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RESEARCH ARTICLE

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Energy-related influences on variation in breastfeeding duration among indigenous Maya women from Guatemala

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Abstract

Objectives: The causes of variation in breastfeeding duration in humans are poorly understood, but life history factors related to maternal energetics drive much of the variation in lactation duration in nonhuman animals. With this in mind, we investigated whether four energy-related factors influence variation in breastfeeding duration in a non-industrial human population: (1) mortality risk during mother's development (assessed via mother's adult height), (2) reliance on nutrient-dense weaning foods, (3) access to and need for help with infant feeding and care ("allomaternal care"), and (4) maternal tradeoffs between current and future reproduction (measured via child's birth order).

Materials and methods: The data pertain to 51 Kakchiquel-speaking Maya mothers and 283 children from a village in rural Guatemala. We developed a linear mixed model to evaluate the relationships between breastfeeding duration and the energy-related factors.

Results: Duration of breastfeeding was associated with two of the energy-related factors in the ways we predicted but not with the other two. Contrary to predictions, taller mothers breastfed for shorter periods and we found no evidence that weanling diet quality impacts breastfeeding duration. As predicted, women who had more help with infants breastfed for shorter periods, and later-born infants breastfed longer than earlier-born ones.

Discussion: The results regarding allomaternal care suggest that help reduces mothers' lactation demands. The energy saved may be redirected to increasing fecundity or investment in other children. The birth order result suggests that children born to mothers nearing reproductive senescence receive higher levels of investment, which likely impacts children's fitness.

KEYWORDS
allocare, demography, lactation, life history, wean

1 | INTRODUCTION

Breastfeeding duration varies markedly among and within human populations. This variation warrants attention because it appears to affect both health and demography. Longer durations of breastfeeding are associated with reduced offspring morbidity and mortality in infancy and early childhood (Adair et al., 2013; Kramer & Kakuma, 2012; Kay et al., 2014; Rollins et al., 2016; Victora et al., 2016). Extended breastfeeding is also associated with positive somatic and psychological outcomes in later life (Godfrey, Gluckman, & Hanson, 2010; Victora et al., 2015). In addition to benefitting children, longer breastfeeding appears to reduce a mother's risks of developing a number of noncommunicable diseases, including some reproductive cancers, heart disease, and diabetes (Rollins et al., 2016; Victora et al., 2016). With regard to demography, the duration of breastfeeding impacts interbirth interval and fertility (Howie & McNeilly, 1982; Valeggia & Ellison, 2001; Vitzthum, 2009). As such, when women stop breastfeeding their children affects the size, growth rate, and structure of the population

to which they belong (Hamilton et al., 2009; Kuzawa & Bragg, 2012; Newson & Richerson, 2013; Wells & Stock, 2007). Given the health and demographic effects of breastfeeding duration, identifying the factors that influence its variation has the potential both to improve understanding of the history of our species and to inform public policy.

Work carried out over the last 25 years suggests that many of the differences in duration of lactation among species can be accounted for by maternal energetic status as well as by long- and short-term factors that influence that status over the course of a mother's life (hereafter "energy-related factors") (Charnov & Berrigan, 1993; Hamilton, Davidson, Sibly, & Brown, 2011; Isler & van Schaik, 2012; Lee, 1996; Psouni, Janke, & Garwicz, 2012). The relationships between energy-related factors (such as body size, brain size, and diet quality) and lactation duration can be explained by life history theory. Life history theory is based on the assumption that the time and energy available to an organism for growth and development, reproduction, and body maintenance are limited. The theory holds that, because time and energy allocated to one purpose (e.g., lactation) cannot be allocated to others (e.g., conception and gestation of subsequent offspring), investments in one part of the life course require tradeoffs in others. The main corollary of this idea is that organisms seek to distribute their time and energy in a way that maximizes reproductive fitness, given their environmental circumstances (Stearns, 1976, 1992).

