in the main text (see S Tables 3a-4e). We therefore report them only in the Appendix.

## **2.5 Discussion**

### **2.5.1 Summary of main results**

We carried out two sets of analyses in which we used population means for breastfeeding and energetics-related variables from small-scale human societies to test predictions of the Live Fast-Die Young (LFDY) hypothesis, the alloparental care hypothesis, and the weanling food quality hypothesis. With regard to the LFDY hypothesis, we found that duration of breastfeeding was negatively associated with adult female BMI. This finding is consistent with the predictions of the LFDY hypothesis. Regarding the weanling food quality hypothesis, we found evidence that duration of breastfeeding was negatively associated with use of high quality, animal-based weaning foods, after adjusting for maternal body size and access to alloparental care. This result is consistent with the predictions for the weanling diet quality hypothesis. As regards the allocare hypothesis, our analyses failed to reject the null hypothesis that allocare does not impact duration of breastfeeding.

### **2.5.2 Interpretations and relation of findings to wider literature**

The results reported here suggest that maternal and infant energetic factors (i.e. body size and diet quality) affect human breastfeeding duration. With regard to body size, our findings are consistent with the idea that the conditions in which mothers develop may influence how long they breastfeed their infants. Specifically, we found that women from higher BMI populations are likely to have relatively fast life history strategies, featuring reduced durations of breastfeeding. The underlying logic that may account for these observations is that exposure of mothers to extrinsic mortality risks during their infancies and childhoods is associated with both

shorter adult stature (Migliano et al. 2007; 2010; Walker et al. 2006; Walker and Hamilton 2008) and increased adult adiposity (Adair 2008; Adair et al. 2009; 2013; Baker et al. 2009; Wells 2009; 2010; 2012a; 2011; 2014). So short, adipose adult phenotypes likely reflect developmental conditions of high mortality risk. Women that developed under such conditions may truncate breastfeeding durations in a strategy that maximizes early and rapid reproduction when lifespan is relatively likely to be cut short. These patterns are consistent with a growing body of research on small-scale human populations that suggests that human life history decisions in general and breastfeeding decisions in particular are mediated by maternal energy balance (e.g. Vallengia and Ellison 2001; 2004; 2009; Wood et al. 1985; Worthman et al. 1993). Maternal energy balance is in part constrained by environmental risk during maternal development (Gawlik et al. 2011; Migliano et al. 2007; Nettle 2010; Walker et al. 2006; Walker et al. 2008).

With respect to other factors that influence maternal energy budgets, we found that use of high quality, animal-based weaning foods is associated with relatively short durations of breastfeeding, consistent with the prediction of the weanling diet-quality hypothesis. This result suggests that infants who receive denser nutrition from non-breastmilk foods than other infants also receive less time and energy investment through lactation. While this specific prediction has not been tested previously in humans, it does accord with a number of findings from the infant nutrition and public health literature, as well as evidence from studies of cross-species variation in duration of lactation. Specifically, human epidemiological and public health research indicates that cow's milk (an animal-based weaning food) is frequently used as a replacement for breastmilk in dairying populations, with this replacement process often leading to the termination of breastfeeding (e.g. Heath et al. 2002; Sellen 2001a; Wijndaele et al. 2009). This pattern thus

accords with the prediction of the weanling diet quality hypothesis that introduction of animal-based supplements relates to relatively shorter durations of breastfeeding. Nonhuman animal studies further suggest that species in which infants are provisioned with nutrient-dense, animal-based foods end lactation relatively earlier than other species (Langer 2003; Langer 2008; Psouni et al. 2012). So, taking the cross-species evidence and epidemiological evidence together with this new cross-cultural evidence, it appears that use of animal-based weaning foods may reduce the costs of extended lactation to mothers, while supplying offspring with high quality nutrition for growth. Notably, this conclusion contrasts with previous suggestions that use of cereal or starch-based weaning foods may have been instrumental in facilitating relatively early weaning in humans .

A final point regarding influences on maternal energy budgets concerns access to alloparental care. We were unable to reject the null hypothesis of no relationship between duration of breastfeeding and allocare. But, we did observe a slight negative association between the variables of interest. This trend is in the direction consistent with the widely held view that reliance on alloparental care effectively increases maternal energy budgets and thus facilitates earlier weaning and higher fertility (Haig 2010; Hrdy 2009; Kramer and Ellison 2010; Meehan et al. 2013). The trend is also consistent with empirical evidence from one previous study on among-population variation in breastfeeding duration in humans (Quinlan and Quinlan 2008) as well as a handful of within-population studies (McKerracher et al. in prepb; Quinlan et al. 2003) and cross-species studies (Isler and van Schaik 2012; Ross and MacLarnon 2000). Our failure to reject the null hypothesis here might be a result of low statistical power associated with the small sample size. On the other hand, our finding of no clear, statistically detectable effect of allocare

score on duration of breastfeeding may suggest a need for caution when interpreting previous theoretical and empirical work. It is possible that earlier evidence consistent with the alloparental care hypothesis may actually be capturing variation associated with maternal body size and/or with weanling diet quality, rather than access to help per se, since previous studies have not adjusted for such factors when testing the hypothesis. Determining which of these possibilities is correct will require data on reliance on alloparental care for additional populations.

### **2.5.3 Limitations of study**

There are at least four reasons to be cautious when interpreting the findings reported here: 1) the sample is small, 2) the sample is biased towards equatorial populations, 3) we were unable to use the best available method to control for phylogenetic non-independence due to a lack of a reliable phylogeny, and 4) we relied on the untested assumption that high Body Mass Index (BMI) is a reasonable indicator of maternal developmental conditions.

Regarding the first point—sample size—we suggest that the hypotheses should be evaluated further in future using a larger sample once additional high quality breastfeeding, demographic, and socio-ecological data from small-scale populations become available. Until such data are published, our sensitivity analyses, which suggest that the findings are consistent across analytical approaches, may at least partly mitigate this problem (Ader et al. 2008).

With respect to the sample bias issue, while ideally we would have incorporated data from a wider range of human populations had such data been accessible, the predictions tested here do not necessarily require wide geographic coverage. Rather, the LFDY, weanling diet quality, and alloparental care hypotheses predict negative associations between duration of breastfeeding and

maternal adiposity, weanling food quality, and allocare, regardless of underlying or extrinsic causes of variation for the predictors. Again, though, as with the sample size issue, further analyses should be carried out in future to assess whether the patterns observed in our equatorially-biased sample hold in high latitude populations, once reliable data from such populations are available.

Regarding the third point, it is possible that shared ancestry and/or cultural interactions among populations may have inflated the effect sizes we observed in our analyses. More closely related populations are likely to be more similar to one another in both duration of breastfeeding and various ecological factors influencing maternal energetics than more distantly related populations, simply because of their shared history (Mace and Pagel 1994; Mace and Holden 2005; Nunn et al. 2006). As such, the effects we observed of maternal body size and weanling diet quality on duration of breastfeeding in our main analyses could partly reflect these effects of statistical non-independence among the populations in our samples. To partly address this problem, we carried out supplementary analyses in which we controlled for continental group and for linguistic group, and found that doing so had little effect on the results (S Table 3a, 3d, 4a, 4d). However, these approaches do not account for any phylogenetic structure within clusters, so even these more complex models may have produced somewhat inflated estimates (Felsenstein 1985; Nunn et al. 2006). As such, we suggest that, when a phylogenetic tree that represents the populations in our sample becomes available, the predictions tested here should be reevaluated.

The last limitation concerns whether BMI serves to indicate maternal conditions during development. Data from industrialized populations strongly indicates that both short stature and high adiposity relative to height associate positively with relatively poor conditions during development, both within and among socio-economic strata (e.g. Adair 2008; Adair et al. 2013; Godfrey et al. 2010). Additionally, longitudinal data from at least one small-scale population (the Aché of Paraguay) indicates that children born into more challenging conditions are generally born relatively small and then develop greater peripheral fat than other members of their cohorts (Baker et al. 2009). However, in non-human animals, high adiposity may track good, low-risk conditions (Bowman and Lee 1995; Gawlik et al. 2011; Lee et al. 1991). Furthermore, a previous study on life history scheduling and BMI across small-scale human populations suggests that BMI correlates negatively with population density. The authors of the previous study in question assume that high population density indexes high competition for resources and thus relatively poor environmental conditions for development (Gawlik et al. 2011). And, there is also evidence from the Bolivian Tsimane, small-scale forager-horticulturalists, that suggests poor conditions in early childhood are associated with lower BMIs in later childhood/adolescence (Leonard et al. 2015). So, it may be the case that high BMI indicates good rather than poor energetic conditions for mothers in small-scale societies. These conflicting stories regarding the etiology of high BMI deserve further attention when making sense of our findings.

Given the above concern about whether or not the association between BMI and duration of breastfeeding indeed accords with the LFDY hypothesis, we carried out a supplementary analysis. We reasoned that, if the LFDY accounts for the negative association between BMI and duration of breastfeeding in our sample, we should observe a positive effect of height on duration

of breastfeeding and a negative effect of mass-adjusted-for-height. We expected this to be the case because, unlike the predicted but controversial positive association between BMI and the riskiness of the environment, the negative association between the riskiness of an environment and female height is relatively well-established (Migliano 2005; 2010; Migliano et al. 2007; Walker et al. 2006; Walker and Hamilton 2008). So, we assessed the impact of short height and high mass/adiposity on duration of breastfeeding. To this end, we regressed duration of breastfeeding on mass while controlling height, weanling diet quality score and allocare score as well as height while controlling mass, weanling diet quality score and allocare score.

The findings of this follow-up analysis are summarized in Table 2-5. We found that, consistent with the logic of the LFDY hypothesis, duration of breastfeeding is positively associated with height after adjusting for mass, diet quality score, and allocare score. We also found a negative association between duration of breastfeeding and mass after adjusting for the other predictors. These results also suggest that mothers from higher BMI populations that favour investing early and heavily in storage of energy for reproduction (fat) over linear growth schedule relatively fast life histories, consistent with the LFDY hypothesis' predictions.

**Table 2-5: Results of supplemental multivariate linear regression analysis of effects of mass and height on among-population variation in duration of breastfeeding, controlling weanling diet quality score and allocare score.**

Predictor	Estimate	Standard Error	95% CI	One-tailed p
Intercept	-75.984	63.001		0.1366
Adult female body mass	-0.925	0.247		0.0048**
Adult female height	1.074	0.458		0.0288*
Weanling diet quality	-11.682	2.616		0.0022**
Allocare score	-3.806	4.060		0.1924

Model summary	$R^2=0.806$ , adjusted $R^2: 0.695$ , two-tailed model $p=0.0123^*$
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#### 2.5.4 Implications and avenues for future research

The findings of this study have implications for understanding variation in human breastfeeding patterns in relation to contemporary public health and for understanding human evolutionary demography. They also point us towards several avenues for future research.

Our findings highlight three ideas pertaining to public health. First, as with previous investigations of duration of breastfeeding in small-scale populations (e.g. Dettwyler 1987; 2004; Fouts et al. 2005; 2012; Gawlik et al. 2011; Hewlett 1998; Kennedy 2005; Quinlan 2007; Sellen and Smay 2001; Sellen 2001b; Van Esterik 2002; Vitzthum 1994) the data reported here indicate a wide range of variation in duration of breastfeeding. Furthermore, our data suggest that among-population variation in mean duration of breastfeeding is associated with variation in local ecology. These patterns suggest that there is likely no universal optimum duration. Rather, at least from the perspective of mothers, optima shift according to constraints on energy (Dettwyler 2004; Kennedy 2005; Sellen 2007). This plasticity should be considered when developing public health recommendations for infant feeding practices in different locations.

Secondly, the results reported here suggest that maternal body size and adiposity are key factors mediating relationships between life history scheduling – including duration of breastfeeding – and extrinsic ecological risk. In so doing, they accord with several recent findings that indicate tradeoffs between growth and reproduction in humans (e.g. Gawlik et al. 2011; Migliano et al. 2007; Walker et al. 2006; Walker and Hamilton 2008). Evidence from a number of Western,

industrialized populations shows that obesity and adiposity are associated with short durations of breastfeeding (e.g. Baker et al. 2004; 2007; Hauff and Demerath 2012; Hauff et al. 2014). This obesity effect on duration of breastfeeding has previously been assumed to be the result exclusively of proximate, cultural factors such as low body confidence among more adipose women in Western populations (e.g. Hauff and Demerath 2012; Hauff et al. 2014). However, the cross-cultural evidence presented here may indicate that there are evolved reaction norms that underpin the proximate drivers. Such ultimate factors should perhaps be taken into account when developing breastfeeding intervention strategies, for both Western and non-Western populations. Given that the role of infant and young child feeding in inter-generational transmission of obesity risks is becoming increasingly well-known (e.g. Adair et al. 2013; Agostoni 2014; Wells 2014), interventions that target obese mothers may reduce compounded risks across generations.

The final insight pertaining to contemporary public health offered by our results concerns weaning diet. The evidence may suggest that use of animal foods (or possibly other protein- and micronutrient-rich foods) as preferred weaning foods allows mothers or other care-givers to end breastfeeding relatively early and thus channel time and energy into other things (e.g. taking care of and providing for other children or maintaining their own health). As such, there are obvious potential benefits for mothers who utilize high quality, nutrient-dense complementary foods once infants can process them efficiently (~four-six months of age). It remains an open question as to what the costs and benefits to offspring might be, but some evidence tentatively suggests that use of high quality, animal-based weaning foods may be advantageous to them as well, at least if used in moderation and if introduced in a timely fashion (Krebs 2007; Marquis et al. 1998). We do caution, however, that evidence from Western populations suggests that animal foods should

not be given in very high quantities, because infants between 6 and 24 months of age that derive large proportions (e.g. greater than ~10%) of energy from protein are at elevated risk for rapid weight gain and subsequent overweight and obesity (Gunther et al. 2007; Hardwick and Sidnell 2014; Lennox et al. 2013; Michaelsen 2013; Weber et al. 2014). We suggest that future investigations should more rigorously assess the longitudinal effects of use of animal-based weanling diets in non-Western environmental contexts, and develop feeding recommendations accordingly.

Our results offer at least two insights regarding human evolutionary demography. The first is that body size reaction norms likely represent important mediators or even drivers of among population variation in duration of breastfeeding within *Homo sapiens*. Such ontogenetic variation/phenotypic plasticity may contribute to our capacity for flexibility in infant and young child feeding behaviour. Body size plasticity may operate alongside socio-ecological factors that previous theoretical and empirical research has suggested as main drivers of breastfeeding variability, such as alloparenting (e.g. Haig 2010; Hrdy 2009; Hrdy 1999; Quinlan and Quinlan 2008) and maternal workload/ subsistence economy (Levine 1988; McDade and Worthman 1998; Nerlove 1974; Sellen and Smay 2001). If maternal body size mediates between external environmental cues and investment in offspring, and this mediation has consequences for offspring life history strategy, drivers of among-population variation in body size may influence key demographic parameters including fecundity, birth spacing, and fertility. Humans differ substantially from other apes in these parameters, so pinpointing the biological mechanisms involved in their evolution is likely central to understanding how and why humans have been far more demographically successful than the other living primates (Hamilton et al. 2009; Wells and

Stock 2007). That being said, while this study suggests that maternal body size may be a factor of interest, we did not fully probe some of the key assumptions of the LFDY, the hypothesis proposed to account for the links between maternal developmental energetics and duration of breastfeeding. In particular, we did not directly test the assumption that high adult maternal adiposity, measured coarsely by BMI, results from poor energetic conditions during development. Future research should test this assumption when pertinent data regarding the following become available: ecological conditions during mothers' infancies and childhoods (e.g. historical disease prevalence or historical food security measures) and mothers' fat deposition patterns. Furthermore, we should also consider the possibility that other mechanisms instead of or in addition to maternal height and adiposity may mediate relationships between the extra-maternal environment and investment in offspring. Birth and weaning weights of offspring (see, for example, Lee et al. 1991; Wander and Mattison 2013) may also represent intermediaries between environmental cues, life history scheduling, and demographic outcomes. Future research should investigate the roles of other sources of variation in growth, development, and fat deposition in duration of breastfeeding and in fertility.

The second insight regarding human evolutionary demography relates to selection of weaning foods. Bioarchaeological evidence suggests a demographic shift to higher fertility and possibly higher infant mortality was associated with the transition from foraging to farming (e.g. Bentley et al. 1994; Bocquet-Appel 2011). This association has been thought to have been partly enabled by the increased availability of cereal grains as weaning foods with the advent of farming (Sellen and Smay 2001). The logic is that increased availability of energy-dense weaning foods associated with farming may have enabled mothers to reduce the cost of lactation to themselves

while continuing to supply infants with sufficient energy. However, previous work by Sellen and Smay (2001) and by Meehan and Roulette (2013) did not indicate any obvious differences between farmers and hunter-gatherer-fishers regarding access to starchy, energy-dense weaning foods. The evidence reported here also contrasts with the hypothesis that cereal farming increased the availability of weaning foods and increased fertility. Rather, our findings suggest that use of animal-based weaning foods is associated with relatively *shorter* duration of breastfeeding than exclusive reliance on plant-based ones. This pattern is striking because use of animal-based weaning foods is more prevalent among hunter-gatherer-fishers than among farmers (Sellen and Smay 2001). Thus, it appears that increased use of cereals as weaning foods is unlikely to explain the demographic shift associated with the transition to agriculture. Other changes related to maternal energy balance during both development and reproduction – such as increased sedentism and/or altered adult diet composition – are more likely to account for shortened duration of breastfeeding, shorter interbirth intervals, and higher fertility in farmers relative to their foraging predecessors. But what these specific changes may have been and how they may have influenced human lactation biology and demography remain open questions and represent obvious avenues for future inquiry.

### **3 Duration of breastfeeding and maternal energetics in a sample of indigenous Maya women from Guatemala**

### 3.1 Abstract

Human mother-infant pairs vary in duration of breastfeeding, within and among families as well as among populations. Breastfeeding behaviour affects morbidity, mortality, birth spacing, fertility, and wellbeing. Yet, despite these demographic and health effects, the ecological causes of and constraints on this variation remain poorly understood.

Here, we report results of analyses designed to test predictions of four hypotheses from evolutionary ecology regarding variation in duration of breastfeeding, using new data on breastfeeding and ecology from 51 indigenous Maya women from Guatemala and their 283 children. In particular, we evaluated the predictions that shorter durations of breastfeeding would be associated with: shorter maternal height and higher maternal adiposity, with use of animal-based weaning foods, with increased help with feeding infants, and with early parity.

The results were mixed vis-à-vis the predictions. Contrary to the predictions, we found that, on average, taller mothers breastfeed for less time than shorter mothers in this population. Furthermore, we found no statistical evidence that adiposity variation affects variation in duration of breastfeeding. Consistent with expectations, help with infant feeding was associated with relatively shorter durations of breastfeeding. Lastly, as predicted, latter-born infants were breastfed substantially longer than their older sibs.

These findings suggest that mother-infant pairs in this Guatemalan population tailor durations of breastfeeding to some features of local ecology. Access to energetic and time subsidies to infant feeding and opportunity costs of continuing to breastfeed versus investing in a new pregnancy appear to be among the key factors. We suggest that both infant feeding help and changing energetic allocations across the lifespan have implications for understanding human evolutionary demography.

## 3.2 Introduction

### 3.2.1 Background

This paper reports a study that investigated the role of maternal energetic conditions and circumstances in driving variation in the duration of breastfeeding. Specifically, we evaluated predictions derived from four leading evolutionary ecological hypotheses. These hypotheses focus on factors related to maternal energy balance. The energy-related factors are proposed to influence intra- and inter-individual variation in duration of breastfeeding. We use new data concerning durations of breastfeeding obtained from a sample of indigenous, Kakchiquel-speaking Maya women and children from a village in Sololá, Guatemala to evaluate the predictions.