Some evidence indicates that the breastfeeding patterns of human mother–child pairs are likely to be constrained and/or driven by at least some of the same energy-related life history factors that affect cross-species variation in lactation duration (Gray, 1996; Meehan, Quinlan, & Malcom, 2013; Quinlan, Quinlan, & Flinn, 2003; Valeggia & Ellison, 2004, 2009; Worthman, Jenkins, Stallings, & Lai, 1993). Yet, the majority of anthropological studies on human breastfeeding variation have concentrated on social, cultural, and economic influences on breastfeeding (Gray, 1995; Levine, 1988; Nerlove, 1974; Quinlan & Quinlan, 2008; Sellen, 2001; Veile & Kramer 2015; Veile, Martin, McAllister, & Gurven, 2014; Wander & Mattison, 2013), often to the exclusion of some or all of the life history drivers and constraints that affect among-species variation. This approach, while offering important insights into the ecology of human breastfeeding, offers us only part of the picture. Focusing on socioeconomic and cultural drivers unique to humans limits our ability to identify the ways in which and the extent to which human patterns derive or deviate from those of other species.

With this in mind, we used data from an indigenous community in Central America to test several hypotheses concerning the impact of maternal life history factors on within-population variation in breastfeeding duration. The hypotheses we tested focus on energy-related factors that appear to affect duration of lactation in other species. We will refer to the hypotheses as the "live fast-die young" (LFDY) hypothesis, the "weanling diet quality" hypothesis, the "allomaternal care" hypothesis, and the "declining opportunity costs" hypothesis.

The LFDY hypothesis is based on the well-established life history tradeoff in energy allocation between breastfeeding and ovarian function (Ellison, Panter-Brick, Lipson, & O'Rourke, 1993; Valeggia & Ellison, 2001, 2004, 2009; Vitzthum, 1994). It contends that whether a mother favors continued breastfeeding of a current child over energetic investment in the conception of an additional child depends on the mortality risk she experienced during development (Charnov & Berrigan, 1993; Walker et al., 2006; Walker & Hamilton, 2008). If death is likely to occur before reproductive senescence, women's fitness will benefit from reproducing early and often. As such, mothers who develop under conditions of high mortality risk should favor 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 strategy 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. These same women are expected to have instead allocated resources to reproduction and to the storage of adipose tissue that can be readily mobilized for future reproduction. Thus, the LFDY hypothesis predicts that shorter, more adipose women will breastfeed for less time than taller, leaner women.

The weanling diet quality hypothesis holds that mothers can partially reduce the costs of extended breastfeeding while continuing to provide adequate nutrition to offspring by feeding them high quality alternatives to breast milk (Langer, 2003, 2008; Psouni et al., 2012). Under this hypothesis, these alternative foods must be liquids, solids, or semi-solids from which infants may easily extract essential nutrients even with short, immature digestive tracts. Cooked meat/fish/insects and other animal products constitute such high quality foods. This hypothesis predicts that mothers who provide their infants with animal foods and other protein-dense foods are likely to cease breastfeeding those infants relatively early.

The allomaternal care hypothesis has been put forward to account for the shorter durations of breastfeeding in humans relative to other apes (Hrdy, 1999, 2009; Kramer, 2010; Newson & Richerson, 2013; see also Bogin, Bragg, & Kuzawa, 2014). The hypothesis argues that non-maternal caregivers can subsidize the energetic costs of infant feeding, carrying, and care that would otherwise be borne exclusively by mothers. Mothers who receive help with infant feeding can invest less via breastfeeding without compromising the supply of energy to infants. They can instead redirect their time and energy towards other things, such as maintenance of their own bodies, support of older children, or conception of a new child. 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 declining opportunity costs hypothesis derives from parent-offspring conflict theory. Parent-offspring conflict theory argues that mothers' and offspring's interests in offspring survivorship differ because offspring only share ~50% of their genes with their mothers (Trivers, 1974). Offspring also share only approximately 50% of their genes with the siblings with whom they compete for maternal investment. As such, individual offspring are expected to favor their own direct fitness interests over their siblings' and thus to seek relatively long, intensive investment via breastfeeding at the expense of their siblings. Mothers' fitness, in contrast, generally benefits from dividing energetic resources among several offspring. That is, mothers are

expected to end breastfeeding earlier than offspring ideally would like, resulting in weaning conflict (McDade, 2001; McDade & Worthman, 1998; Wells, 2003). But, as mothers age, the likelihood of conceiving and producing additional healthy offspring declines. Thus, according to the declining opportunity costs 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 in that child does not come at the cost of a lost opportunity to conceive again. As such, the declining opportunity costs hypothesis predicts that mothers should breastfeed later-born children longer than they breastfed children produced earlier in their reproductive careers.

In keeping with these hypotheses, previous research suggests that duration of breastfeeding is associated with pace of maternal life history schedule, weanling diet quality, and reliance on allomaternal care (Gawlik, Walker, & Hochberg, 2011; Psouni et al. 2012; Quinlan & Quinlan, 2008). In addition, some evidence supports the prediction that later-born children should be breastfed longer than earlier-born children (Wander & Mattison, 2013). There are, however, a number of reasons why additional work is required. 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 bias in effect estimates. Second, though their logic extends from the cross-species and cross-populations scales to the inter-individual scale, neither the LFDY hypothesis nor the weanling diet quality hypothesis has been formally tested within a single human population with respect to their implications for breastfeeding duration. The variables relevant to these hypotheses—maternal body size and choice of weaning foods—are central to both contemporary public health research (Carling, Demment, Kjolhede, & Olson, 2015; Kramer & Kakuma, 2012) and human evolutionary studies (Bogin et al., 2014; Schwartz, 2012). So, it is important that we assess the effects of these variables on breastfeeding as rigorously and in as many contexts as possible. Lastly, the currently available evidence regarding the declining opportunity costs and the allomaternal care hypotheses is mixed, possibly due to weaknesses in previous studies. Given these concerns, additional evaluations of the allomaternal care and declining opportunity costs hypotheses are needed. The study reported here uses new data from a traditional, subsistence-level village in the Highlands of Guatemala to begin to address these issues.

2 | MATERIALS AND METHODS

2.1 | Ethnographic context

The data were collected as part of a long-term field project directed by PN. The project's main goal is to investigate the evolutionary ecologies, life histories, and physiologies of the women, men, and children of two Maya villages located in the Sololá Department of Guatemala's Highlands.

The data were collected from one of the two villages. This village was chosen because, unlike the other, it appears to be predominantly natural fertility, based on reports of low contraception use, limited access to biomedical care, and high average parity. Situated at ~1,500 to 1,600 m above sea level in rugged, mountainous terrain and accessible to other communities only by boat, the village is home to approximately 1,300 indigenous Kakchiquel-speaking Maya people (Dowsett, Eckert, & Kowolik, 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 make regular trips to city markets to sell surplus coffee and corn and, for 25% of households, at least some of these market sales trips were by mothers (unpublished data). Women, men, and children all participate in food production, but men are more likely than women or children to do small amounts of farm-related wage labor—only 8% of mothers sampled reported earning hourly wages for domestic or farm labor. All family members contribute to the collection and carrying of the firewood required for heating and cooking. Women and adolescent girls carry out the bulk of the domestic work in addition to their food production tasks: they are responsible for cooking, cleaning, textile production, and some of the sales of food and textiles at the market. Most of the childcare for infants and toddlers is provided by their mothers and older sisters, although some grandmothers also provide substantial amounts of care.

The diet in the village, regardless of life history stage or sex, is limited in diversity and nutrients, especially with respect to sources of fat, protein, and many micronutrients. Corn is 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 are the 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).

The diets of infants and young children generally consist predominantly or exclusively of breast milk until ~6 to 8 months of age. After this, mothers and/or other caregivers begin to introduce a variety of weaning foods, the most common of which are maize porridge, maize tortillas, mashed vegetables, and a fortified porridge called "Incaparina." Approximately 15% of mothers also report that beans, eggs, and/or chicken broth are important foods to introduce during the second half of an infant's first year of life. A handful of mothers consider coffee and/or soda to be suitable first liquids for babies (unpublished data).

2.2 | Data collection

Interview data were collected from 60 married, multiparous women of reproductive age. We selected the individuals in question for interview because longitudinal data on anthropometry and reproductive history were available for them. Participants provided consent before commencement of the study, and they 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). The interviews were carried out in 2013.