Longer durations of exclusive and all breastfeeding in humans are generally associated with reductions in offspring morbidity and mortality throughout infancy and childhood (Adair et al. 1993; 2009; 2013; Kramer and Kakuma 2007; 2012; but see Marriott et al. 2012). They also appear to be associated with positive somatic and psychological outcomes in later life (Godfrey et al. 2010; Victora et al. 2015). Yet, the length of time for which a human infant is breastfed varies considerably within families as well as among families and populations. Complete cessation of breastfeeding frequently occurs well before its health and growth benefits to offspring have fully dropped off. Short breastfeeding durations can result in poorer offspring survivorship and wellbeing (e.g. Kay et al. 2014; Tenfelde et al. 2012). Understanding why such variation occurs has implications for contemporary public health because it can help identify

causes of variation in rates of infant and young child mortality. Understanding sources of this variation can also help identify causes of variation in prevalence of non-communicable diseases in adults because there is now clear evidence that early life nutrition affects risks of developing metabolic pathologies such as heart disease and diabetes mellitus in adulthood (Godfrey et al. 2010; Lanigan and Singhal 2009; Owen et al. 2005a; 2005b; Sellen 2007). Additionally, variation in duration of breastfeeding is associated with, and has been proposed to be a driver of, variation in length of inter-birth intervals and, ultimately, in fertility (Hamilton et al. 2009; Howie and McNeilly 1982; Kuzawa and Bragg 2012; McNeilly 1993; 1997; Newson 2013; Wells and Stock 2007). Given the influence of breastfeeding duration on fertility, morbidity, and mortality, understanding why duration of breastfeeding varies within and among human mothers is crucial to understanding past and present human evolutionary demography and health.

Data from nonhuman animal studies and previous cross-cultural human studies suggest that variation in duration of lactation/breastfeeding is associated with a number of ecological factors. These factors include extrinsic mortality risk to both juveniles and adults, maternal body size, maternal brain size, offspring brain size, offspring growth rate and weaning weight, and access to energetic subsidy through high quality diet and/or through help with infant provisioning (e.g. Dubman et al. 2012; Gawlik et al. 2011; Hamilton et al. 2011; Isler and van Schaik 2012; Langer 2003; 2008; Lee 1996; Psouni et al. 2012; Quinlan 2007; Quinlan and Quinlan 2008; Ross and MacLarnon 2000). We suggest that several of these factors may also affect duration of breastfeeding within a single human population and even within an individual sib-ship or family. The same logic—described in the section below—that appears to account for the cross-species and

cross-cultural impacts of morbidity and mortality rates, quality of non-breastmilk infant food supplements, maternal condition, and maternal access to help with infant care extends to variation among mother-infant dyads.

### **3.2.2 Hypotheses and predictions**

At least four hypotheses may offer insights into duration of breastfeeding in a single human population: the Live Fast-Die Young (LFDY) hypothesis (Gawlik et al. 2011; Walker et al. 2006; Walker and Hamilton 2008; see also Wells 2014), the weanling diet quality hypothesis (Langer 2003; 2008), the alloparental care hypothesis (Haig 2010; Hrdy 1999; 2007; 2009; Kramer 2010; Kramer and Ellison 2010; Newson and Richerson 2013; Quinlan and Quinlan 2008; Sear and Coall 2011; RW.ERROR - Unable to find reference:613), and the declining opportunity costs (DOC) hypothesis (Bowen et al. 2006; Paul et al. 1993; Pennington and Harpending 1988; Wander and Mattison 2013).

The LFDY hypothesis assumes that there is a reproductive tradeoff between breastfeeding and resumption of ovarian function. That is, mothers in negative energy balance (i.e. mothers using more calories than they consume and thus not storing fat) following the birth of an infant generally suppress ovulation while breastfeeding. Ovulation resumes when mothers return to positive energy balance, and it is more difficult to return to positive energy balance while breastfeeding (e.g. Ellison et al. 1993; Valeggia and Ellison 2004; 2009; Vitzthum 1994). The LFDY hypothesis contends that whether or not mothers favour continued breastfeeding over energetic investment in the conception of an additional child is constrained by maternal mortality risks during development. If death is likely to occur before reproductive senescence, women's

fitness benefits from reproducing as early and as often as possible. As such, mothers who developed under conditions of high mortality should favour a “fast” life history strategy characterized by relatively short periods of growth and development, early ages at first birth, and shorter periods of investment in each offspring. Such a life history schedule is expected to be associated with short, high adiposity maternal phenotypes. The reason for this expectation is that women who developed under adverse conditions are likely to have stopped allocating energy to linear growth early and instead allocated resources to reproduction and the storage of adipose tissue that can be readily mobilized for future reproduction (Hill et al. 2013). With respect to breastfeeding duration, then, the LFDY hypothesis predicts that shorter, fatter-for-height women will breastfeed for relatively shorter durations than taller, less adipose women.

The weanling diet quality hypothesis holds that mothers may partially reduce the costs of extended breastfeeding while continuing to provide adequate nutrition to offspring by feeding them alternatives to breastmilk. Under this hypothesis, these alternative foods must be liquids, solids, or semi-solids from which infants may easily extract high quality nutrients even with short, immature digestive tracts. Protein-dense foods such as meat and other animal products constitute such high quality foods. This hypothesis predicts that infants provided with protein-dense foods may begin and end the weaning process relatively early.

The alloparental care hypothesis is one of the key hypotheses advanced to account for the shorter durations of breastfeeding in humans relative to other large-bodied apes (e.g. Haig 2010; 2009; Hrdy 1999; Newson and Richerson 2013). The human breeding system is much more

cooperative than breeding systems found in most other primates—all human infants receive at least some care from people other than their mothers (Hrdy 2009). The hypothesis argues that non-maternal caregivers can subsidize the energetic costs of infant feeding which would otherwise be borne exclusively by mothers. Mothers who receive help with infant feeding can invest less in infants via breastfeeding without necessarily compromising the supply of energy to infants and instead redirect their time and energy towards other things. The hypothesis predicts that infants who receive energy transfers from non-mothers are likely to breastfeed for less time than infants who do not receive such transfers.

The DOC hypothesis derives from parent-offspring conflict theory. Parent-offspring conflict theory argues that mother's and offspring's interests in offspring survivorship differ because they share only approximately 50% of their genes (Trivers 1974). Because offspring also share only approximately 50% of their genes with the siblings with whom they compete for maternal investment, individual offspring are expected to seek relatively long, intensive investment via breastfeeding. Mothers, in contrast, may benefit from dividing energetic resources among several offspring. That is, mothers are generally expected to end breastfeeding earlier than offspring ideally would like, resulting in weaning conflict (Fouts et al. 2005; McDade and Worthman 1998; McDade 2001; Wells 2003). But, as mothers age, the likelihood of conceiving and producing additional healthy offspring declines. Thus, according to the DOC hypothesis, as mothers near reproductive senescence, their interests in continuing to invest in a given offspring converge with those of the child, since continuing to invest does not come at the cost of a lost opportunity to conceive again. As such, the DOC hypothesis predicts that mothers are likely to

breastfeed latter-born children for longer than they breastfed children produced earlier in their reproductive careers.

### **3.2.3 Justification and aims of study**

In keeping with these hypotheses, previous research generally suggests that, across species, across populations, and possibly across individuals, duration of breastfeeding is associated with variation in pace of maternal life history schedule, in weanling diet quality, and in reliance on alloparental care (Gawlik et al. 2011; Langer 2003; 2008; Quinlan and Quinlan 2008). Additionally, some evidence may be consistent with the prediction that latter-born children are likely to be breastfed for relatively long durations (e.g. Wander and Mattison 2013). But, there are a number of reasons to evaluate predictions of these hypotheses using new data and methods.

To begin with, even though they are not mutually exclusive, these hypotheses have not been evaluated simultaneously in a single analytical framework that controls for likely sources of estimate bias. Integrated, multivariate models are appropriate for evaluating predictions related to life history variables such as duration of breastfeeding, since many factors play into how organisms allocate limited time and energy.

Second, neither the LFDY hypothesis nor the weanling diet quality hypothesis has been formally tested within a single human population, even though their logic extends from the cross-species and cross-population scales to the inter-individual scale. The variables relevant to these hypotheses – maternal body size and choice of weaning foods – are of central importance to both contemporary public health research (Carling et al. 2015; e.g. Kramer and Kakuma 2007; 2012)

and human evolutionary studies (Bogin et al. 2014; e.g. Schwartz 2012). So, it is essential that we assess the effects of these variables on breastfeeding as rigorously and at as many analytical scales and in as many contexts as possible.

Lastly, the currently available evidence regarding the DOC and the alloparental care hypotheses is mixed, possibly due to weaknesses in previous study designs. In the case of alloparental care, some previous studies have used coarse proxies for availability of help, rather than measures of whether mothers actually received help with infant care. In the case of the DOC, the conflicting results may in part be due to the cross-sectional study designs of earlier studies, whereas inter-familial/longitudinal study is likely to provide the most sensitive evaluation of its main prediction. Given these concerns, additional evaluations of the alloparental care and DOC hypotheses are needed.

With these points in mind, we sought to evaluate predictions of these four hypotheses using a single linear mixed effects model that accounts for both intra- and inter-family variation in durations of breastfeeding.

### **3.3 MATERIALS AND METHODS**

#### **3.3.1 Background/ Ethnographic context**

The data were collected as part of a long-term field study entitled Society, Environment and Reproduction (SER). Directed by Dr. Pablo Nepomnaschy, SER's main goal is to investigate the evolutionary ecologies, life histories, and physiologies of the women, men, and children of two

Maya villages located on the northern shore of Lake Atitlan in the Sololá region of Guatemala's Highlands.

The data derive from one of the two villages. This village was chosen based on reports of low contraception use, limited access to biomedical care, and high average parity. These reports suggest predominantly 'natural' fertility in the community. Reports from the other village, in contrast, suggest that nearly half of the women manage their fertility, with varying degrees of success (unpublished data). Situated at ~1500-1600 m above sea level in rugged, mountainous terrain and accessible to other communities only by boat, the study village is home to approximately 1300 indigenous Kakchiquel-speaking Maya people (Dowsett et al. 2002; Nepomnaschy 2005).

The majority (~71%) of the village's people live traditional, near-subsistence-level lifestyles, either owning or leasing land to produce corn, beans, coffee, fruit and vegetables for consumption (unpublished data). Approximately 36% of families surveyed at least occasionally make trips to city markets to sell surplus coffee and corn (unpublished data). Women, men, and children all participate in food production, but unpublished interview data suggest that men are more likely than women or children to do small amounts of farm-related wage labour. All family members contribute to the collection and carrying of large bundles of firewood necessary for heating and cooking. Women and adolescent girls carry out the bulk of the domestic tasks in addition to their food production tasks: they are responsible for cooking, cleaning, textile

production, and sales of food and textiles at the market. Most of the childcare for infants and toddlers is provided by their mothers and older sisters (unpublished data).

The diet in the village is limited, especially with respect to sources of fat, protein, and many micronutrients. Corn constitutes the most important caloric staple, followed distantly by purchased rice and wheat products. Beans, eggs from husbanded chickens, and fish and crustaceans from the lake represent main sources of protein and fat, although animal foods are generally not consumed daily or in large quantities. Fruits and vegetables, many grown in the village and some purchased at market, contribute vitamins and trace elements (unpublished data).

### **3.3.2 Data Collection**

The data were collected using structured interviews with 60 women from the Maya village; we also gathered anthropometric measurements of these women. We selected these 60 women for interview in 2013 because longitudinal data on anthropometry and reproductive history were available for them. All participants provided consent before commencement of the study, and all were made aware in both Spanish and Kakchiquel that they had the right to withdraw from participation at any point during the field season. The data collection protocol was approved by Simon Fraser University's Research Ethics Board (study #: 2012so668).

We used two interviews with each of the participants to gather the relevant data. The first focused on breastfeeding behaviour and on maternal access to/reliance on alloparental care during infancy and early childhood. The second was a broader questionnaire on household composition, household member workloads, maternal reproductive histories, and other

demographic factors. All interviews were carried out in Kakchiquel by six trained, bilingual field assistants from neighbouring villages. Kakchiquel responses were translated on the fly and recorded in Spanish. We subsequently translated these written responses into English. The quality of the Spanish-to-English translations for a random subsample of 12 of these was verified with one of the local field assistants using a standard translation-back translation method.

Anthropometric assessments (height in cm and mass in kg) were collected monthly in 2000 and then in one session in March of 2013. All measures were taken three times during each observation session and averaged. Observations on pregnant women were excluded because this study investigates the effects of women's energetic reserves measured partly via weight and adiposity in non-pregnant women. Women who did not complete all components of anthropometric assessments at least once in each field season were excluded from the final sample.

The final dataset (containing complete measures for all subjects and excluding inexplicable outliers) pertains to 51 mothers and 283 children born to those mothers. The dataset comprises eight variables. These variables are 1) recalled duration of breastfeeding for each child estimated to the nearest month, 2) mother's height, 3) estimated maternal weight around the time of a child's conception, 4) whether or not the mother reported regularly giving her children protein-dense complementary foods, 5) whether or not the mother reported receiving help with infant feeding, 6) whether or not the mother generates and controls some of the family's financial

resources<sup>1</sup> 7) whether or not the child is one of the last two of a mother’s reproductive career<sup>2</sup>, and 8) a meta-variable that we call “traditional-ness”<sup>3</sup>. Further information on how the estimated weight variable and traditional-ness meta-variable were calculated is available in the supplementary materials (Appendix 2, S Text 2.1; and Appendix 2, S Text 2.2 respectively).

### 3.3.3 Analyses

To test the predictions of the hypotheses, we developed a linear mixed effects model that included all measured variables expected to influence variation in duration of breastfeeding (including the aforementioned “traditional-ness” meta-variable to control for outside influences on lifestyle and infant care), and a random intercept effect term for each mother. Recalled duration of breastfeeding for each child constituted the response variable. The fixed effects variables (introduced above) – along with how they relate to each of the four hypotheses and their predictions – are presented in Table 3-1.

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<sup>1</sup> This variable serves as a proxy for work outside the home/farm and thus for need of alloparental care.

<sup>2</sup> Many of the mothers had not yet finished their reproductive careers at the time of data collection. So, to operationalize this variable, we assumed a standard human age at menopause of 45 years (Robson and Wood 2008), then subtracted 2\*(sample mean IBI of ~3.5), yielding a maternal age cutoff of ~38 years. We then scored any children born on or after mothers’ 38<sup>th</sup> birthday as latter-born children.

<sup>3</sup> The traditional-ness meta-variable was designed to capture the extent to which a family has been influenced by sources of information about lifestyle and infant care external to the community. Higher values for traditional-ness indicate households with higher adherence to small-scale, traditional ways of life (e.g. less contraceptive use, less consumption of fortified or other imported foods). It was included to control for possible outside influence on lifestyle and infant care.

**Table 3-1: Summary of fixed effects variables included in linear mixed effects model, the hypotheses to which they relate, and their predicted effects on variation in duration of breastfeeding.**

<b>Fixed effect</b>	<b>Variable type</b>	<b>Hypothesis</b>	<b>Predicted relationship with duration of breastfeeding</b>
Mother's height	Continuous	Live fast-die young	Positive association
Estimate of mother's estimated weight at conception of child	Continuous	Live fast-die young	Negative association
Use of protein-dense foods as preferred weaning foods	Categorical	Weanling diet quality	Negative association
Reliance on help with infant feeding and care	Categorical	Alloparental care	Negative association
Whether mother sells at the market or carries out wage labour	Categorical (proxy)	Alloparental care	Negative association
Child's status as a last or second-to-last born child	Categorical	Declining opportunity costs	Positive association
Traditional-ness of family	Continuous	Control variable	Positive association

### 3.4 RESULTS

Duration of breastfeeding varies substantially both within and among families. The minimum duration of breastfeeding was reported to be 5 months and the maximum 84 months. Variation within some families is nearly as great, with more than one mother reporting breastfeeding ranges from 24 to 84 months. The mean (and standard error) for duration of breastfeeding across all children in the sample was 28.21 (+/-1.54) months.

We present estimated mixed effects in the linear effects model in Table 3-2 and describe the results pertaining to each hypothesis separately. All fixed effects described are adjusted for the effects of the other predictors in the model.

Regarding the LFDY hypothesis, we found that duration of breastfeeding was *negatively* associated with maternal height. Although the one-tailed p-value of this association (0.950) indicates that we cannot reject the null hypothesis of no effect of height on duration of breastfeeding, the 95% confidence intervals for this estimate suggest that the slope of the relationship is very likely to be negative. We also found that duration of breastfeeding was not significantly associated with estimated weight at conception of each child. Neither of the results regarding effects of anthropometric factors on duration of breastfeeding offer support for the predictions of the LFDY hypothesis as currently formulated.

**Table 3-2: Estimated effects of mother's height, estimated maternal mass, weaning food quality, reliance on alloparental care, and declining opportunity costs on variation in duration of breastfeeding.**

<b>Fixed Effect</b>	<b>Estimate</b>	<b>95% Confidence Interval</b>	<b>One-tailed p-value</b>
<b>Intercept</b>	92.920	92.821 to 154.963	0.0019**
<b>Mother's height</b>	-0.469	-0.903 to -0.034	0.9501
<b>Estimated maternal weight at conception of child</b>	0.093	-0.125 to 0.335	0.8566
<b>Use of protein-dense foods as preferred weaning foods</b>	0.171	-5.758 to 5.972	0.9502
<b>Reliance on help with infant feeding and care</b>	-2.649	-5.229 to -0.004	0.0171*
<b>Whether mother sells at the market or carries out wage labour</b>	-5.163	-10.225 to -0.113	0.0168*
<b>Child's status as a last or second-to-last born child</b>	5.585	2.765 to 8.146	0.0001***
<b>Traditional-ness of family</b>	0.635	-1.433 to 2.667	0.2552

With respect to the weaning diet quality hypothesis, we found that duration of breastfeeding was not significantly negatively associated with reported use of high quality, protein-rich weaning foods. As such, these analyses do not provide support for the weaning diet quality hypothesis.

Concerning the alloparental care hypothesis, we did find that duration of breastfeeding was significantly negatively associated with both reported reliance on relatively higher levels of help

with infant feeding and care and reported maternal participation in work away from home. These findings are consistent with the predictions of the hypothesis.

The last test concerns the DOC hypothesis. Duration of breastfeeding was positively associated with the child's status as last or second-to-last-born. This result is consistent with the predictions of the hypothesis.

In sum, the analyses yielded no support for the LFDY and no support for the weanling diet quality hypothesis. The results were consistent with the predictions of the alloparental care hypothesis and the DOC hypothesis.

## **3.5 DISCUSSION**

### **3.5.1 Summary of main findings**

In the study reported here, we evaluated predictions of four hypotheses regarding inter-individual variation in duration of all breastfeeding and maternal energy budgets, using data from 283 Kakchiquel-speaking Maya women from the rural Central Highlands of Guatemala. Specifically, we found tentative evidence that taller mothers actually have shorter durations of breastfeeding than shorter mothers and we found no evidence that relatively adipose mothers have relatively short durations of breastfeeding. Thus, the predictions we derived from the LFDY hypothesis were not supported by the analyses reported here. Next, we found no evidence of an association between shorter durations of breastfeeding and use of higher quality weaning foods from which infants may more easily extract crucial nutrients. Thus, we failed to reject the null hypothesis

that weanling diet quality does not impact duration of breastfeeding in this sample. Third, we found that duration of breastfeeding was negatively associated with both our direct measure of maternal reliance on alloparental care and our proxy for maternal non-domestic workload (assumed to reflect increased *need* for alloparental care). These results are consistent with the predictions of the alloparental care hypothesis. Lastly, the data indicate that duration of breastfeeding was positively associated with child's parity status as a last or second-to-last-born child, consistent with the DOC hypothesis.

### **3.5.2 Limitations of this study**

The findings reported here suggest some variables that drive or constrain variation in a mother's energy budget influence duration of breastfeeding. However, there are a number of reasons for caution when interpreting our results. In particular, the breastfeeding, weanling diet, and alloparental care data all derive from recall-based interviews and the maternal adiposity-for-height estimates derive from relatively simple extrapolations concerning maternal weight change through time. Additionally, our sample was based on convenience, perhaps suggesting a need for caution when generalizing.