We interviewed each participant twice. The first interview focused on breastfeeding behavior–including the selection and timing of

TABLE 1 Summary of fixed effects (explanatory variables) included in linear mixed effects model, the hypotheses to which they relate, and their predicted effects on variation in duration of breastfeeding

Fixed effect	Variable type	Units/scoring	Hypothesis	Predicted relationship with duration of breastfeeding
Mother's height	Continuous	cm	Live fast-die young	Positive association
Use of protein-dense foods as preferred weaning foods	Categorical, binary	"1" if meat, fish, eggs, and/or beans reported as preferred weaning food, "0" if otherwise	Weanling diet quality	Negative association
Reliance on help with infant feeding and care	Ordinal	"2" if "a lot" of help reported, "1" if "a little" help reported, "0" if "no" help reported	Alloparental care	Negative association
Mother earns	Categorical, binary (proxy)	"1" if wage earning or market selling reported, "0" if otherwise	Alloparental care	Negative association
Child's status as a last or second-to-last born child	Categorical, binary	"1" if last- or second-last born, "0" if otherwise	Declining opportunity costs	Positive association
Traditional-ness of family	Continuous	Higher score if more "traditional," lower if more "modernized"	Control variable	Positive association

introduction of preferred weaning foods–and on maternal access to/reliance on allomaternal care during infancy and early childhood. The second interview was a broader questionnaire on household composition, household member workloads, maternal reproductive histories, and other demographic factors. These demography-focused interviews revealed that participants ranged in age from 28 to 55 years (mean = 40.7), in age at first birth from 15 to 28 years (mean = 20.3), and in interbirth interval from 1.9 to 7 years (mean = 3.0). Among the post-menopausal participants, mean total fertility was 8.2, with a range from 4 to 14. Both sets of interviews were carried out in Kakchiquel by six trained, bilingual field assistants from neighboring villages. Kakchiquel responses were translated instantaneously 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 participants was verified with one of the local field assistants using a standard translation-back translation method.

We also gathered anthropometric data for the majority of the women. Height (in cm) and weight (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 weight-for-height in non-pregnant women. Women who did not complete all components of anthropometric assessments at least once in each field season were also excluded from the final sample.

Seven data points were excluded because they were missing data for one or more of the independent variables. Two others were excluded because they were inexplicable outliers. Thus, the complete dataset pertains to 51 mothers and 283 children born to those mothers.

The dataset includes values for nine variables: (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 her first conception, (4) mother's age, (5) whether or not the mother reported preferring to regularly give her children protein-dense complementary foods (hereafter "weanling diet quality"),[1] (6) whether the mother reported receiving "no help," "a little help," or "a lot of help" with infant feeding (hereafter "help with infant feeding"), (7) whether or not the mother generates and controls some of the family's financial resources (hereafter "mother earns")[2] (8) whether or not the child is one of the last two of a mother's reproductive career,[3] and (9) a meta-variable that we call "traditional-ness." The "mother earns" variable was used as a proxy for work outside the home/farm and thus for need of allomaternal care, while the "traditional-ness" 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. Further information on how the estimated weight and "traditional-ness" variables were calculated is available in the supplementary materials (S Text 1 and S Text 2, respectively).

2.3 | Analyses

To test the predictions of the four hypotheses, we developed a linear mixed effects model. The model included seven of the nine variables. It also included a random intercept effect term for each mother to allow for random error attributable to individual factors. Recalled duration of breastfeeding in months for each child was the response variable, and the other six variables were treated as explanatory variables. How each of explanatory variables relates to the predictions of hypotheses is outlined in Table 1. The two variables we excluded from the model were mother's estimated weight at first conception and mother's age. They were not used in our main analyses because the weight variable is highly correlated with maternal height (the most standard and reliable proxy for maternal developmental conditions) and the age variable is highly correlated with mother's reproductive career stage. Thus, the

TABLE 2 Summary of distributions of duration of breastfeeding and of continuous fixed effects (explanatory variables) included in linear mixed effects model

Fixed effect	Mean	Standard error	Range
Duration of breastfeeding (months)	28.2	1.5	5–84
Mother's height (cm)	146.7	0.03	134.5–158.8
Reliance on help with infant feeding and care	1.0	0.11	0–2
Traditional-ness of family	6.4	1.85	2–9

inclusion of these variables in the model created multi-collinearity and variance inflation problems. That said, we included both variables in a supplementary analysis with the aim of clarifying our main results pertaining to the LFDY hypothesis (see S Text 3). Because we had clear *a priori* expectations regarding the direction of the relationships between the response and explanatory variables, we used one-tailed significance tests in both the main and supplementary models. The main and supplementary models were created using the nlme package in R (Pinheiro, Bates, DeBroy, Sarkar, & R Core Team, 2015).

3 | RESULTS

In our sample, duration of breastfeeding varies substantially both within and among families. The minimum duration of breastfeeding was 5 months and the maximum was 84 months. The range of duration of breastfeeding within a family could also be large. We observed within-family ranges of 24–84 months. The mean (and standard error) for duration of breastfeeding across all children in the sample was 28.2 (±1.5) months. These descriptive statistics, along with information regarding the spreads and central tendencies of the non-dichotomous explanatory variables, are summarized in Table 2.

We present estimates of the fixed effects (explanatory and control variables) in our model in Table 3 and describe the results pertaining to each hypothesis separately. All effects described are adjusted for the effects of the other predictors in the model.

Regarding the LFDY hypothesis, contrary to expectations, we found that duration of breastfeeding (in months) was *negatively* associated with maternal height (although the one-tailed test result was non-significant, the 95% CI for the effect indicates a negative impact). This result does not offer support for the predictions of the LFDY hypothesis as currently formulated. To make sense of this unexpected result, we looked at our supplementary models in which we adjusted for maternal age and/or estimated maternal weight at the beginning of a woman's reproductive career. This follow-up analysis indicated that duration of breastfeeding was negatively associated with maternal heaviness-for-height. These results also showed that, after adjusting for estimated weight around the time of first conception, the slope of the relationship between duration of breastfeeding and maternal height was not significantly different from zero (see S Text 3). These supplementary findings *may* be consistent with the predictions of the LFDY hypothesis, but they provide neither clear evidence that we should reject the null hypothesis nor clear evidence that we should seek alternative explanations for relationships between duration of breastfeeding and maternal anthropometric factors.

With respect to the weanling diet quality hypothesis, we found that duration of breastfeeding (in months) 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 weanling diet quality hypothesis as formulated here.

Concerning the allomaternal care hypothesis, we did find that duration of breastfeeding (in months) 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 declining opportunity costs hypothesis. Duration of breastfeeding (in months) was significantly positively associated with the child's status as last or second-to-

TABLE 3 Estimated effects of mother's height, weanling food quality, reliance on alloparental care, need for alloparental care (mother earns), and declining opportunity costs (child's status as last or second-to-last born) on variation in duration of breastfeeding (months)

Fixed Effect	Estimate	95% Confidence interval	One-tailed p-value
Intercept	90.788	33.136–148.441	0.0011**
Mother's height (cm)	−0.414	−0.796 to −0.031	0.9807
Use of protein-dense foods as preferred weaning foods	−0.096	−5.398 to 5.206	0.4859
Reliance on help with infant feeding and care	−2.845	−5.158 to −0.531	0.0098**
Mother earns	−4.989	−9.486 to −0.312	0.0189*
Child's status as a last or second-to-last born child	6.050	3.578–8.523	0.0000****
Traditional-ness of family	0.611	−1.233 to 2.456	0.2587

*$p \geq 0.05$; **$p \geq 0.01$; ***$p \geq 0.001$; ****$p \geq 0.0001$.

last-born. This result is consistent with the predictions of the hypothesis.

4 | DISCUSSION

4.1 | 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 energy-related maternal life history factors, using data from 51 Kakchiquel-speaking Maya mothers and 283 children from the rural Central Highlands of Guatemala. Our analyses suggested that taller mothers have shorter durations of breastfeeding than shorter mothers, which is inconsistent with the predictions of the LFDY hypothesis. The analyses yielded no evidence of an association between duration of breastfeeding and our measure of weanling diet quality (i.e., whether or not a mother listed a protein-dense food among her preferred weaning foods). Thus, our analyses did not offer support for the predictions we derived from the weanling diet quality hypothesis. Third, we found that duration of breastfeeding was significantly negatively associated with both our direct measure of maternal reliance on allomaternal care and our proxy for maternal non-domestic workload, "mother earns," which was assumed to reflect increased *need* for allomaternal care. These results are consistent with the predictions of the allomaternal care hypothesis. Lastly, duration of breastfeeding was positively and significantly associated with child's parity status as a last or second-to-last-born child, which is consistent with the predictions of the declining opportunity costs hypothesis.