The use of maternal recall, in some cases years after the behaviour of interest ended, may or may not be a cause for concern. Evidence from other populations generally suggests that the majority of women recall duration of breastfeeding fairly accurately even decades after weaning, especially if duration of breastfeeding exceeds 13 months (Li et al. 2005; Natland et al. 2012; Promislow et al. 2005), as was the case for almost all of the children in the study population. But, this same body of evidence also suggests a non-trivial minority of women substantially over- or

under-estimate duration of all breastfeeding when re-interviewed. Additionally, recalled durations are prone to “heaping”, a phenomenon in which participants round their estimates to the nearest common fraction (e.g.  $\frac{1}{4}$  or  $\frac{1}{2}$ ) of a year (Beckett et al. 2001; Holland 1987), which can result in a non-continuous distribution of breastfeeding durations. So, it is likely that at least some of the reported durations in our study are inaccurate or at least imprecise. With this possible shortcoming in mind, we carried out two supplementary analyses. In the first, we re-scored the breastfeeding estimates as discrete data points in six month intervals, such that infants that ceased breastfeeding between birth and three months were scored as 1, infants weaned between three months and nine months as two, infants weaned between nine and 15 months as three, infants weaned between 15 and 21 months as four, and so on. We then fit a Poisson distribution. In the second, we used the original, continuous breastfeeding data and fit a generalized estimating equation, which is robust to the mis-specified correlation that may result from recall error and/or heaping (further methods details and results reported in Appendix 2, S Text 2.3). Both of these alternative methods returned results consistent with our main findings. The consistency among the results suggests that our results are reliable, despite some likely reporting error. Nonetheless, future work should focus on obtaining observational or at least prospective interview data on breastfeeding duration and related variables with subsequent follow-ups to assess the level and direction of recall bias in this particular population, further improving our confidence in these results.

Estimates of past maternal weight used in this study also call for caution. We only have two time periods for which observations on maternal weight were recorded – actual maternal weights

immediately prior to pregnancies are not known. The extent to which the estimating curve we used approximates weight changes in individual women cannot be evaluated with only two sets of observations per woman. That being said, the method we used allows us to borrow strength from the curve for the full sample in estimating past weights for individual women. As such, it is currently unclear whether the finding of no effect of estimated weights on duration of breastfeeding may be explained by problems with these estimations. In future field seasons, we will collect additional observations on women's weights, which will allow us to develop and validate a more reliable model of adult weight change trajectories in this population.

Lastly, the issue regarding sample structure deserves further scrutiny. With a view to obtaining longitudinal data, the participating mothers were selected based on prior participation in an earlier set of studies, so we cannot assume that they are necessarily representative of the current adult female population of the village. In fact, our approach systematically excluded women who were not yet child-bearing when the project was initiated in 1999. So, the findings reported here suggest that, for older, more conservative members of the population, maternal energetics influence variation in duration of breastfeeding, but we cannot yet assume these patterns generalize to the full population. We intend in future research to expand our sample to include younger women so that we can better assess the extent to which cohort effects impact durations of breastfeeding in this population.

### 3.5.3 Interpretation of results

Despite the aforementioned potential shortcomings, we suggest that the findings of this study may affect our understanding of the evolutionary ecology of maternal energy budgets and their influences on infant feeding behaviours. We focus particularly on interpreting the associations between duration of breastfeeding and height, reliance on and need for help with infant feeding, and child's parity. We also briefly discuss the negative findings regarding the weanling diet quality and maternal adiposity-for-height hypotheses.

That there may be a negative association between maternal height and duration of breastfeeding is surprising both for theoretical reasons and in light of previous empirical results from cross-cultural studies (Gawlik et al. 2011; Walker et al. 2006; Gawlik and Hochberg 2012). However, the result is not unprecedented in within-population studies. Although previous within-population studies have not explicitly evaluated the LFDY hypothesis as it relates to duration of breastfeeding and maternal height, at least three within-population studies have included mother's height as a covariate in regressions aimed at identifying other factors associated with risk of early breastfeeding cessation. The results of these regressions were mixed. Simondon and Simondon (1998) reported a negative association between the variables of interest among Senegalese women. Petrucci Gigante et al. found (2000), a non-significant, positive trend among Brazilian women. Al-Sahab and colleagues (2008) found a significant positive association in Iranian women. When these findings are added to the results of the present study, the implication is that the assumptions underlying the LFDY hypothesis may not hold in all populations. Rather, factors other than extrinsic morbidity and mortality risk may account for both female height

variation and duration of breastfeeding variation in some populations (e.g. Vercellotti et al. 2014), possibly including the study population.

We suggest cohort effects could contribute to height variation and supply an explanation for a negative association between breastfeeding and height. Recent work suggests that short height results from sped up life histories in some cases, childhood growth faltering in response to cohort-specific shocks or cultural patterns in others, and familial/regional effects in still others (Rosenquist et al. 2015; Rozzi et al. 2015; Sear 2010; Vercellotti et al. 2014). If short height in the Guatemalan Maya sample reflects a cohort-related effect rather than the effect of adaptive fast life histories, then the negative association may mean that shorter mothers belong to a particular cohort that also favours an extended breastfeeding strategy. A supplementary analysis indeed suggests that height associates negatively with age in this sample, although this relationship is not statistically significant (Appendix 2, S Text 2.4). There is also a non-significant trend towards older mothers having longer average breastfeeding durations (Appendix 2.4, S Text 4). As it stands, then, it appears that sped up life histories in response to high-mortality developmental conditions are unlikely to account for breastfeeding variation in the study population, but cohort effects might.

With respect to the negative association between duration of breastfeeding and both amount of help with infant feeding and maternal earning, our findings accord with a large body of theoretical literature and a growing body of empirical evidence. The results reported here are consistent with evidence from other small-scale populations that greater access to help reduces

duration of breastfeeding in contemporary humans (Quinlan et al. 2003; Quinlan and Quinlan 2008). These findings also dovetail with evidence from the biomedical literature on proximate explanations for early cessation of breastfeeding, in which mothers report difficulty with continuing to breastfeed when they return from maternity leave to work outside the home (e.g. Baker and Milligan 2008; Scott et al. 2006; 2014b; Van Esterik and Greiner 1981). It seems likely that the association between return to work and cessation of breastfeeding is at least partly due to the fact that a large portion of infant feeding becomes the responsibility of other caregivers under such circumstances. Thus, our findings regarding help with infant feeding and/or earning power are consistent with the view that reliance on alloparental care facilitates relatively early cessation of breastfeeding. This new evidence, especially when combined with the mounting evidence from other studies, is in keeping with a scenario in which reductions in durations of human breastfeeding and birth spacing co-evolved with increased reliance on cooperative infant care.

The finding that duration of breastfeeding is positively associated with last- and second-to-last-born status of a child is consistent with expectations derived from life history theory (Stearns 1976; 1992) and parent-offspring conflict theory (Trivers 1974). As maternal opportunities to conceive healthy subsequent offspring decrease through time (ovarian reserves deplete and quality of oocytes and follicles degrade with age), mother and offspring interests (and therefore duration of breastfeeding optima) are more likely to converge near those of the offspring (Ellison et al. 1993; Pennington and Harpending 1988). The data from the study population support this prediction. Average duration of breastfeeding for children whose mothers have reached or are

reaching reproductive senescence is ~34 months, whereas average duration of breastfeeding for children of earlier parity is only ~27 months.

While this pattern is compelling in its consistency with theoretical expectations, empirically, there is very little comparative evidence from other natural fertility populations that maternal investment via lactation increases over a mother's reproductive career. Only two previous studies evaluated the DOC with a focus on breastfeeding duration. One of these detected the predicted effect (Wander and Mattison 2013) but the other did not (Quinlan et al. 2003). Both studies assessed the impacts of maternal age and parity on this duration cross-sectionally. This cross-sectional approach is far less sensitive than the longitudinal one used in the present study and is therefore less likely to detect the effect predicted by the DOC of declining maternal investment over the reproductive lifespan. Thus, the one null finding may be accounted for by the study's cross-sectional design. Taking the available evidence together, then, it appears that duration of breastfeeding may increase as opportunity costs of breastfeeding decline. That said, there is an obvious need for additional evaluation of this prediction in other natural fertility populations before we can be confident in the robustness and generalizability of this pattern.

We did not find any statistically significant effect of estimated maternal fatness prior to the conception of a given child on duration of breastfeeding or of reported weanling diet quality on duration of breastfeeding. In light of previous evidence, especially with respect to maternal fatness, a finding of no discernable effect is somewhat surprising. A recent cross-cultural study on natural fertility populations found that women from populations with relatively high mean

adiposity measures have relatively short mean durations of breastfeeding (Gawlik et al. 2011). Additionally, there is evidence from the biomedical literature on women from large-scale societies that indicates that overweight and obese women are less likely to initiate breastfeeding, have more difficulty breastfeeding, introduce supplements to breastfeeding earlier, and end all breastfeeding earlier than normal weight women (e.g. Amir and Donath 2007; Baker et al. 2004; 2007; Li et al. 2003). We cannot yet rule out shortcomings of our weight estimation methods as an explanation for our null findings. But, if future research suggests weight estimation error does not account for them, it may be that, in this study population, other factors are more important than adiposity in determining length of maternal investment via lactation. We also suspect that other factors may be more important than selection of weaning foods in this population. Our data suggest that child's parity status and mother's reliance on alloparental care represent such key factors. Maternal height and the constraints it places on maternal energy budget may also have an impact.

#### **3.5.4 Implications and significance of study**

This research offers insights pertaining to the evolution and ecology of variation in duration of breastfeeding in humans, and may have implications for understanding human demography. Specifically, we found that duration of breastfeeding may be negatively associated with maternal height in our sample. Although it is certainly not clear that this pattern is common across small-scale populations, the result does hint that a mother's own growth and development may affect how she allocates energy to reproduction once she reaches adulthood. If supported by future investigations in other small-scale populations, this finding may offer an additional line of evidence (along side, for example, biomolecular methods, see review by Jay 2009) useful for

reconstructing breastfeeding behaviour in past human populations for which adult female heights can be estimated.

More importantly, we found evidence that greater access to and need for help with infant feeding was associated with reduced duration of breastfeeding. This finding suggests that access to alloparental care relaxes the constraints on mothers' energy budgets and frees them to allocate energy to purposes other than lactation. This constraint relaxation associated with cooperative infant care may have had a profound impact on human fertility vis-à-vis the fertility of other apes. As a number of other researchers have suggested, reliance on alloparental care may have been a crucial factor facilitating the development of short birth spacing and high fertility in humans (e.g. Hrdy 1999; 2009; Newson 2013).

Lastly, our finding regarding the positive association between duration of breastfeeding and latter born status may allow us to identify breastfeeding optima for infants in the ecological setting of the Guatemalan Central Highlands. In general, mothers have a substantial advantage over offspring when parent-offspring conflict occurs outside of the womb (Kilner and Hinde 2008). So, it is likely that much of what we observe with respect to breastfeeding behaviour reflects mothers asserting their interests. However, if the assumptions of the declining opportunity costs hypothesis are correct, duration of breastfeeding for last-born children probably reflects infant preferences. Paying attention to how long latter born children choose to breastfeed may inform us about the breastfeeding strategies most beneficial to infant health and wellbeing in a particular ecological context, and may also allow us to assess how infant optima differ from maternal ones. Ultimately, this and similar observations in other ecologies may offer

insights into how mother-infant pairs negotiate resource allocation in the face of both risks and opportunities.

## **4 Breastfeeding durations are associated with culture and modernization in indigenous Maya women from Guatemala**

## 4.1 ABSTRACT

The duration of the period of exclusive breastfeeding (exBF) and the total length of all breastfeeding (allBF) vary substantially within and among contemporary human populations. Ecological factors at least partly drive this variation. However, the mechanisms by which durations of breastfeeding shift in response to changes in ecology are currently poorly understood. In theory, ecology may affect breastfeeding behaviour via individual plasticity (e.g. endocrinological/physiological processes, trial-and-error learning) or through cultural processes (i.e. as a result of socially transmitted information). At the moment, however, we lack data on the relative importance of these mechanisms. With this mind, we designed a study that assesses the impact of rapid socio-ecological change on the duration of exBF and the duration of allBF. The study also explored whether there is evidence that individual plasticity and/or mode of cultural learning accounts for variation among children in durations of exBF and allBF.

We collected data from 82 women and their 419 children in a population of indigenous Maya people, living in two Guatemalan villages. This population is currently undergoing an economic and fertility transition. We used linear mixed models to compare the breastfeeding durations of children from more modernized households with those of less modernized households. Household modern-ness was measured via mothers' self reports on the extent to which a household diverged from traditional economic, health care, and dietary practices. To assess whether cultural learning affects duration of exBF and/or duration of allBF, the conservativeness of the source(s) from which a mother reported learning about how to feed infants and young children was included as a covariate in the models.

We found that duration of exBF was associated with mode of cultural learning. Mothers who learned about infant and young child feeding from conservative sources were more likely to cease exBF relatively late, generally at ~six months of age. Duration of exBF was not associated with household modern-ness. In contrast, duration of allBF was associated with household modern-ness but was not associated with mode of cultural learning. These findings suggest that duration of exBF may be more culturally conserved and less individually responsive to socio-ecological change than duration of allBF and vice-versa. This in turn suggests that the two durations may respond to changing ecological conditions via different mechanisms (cultural learning versus individual plasticity). The impact of social learning on duration of exBF has implications for understanding breastfeeding behaviours in our ancestors, as does the impact of socio-ecological conditions on duration of allBF. Understanding the mechanisms through which breastfeeding patterns change in response to changing socio-ecology can also inform the development of contemporary public health policy regarding infant feeding.

## 4.2 INTRODUCTION

In this paper, we investigate the impact of cultural and socio-ecological factors that affect when the period of exclusive breastfeeding (exBF) ends and when complete cessation of all breastfeeding (allBF) occurs. We do so using data from a population of indigenous Maya women living in two villages in the Sololá region of the Guatemalan Central Highlands. The socio-ecology of this population, especially with respect to economy and demography, is currently undergoing substantial changes (Berry 2010). In particular, the economy is shifting from predominantly subsistence agriculture to steadily increasing participation in wage labour and market exchange. The number of female earners and female-headed households, particularly in one of the villages, also appears to be increasing. A small number of these women are beginning to manage their fertility biomedically. These changes are likely primarily driven by the presence of growing numbers of people from North American and Europe visiting the area as tourists, buying and leasing property in the region, and financing economic development in and near the villages (Berry 2010).

Evidence suggests that demographic and economic changes such as the ones affecting the study population are associated with changes in breastfeeding duration in a number of Latin American indigenous populations (e.g. Veile et al. 2014; Veile and Kramer 2015). However, it is currently unclear whether these kinds of changes generally result in shorter or in longer durations of exBF and/or of allBF. The directions of the effects of modernization on duration of breastfeeding seem to vary by context (González de Cossio et al. 2013; e.g. Veile et al. 2014; Veile and Kramer

2015). Even less clear are the mechanisms by which the duration of exBF and the duration of allBF respond to changing socio-ecological conditions (Snopkowski and Kaplan 2014). One possibility is that mother-infant dyads adjust breastfeeding behaviour to ecology through individual physiological mechanisms and/or individual learning (e.g. the underlying assumptions of these studies: Gawlik et al. 2011; Quinlan 2007; Quinlan and Quinlan 2008). Another possibility is that mothers adjust their breastfeeding behaviour to ecology in part or even primarily through cultural information acquired from other members of their families and/or communities. (Dettwyler 2004; Fouts et al. 2012; Hadley et al. 2010b; McDade and Worthman 1998; Meehan and Roulette 2013; Newson 2013; Schafer et al. 2015; Snopkowski and Kaplan 2014; Stewart et al. 2013; Wells 2006).

#### **4.2.1 Background**

In this section, we outline the reasons to study variation in the duration of exBF and the duration of allBF. We also introduce some of the key theoretical tools used to examine why these durations may vary. Understanding variation in the duration of exBF and the duration of allBF as well as how socio-ecology influences this variation constitute important foci of study for two main reasons. First, the duration of breastfeeding exclusivity and the duration of continued breastfeeding impact infant health (Roberts et al. 2013). Second, variation in these durations affects life history and demography (Hamilton et al. 2009; Harris and Vitzthum 2013; Hochberg 2011; Newson 2013; Vitzthum 2009; 1994; Wells and Stock 2007).

#### *4.2.1.1 Infant health*

Breastfeeding represents a set of behavioural and physiological processes during which mothers transfer energy, nutrients, immune primers, growth factors, and microbial communities to infants (Allen-Blevins et al. 2015; Hinde and German 2012; Labbok et al. 2004; McDade and Worthman 1998). Ending exBF via the introduction of non-breastmilk liquids, semi-solids, and/or solids disrupts and reconfigures these patterns of transfer. Ending allBF reflects a complete termination of direct somatic transfers from mother to offspring. Immature infant dentition and digestive systems (including commensal microbes) cannot efficiently process solids or semi-solids (Langer 2003; Palmer et al. 2007; Sellen 2007). Under-developed infant immune systems are poorly equipped to respond to food- or water-borne pathogens introduced through supplementation of infant diets with non-breastmilk foods, especially in the first four to six months of post-natal life (McDade and Worthman 1998; McDade 2003).

Not surprisingly, then, relatively short duration of exBF is associated with increased risk of infant infection, morbidity, and mortality (Kramer and Kakuma 2012; Lamberti et al. 2011). It is also associated with increased risk of developing an adult phenotype prone to obesity and metabolic complications (Schack-Nielsen et al. 2010). Very long durations of exBF (much beyond ~six months of age) can result in growth faltering and micronutrient deficiency (Caulfield et al. 1999; Dewey 2001).

After the period of exBF ends and the nutritional needs of infant growth begin to outstrip what can be provided through breastmilk alone (at ~six months of age), continuing breastfeeding for at

least an additional 6-18 months confers a number of benefits to infants.<sup>4</sup> In particular, extended breastfeeding continues to provide infants with nutrition and passive immunity (Jones et al. 2003; Labbok et al. 2004). It also facilitates the development of healthy oral and gut microbiomes (Palmer et al. 2007; Thompson et al. 2011; Thompson 2012). Relatively long duration of allBF may also be associated with increased immune competence (Mortensen and Tawia 2013), higher capacity for formation of secure psychological and emotional attachments (Kim et al. 2011; Tasnim 2015), and improved cognitive performance (Tasnim 2015; Victora et al. 2015) as offspring mature.

#### *4.2.1.2 Parent-offspring conflict and demography*

In addition to their impacts on infant health, the duration of exBF and the duration of allBF affect how mothers and children allocate their limited time and energy resources to different aspects of the life cycle (Hawkes and Paine 2006). Maternal and offspring fitness interests in how much energetic investment an infant should receive do not fully align because of asymmetries in genetic relatedness (Trivers 1974). Mothers are equally closely related to each of their offspring but individual offspring are (obviously) more closely related to themselves than to their siblings. Given these patterns of genetic relatedness, maternal fitness most often benefits from equitable division of time and energy resources among children. Infant fitness most often benefits from investment beyond what mothers are generally willing to provide to an individual child. This difference between the maternal and infant perspectives on energy allocation can result in physiological and/or behavioural conflict between mothers and offspring (Trivers 1974).

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<sup>4</sup> Continued breastfeeding after ~six months of age should be combined with safe and adequate non-breastmilk foods to reduce risks of stunting, wasting, and other forms of malnutrition (Labbok et al. 2004)

At the proximate level, breastfeeding inhibits the ovarian function of mothers in negative energy balance, preventing them from redirecting time and energy to the conception and support of additional offspring (Valeggia and Ellison 2004; Valeggia and Ellison 2009; Worthman et al. 1993). So, mothers may seek to reduce their direct energetic costs of feeding infants from the breast by introducing non-breastmilk supplements (Haig and Wharton 2003; McDade 2001) and/or by tapering off continued breastfeeding once returns on lactational investment in infant survivorship have diminished but before returns in infant quality have been fully realized (Trivers 1974). Infants may meet maternal attempts to redirect energy towards their future siblings with fussing, crying, tantrums, or other behaviours used to elicit prolonged breastfeeding (Fouts et al. 2005; Wells 2003). The outcomes of such conflicts – whether or not an individual infant continues to receive heavy maternal investment via breastfeeding – affects major demographic parameters including interbirth intervals and completed fertility (Harris and Vitzthum 2013; Hochberg 2011; 2009; Vitzthum 1994). On average, mothers that successfully wean early, all else equal, tend to have more children than mothers that prolong breastfeeding (Bongaarts and Potter 2013; Vitzthum 2008). In sum, duration of exBF and duration of allBF influence population dynamics (Hamilton et al. 2009; Wells and Stock 2007).

#### *4.2.1.3 Socio-ecological/cultural correlates of breastfeeding durations*

The duration of exBF and especially the duration of allBF vary substantially both within and among human populations (Sellen 2001b). Given the aforementioned impacts of breastfeeding and weaning strategies on morbidity, mortality, and fertility and thus on differential survival and reproduction, it is likely that these strategies have been subject to strong selection over our evolutionary history (McDade 2001; Sellen 2009). In keeping with this reasoning, there is at

least some evidence suggesting that both duration of exBF and duration of allBF are related to underlying variation in the maternal expression of a gene implicated in crucial aspects of human lactation biology (Jonas et al. 2013; see also Colodro-Conde et al. 2013). We can thus infer from the observed variability in the timing of key breastfeeding milestones that selection has favoured high levels of behavioural and physiological plasticity and perhaps an important role for cultural learning in approaches to infant feeding.

The evidence available suggests three things consistent with this inference about adaptive plasticity in breastfeeding. First, both milestones are influenced by variation in cultural models of infancy and by culturally transmitted advice concerning infant feeding (Demirtas et al. 2012; Fouts et al. 2012; Hadley et al. 2010b; Hewlett 1998; Veile and Kramer 2015; Wells 2006; Wren et al. 2015). That is, the extent to which a group of people conceive of infants as autonomous actors versus subjects of parental obedience seems to affect whether or not mothers closely follow their baby's cues about breastfeeding needs and wants (Fouts et al. 2012). Parents from populations that do not follow this baby-led approach to breastfeeding appear to rely heavily on parent-centered cultural guidelines on when and how to introduce non-breastmilk foods and when to terminate breastfeeding (e.g. Demirtas et al. 2012; Fouts et al. 2012; Schafer et al. 2015).

Second, duration of exBF may respond to variation in subsistence strategy and maternal nondomestic workload. Specifically, some evidence suggests that infants from subsistence farming and herding populations, especially those in which women carry out much of the

farming labour, end exBF earlier than infants from foraging populations (Levine 1988; Nerlove 1974; Sellen and Smay 2001).

Third, the duration of allBF may be affected by a number of ecological factors. In particular, the duration of allBF may be shortest in environments with either very low or very high disease risk and longest in environments with moderate disease risk (Quinlan 2007). Mothers that receive large amounts of help with infant care may have shorter durations of allBF than mothers that receive less help (Quinlan et al. 2003; Quinlan and Quinlan 2008). Smaller infants may not be breastfed for as long as their larger counterparts (Wander and Mattison 2013). And, variation in the duration of allBF is associated with variation in maternal condition (e.g. adiposity, reproductive career stage), such that younger, fatter-for-height mothers terminate breastfeeding earlier than older, thinner-for-height mothers (Gawlik et al. 2011; Mckerracher et al. in prep.; Wander and Mattison 2013).

#### **4.2.2 Objectives: Investigating mechanisms of change in durations of breastfeeding**

While it appears that duration of exBF and duration of allBF may vary with ecological cues and cultural guidelines, as suggested above, we do not yet understand through which mechanisms these milestones respond to ecological (including cultural, economic, and demographic) changes. Furthermore, we have little understanding of whether the duration of exBF and the duration of allBF respond to socio-ecological changes in similar ways, or if there are key differences between the two variables that affect how they each respond to changing socio-ecology. The few studies to date directly relevant to these questions have produced conflicting and often difficult-to-interpret results, with both durations increasing in some populations exposed to rapid

ecological changes, decreasing in other such populations and, in still others, responding in opposite ways (González de Cossio et al. 2013; Veile et al. 2014; Veile and Kramer 2015).

With the foregoing in mind, we have three objectives in this paper. The first is to describe breastfeeding behaviours in the focal population. The people of the population's two villages (designated here as Villages "A" and "B" to preserve the identities of the communities) are, as mentioned above, becoming more reliant on participation in the market economy and are in the process of changing the extent to which they manage health and fertility via biomedical means. Hereafter, we call these changes "modernization." We do so for the sake of convenience. We do not intend to imply that lifeways based on subsistence agriculture and natural fertility are in some way lesser. Modernization is affecting Village A much more than Village B. Our second aim is to assess the extent to which modernization impacts the duration of exBF and the duration of allBF. Our third objective is to investigate the effects of culture and social learning strategies on breastfeeding behaviours. We include this last aim to shed light on the mechanisms through which variation in the duration of exBF and the duration of allBF become associated with variation in socio-ecological factors.

## **4.3 MATERIALS AND METHODS**

### **4.3.1 Data collection**

The data were collected between Jan. 1 and March 10 of 2013. These data pertain to 82 women and their 419 children from the two rural villages in the Sololá region of the Guatemalan Central Highlands. The dataset comprises information collected on duration of exBF, duration of allBF, 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 selection of weaning foods.

With the exception of the anthropometric measures, the data were collected via two sets of recall-based, structured interviews with mothers, carried out by trained, local research assistants. The research assistants administered the interviews in the local Kakchiquel Mayan dialect, and then reported the responses in Spanish. Subsequently, the responses were translated from Spanish to English in preparation for coding and analysis. The translations were verified by back-translating a sub-sample of approximately ten per cent. Anthropometric data – height (cm), mass (Kg), and upper arm skinfold thickness (mm) – 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.

The raw data generated through the interviews and anthropometric measurements were used to create the following variables used in our main analyses: 1) the duration of exBF, 2) the duration of allBF, 3) modernization to traditional-ness score (hereafter ModTrad Score), 4) mode of cultural learning, 5) village, 6) parity status, and 7) access to help with infant feeding. The variables and how they were collated are described in detail below.

ExBF: We used recalled number of months for which each child consumed only breastmilk to estimate exBF. Interviewees were instructed that introduction of any liquids or solids, including formula, animal milk, or water, would indicate an end of exBF. Women generally reported these values in months, but a few women with children that ended exBF after more than one year reported these values in compound fractions of years. In such cases, we converted reported

values in years into estimates in months. These raw values were positively skewed, so we used a log 10 transform to better approximate 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 (R Development Core Team 2014).

AllBF: This variable was estimated using recalled number of months for which each child was breastfed, including occasional feeds and comfort feeds. Some women initially reported these values in months but many women reported values in years and/or fractions of years. Again, values reported in years were converted into months. These values were also positively skewed, so we again used a log 10 transform to better approximate a normal distribution.

ModTrad Score: We devised this variable to characterize the extent to which each woman and her family has been influenced by any norms and behaviours likely related to increased market integration that have been incorporated into her community in recent decades. ModTrad score encompasses eight continuous and factor variables pertaining to demography, anthropometry, diet, and the woman's control of a share of household resources. 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; 2012b; Wells 2010). The contributing variables and descriptions of the variable scorings are presented in Table 4-1. Details concerning the justification for variable inclusion are available in the supplement (see S Text 3.1).

Adding these scores together resulted in each family's receiving a ModTrad score of between two and nine. Two represents the most modernized, market-integrated households and nine

**Table 4-1: Subsidiary variables used in calculating ModTrad Score.**

Type	Variable	Scoring (+1 per variable if more traditional, 0 if more modernized)
<b>Demography</b>	Fertility Status	0 if contraception reported and all IBIs less than $2\bar{x}$ IBIs ( $2 \times 3.14 \text{ yrs} = 6.28 \text{ yrs}$ ) during fertile years (15-45), 1 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	0 if a woman began her reproductive career (first gave birth) after 1996, 1 if reproductive career began prior to or during 1996.
	Under five mortality	0 if # of reported infant and child deaths/ #of births < 0.2, 1 if # of reported infant and child deaths/ #of births $\geq 0.2$ <sup>1</sup>
<b>Anthropometry</b>	Body Mass Index (BMI)	0 if over standard overweight threshold of 25, 1 if below this threshold
	Upper arm skinfold thickness	0 if over $\geq \bar{x}$ (10.15 mm), 1 if $< \bar{x}$ (10.15 mm)
<b>Weanling diet</b>	Use of protein and micronutrient supplement porridge (Incaparina) in infant diet	0 if supplement, recommended by Guatemalan government representatives, used; 1 if not used.
	Use of naturally occurring protein- and micronutrient-dense foods in infant diet	0 if biomedically recommended but expensive foods such as beans, eggs, fish, meat used; 1 if not used.
	Use of stimulants in infant diet	0 if coffee or tea not used, consistent with biomedical recommendations, as weaning food; 1 if used as preferred weaning food
<b>Participation in Market Economy</b>	Woman's participation in sale of products or labour	0 if woman reports regularly doing paid work or in selling products at market; 1 if she does not.
<sup>1</sup> 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.		

represents the most traditional ones. This score represents the final ModTrad score used in our models reported in the main text. In the supplement, we report sensitivity analyses in which we evaluate the effects of varying the composition of ModTrad score (see S Text 3.2).

Mode of cultural learning was 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 reported knowledge sources that were likely to provide culturally normative or conservative advice (i.e. older female family members, older female friends/neighbours/members of the community, or from indigenous midwives) 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 that reported teaching themselves, learning from their infants and young children, learning through practice, learning from 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 three control variables in the analysis pertaining to allBF – "village", "parity status", and "access to help with infant feeding". We included one control variable – "village" – in the analysis pertaining to exBF. Parity status and access to help with infant feeding were revealed by other work we have in preparation to impact allBF in this population (McKerracher et al. in prepb). Village was included because there are differences between the two villages in layout<sup>5</sup> and in access to

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<sup>5</sup> Houses in Village A are grouped tightly together, with neighbours frequently sharing walls or yards; there are no crop fields within this village (Berry 2010, p. 24). Houses in Village B are spaced more widely, and small clusters of houses are separated from one another by crop fields.

biomedical health care<sup>6</sup> that we reasoned could influence the flow of information on how to breastfeed, which in turn could impact both exBF and allBF. Village was scored as 0 or 1 to represent A or B, respectively. Parity status was scored as a dummy variable in which 1 represents a latter born child (a child last or second-to-last in birth order if his/her mother was age 38 or greater when he/she was born) and 0 represents all other children. 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” with providing, preparing, or giving food or drinks to infants, was scored as 0 for women who reported no help, 1 for women who reported a little help with some infants, and 2 for women who reported a lot of help.

#### 4.3.2 Analyses

We began by visually inspecting histograms and tabulating counts of convergence on a single value to explore the extent to which women agreed about duration of exBF and duration of allBF. We did so on the assumption that the most frequently reported values represent cultural norms regarding how long these durations should be.

Next, we investigated the effects of socio-economic change and cultural transmission of infant feeding behaviour on breastfeeding behaviours. To this end, we used a linear mixed effects approach to estimate the effects of both ModTrad score and mode of cultural learning on exBF and allBF. Because it seemed likely that there are woman-specific effects on breastfeeding durations and given that each woman provided data pertaining to multiple children, we added a

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<sup>6</sup> At the time of data collection, the health post in Village A was staffed five days/week by at least one doctor, two or three nurses, and an administrative assistant. The relatively small health post in Village B was only open two mornings/week and was generally only staffed by two nurses. A doctor visited the post only sporadically.

woman-specific random intercept term. We also controlled for the effects of village, parity status, and access to help with infant feeding in the allBF model and for village in the exBF model. These analyses were implemented using the nlme package of R (Pinheiro et al. 2015).

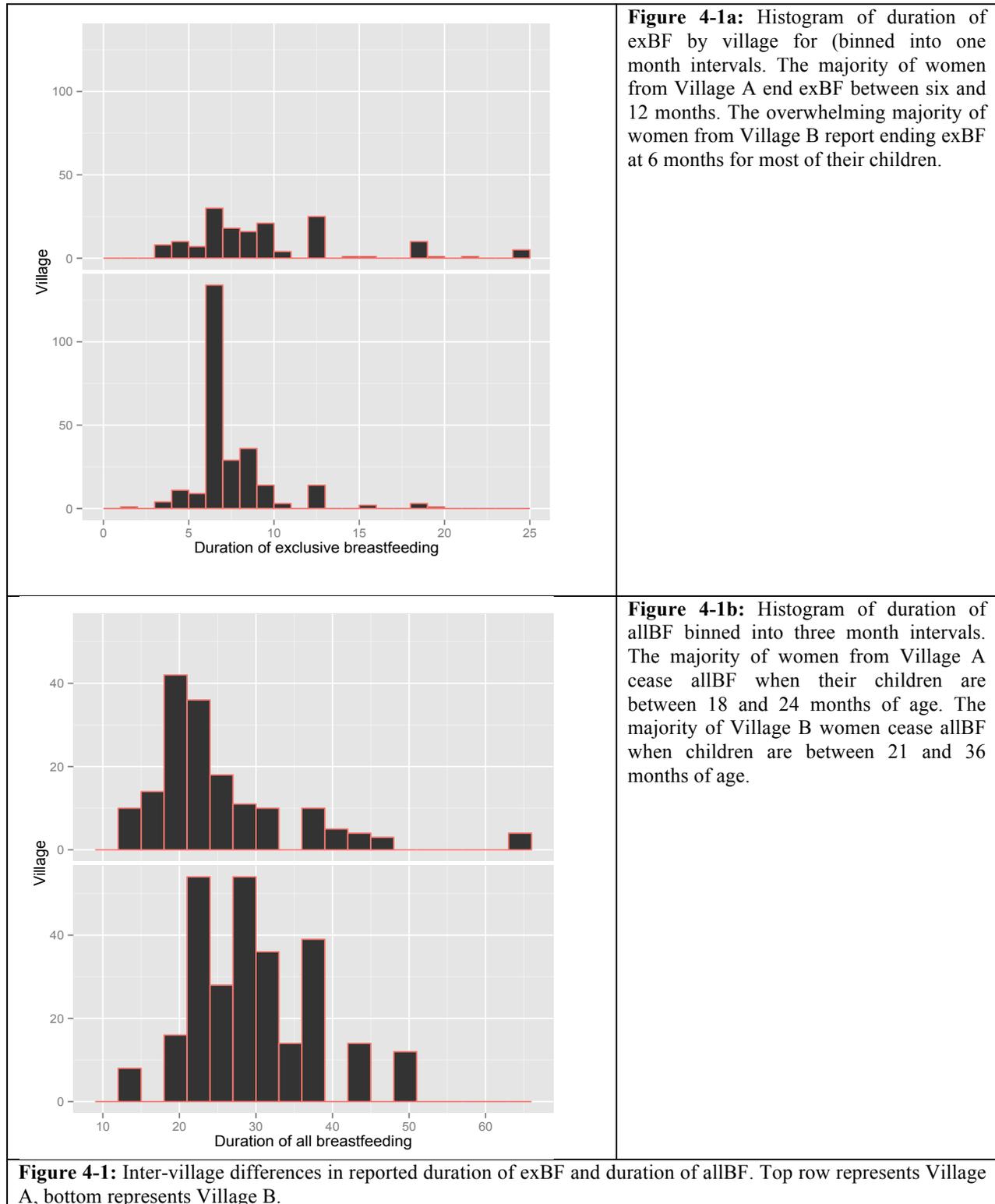
#### 4.4 RESULTS

Descriptive statistics for the duration of exBF and the duration of allBF are summarized in Figure 4-1 and Tables 4-2 and 4-3. After excluding a substantial outlier of 60 months,<sup>7</sup> exBF for the full sample ranged from one month to 24 months, with a mean of ~six months. AllBF ranged from six months to 84 months in the full sample, with a mean of ~28 months.

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<sup>7</sup> The extreme outlier was excluded from analyses because it is probably biologically impossible for a human child to survive on breastmilk alone for 60 months (Kramer and Kakuma 2012, McDade and Worthman 1998). A member of our team re-interviewed the child's mother to probe her about this estimate and received the same response of ~five years of exclusive breastfeeding. Nevertheless, we think the data point likely represents an error in recall.

**Figure 4-1**



**Table 4-2: Descriptive statistics for duration of exBF. Unit for all values is months.**

Sample	Min	Mean	Median	Mode	Max
<b>Full sample</b>	1	7.8	6	6	24
<b>Village A</b>	3	9.1	8	6	24
<b>Village B</b>	1	7.0	6	6	19

**Table 4-3: Descriptive statistics for duration of allBF. Unit for all values is months.**

Sample	Min	Mean	Median	Mode	Max
<b>Full sample</b>	6	27.57	24	24	84
<b>Village A</b>	6	23.5	20	24	72
<b>Village B</b>	8	29.8	24	24	84

With regard to consensus/agreement among women in reported values for exBF and allBF, we found that 163 out of 419 (38.9%) children for which we have data were reported to have been exclusively breastfed for ~six months, the modal value for the sample. This tendency to report exBF durations of ~six months was especially prevalent among Village B mothers, who reported that 133 of their 260 children (51.2%) had exBF values that reflected the sample mode; only 30 out of 158 children (19.0%) from Village A were reported to have modal exBF values. There was lower consensus with regard to allBF: 113 out of 419 children (27.0%) were reported to have stopped breastfeeding at or near the sample mode of 24 months. The differences in consensus in allBF between the two villages were minor relative to the exBF differences, with 37 out of 158 (23.4%) mother-infant pairs from Village A reported to have modal allBF values and with 76 out of 259 (29.3%) mother-infant pairs from Village B reported to have modal allBF values.