4.2 | Limitations of study

There are a number of reasons for caution when interpreting the results of the present study. The use of maternal recall, in some cases years after the behavior of interest ended, may be a cause for concern. Evidence from other populations 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, Scanlon, & Serdula, 2005; Natland, Andersen, Nilsen, Forsmo, & Jacobsen, 2012; Promislow, Gladen, & Sandler, 2005), as was the case for almost all of the children in the study population. However, the aforementioned studies also indicate that a non-trivial minority of women substantially over- or underestimate duration of breastfeeding when re-interviewed. In addition, 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, Da Vanzo, Sastry, Panis, & Peterson, 2001; Holland, 1987). This can be a problem because it often results 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 and/or imprecise.

With this possible shortcoming in mind, we carried out two supplementary analyses. In the first, we classified the breastfeeding durations by 6-month intervals, with the exception of the interval following birth, which was 3 months. Specifically, infants that ceased breastfeeding between birth and 3 months were scored as "1," infants weaned between 3 and 9 months as "2," infants weaned between 9 and 15 months as "3," infants weaned between 15 and 21 months as "4," and so on. We then used a Poisson generalized linear mixed model to describe these classificatory scores as a function of our predictors. In the second analysis, we used generalized estimating equations (GEEs) to assess the effects of the predictors on the original, continuous breastfeeding data. GEEs are robust to misspecifications of the variance and to correlation that may result from heaping and/or increases in recall error over time (further methods details and results reported in S Text 4). Both of these alternative methods returned results that are consistent with our main findings. Thus, we think the data and therefore our results are reliable. Nonetheless, future prospective studies on breastfeeding duration and related variables will be needed to confirm these findings.

An issue regarding sample structure also warrants consideration. The participating mothers were selected on the basis of prior participation in an earlier set of studies so that we would have longitudinal data for analysis. Our approach thus intentionally excluded women who were not yet childbearing when the project was initiated in 1999. In light of this, the findings reported here suggest that, for older, more conservative members of the population, maternal energy-related life history factors influence variation in duration of breastfeeding. This older subset of the population for which our results appear to apply may be especially of interest, because they have nearly completed their fertility and thus can inform us about the role of breastfeeding ecology in population dynamics. But, future research should include younger women to assess the extent to which our results may be generalizable to the whole population.

We also note that several of our explanatory measures are relatively coarse, especially regarding allomaternal care and weanling diet quality. Our primary measure of allomaternal care does not distinguish among care providers, who presumably have differing social and fitness interests in the health and wellbeing of the children. Our measure of need for allomaternal care does not distinguish among reasons for leaving children in the care of non-mothers. This measure also does not discriminate between the ~25% of mothers who occasionally sell things at market and the ~8% of mothers who undertake long hours of wage labor, even though these different kinds of participation in the market economy may place different kinds of time and energy constraints on breastfeeding. The measure of weanling diet quality focuses only on preferences regarding protein-density of weaning foods, not on the structure of the weaning food or its method of preparation. Furthermore, it does not take into account within- or between-caregiver variation with which a reported preferred weaning food was given.

Yet, despite the above-mentioned need for caution, we view our evaluations of the allomaternal care hypothesis and the weanling diet quality hypothesis as reliable. Regarding allomaternal care, we observed that duration of breastfeeding was negatively associated with the help with infant feeding variable and with the mother earns variable, despite the coarseness of our measures. This suggests that there is a strong allomaternal care signal that is detectable in the noise. With respect to

weanling diet quality, our variable, while coarse, is of the same grain as what has been used in cross-species studies (Langer, 2003, 2008; Psouni et al., 2012). As these cross-species studies did detect a negative effect of weanling diet quality on duration of lactation using a metric of diet quality similar to ours (i.e., a categorical one based on protein richness), it appears that such measures can be sufficient for modeling the relationship of interest. Nevertheless, it is possible that there is a diet quality effect in our data that we failed to identify. Future work using a finer-grained weanling food quality measure will allow us to make stronger claims about our assessment of the weanling diet quality hypothesis.