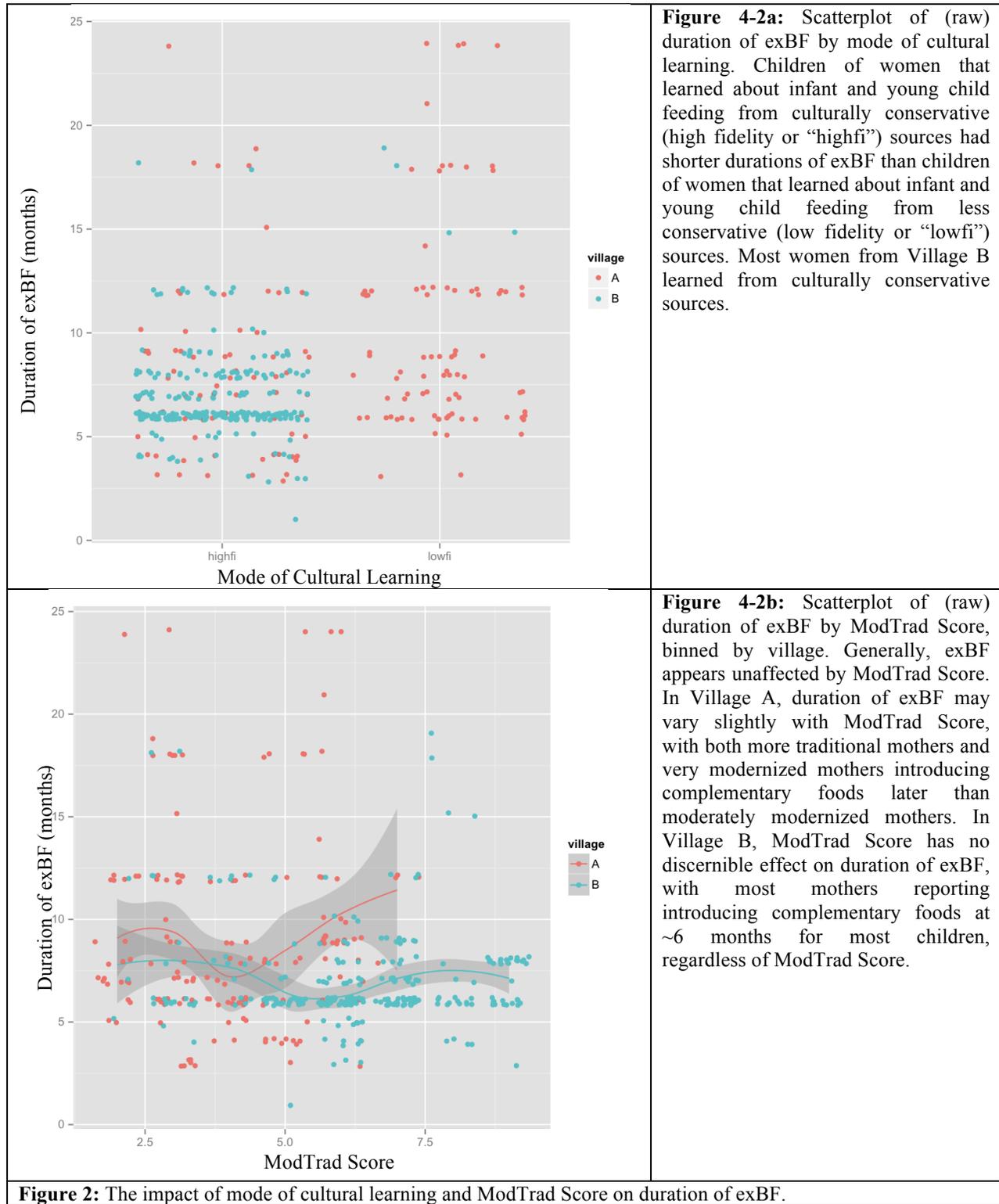
We present the main results regarding exBF in relation to ModTrad score and mode of cultural learning in Table 4-4 and Figure 4-2. We found that mode of cultural learning is the only

significant predictor of variation in exBF, with mothers who learned about infant and young child feeding from low fidelity sources reporting introduction of complementary foods later than mothers who learned from high fidelity sources. We found no evidence of an association between exBF and ModTrad score.

**Table 4-4: Model summaries for analyses of effects of modernization (ModTrad Score) and mode of cultural learning on log 10 duration of exBF.**

Fixed effect	Estimate	Standard Error	95% CI	One-sided p-value
<b>Intercept</b>	0.839	0.039	0.738 to 0.940	0.000 <sup>****</sup>
<b>ModTrad Score</b>	0.008	0.018	-0.027 to 0.043	0.325
<b>Mode of cultural learning</b>	0.142	0.045	0.054 to 0.231	0.001 <sup>**</sup>
<b>Village</b>	-0.020	0.046	-0.110 to 0.070	0.655

**Figure 4-2**



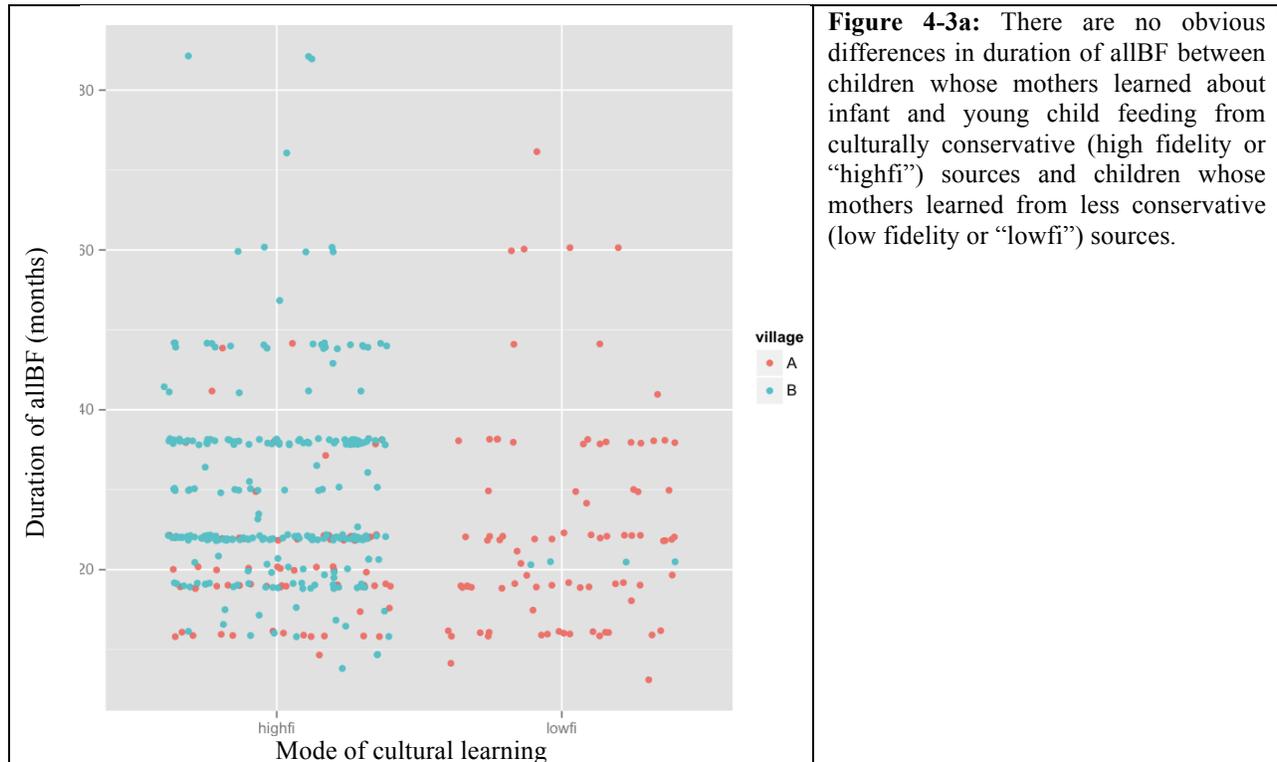
**Figure 2:** The impact of mode of cultural learning and ModTrad Score on duration of exBF.

The main results pertaining to allBF in relation to ModTrad score and mode of cultural learning are presented in Table 4-5 and Figure 4-3. We found that ModTrad score is the only significant predictor of variation in allBF, with more traditional mothers breastfeeding longer. We found no evidence that allBF is associated with mode of cultural learning.

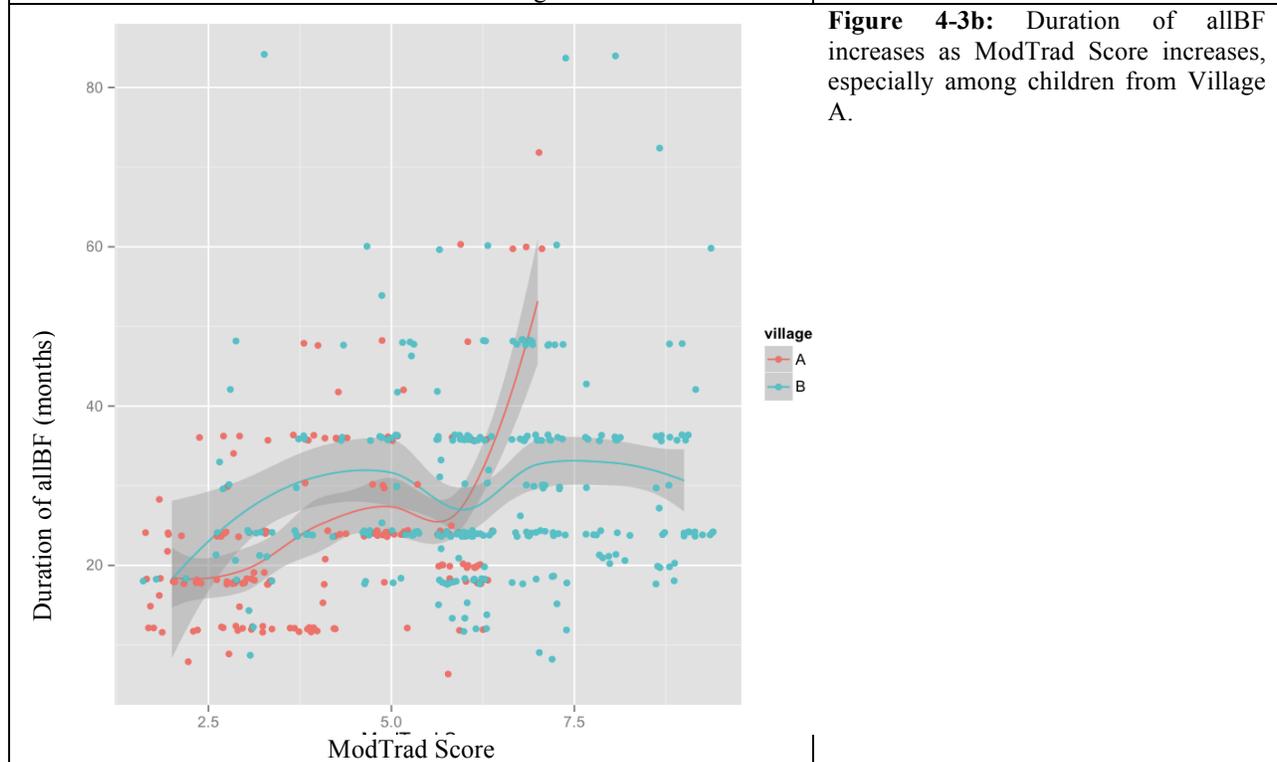
**Table 4-5: Model summary for analyses of effects of modernization (ModTrad Score) and mode of cultural learning on log 10 duration of allBF.**

Fixed effect	Estimate	Standard Error	95% CI	One-sided p-value
Intercept	1.662	0.105	1.456 to 1.868	0.000****
ModTrad Score	0.111	0.035	0.042 to 0.180	0.002**
Cultural learning fidelity score	-0.022	0.046	-0.112 to 0.068	0.319
Village	0.073	0.044	-0.014 to 0.160	0.051
Parity status	0.066	0.014	0.038 to 0.094	0.000****
Access to help with infant feeding	-0.019	0.017	-0.052 to 0.014	0.137

**Figure 4-3**



**Figure 4-3a:** There are no obvious differences in duration of allBF between children whose mothers learned about infant and young child feeding from culturally conservative (high fidelity or “highfi”) sources and children whose mothers learned from less conservative (low fidelity or “lowfi”) sources.



**Figure 4-3b:** Duration of allBF increases as ModTrad Score increases, especially among children from Village A.

**Figure 3:** The impact of mode of cultural learning and ModTrad Score on duration of allBF.

## 4.5 DISCUSSION

### 4.5.1 Summary of main findings

The study reported here examined the self-reported duration of exclusive breastfeeding (exBF) and of duration of all breastfeeding (allBF) in a sample of 82 indigenous, Kakchiquel-speaking Maya women and 419 children from two villages in Guatemala. We found that the women generally report beginning to introduce complementary liquids and solids and thus ending exclusive breastfeeding when infants reach six to eight months of age. Many children in these villages cease allBF at 24 to 28 months of age, although a non-trivial number from Village B continue to breastfeed until ~36 months. Mother-offspring pairs vary substantially within and among families in the duration of these breastfeeding phases, seemingly with greater variation (and reduced tendency to heap their responses on the community's cultural norms, as measured by the sample modes for the two durations) in allBF than in exBF.

Our regression analyses suggest that sources of cultural knowledge about infant and young child feeding strategy account for some of the variation in exBF, controlling for extent of family's engagement in the population's economic and demographic modernization transition (ModTrad score) and village effects. There is no evidence that exBF is associated with ModTrad score. In contrast, allBF appears to vary with ModTrad score, while controlling for mode of cultural learning, village effects, parity status of child, and access to help with infant feeding. Children from more traditional households appear to cease allBF later than children from more economically and demographically modernized households.

#### 4.5.2 Limitations

There are reasons to be cautious when interpreting these results. Most obviously, our study was retrospective and relied on recall data. The limitations of self-recall for understanding human behaviour in general and breastfeeding behaviour in particular are well known. Comparisons of prospective and observational data with retrospective recall data show that some mothers may make non-trivial errors when asked to recall duration of allBF years after a child's weaning (Li et al. 2005; Natland et al. 2012; Promislow et al. 2005). Errors in recall are even more common for duration of exBF (Burnham et al. 2014). That being said, the vast majority of mothers can accurately recall duration of allBF years or even decades after a child's weaning, and many mothers can also do so with exBF (Li et al. 2005; Natland et al. 2012; Promislow et al. 2005). So, while we would ideally use prospective observational data if they were available, the recall data are likely sufficient to assess the ecology of breastfeeding durations in broad strokes (e.g. Veile and Kramer 2015). Furthermore, some evidence indicates that Western mothers that recall duration of exBF and/or duration of allBF incorrectly tend to bias recalled durations towards public health recommendations (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 perhaps yielding inaccurate information on a fraction of the breastfeeding durations of individual participants, then, responses may actually offer unique insights into cultural norms and values about breastfeeding duration.

Another possible limitation of the study is that the variable used to measure the relative modernization of a household was a composite one, comprising a number of variables originally

collected for other purposes. Unfortunately, we do not yet have data regarding the proxies most commonly used to measure modernization versus traditional-ness such as accessibility of transport to nearest urban center; years of formal, state-run education; or competency in a dominant/colonial language (e.g. Snopkowski and Kaplan 2014; Veile et al. 2014). With these shortcomings of our ModTrad variable in mind, we carried out two sets of sensitivity analyses involving alternate scoring methods for ModTrad Score. Generally, the findings of these sensitivity analyses (reported in the supplement, see S Text 3) accorded with the findings reported in the main text, suggesting our main findings are reliable. Nonetheless, caution should be exercised until standard measures of modernization versus traditional-ness become available.

#### **4.5.3 Breastfeeding and Modernization**

Our findings regarding both the lack of impact of ModTrad score on exBF and the positive impact of ModTrad score on allBF 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 have been conflicting, with two studies indicating a negative impact of modernization on exBF, one not detecting any impact, and one finding a positive impact. Specifically, both a study based on a pair of retrospective national surveys from Mexico (González de Cossio et al. 2013) and a study based on prospective interviews carried out in rural Vietnam (Duong et al. 2005) found that exBF declines as populations become less rural, less insular, and more market-integrated. In contrast, using retrospective recall data augmented with observation, Veile et al. (2014) found the opposite effect among Bolivian Tsimane people: exBF was generally longer in more modernized villages than in less modernized villages. Lastly, Veile and Kramer (2015) reported findings that are in line with ours but inconsistent with those

pertaining to the Bolivian Tsimane, the rural Vietnamese, and the indigenous Mexicans (Maya, Aztecs, and Tarahumara). That is, in their study, based on retrospective recall data from Xculoc-speaking Maya women, exBF was not associated with variables that serve as indicators of economic and demographic modernization.

Differences in research design, in methods of assessing duration of exBF, and in choice of indicators of economic and cultural changes among studies may account for some of the discrepancies among these results pertaining to exBF. Alternatively, it may be that the economic change processes themselves vary depending on ecological (including cultural) context, and thus exert different pressures and constraints on mothers and infants, resulting in different behavioural and physiological responses. Consistent with this latter possibility, recent work indicates that local socio-ecology and the structure of socio-cultural networks impacts the rate at which populations undergo changes in fertility patterns in response to modernization (Snopkowski and Kaplan 2014). Given close links between fertility and breastfeeding durations (see Bongaarts and Potter 2013 for a recent synthesis of the evidence regarding fertility and breastfeeding), it is reasonable to infer that similarly complex interactions influence how breastfeeding behaviours change as indigenous populations modernize. If this hypothesis that the process of modernization and its influence on breastfeeding varies by context is correct, the findings of the four studies together suggest that the duration of exBF responds to increased market integration in diverse ways.

Regarding the impact of modernization on duration of allBF in indigenous populations, previous studies have also produced conflicting results. There is at least one case – again, the Tsimane

people of Bolivia – in which allBF duration increases as market integration increases (Veile et al. 2014). The most common finding, however, appears to be the pattern reported in the present study. Namely, the average duration of allBF most often 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 (Gebreselassie et al. 2008; Grummer-Strawn 1996; Trussell et al. 1992).

Currently, it is unclear what drives this negative association between allBF and modernization. There are two obvious possible explanations compatible with our data. One is that market integration brings with it substantial increases in energy availability and substantial decreases in energy expenditures (Lieberman 2003). Energy surpluses can enable mothers to continue to breastfeed intensively while also resuming ovarian cycling and conceiving additional children (Valeggia and Ellison 2004; Valeggia and Ellison 2009; Vitzthum 2009). 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 (Guthrie et al. 1983; Jakobsen et al. 2003; Sellen 2001a). So, more rapid conception associated with modernization and increases in energy balance may lead to relatively early cessation of breastfeeding.

The other plausible explanation for the negative association between allBF and modernization 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 labour or selling things at a market may separate mothers from infants, prohibiting frequent, on-demand breastfeeding and encouraging

relatively rapid replacement of breastmilk with other sources of nourishment (Dennis 2002; Jones et al. 2012; McDade and Worthman 1998; Thulier and Mercer 2009).

Given that our proxy for assimilation into the Guatemalan market economy – ModTrad score – comprises indicators of both energy balance and women’s nondomestic labour, it is possible that either or both of the above explanations may contribute to the effects of market integration on variation in duration of allBF. However, we favour the maternal work hypothesis. We do so because, in another study that focuses exclusively on data from Village B (where fertility is predominantly natural and thus relatively likely to track variations in energy balance and diet), we found two things that shed light on this question (McKerracher et al. in prepa). First, we found evidence that allBF correlates negatively with maternal work outside the home. Second, we found no evidence of an effect of maternal body size on the duration of allBF. These observations suggest that maternal work has a more direct influence on duration of allBF than energy balance. In addition to these findings from our previous study, it is worth noting that increasing market integration appears to go hand-in-hand with increasing female wage earning in the study population (Berry 2010). So, the data suggest that maternal nondomestic workload contributes to changes in the duration of allBF associated with changes in economic scale. That said, we cannot completely reject the hypothesis that maternal body size may also be a contributing factor. As such, there is a need for additional research that explicitly and prospectively evaluates these competing hypotheses. Such research will allow a better understanding of why the duration of allBF generally appears to be inversely related to market integration.

#### 4.5.4 Duration of Exclusive Breastfeeding and Mode of Cultural Learning

Our finding that the duration of exBF correlates with mode of cultural learning suggests that the strength of cultural norms influences exBF. We hypothesize that such norms may mediate or inhibit the way exBF responds to non-cultural factors that influence the length of the period of breastfeeding exclusivity. Cultural norms can reinforce breastfeeding behaviours likely to improve infant survivorship on average when socio-ecology is fairly stable (McDade and Worthman 1998; Snopkowski and Kaplan 2014). On the other hand, when key socio-ecological factors change rapidly (i.e. within a human generation or two), strong, culturally-conserved breastfeeding norms may reduce the responsiveness of behaviour to ecological change. This reduced responsiveness may, in turn, sometimes lead to breastfeeding maladaptations in the short term (Newson 2013; Richerson et al. 2009).

The cultural mediation hypothesis has not previously been tested. But, a number of studies from both the biomedical literature and the evolutionary anthropological literature indicate that culture, broadly construed, probably plays an important role in when non-breastmilk liquids, semi-solids, and solids are introduced (Demirtas et al. 2012; Dettwyler 2004; Hadley et al. 2010b; Mueffelman et al. 2014; Van Esterik 2002; Veile and Kramer 2015; 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 or more plastic systems for transmitting infant and young child feeding knowledge than others. Under this view, populations with more conservative modes of cultural learning are expected to be relatively slow to respond to changing ecological conditions, thus accounting for seeming misfits between breastfeeding durations and

modernizing ecologies in such circumstances. Populations with less conservative cultural learning modes, in contrast, may be able to respond more flexibly and more rapidly to socio-ecological change.

It appears likely that cultural learning and social norms may have especially profound effects on the duration of exBF, perhaps explaining why we found an association between duration of exBF and mode of cultural learning but not between duration of allBF and mode of cultural learning. The logic underpinning this hypothesis is that the infant morbidity and mortality costs of timing the introduction of non-breastmilk foods incorrectly are very high (Kramer and Kakuma 2004; 2007; 2012; McDade and Worthman 1998; Stewart et al. 2013). Ending allBF early or late impacts morbidity and mortality, but many of these risks mainly impact later post-reproductive years (Schack-Nielsen and Michaelsen 2007), meaning that potential fitness variation associated with variation in allBF is relatively low. In keeping with this suggestion, some previous work on maternal diet during pregnancy and breastfeeding indicates that cultural norms can evolve to solve locally-specific, severe ecological challenges when the stakes regarding infant morbidity and mortality are high (Henrich and Henrich 2010).

#### **4.5.5 Do High Levels of Consensus among Responses about Duration of Exclusive Breastfeeding and Duration of All Breastfeeding Reflect Cultural Norms?**

Our findings regarding among-woman consensus in duration of exBF and in duration of allBF align with our *post hoc* hypothesis introduced above regarding differences in the extent to which social norms control each of these variables. Nearly 40% of mother-infant dyads converged on the sample modal value for duration of exBF (six months) whereas only a little more than a quarter did so with the sample modal value for duration of allBF (24 months). This pattern hints

that there is closer agreement in the population with regard to the ideal duration of exBF relative to the ideal duration of allBF. Moreover, it is consistent with the idea that especially high costs in terms of morbidity and mortality associated with inappropriately short or long duration of exBF mean that this variable is more likely to be more tightly constrained and less plastic than duration of allBF.

To the best of our knowledge, no previous study has specifically assessed the extent to which mother-infant pairs converge on the sample mode for duration of exBF relative to duration allBF. Nonetheless, a number of studies have examined differences in “heaping” (the tendency to bias recalled responses towards round, easily conceptualized time intervals, Beckett et al. 2001; Holland 1987) between the two variables. Additionally, other studies have compared the spreads and central tendencies of duration of exBF and duration of allBF in other ways. The majority of findings on heaping suggest duration of exBF reports are more likely than duration of allBF reports to be heaped on normative, round month values and are generally more likely than duration of allBF values to be recalled inaccurately (e.g. Burnham et al. 2014; Coit et al. 2012; Duong et al. 2005). This heaping pattern is consistent with the view that mothers are affected by the high stakes – culturally and/or in terms of risks to infant survivorship and health – associated with appearing to deviate from a normative or recommended period of exBF. Other work on dispersion of the duration of exBF and of allBF also suggests that mother-infant pairs in some populations may reach consensus or near consensus on duration of exBF quickly, but duration of allBF drops off very gradually and continuously (e.g. Anderson et al. 1986). Our finding of relatively high consensus for recalled duration of exBF accords with these general patterns described in earlier work on other populations.

This tendency towards relatively high levels of consensus regarding duration of exBF compared to duration of allBF calls into question the assumption that variation in the two durations reflects similar patterns of negotiation between mother and offspring over maternal investment (e.g. McDade 2001). The recalled patterns point to a cognitive or cultural bias towards convergence on duration of exBF reports and not duration of allBF reports. Given that there are substantial risks to infant wellbeing and possibly substantial fitness costs to mothers associated with very short or very long durations of exBF (McDade 2001; 2003), we might expect mothers to be particularly attuned to absorbing cultural cues from their group members or from expert sources about how to time the end of exBF. Such cognitive biases could perhaps account for a tendency to be aware of and then to report community modal values of exBF. They could also account for the observed association between duration of exBF and mode of cultural learning discussed above. Unfortunately, the data used in the present study cannot shed light on how such biases might operate. Future research should directly – through field experiments – investigate how cultural learning shapes duration of exBF relative to duration of allBF. Additionally, there is a need for future work that explicitly focuses on the fitness consequences associated with deviating from norms for duration of exBF versus those for duration of allBF. We suspect that allBF is under relatively loose control culturally because it is under only weak mortality selection. If so, mother-infant pairs may have the freedom to negotiate the duration of allBF in accordance with individual factors such as maternal age/nearness to reproductive senescence, infant sex, and/or infant quality (Trivers 1974; see also Fujita et al. 2012; McKerracher et al. in prepb; Wander and Mattison 2013).

#### 4.5.6 Implications for Public Health and for Human Life History Evolution

The findings reported here have implications for understanding human life history evolution. They may also be useful in developing implementation strategies for public health interventions.

With respect to evolved life history, our data provide evidence that variation in the duration of exBF associates with variation in mode of cultural learning. These findings suggest that the response of duration of exBF to socio-ecological changes may be mediated through where mothers learn about infant and young child feeding behaviour. Although the kinds of changes that this study focuses on – namely exposure to and integration into a large-scale, market-based economic system – are human made, they provide an opportunity to examine the pace at which duration of exBF and related life history variables respond to ecological changes that occur over the course of a single human generation. These modes of response may also apply to other kinds of ecological/environmental changes operating on a similar time scale, that is, within one or two human generations. Interestingly, modeling work indicates that ecological variability on this same time scale favours relying on culturally transmitted information to solve ecological problems (Richerson et al. 2009; 2010). It may be that the proposed effects of cultural transmission on the sensitivity of duration of exBF relative to ecological change relative to that of allBF have roots deep in the evolution of our species. If so, sharing of information about when to introduce non-breastmilk foods into infant diets likely impacted the survivorship of many of our distant ancestors.

With respect to public health, these findings, concordant with other studies on other populations, suggest that assimilation of indigenous populations into market economies is associated with

changes breastfeeding behaviours, especially the duration of allBF. At the same time, our results suggest that these behaviours, particularly the duration of exBF, may be shaped by sources of cultural knowledge transmission. If supported by further work, these observations suggest two sets of public health recommendations. First, if increasing market integration drives decreases in breastfeeding duration, small-scale populations in the process of being assimilated into market economies perhaps deserve prioritization when allocating resources to breastfeeding promotion and institutional support. Second, if breastfeeding durations are associated with sources of cultural knowledge transmission, recommendations, reassurance, and support should be provided not only to mothers, but to the women in their communities from which they learn. Such an approach would not only offer benefits to infants in terms of decreased exposure to gastrointestinal and respiratory infections during the first six months of life and thus decreased morbidity and mortality risks but would also likely improve mother's breastfeeding confidence via increased social and cultural support.

## 5 General discussion and significance

### 5.1 Recap of main findings of three studies

This dissertation investigated the impact of energetic, socio-economic, and cultural factors on variation in the duration of exclusive breastfeeding and in the duration of all breastfeeding. The investigations were carried out at three, nested scales of analysis. I took the view that, regardless of scale, the factors under investigation were likely to be connected with one another in terms of their current and evolutionary ecology. As such, I framed them as compatible hypotheses rather than mutually exclusive, competing hypotheses. The first study took the widest view of the three, and focused on variation across a sample of small-scale human societies. The second zoomed in and looked at variation within and among families/households within a single village of a small-scale farming population of indigenous Maya from the Guatemalan Highlands. The third investigated variation within and among families and between two villages from that same Maya population. The first two studies were primarily concerned with proposed energetic drivers of durations of breastfeeding. The third was focused on the effects of culture and socio-ecological change on breastfeeding durations.

The first, among-populations study evaluated predictions of the live fast-die young (LFDY) hypothesis, the weanling diet quality hypothesis, and the alloparental care hypothesis. The LFDY hypothesis predicts that the duration of exclusive breastfeeding and the duration of all breastfeeding should be positively associated with maternal developmental conditions (and body size-related markers thereof). The weanling diet quality hypothesis predicts that the duration of

exclusive breastfeeding and the duration of all breastfeeding should be negatively correlated with the quality of weaning foods. Under the alloparental care hypothesis, the durations of exclusive and all breastfeeding are expected to be negatively correlated with availability and use of alloparental care (i.e. help with infant feeding and care). This study found that, across populations, mean duration of all breastfeeding was positively associated with mean maternal height, negatively associated with mean maternal weight and mean maternal adiposity-for-height, and negatively associated with quality of weanling diet. There was no evidence that mean duration of all breastfeeding was associated with the amount of time infants are held by non-mothers. These findings are broadly consistent with the predictions of the live fast-die young hypothesis and the weanling diet quality hypothesis. They do not support the alloparental care hypothesis.

The second study tested the same three hypotheses for causes of variation in the duration of all breastfeeding as the first. It examined the predictions of these hypotheses using among-household data from mothers from one Maya village. In addition to evaluating the live fast-die young hypothesis, the weanling diet quality hypothesis, and the alloparental care hypothesis, this study also tested the Declining Opportunity Costs (DOC) hypothesis. The DOC predicts that the duration of all breastfeeding will increase as mothers near reproductive senescence. The study found that, while controlling for potential confounds, the duration of all breastfeeding is negatively associated with maternal height, negatively associated with a proxy for need for allocare, and negatively associated with a direct measure of use of allocare. The study yielded unequivocal evidence that duration of all breastfeeding is positively associated with a child's status as being born near the end of his/her mother's reproductive career. There was no evidence

that the duration of all breastfeeding associates with mother's weight. There was also no evidence of an association between duration of all breastfeeding and the quality of the foods the mother preferred to use for supplementation.

The third and last study evaluated the predictions that the duration of exclusive breastfeeding and the duration of all breastfeeding would be negatively associated with extent of socio-economic modernization. It also evaluated the predictions that whether women learned about how to feed their infants and young children from culturally conservative sources (e.g. from parents, parents-in-law, or traditional midwives) or through more flexible, liberal means (e.g. following a baby-led weaning approach or self teaching) would affect the durations of exclusive and all breastfeeding. This last study found that, after adjusting for the most obvious potential confounds, the duration of exclusive breastfeeding was associated with variation in the informational sources from which mothers learned about infant and young child feeding behaviours. In particular, women that reported following the norms of their communities or learning from their mothers or mothers-in-law tended to end exclusive breastfeeding when their infants reached ~six months of age. Mothers that learned about infant and young child feeding through self-teaching, baby-led weaning, or from sources whose knowledge derived from outside of the community generally ended exclusive breastfeeding later than mothers that learned from culturally conservative sources. There was also a greater range of variation among the women that learned from less culturally conservative sources compared to mothers that learned from sources that were likely to pass on/enforce community norms. There was no evidence that the duration of all breastfeeding was associated with type of cultural sources of infant feeding knowledge. Rather, the duration of all breastfeeding was associated with a variable used as a

proxy for the extent to which a household was “modernized” at the time of data collection. Children from the most “traditional” households (i.e. households that live lifestyles based on subsistence farming and natural fertility) were breastfed longer than children from the most “modern” households (i.e. households whose heads participated extensively in the market economy and relied heavily on biomedical health and fertility interventions). This latter relationship between the duration of all breastfeeding and “modernization” held after controlling for variables revealed by the second study to influence the duration of all breastfeeding.

## **5.2 Maternal energetics, culture and breastfeeding durations**

At first glance, the results of the first two studies, when taken together, are somewhat puzzling. These studies evaluated the same, energy-related hypotheses and produced different results. Specifically, the prediction that the duration of all breastfeeding would be positively associated with maternal height and negatively associated with maternal adiposity-for-height was supported by the first study but not by the second. Additionally, the prediction that duration of all breastfeeding should be negatively associated with the nutritional quality of weaning foods was supported by the first study but not by the second. The prediction that duration of all breastfeeding should be negatively associated with reliance on and/or access to help with infant care was supported by the second study but not the first.

There are two possible explanations for the conflicting results between the first and second studies. The first explanation is that the materials and methods of one or both of the studies had important shortcomings. The sample and the analytical approach employed in the first, among-populations study especially requires scrutiny. To reiterate, the analyses in that study used

population-wide mean values for all independent and dependent variables. Those analyses thus ignored within-population variation. Evidence from both epidemiological studies and from cross-species comparisons suggests that averaging and pooling data and carrying out analyses at relatively high taxonomic levels can obscure underlying processes and mechanisms involved in ecological constraint and/or adaptation (Greenland and Robins 1994). Consistent with this reasoning, supplementary analyses at the *within*-population level suggest that, if average, per-woman values of the duration of all breastfeeding are regressed on maternal weight and/or maternal Body Mass Index (BMI), the results closely resemble those of the among-populations study. Each woman's mean duration of all breastfeeding is strongly and significantly negatively correlated with her weight and BMI (see Tables 5.1 and 5.2). When within-woman variation is investigated at the within-population level (as in the second study), however, the weight effect disappears and nearness to reproductive senescence appears to be among the most important, if not the most important correlate, of the duration of all breastfeeding. This approach that accounts for within-woman variation within a population is roughly analogous to examining inter-woman variation in an among-populations study. Furthermore, cross-sectionally in the within-village sample, there is a trend towards a negative correlation between height and age (see Appendix 2, S Text 2.3), so it is plausible that the results derived from the averaged data reflect age/cohort/reproductive senescence effects that can only be identified longitudinally. In other words, height, weight, and BMI may not reflect genuine effects of maternal developmental condition. With this in mind, moving back to the among-populations scale, the finding of negative associations between the duration of all breastfeeding and both maternal weight and maternal adiposity-for-height may relate to underlying and systematic heterogeneity in ages,

parity, and timing of reproductive senescence among populations. Again, these relationships may not represent genuine impacts of maternal body size on the duration of all breastfeeding. Future analyses at the among-populations level should, when the relevant data become available, use a mixed effects and/or a phylogenetic comparative design that accounts for within-population and, ideally, within-woman variation in age, parity, and maternal condition. Such data will allow us to assess whether the support the original study appears to offer for the live fast-die young and the weanling diet quality hypotheses reflects statistical artefacts or biologically meaningful phenomena.

**Table 5-1: Mother's average duration of breastfeeding, regressed on her weight**

Predictor	Estimate	Standard Error	p-value
<b>Intercept</b>	45.165	5.054	0.0000 <sup>***</sup>
<b>Maternal Weight (Kg)</b>	-0.2947	0.0872	0.0011 <sup>**</sup>

**Table 5-2: Mother's average duration of breastfeeding, regressed on her BMI**

Predictor	Estimate	Standard Error	p-value
<b>Intercept</b>	45.981	5.629	0.0000 <sup>***</sup>
<b>Maternal BMI</b>	-0.677	0.213	0.0021 <sup>**</sup>

Although analytical limitations may indeed account for the discrepancies between the within- and among-populations studies, a second, more intriguing, possibility is that real differences exist with respect to adaptation, phenotypic plasticity, and evolutionary ecology between different scales of analysis. That is, gross ecological conditions of a generation or generations for a particular population may govern maternal development and thus body size. Maternal development and adult body size then, in turn, influence life history scheduling (including the duration of exclusive breastfeeding and the duration of all breastfeeding). Emergent norms in infant and young child feeding behaviour may yield a strategy or set of strategies that reflect a

reasonably good fit with a population's ecology (e.g. relatively short durations of exclusive breastfeeding and of all breastfeeding if the population's conditions are adverse and the life history schedules of its people are generally fast). But, this normative strategy or set of strategies may not be particularly well-suited to the conditions of individual women living within populations. For individual women, other factors – such as their reproductive career stage and their access to reliable allocare – may be more important in fine-tuning their behaviours to the specifics of their individual environments and their particular developmental histories. According to this view, the apparent discrepancies between the first two studies may in fact represent different kinds of responses to environmental context that operate differently at different scales. If future probing reveals that adaptations or adaptive fits genuinely differ across levels, such evidence would call into question a core assumption of this dissertation. Namely, such a finding would be inconsistent with the assumption that adaptations arise through the same or similar mechanisms and in response to the same or similar constraints/drivers irrespective of scale. It essentially calls into question the assumption that the best hypothesized explanation or explanations for variation should hold across scales of analysis.

Appropriate data to fully discriminate between the methodological shortcomings explanation and the genuine differences among ecological scales explanation for the discrepancies between the first and second studies are not yet available. As suggested above, confidently rejecting the methodological shortcomings hypothesis requires accounting for inter-individual variation when examining among-population patterns. Nonetheless, there is relevant circumstantial evidence available that can be used to evaluate which explanation is most likely to account for the difference between findings. In particular, the results of third, among-Maya-households-and-

villages study reported here point us towards the genuine differences among ecological scales explanation.

Parts of the third study were dedicated to investigating mechanisms through which infant and young child feeding behaviours may respond to ecological changes (IE individual learning/phenotypic plasticity versus cultural learning). This study can thus shed light on the assumption regarding similarity of mechanisms across scales. Its findings suggest that the majority of the women in the focal population learn about how to feed infants and young children (including when to end exclusive and all breastfeeding) from conservative cultural sources such as mothers, mothers-in-law, and traditional midwives. This finding is consistent with one of Hewlett and Cavalli-Sforza (1986). Their work suggests that, similar to what my colleagues and I found for Maya women from the Guatemalan Central Highlands, the Aka foragers of Central Africa generally transmit childcare knowledge vertically, i.e. from parents to children. As with the Maya, the Aka finding indicates that infant and young child feeding knowledge is predominantly transmitted via a relatively conservative cultural learning process. The finding also accords broadly with a growing body of data suggesting that cultural conceptions of infancy affect the duration of exclusive breastfeeding, the duration of all breastfeeding, and the abruptness with which these phases end (e.g. Duong et al. 2005; Fouts et al. 2012; Hadley et al. 2010b; Meehan and Roulette 2013; Veile and Kramer 2015). Together, these observations offer some evidence pertinent to evaluating the proposal that the discrepancies between the results of the among-populations study and the within-a-single-village study reflect biologically meaningful patterns. The evidence presented in the third paper as well as in other, previous ecological studies on the effects of culture on breastfeeding indicates that socially

transmitted information contributes to normative patterns of infant and young child feeding behaviour. It may be that such normative patterns on average (i.e. across a whole population) offer fitness payoffs to mothers and/or infants, but these payoffs may sometimes come at the cost of individual fitness, leading some individual mother-infant pairs to deviate from a population's norms. This 'on average' adaptation via social learning hypothesis represents a plausible one, given two things. The first is that humans are over-imitators that often elect to learn socially even when individual learning is more efficient (McGuigan et al. 2011; Whiten et al. 2009). The second is that human breastfeeding appears to pose some unique physical challenges relative to the ease with which other infant primates latch onto the nipple – the round, protruding shape of human breasts and the mechanics of human infant suckling both complicate latching – that require patience, practice and, ideally, instruction to overcome (Neifert 2004).

The upshot of the above discussion is that it is certainly possible that what appear to be intra- and inter-individual adaptations to fine-scale ecological conditions may arise through different mechanisms than what appear to be population-level or species-level adaptations to coarser-scale ecological conditions. With this possibility in mind, one interpretation of the findings of this dissertation is that, at least for Maya women from the Guatemalan Highlands, the duration of all breastfeeding is influenced by whether women have need for and access to allocare, with shorter durations of all breastfeeding associated with greater need for and greater access to help with infant feeding and care. As these women approach reproductive senescence, despite having increased access to allocare, they appear to rely less on such help with infant feeding and instead continue to breastfeed their last born children much longer than their earlier born children. They can afford continued lactational investment in last children because these investments do not

come at the cost of lost opportunities to invest in subsequent children. So, women from this population generally time ending breastfeeding such that they capitalize on the energy available within their households via allocare. The shortened breastfeeding durations facilitated by allocare may lead women to have relatively larger numbers of children than they would without help. But, these same women then also opt to invest directly and heavily in their children via lactation when they can afford to do so. In other words, women pursue breastfeeding strategies that make the most of the energy they have available to them. Scaled up to the among-populations level of analysis, these general tendencies may be solidified through social transmission of information regarding infant and young child feeding behaviour. Whole populations may then collectively adjust breastfeeding durations in response to ecological conditions via cultural transmission. This could result in, for example, short breastfeeding durations in high adiposity populations even if individual mothers within those populations base their breastfeeding strategies on their allocare availability and/or their reproductive career stages, which may or may not be related to their adiposity.