4.3 | Duration of breastfeeding and life history tradeoffs

Although there is a need for some caution regarding the results, this study suggests that a number of energy-related life history factors that influence duration of lactation in nonhuman animals also affect duration of breastfeeding in humans. 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 status.

That there is a negative association between maternal height and duration of breastfeeding is surprising both from a theoretical perspective and in light of some previous empirical results (Charnov & Berrigan, 1993; Walker et al., 2006; Walker & Hamilton, 2008). To reiterate, the LFDY hypothesis is grounded in life history theory, which predicts trade-offs between growth and reproduction (Migliano, Vinicius, & Lahr, 2007, 2010; Walker et al., 2006; Walker & Hamilton, 2008). As such, we expect reductions in investment in growth to be associated with increased investment in quantity of offspring and thus also in decreased investment via lactation in individual offspring. As regards previous empirical results, several earlier studies found that women who develop under conditions of high mortality risk tend to stop growing early (and thus have shorter adult heights) and to have fast life histories (Migliano et al., 2007, 2010; Walker et al., 2006; Walker & Hamilton, 2008). The available cross-population evidence indicates that this positive association between height and pace of life history holds for duration of breastfeeding (Gawlik & Hochberg, 2012; Gawlik et al., 2011). That being said, a negative association between duration of breastfeeding and height is not unprecedented, at least in within-population studies. Although previous within-population studies have not explicitly evaluated predictions of the LFDY hypothesis as it relates to duration of breastfeeding and maternal height, several such 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. For example, Simondon and Simondon (1998) reported a negative association between the variables of interest in a sample of Senegalese women. Petrucci Gigante, Victora, and Barros (2000) found 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.

There are two main potential explanations for our analysis's failure to support the LFDY hypothesis. First, factors other than extrinsic morbidity and mortality risk may contribute to female height variation in some populations (Vercellotti et al., 2014). Recent work suggests that short height results from sped up life histories in some cases; in other cases, it can be attributed to childhood growth faltering in response to cohort-specific shocks or cultural patterns; in still others, familial/regional effects contribute to short height (Rosenquist et al., 2015; Rozzi, Koudou, Froment, Le Bouc, & Botton, 2015; Sear, 2010; Vercellotti et al., 2014). In our sample, cohort effects could contribute to height variation and explain the negative association between breastfeeding and height. That is, the association may suggest that shorter mothers belong to a particular cohort that happens to also favor an extended breastfeeding strategy. However, adjusting for mother's age (a loose proxy for cohort) in our supplementary analyses had little effect on these or the main results (see S Text 3), suggesting that the cohort-based explanation is unlikely to account for the height effect.

The second potential explanation for the negative association between duration of breastfeeding and maternal height is one that is consistent with our supplementary analyses. To reiterate, these analyses adjusted for estimated maternal weight around the time of first conception. According to this view, the association between duration of breastfeeding and height may not reflect a height effect per se. Rather, it may reflect the impact of maternal weight on duration of breastfeeding, since weight is, of course, highly positively correlated with height. Importantly, like height, adiposity, coarsely measured as weight-for-height, can be an indicator of maternal developmental conditions (Gawlik & Hochberg, 2012; Gawlik et al., 2011). But—unlike height—a woman's weight-for-height at the beginning of her reproductive career is *expected* to be negatively associated with duration of breastfeeding under the LFDY hypothesis. Women who developed under high mortality are predicted to begin storing easily mobilizable fat for reproduction relatively early in adolescence rather than continuing to grow in height. Our supplementary analyses indicate that duration of breastfeeding is indeed negatively associated with estimated weight around the time of first conception, after adjusting for height (S Text 3). This finding suggests that, at least in this population, weight adjusted for height may be a more important indicator of maternal developmental conditions than height. That being said, the reliability of this assessment is unclear for two reasons. First, multi-collinearity constitutes a substantial shortcoming of the full supplementary model that adjusts for weight and age. Second, the weight measures are retrospective estimates rather than direct measures. Given these concerns, prospective data explicitly focused on adolescent weight as it relates to developmental conditions are needed to confirm the findings of our supplementary analyses.