### **5.3 Implications and future directions**

The three studies reported here aimed to shed new light on factors that may have contributed to the human tendency to end exclusive and all breastfeeding relatively early and with greater flexibility compared to other apes. Its main objective was to use the comparative method and new data at multiple scales of analysis to evaluate a series of hypotheses from the literature regarding factors likely to have facilitated the evolution of these tendencies in our lineage. One of the original, overarching assumptions was that consistency of patterns across multiple scales

of analysis – across species, across cultures, and across both villages and households within a population – would offer compelling support to the hypothesis or hypotheses that predicted those patterns. However, the studies provided no such evidence of consistency/generalizability. Each study identified different potential constraints and/or drivers of variation in the duration of breastfeeding. Furthermore, none of the findings accorded perfectly with those regarding constraints and/or drivers of variation in the duration of lactation in nonhuman animals. Taken together, then, the studies suggest that different factors influence the duration of exclusive breastfeeding and the duration of all breastfeeding at different ecological scales.

Despite this lack of consistency among the results, this body of work offers a number of insights relevant to understanding the evolution and ecology of human life history and demography. The studies also may have implications for evolutionary medicine and/or public health. Additionally, given that the discrepancies among the results of the studies appear to raise more questions than provide clear answers, this dissertation points to several obvious avenues for future inquiry.

As regards the evolution of human life history and demography, while the specific patterns of associations between the duration of all breastfeeding and energetic factors differed, both of the first two studies as well as a host of nonhuman animal studies (e.g. Dubman et al. 2012; Isler and van Schaik 2012; Jackson et al. 2014; Psouni et al. 2012) suggest that factors related to maternal condition and energy availability contribute to variation in when breastfeeding/lactation ends (or possibly vice versa). The implications of this general tendency for variation in the duration of breastfeeding to associate with energetic factors – especially body size variables – for human evolution are at least twofold. First, they suggest that maternal energetics should be accounted

for or possibly added as interaction effects in future analyses pertaining to other predictors of the duration of exclusive breastfeeding and/or the duration of all breastfeeding. Adjusting for body size enabled us to identify relatively unbiased estimates of the impacts of weanling diet quality and variation in alloparental care on duration of all breastfeeding. In this vein, access to high quality foods likely affects and/or is affected by maternal body size. That is, women who can access better nutrition are likely to be in better condition (indexed by body size) to procure additional food; women who can procure better nutrition are likely to be in better condition. Similarly, women with relatively high quality nutrition and in relatively robust condition may be better equipped to have more children, and some of these children may serve as alloparents to their younger sibs. So, there are connections between the body size-related hypotheses, the alloparental care hypothesis, and the weanling diet quality hypothesis. These connections suggest that it was important to hold maternal condition constant when estimating the effects of diet quality and allocare on duration of all breastfeeding. Making similar statistical adjustments in future studies may facilitate clearer understandings of the extent to which other variables influence the ways in which mothers allocate time and energy to lactation versus other aspects of reproduction and maintenance. In particular, these kinds of adjustments may clarify the relationships between women's reproductive tradeoffs and extrinsic ecological risk (e.g. Quinlan 2007), type of subsistence economy (e.g. Sellen and Smay 2001), and maternal non-domestic workload (e.g. Nerlove 1974).

Second, although the mechanisms underpinning the associations between the duration of all breastfeeding and maternal body size remain unclear, the associations in and of themselves may allow us to better model breastfeeding and related behaviours in our extinct relatives, since body

size is to some extent visible in the bioarchaeological and hominin fossil records (Humphrey 2010; Kennedy 2005; Robson and Wood 2008). It has been suggested previously that human-like life history strategies, including relatively short length of lactation and relatively short interbirth intervals, may have arisen in our lineage with the species *Homo erectus/ergaster* (e.g. Aiello and Key 2002; Aiello and Wells 2002; O'Connell et al. 1999; Robson and Wood 2008; Wells and Stock 2007). This suggestion is based predominantly on the fact that *H. erectus/ergaster* was the first member of our lineage that was similar in size to our own species, *H. sapiens*, and thus may also have been the first of our ancestors with similar energetic requirements and constraints to those of contemporary humans (Aiello and Key 2002; Wells and Stock 2007). The evidence from the first study in this dissertation that suggests that duration of breastfeeding correlates with height, adiposity, and access to high quality weaning foods is consistent with this reasoning. The evidence from the second study that suggests that need for and access to alloparental care are associated with relatively shorter durations of breastfeeding may imply, as suggested in previous theoretical work, that cooperative and social forms of child care represent part of the modern human life history package likely to have emerged in *H. erectus/ergaster* (Bogin et al. 2014; O'Connell et al. 1999). In other words, these lines of evidence are consistent with the view that the similarity in size and socio-ecology between *H. sapiens* and *H. erectus/ergaster* may indicate that *H. erectus/ergaster* shared a similar set of life history tactics with us and our similarly-sized immediate ancestors, to the exclusion of earlier, smaller-bodied hominin taxa.

Another insight offered by this dissertation with respect to human evolutionary demography concerns the role of cultural learning in breastfeeding behaviour. In keeping with a growing body of research (e.g. Bogin et al. 2014; Dettwyler 2004; Fouts et al. 2012; Meehan and Roulette

2013; Wells 2006), the third study in this dissertation provides evidence consistent with the view that social transmission of information about infant and young child feeding is integral to breastfeeding behaviours in our species. The results of the third study further imply that social transmission of such information may help in tailoring these behaviours to local ecological conditions. The role of social transmission of information in driving variation in the duration of exclusive breastfeeding and the duration of all breastfeeding may help us to refine our understanding of when and why the modern, highly flexible pattern of human infant and young child feeding behaviours emerged. It appears that social learning in general offers fitness payoffs under conditions of unpredictable, medium-amplitude environmental changes that unfold over the course of a few long (i.e. human-like) generations, combined with conditions of sufficient population sizes to spread, retain, and elaborate on beneficial cultural innovations (Henrich 2004; Powell et al. 2009; Richerson et al. 2009). Climatic records, human demographic records, and archaeological records all suggest that ecological conditions would have favoured increased reliance on socially-learned information – culture – during the terminal Pleistocene, perhaps following the origins of our own species, *H. sapiens* (Richerson et al. 2009).

It is currently unclear what the direct implications of an ecological context that favours cultural learning for the evolution of infant and young child feeding behaviours are. But, we might infer that cultural learning influenced human life history strategies in general and breastfeeding behaviours in particular for the majority of the history of *H. sapiens* (Wells and Stock 2007). If it has indeed been the case that infant and young child feeding have been shaped by population norms for tens of thousands or even hundreds of thousands of years, we can make some novel predictions about the bioarchaeological/palaeoanthropological record. For example, we might

predict relatively low levels of within-population variation relative to among-population variation in breastfeeding strategies. We might also predict occasional instances of cultural maladaptations in the record. This last prediction regarding maladaptations is based on the idea that culture is generally expected to offer fitness benefits but can sometimes lead to otherwise biologically inexplicable, non-adaptive outcomes, if people adhere widely to an idea that is compelling but ultimately harmful to survivorship and/or reproduction (Newson 2013; Richerson et al. 2009).

Beyond these considerations with respect to past human behaviour and demography, this dissertation may also have implications for public health. In particular, inasmuch as promoting extended exclusive and all breastfeeding remains a global public health objective (e.g. World Health Organization 2010), several of the findings may be of interest to public health policy-makers seeking to identify populations and subsets of populations to be targeted for breastfeeding-related interventions. The findings of the first two studies suggest that short, adipose women in the early stages of their reproductive careers are at elevated risk of having relatively short durations of all breastfeeding. These findings might suggest that mother-child pairs in which the mother is relatively adipose-for-height and/or in which the child is of low parity should receive extra attention and breastfeeding support from clinicians and other front line workers. The findings of the third study that, in line with the results of a number of other studies (e.g. Duong et al. 2005; Veile and Kramer 2015), indicate a negative association between the duration of all breastfeeding and abandonment of traditional lifeways. This finding points to the need for clinicians and for public health policy-makers to prioritize indigenous populations undergoing transitions when promoting extended breastfeeding, assuming public healthy policy-

makers aim to reduce developmental and health inequalities between indigenous and non-indigenous children. The other findings of the third study – the findings that indicate that the kind of source from which a mother acquires socially-transmitted information about how to feed infants and young children – highlight that promotion of extended exclusive and all breastfeeding should be targeted not only at mothers but also the people from which they are most likely to learn about infant feeding.

In terms of future research, there are a number of obvious next steps that will help to clarify and/or expand on the results of the three studies reported here. The first such step pertains to addressing shortcomings of the among-populations study. The results of the among-populations study cannot be taken at face value and should be treated with caution. The study did not account for inter-individual, within-population variation in breastfeeding behaviour or in ecology and did not use the best available methods to control for the effects of relatedness among the populations in the sample. As suggested above, once high quality data regarding the inter-individual variation of interest and regarding the phylogenetic histories of the populations in the dataset are made available, the predictions tested in the first study should be re-evaluated.

The next set of possibilities for future research pertains to the second study. This within-a-single-village study suffers from two major limitations. The first of these concerns its heavy reliance on maternal recall to measure the duration of all breastfeeding. The problems with retrospective, recalled data are well known: they may reflect systematic biases in memory and reporting. While some evidence suggests that most women can accurately recall duration of all breastfeeding reasonably accurately years after weaning when the duration of breastfeeding exceeds 13 months

(Li et al. 2005; Natland et al. 2012; Promislow et al. 2005), future work should nevertheless use prospective observations and interviews to assess the reliability and validity of the recalled data. The second shortcoming pertains to the evaluation of predictions derived from parent-offspring conflict theory. The second study only tested predictions of the Declining Opportunity Costs hypothesis as regards parent-offspring conflict. To reiterate, the DOC test prediction was that latter-born children were breastfed longer than their older siblings. The results of that test suggest that parent-offspring conflict may play an important role in intra- and inter-individual variation in duration of all breastfeeding. It offered evidence consistent with the prediction that mothers should adjust the amount of time and energy transferred to infants via lactation depending on their reproductive career stage rather than transferring as much time and energy to infants as infants would ideally procure. This raises the question of whether or not mother-infant pairs struggle over allocation of resources on other axes. In particular, future research should assess the effects of offspring quality, offspring sex, and mother's socio-economic status on within-family variation in the duration of all breastfeeding in this and in other small-scale human populations.

The last set of opportunities for future research raised by this dissertation concern the roles of culture and cultural change in the evolutionary ecology of breastfeeding. The third study reported here suggests that mode of cultural learning influences how mother-child pairs adjust infant and young child feeding behaviours in response to changing social and economic circumstances. Unfortunately, however, the interview questions concerning social learning about infant and young child feeding behaviour and about cultural change/modernization have shortcomings. With regards to social learning, the interview question we designed lumped all infant and young

childfeeding behaviours together – participants were asked about from whom or through what method they learned to feed their babies and toddlers. Future research should aim to identify specific learning sources of information or “models” and methods for different infant and young child feeding behaviours. Doing so would allow us to identify the modes of transmission for a number of behaviours. Behaviours of interest might include: initiation of breastfeeding/colostrum use, the mechanics of breastfeeding, when to end exclusive breastfeeding, what complementary foods to introduce and in what order to introduce them, when to begin to decrease breastfeeding frequency, and when and how to terminate comfort feeds. Such an approach will offer a fuller understanding of how information moves among community members within and between generations. It could also help identify central informational hubs (i.e. the people and/or places from which many mothers obtain key information regarding health/nutrition) that could allow expedient dissemination of public health recommendations within the community.

With regards to cultural change/modernization, a future study should seek to measure modernization via means that will allow results to be more easily compared to those of other studies. Specifically, proficiency in the language of a dominant/colonial power, distance of a household or a village to a larger-scale social and economic hub, and years of formal education constitute conventional metrics for extent of modernization (e.g. Snopkowski and Kaplan 2014; Veile et al. 2014). Such metrics should, in future, be acquired for the study population so as to validate the ones used here.

## 6. Conclusions

The periods of exclusive breastfeeding and supplemented breastfeeding in humans are considerably shorter than those of other large-bodied apes, including those of our closest living relatives, the chimpanzee and the bonobo (Emery Thompson 2013; Humphrey 2010; Kennedy 2005; Lee et al. 1991; Sellen 2001b). There is also some evidence to suggest that the duration of exclusive breastfeeding and the duration of all breastfeeding are more variable in humans than in other primates (Emery Thompson 2013; Sellen 2009; Sellen 2007).

These human tendencies to end exclusive breastfeeding and all breastfeeding relatively earlier than other similarly-sized primates as well as the human capacity to be very flexible in infant and young child feeding behaviours have implications for infant health. Comparatively short durations of exclusive breastfeeding are associated with 20- to 25-fold increases in the risk of infant respiratory infection and infant gastrointestinal infection (Kramer and Kakuma 2004; 2007; 2012; Labbok et al. 2004; McDade and Worthman 1998). Respiratory and gastrointestinal infections constitute the leading causes of infant mortality in developing countries (Kramer and Kakuma 2004; 2007; 2012; Labbok et al. 2004). In addition, comparatively long durations of exclusive breastfeeding (in excess of six or seven months) are associated with stunting, wasting, and other major risks for infant morbidity and mortality (McDade and Worthman 1998; Wilson et al. 2006). Lastly, cessation of supplemented breastfeeding in the first one to two years of life appears to be associated with increased risks of overweight, obesity, and negative impacts on

cognition and attachment (Gluckman and Hanson 2004; Gluckman et al. 2013; Schack-Nielsen and Michaelsen 2007; Tasnim 2015; Victora et al. 2015).

In addition to effects on infant health, the duration of exclusive breastfeeding and the duration of all breastfeeding can impact maternal fertility (Bongaarts and Potter 2013; Vitzthum 2008). The relationship between breastfeeding durations and fertility appears to be regulated largely by maternal energy balance (whether or not a mother's energy use outstrips her energy consumption) (Valeggia and Ellison 2001; 2004; 2009; Vitzthum 2009; Worthman et al. 1993). A mother's energy balance in turn affects her ovarian function, with mothers in negative energy balance often being anovulatory, while mothers in positive energy balance are relatively likely to ovulate regularly (Valeggia and Ellison 2001; 2004; 2009; Vitzthum 2009). Thus, unless a woman is regulating her fertility behaviourally or pharmaceutically, her breastfeeding patterns and energetic status affect the length of intervals between her births. Shorter interbirth intervals are associated with higher total fertility (e.g. Bongaarts and Potter 2013; Vitzthum 2008).

Given the aforementioned implications for both health and demography, identifying the factors that enabled humans to wean relatively early and flexibly is an important goal for evolutionary anthropology. In the three studies presented here, I sought to identify some of these factors. Each study evaluated multiple hypotheses pertaining to causes of variation in breastfeeding duration. The first study investigated associations between variation in the population mean duration of all breastfeeding and variation in three factors that have been hypothesized to impact maternal energy balance – maternal size, quality/energy-density of weaning foods, and maternal access to

help with infant care. The second study also examined the effects of maternal size, weaning food quality, and access to help, but focused on within-population variation rather than among-population variation. This study was carried out using newly collected field data from indigenous Maya women living in a village in the Sololá region of the Guatemalan Central Highlands. The third study also used field data from Maya women. However, rather than focusing on energetics, this last study investigated the role of socio-ecological/socio-economic change and the social transmission of information about how to feed infants in driving variation in the duration of exclusive breastfeeding and the duration of all breastfeeding. It also differed from the second study in that it employed data from two villages.

The first study provided evidence that, across populations, breastfeeding duration is negatively associated with maternal body mass, positively associated with maternal height, and negatively associated with dietary quality of weaning foods. It yielded no evidence of an association between duration of breastfeeding and maternal reliance on other people for help with infant care. The second study showed that variation in breastfeeding duration among Maya mother-infant pairs is negatively associated with maternal height, negatively associated with maternal access to help with infant care, and positively associated with mother's nearness to reproductive senescence. These analyses did not provide any evidence that the duration of all breastfeeding associates with maternal weight at conception or with quality of weaning foods used. The results of the third study indicated that duration of exclusive breastfeeding is negatively associated with conservativeness of the source from which mothers learn about infant feeding behaviour. Its results further suggested that full duration of supplemented breastfeeding is positively associated

with the extent to which a household had departed from traditional, subsistence fisher-farming lifeway. This last study offered no evidence that the duration of exclusive breastfeeding is related to modernization. There was also no evidence that duration of all breastfeeding is affected by a mother's cultural source of infant and young child feeding knowledge.

Taken together, these results suggest two things. One is that maternal energetic factors influence the duration of all breastfeeding. These factors include constraints on maternal energy during development that are assumed to impact height, somatic fat stores, access to energy from other community members in the form of help with infant care, and access to nutritionally-dense supplemental foods. The other thing the results suggest is that socio-ecological factors (including cultural ones) influence variation in the duration of exclusive breastfeeding and in the duration of all breastfeeding in humans. These findings are consistent with the argument that, over the course of our evolutionary history, increases in energy availability and/or development of complex cultural systems for information transmission contributed to the evolution of short, flexible breastfeeding and high fertility in humans (Bogin et al. 2014; Burger et al. 2010; Dettwyler 2004; Ellison 1995; Hamilton et al. 2009; Kaplan et al. 2000; Kramer and Ellison 2010; Meehan et al. 2013; Newson 2013; 2009; Sellen 2007; Wells and Stock 2007). Moreover, human breastfeeding represents a complex physiologic and cultural process, crucial to our demographic history.

To conclude, there are many routes for further inquiry that require exploration before we will understand the evolutionary ecology of human breastfeeding. Nevertheless, the studies that

comprise this dissertation suggest inter-related and primary roles for maternal energetics and culture in the timing of key milestones in the human weaning process.

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## Appendix 1

**S Table 1: Eco-geographic data for populations in sample**

Population	Continent	Country/region	Linguistic Taxon	Absolute Latitude	Pathogen prevalence
<b>Ache</b>	Central/South America	Paraguay	South American isolate/no relatives in sample	25.7	0.17
<b>Aeta</b>	Oceania	Philippines	Malayo-Polynesian	15	0.51
<b>Agta (Cagayan)</b>	Oceania	Philippines	Malayo-Polynesian	17.5	0.51
<b>Agta (Casiguran)</b>	Oceania	Philippines	Malayo-Polynesian	17.5	0.51
<b>Aka</b>	Subsaharan Africa	Central African Republic	Niger-Congo	2	1.19
<b>Amele</b>	Oceania	Papua New Guinea	Trans-New Guinea	5	0.15
<b>Au</b>	Oceania	Papua New Guinea	Trans-New Guinea	3.3	0.15
<b>Bofi farmers</b>	Subsaharan Africa	Central African Republic	Niger-Congo	2	1.19
<b>Bofi foragers</b>	Subsaharan Africa	Central African Republic	Niger-Congo	2	1.19
<b>Burarra</b>	Oceania	Australia	Trans-New Guinea	12.4	-0.14
<b>Efe</b>	Subsaharan Africa	Demographic Republic of the Congo	Nilo Saharan	2.7	0.95
<b>Gainj</b>	Oceania	Papua New Guinea	Trans New Guinea	5.2	0.15
<b>Hadza</b>	Subsaharan Africa	Tanzania	Khoisan	3.8	0.66
<b>!Kung</b>	Subsaharan Africa	Namibia/ Botswana	Khoisan	20	0.36
<b>Makushi</b>	Central/South America	Guayana	South American isolate/no relatives in sample	4	0.64
<b>Mayans (Kaqchikel)</b>	Central/South America	Guatemala	Mayans	14.8	0.56
<b>Mayans (Xuloc)</b>	Central/South America	Yucatan Mexico	Mayans	--	0.56
<b>Pume</b>	Central/South America	Venezuela	South American	6.9	0.8

			isolate/no relatives in sample		
<b>Toba</b>	Central/South America	Argentina	North Central Andes	26.2	0.03
<b>Tsimane</b>	Central/South America	Bolivia	North Central Andes	15	0.3
<b>Yasawa Islanders</b>	Oceania	Fiji	Malayo- Polynesian	16.5	-0.39

**S Table 2: Demographic data for populations in sample**

<b>Population</b>	<b>Mean age at first birth (years)</b>	<b>Mean length of interbirth interval (months)</b>	<b>Mean number of live births per woman</b>	<b>Under 5 mortality rate (%)</b>
Ache	19.5	37.6	8.15	12
Aeta	16	45	--	45
Agta (Cagayan)	20.14	38.8	4.39	49
Agta (Casiguran)	19.5	39	7	46
Aka	18	--	5.54	20
Amele	20	30.9	6.88	5
Au	22	36.4	6.10	15
Bofi farmers	--	30	5.32	31
Bofi foragers	--	54	5.54	41
Burarra	15.9	21	6.4	6
Efe	18.5	--	2.6	18
Gainj	25.7	42.3	42.3	27
Hadza	19	39	6.2	30
!Kung	21.4	40.5	4.69	15
Makushi	--	34.8	7.52	29
Mayans (Kaqchikel)	19.8	38.3	6.26	10
Mayans (Xuloc)	19.5	25.2	7.5	3
Pume	15.5	34.4	7.75	13
Toba	20.6	28.9	6.8	23
Tsimane	18.6	35.6	8.5	13
Yasawa Islanders	21.2	34.0	4.5	2

**S Table 3a: Sensitivity test 1 (bootstrapping 95% confidence intervals) for relationship between duration of breastfeeding and BMI**

	Estimate	Standard Error	Bootstrap 95% CI	p
<b>intercept</b>	56.8713	9.6453	39.5780 to 80.9107	0.0000***
<b>BMI</b>	-1.2244	0.4261	-2.2270 to -0.4589	0.0097**

**S Table 3b: Sensitivity test 2 (excluding two least reliable data points with respect to duration of breastfeeding) for relationship between duration of breastfeeding and BMI**

	Estimate	Standard Error	95% CI	p
<b>intercept</b>	58.956	9.867		0.0000***
<b>BMI</b>	-1.325	0.439		0.0077**
<b>Model Summary</b>	$R^2=0.349$ , Adjusted $R^2=0.311$ , model $p=0.0077^{**}$			

**S Table 3c: Sensitivity test 3 (controlling for continent) for relationship between duration of breastfeeding and BMI**

Predictor	Estimate	Standard Error	95% CI	p
Intercept	76.365	8.356		0.0000***
BMI	-1.782	0.353		0.0000***
South America	-6.779	3.315		0.0617
SubSaharan Africa	-10.712	4.450		0.0317*
<b>Model Summary</b>	$R^2=0.720$ , Adjusted $R^2=0.655$ , model $p=0.0007^{***}$			

**S Table 3d: Sensitivity test 4 (adding random intercept term for linguistic taxon affiliations, fit by maximum likelihood) for relationship between duration of breastfeeding and BMI**

Predictor	Estimate/ (Standard Deviation)	Standard Error/ (Residual)	95% CI	p
BMI	-1.213	0.425		0.0140*
Intercepts (Linguistic Taxon Affiliation)	(0.001)	(5.955)		

**S Table 3e: Sensitivity test 5 (excluding influential data point) for relationship between duration of breastfeeding and BMI**

Predictor	Estimate/ (Standard Deviation)	Standard Error/ (Residual)	95% CI	p
BMI	-1.438	0.852		0.1137
<b>Model Summary</b>	$R^2=0.169$ , Adjusted $R^2=0.110$ , model $p=0.1137$			

**S Table 4a: Sensitivity test 1 (bootstrapping 95% confidence intervals) for relationship between duration of breastfeeding and BMI, weanling diet quality, and allocare score**

Predictor	Estimate	Standard Error	Bootstrap 95% CI	p
intercept	79.7423	13.9975	-0.2288 to 176.7995	0.0003***
BMI	-1.9704	0.6245	-6.4146 to 1.5068	0.0116*
Food diet quality score	-8.2079	3.5700	-22.1092 to 5.520	0.0407*
Allocare score	-2.9281	3.4275	-18.7137 to 6.7950	0.4151
Model summary	R <sup>2</sup> =0.633, Adjusted R <sup>2</sup> =0.512, model p=0.0238			

**S Table 4b: Sensitivity test 2 (excluding two least reliable data points with respect to duration of breastfeeding) for relationship between duration of breastfeeding and BMI, weanling diet quality, and allocare score**

Predictor	Estimate	Standard Error	95% CI	p
intercept	58.956	9.867		0.0000***
BMI	-1.325	0.439		0.0077**
Model Summary	R <sup>2</sup> =0.349, Adjusted R <sup>2</sup> =0.311, model p=0.0077**			

**S Table 4c: Sensitivity test 3 (controlling for continent, weighting for sample size) for relationship between duration of breastfeeding and BMI, weanling diet quality, and allocare score**

Predictor	Estimate	Standard Error	95% CI	p
intercept	81.465	17.480		0.0055**
BMI	-1.929	0.800		0.0609
Food quality score	-2.903	4.918		0.5807
Allocare score	3.611	5.229		0.5206
South America	-7.391	4.527		0.1635
SubSaharan Africa	-9.760	6.168		0.1744
Model Summary	R <sup>2</sup> =0.897, Adjusted R <sup>2</sup> =0.795, model p=0.0164*			

**S Table 4d: Sensitivity test 4 (adding random intercept term for linguistic taxon affiliations, fit by maximum likelihood) for relationship between duration of breastfeeding and BMI, weanling diet quality, and allocare score**

Predictor/Effect	Estimate/ (Standard Deviation)	Standard Error/ (Residual)	95% CI	p
BMI	-1.970	0.624		0.0343*
Food quality score	-8.208	3.570		0.0830
Allocare score	-2.928	3.428		0.4411
Intercepts (Linguistic Taxon Affiliation)	(0.000)	(4.200)		

**S Table 4e: Sensitivity test 5 (excluding influential data point) for relationship between duration of breastfeeding and BMI weanling diet quality, and allocare score**

Predictor	Estimate/ (Standard Deviation)	Standard Error/ (Residual)	95% CI	p
BMI	-2.028	0.547		0.0076**
Food quality score	-10.379	2.771		0.0072**
Allocare score	2.417	4.065		0.5709
Model Summary	R <sup>2</sup> =0.812, Adjusted R <sup>2</sup> =0.732, model p=0.0062**			

## Appendix 2

### **S Text 2.1: Estimation of maternal weight prior to conception**

Maternal weights prior to the conception of individual children were estimated in one of two ways, depending on what year the child was born. For children born between 2000 and 2013, log 10 weights were estimated via linear interpolation using only observations of log 10 mother's weights in 2000 and 2013. For children born prior to 2000, we wrote a multivariate function to predict past mother's weights, based on log 10 weight change patterns between 2000 and 2013, mother's age at child's conception, and mother's height.

### **S Text 2.2: Calculating Traditional-ness**

Traditional-ness of a household was estimated using nine subsidiary variables, each treated as a categorical/dummy variable. These variables included ones concerning demography (fertility status of mother, timing of beginning of mother's reproductive career, percent of household's children that died before age five), anthropometry (status as overweight/obese versus normal weight, assessed via body mass index; upper arm skinfold thickness status as fat or thin, assessed relative to the population mean), weaning diet (use of biomedically-recommended, protein-dense weaning foods; use of biomedically-recommended, specially formulated, micronutrient- and protein-dense weaning supplement; use of contraindicated weaning foods), participation in the market economy by women (mother works outside the home and/or sells products at market). Details on scoring of these variables are as follows:

- 1) **Fertility status of mother:** 0 if mother reported having previously used biomedical contraception, 1 if she reported never having used biomedical contraception.
- 2) **Timing of beginning of mother's reproductive career:** 0 if mother first gave birth prior to the end of the Guatemalan civil war in 1996, 1 if she first gave birth after the end of the war.
- 3) **Under five mortality:** 0 if percentage of a mother's children that survived past age five is greater than or equal to 20%, the mean under five mortality rate in the 1960s (Early 1970a), 1 if less than 20%.
- 4) **Overweight/obesity status:** 0 if mother's Body Mass Index in 2013 was greater than 25, 1 if it was less than or equal to 25.
- 5) **Upper arm skinfold thickness:** 0 if mother's upper arm skinfold thickness was greater than the sample mean (~10.5 mm), 1 if it was less than or equal to it.
- 6) **Use of biomedically-recommended, protein-dense weaning foods:** 0 if mother reported using such foods, 1 if she did not.
- 7) **Use of biomedically-recommended, specially formulated, micronutrient- and protein-dense weaning supplement:** 0 if mother reported using such foods, 1 if she did not.
- 8) **Use of contraindicated weaning foods (mainly coffee, soda):** 0 if mother reported NOT using such foods, 1 if she did.
- 9) **Participation in the market economy by mother:** 0 if mother reported working outside the home or earning money from selling things at market, 1 if she did not.

The scores for these individual variables were then added together to create a composite, meta-variable, used as a proxy for modernization/traditional-ness of each household.

### **S Text 2.3: Methods and results for supplementary analyses robust to mis-specified correlation**

We used two approaches to assess the reliability of our main results, given the possibility that the main results were based on analyses in which correlations among fixed effects and between the fixed effects and the outcome variable were mis-specified. One was to re-score the outcome variable (duration of all breastfeeding) as discrete, with original values less than or equal to 3 months scored as “0”, 3.1-9 months scored as “1”, 9.1-15 months scored as “2”, 15.1-21 months scored as “3”, 21.1-28 months scored as “4” etc. We then fit a poisson general linear mixed model via maximum likelihood to the data. Our other, most robust tactic was to use the raw duration of breastfeeding data but to use a generalized estimating equation approach, which produces estimates robust to incorrect assumptions about variance and correlation structure.

The results of these alternative regressions are presented in S Table 2.3.1 and S Table 2.3.2, respectively. They accord generally with our main results, insofar as they indicate that duration of breastfeeding is associated with the need for and the use of alloparental care (mother participates in market economy, mother reports receiving help with infant feeding) and with the parity status of the child (child is last or second-last born). As with the main results, the supplemental results do not offer evidence that duration of breastfeeding is associated with a

proxy of modernization/traditional-ness of household. The only discrepancy is one between the first (less robust) sensitivity analyses and the main results. These first supplementary analyses indicate that duration of breastfeeding is negatively associated with estimated maternal weight at conception. This difference is likely accounted for by the fact that we did not include all control in the supplemental analyses.

**S Table 2.3.1: Relationship between duration of all breastfeeding and maternal weight, use of infant feeding help, need for help with infant care, child’s parity status, and household traditional-ness, with duration of all breastfeeding scored discretely and fitting a poisson distribution.**

Fixed Effect	Estimate	Standard Error	One tailed p-Value
Intercept	3.34584	0.88094	0.0000***
Mother’s estimated weight at conception	-1.0141	0.53040	0.0280*
Mother’s reported access to help with infant feeding	-0.1088	0.0382	0.0022**
Mother participates in market economy	-0.1973	0.0729	0.0035**
Child is last or second-to-last born	0.2584	0.0716	0.0002***
Traditional-ness of household	0.0501	0.0759	0.2547

**S Table 2.3.2: Relationship between duration of all breastfeeding and maternal weight, use of infant feeding help, need for help with infant care, child’s parity status, and household traditional-ness, using a generalized estimating equation.**

Fixed Effect	Estimate	Naïve Standard Error	Robust Standard Error	Naïve z	Robust z <sup>1</sup>
Intercept	1.8127	0.3027	0.3097	5.9884***	5.8525***
Log 10 Mother’s estimated weight at conception	-0.1940	0.1816	0.0267	-0.1682	-1.0469
Mother’s reported access to help with infant feeding	-0.0396	0.0176	0.0138	-0.2464*	-2.8708*
Mother participates in market economy	-0.0869	0.0331	0.0295	-2.6250*	-2.9511*
Child is last or second-to-last born	0.0798	0.0211	0.0267	3.765**	2.9905*

<b>Traditional-ness of household</b>	0.0066	0.0344	0.0138	0.1909	0.1912
<sup>1</sup> A robust z score below -1.96 or above 1.96 indicates a significant relationship at the 0.05 level.					

#### S Text 4:

To assess whether cohort effects may account for the relationship between duration of all breastfeeding and maternal height, we fit an ordinary least squares model, in which we regressed each mother's height on her age. We subsequently fit a ordinary linear mixed effects model by maximum likelihood in which we regressed duration of breastfeeding on both height and age, controlling mother's weight as measured in 2000 (rather than the estimated pre-conceptual value, which incorporated age) maternal participation in the market economy and access to help with infant feeding. The results, presented in S Table 2.4.1 and S Table 2.4.2, may suggest that maternal height is negatively related to maternal age and indicate that controlling for maternal age causes the otherwise marginally significant height effect to disappear.

**S Table 2.4.1 The relationship between mother's height and her age.**

Effect	Estimate	Standard error	One tailed p-value
Intercept	150.3072	4.1396	0.0000***
Mother's age	-0.0875	0.1012	0.1955

**S Table 2.4.2: The relationship between mother's average duration of all breastfeeding and height and age, controlling adiposity (upper arm skinfold thickness) and help with infant feeding.**

Effect	Estimate	Standard error	One tailed p-value
Intercept	74.39617	36.48683	0.0213*
Mother's height	-0.28291	0.23073	0.1134
Maternal age	0.36740	0.19408	0.0325*
Mother's weight	-0.29304	0.18177	0.0571

Help with infant feeding	-3.95536	1.25135	0.0014 <sup>**</sup>
Maternal participation in market economy	-5.30756	2.3500	0.0015 <sup>**</sup>
Child's status as last- or second-last born	6.29326	1.46807	0.0000 <sup>***</sup>

## Appendix 3

### **S Text 3.1: Further details concerning composition of ModTrad Score**

Because we did not have data pertaining to standard metrics for modernization, we created a meta-variable that could serve as a rough proxy for the extent to which a household is modernized. This meta-variable was based on nine variables concerning demography (fertility status of mother, timing of beginning of mother's reproductive career, percent of household's children that died before age five), anthropometry (status as overweight/obese versus normal weight, assessed via body mass index; upper arm skinfold thickness status as fat or thin, assessed relative to the population mean), weaning diet (use of biomedically-recommended, protein-dense weaning foods; use of biomedically-recommended, specially formulated, micronutrient- and protein-dense weaning supplement; use of contraindicated weaning foods), participation in the market economy by women (mother works outside the home and/or sells products at market). Our justifications/rationales for including each of the variables are as follows:

- 1) **Fertility status:** We reasoned that mothers that reported having used biomedically-prescribed forms of contraception were relatively comfortable using the health post and with interacting with the Westerners and/or formally-educated Guatemalans that staff it.
- 2) **Timing of the beginning of mother's reproductive career:** We assumed that mothers that first gave birth before 1996, when the Guatemalan Civil War Ended, grew up had reduced access to biomedical advice and interventions, especially when she was first learning how to mother.

- 3) **Under five child mortality:** Evidence suggests that child mortality in the region has generally declined with increased access to biomedical treatments, so under five mortality is assumed to partly reflect modernization and modernized attitudes to medicine, health, and fertility (Early 1970a; 1970b).
- 4) **Overweight/obesity status:** Ample evidence from a large number of indigenous populations suggests that overweight and obesity (Body Mass Indexes [BMIs] in excess of 25) are rare in such populations, but become very common as lifestyles increasingly rely on market exchange rather than traditional subsistence practices ((Huneault et al. 2011; McGarvey et al. 1989).
- 5) **Upper arm skinfold thickness:** Again, overweight/obesity rates increase with modernization and market integration. Skinfold thickness represents another way of identifying excess adiposity in addition to BMI.
- 6) **Use of protein-dense weaning foods:** Signs in the health post in Village A recommend use of protein-dense weaning foods, introduced after an infant is at least six months of age. Conversations with local research assistants suggest that these recommendations differ from traditional weaning foods, which most often include watery maize porridge and pureed vegetables.
- 7) **Use of “incaparina”, a specially-formulated food supplement for infants and young children:** We assumed that regular use of this product indicates interaction with and receptiveness to nurses, doctors, and/or other people from outside of the villages developing public health interventions.

- 8) **Use of contraindicated weaning foods:** The health post nurses and staff recommend that women should not give infants and young children soda, coffee, or tea. So, we reasoned that mothers that reported using these liquids as preferred supplementary foods were unlikely to have interacted extensively with the non-local health professionals.
- 9) **Maternal participation in the market economy:** This variable is our most direct measure of market integration, but it also indicates a deep, systemic level of modernization because it is also enabling women to successfully head households, encouraging women to learn Spanish, and encouraging women to interact with non-locals, including Westerners (Berry 2010).

### **S Text 3.2: Alternative scorings of ModTrad**

Given the non-standard nature of our measure of modernization, we developed two, more conservative metrics for this variable. These alternative scorings were used in sensitivity analyses, so that we could assess whether using slightly different proxies for modernization would produce results similar to our main ones. These other scorings were:

- 1) One in which we excluded under five child mortality and the anthropometric variables. As regards the under five mortality rate, we reasoned that there could be reverse causality, with changes in breastfeeding affecting mortality rates rather than the other way around. As regards anthropometry, in a similar vein, we reasoned that declines in breastfeeding durations could contribute to increased risks of overweight, obesity, and peripheral adiposity. This new composite variable comprised: Fertility status, Timing of

the beginning of mother’s reproductive career, the three variables related to weaning food choice, and maternal participation in the market economy.

- 2) One using only three sub-variables, each with direct links to modernization: Fertility status, Reported taking of advice from biomedical professionals regarding infant and young child feeding, and Maternal participation in the market economy.

### **S text 3.3: Results of sensitivity analyses using alternative scorings of ModTrad**

The results of our sensitivity analyses regarding alternative scorings of ModTrad are reported in S Tables 1-4. These results are broadly consistent with our main results. ExBF is associated with mode of cultural learning but not with ModTrad Score. AllBF is associated with ModTrad Score, but not with mode of cultural learning.

**S Table 3.3.1: Model summary for analyses of effects of modernization (ModTrad alternative score 1) and mode of cultural learning on log 10 duration of exBF.**

Fixed effect	Estimate	Standard Error	p-value
Intercept	0.8254	0.0519	0.0000***
ModTrad Score Alt 1	0.0019	0.0118	0.8695
Cultural learning fidelity score	0.1440	0.0451	0.0020**
Village	-0.0117	0.0408	0.7744

**S Table 3.3.2: Model summary for analyses of effects of modernization (ModTrad alternative score 1) and mode of cultural learning on log 10 duration of exBF.**

Fixed effect	Estimate	Standard Error	p-value
Intercept	0.8104	0.04778	0.0000***
ModTrad Score, Alt 2	0.0138	0.0203	0.4972
Cultural learning fidelity score	0.1386	0.0430	0.0041**
Village	-0.0191	0.0430	0.6574

**S Table 3.3.3: Model summary for analyses of effects of modernization (ModTrad alternative score 2) and mode of cultural learning on log 10 duration of allBF.**

Fixed effect	Estimate	Standard Error	95% CI	p-value
Intercept	1.2165	0.05466		0.0000***
ModTrad Score, Alt 2	0.0290	0.0117		0.0155*
Cultural learning fidelity score	0.0327	0.0468		0.4870
Village	0.1210	0.0414		0.0046**
Parity status	0.0695	0.0144		0.0000***
Access to help with infant feeding	-0.0149	0.0178		0.4057

**S Table 3.3.4: Model summary for analyses of effects of modernization (ModTrad alternative score 1) and mode of cultural learning on log 10 duration of allBF (log 10 duration of allBF).**

Fixed effect	Estimate	Standard Error	95% CI	p-value
Intercept	1.2466	0.0514		0.0000***
ModTrad Score, Alt 2	0.0408	0.0207		0.0501
Cultural learning fidelity score	0.0233	0.0483		0.6314
Village	0.1173	0.0430		0.0079**
Parity status	0.0690	0.0144		0.0000***
Access to help with infant feeding	-0.0172	0.0182		0.3491