The negative associations between duration of breastfeeding and both amount of help with infant feeding and maternal earning (which was treated as a proxy for need for help with care) accord with theoretical work 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 & Quinlan, 2008; Quinlan et al., 2003). Our findings also dovetail with evidence from the biomedical sociology 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 (Baker & Milligan, 2008; Scott, Binns, Oddy, & Graham, 2006; Van Esterik & 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 allomaternal care facilitates relatively early cessation of breastfeeding. This new evidence, especially when combined with the mounting evidence from other studies, supports the suggestion that reductions in the duration of human breastfeeding and birth spacing co-evolved with increased reliance on cooperative infant care (Hrdy, 1999, 2009; Kramer & Ellison, 2010).

The effects of the variables related to allomothering are substantial. Mothers who reported receiving "a lot" of help with infant feeding breastfed for an average of ~3 months less than mothers who received "no" or "a little help," adjusting for other factors in the model. Mothers who reported earning breastfed for an average of ~5 months less than mothers who did not report earning. Insofar as duration of breastfeeding impacts birth spacing, a 5-month reduction in breastfeeding from the population's mean of ~28 months and thus in interbirth interval relative to the population's mean birth interval of ~3 years could lead to a total fertility increase of ~1.5 children (from 8.2 children to 9.7) over a 25-year reproductive lifespan. This means our data are consistent with the hypothesis that reductions in the costs to mothers of extended breastfeeding afforded by allomaternal care can contribute to higher fertility, with downstream effects on other kinds of population dynamics (Hamilton et al., 2009; Wells & Stock, 2007).

Our 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). Because ovarian reserves deplete through time and quality of oocytes degrade as women approach menopause, mothers' opportunities to conceive healthy offspring decrease with age. As such, mother and offspring interests and therefore duration of breastfeeding optima become increasingly likely to converge near those of the offspring as maternal age and child's birth order increase (Ellison et al., 1993; Pennington & Harpending, 1988). Our results 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 last-born pattern is compelling in its consistency with theoretical expectations, empirically, there is little comparative evidence from other natural fertility populations that maternal investment via lactation increases over a mother's reproductive career. Only two previous studies have explicitly evaluated the declining opportunity costs hypothesis with a focus on breastfeeding duration. One of these detected the predicted effect (Wander & Mattison, 2013) but the other did not (Quinlan et al., 2003). Both studies assessed the impacts of maternal age and parity on breastfeeding duration cross-sectionally. There is reason to think that the cross-sectional approach is less sensitive than the longitudinal one used in the present study and is therefore less likely to detect the effect predicted by the declining opportunity costs hypothesis 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 investing energy in breastfeeding decline. That said, there is need for additional evaluation of this hypothesis in other natural fertility populations before we can be confident in the robustness of this pattern.

We did not find a statistically significant effect of reported weaning food preferences on duration of breastfeeding. This finding may be somewhat surprising, because there is evidence from large-scale societies suggesting that weaned infants may consume more protein-dense diets than partially breastfed infants of the same age (Gondolf, Tetens, Michaelsen, & Trolle, 2012). So, it may be that, in this study population, other factors are more important than use of animal-based or other protein-dense weaning foods in determining length of maternal investment via lactation. Our data suggest that child's birth order and mother's reliance on allomaternal care may represent such key factors. Alternatively, the lack of evidence for a weanling diet quality effect may be attributable to the coarseness of the approach we used to assess the protein-richness of infants' diets in our sample.

4.4 | Implications

The study reported here has implications for the evolution and ecology of duration of breastfeeding in humans, for human demography, and possibly for public health. Specifically, we found that duration of breastfeeding may be negatively associated with maternal height and/or weight-for-height in our sample. Although it is certainly not clear that this pattern is common across small-scale populations or even robust in the study population, the result does hint that a mother's own growth and development may influence 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 (alongside, for example, biomolecular methods; see review by Jay [2009]) for reconstructing breastfeeding behavior in past human populations for which adult female heights and/or weights can be estimated.

In addition, our findings indicate that greater access to and need for help with infant feeding is associated with reduced duration of breastfeeding. Access to allomaternal care likely relaxes the constraints on mothers' energy budgets, freeing maternal energy for allocation to purposes other than lactation. The extra energy made available to mothers through 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 allomaternal care may have been a crucial factor facilitating the development of short birth spacing and high fertility in humans (Hrdy, 1999, 2009; Newson, 2013). This allomaternal care finding may also be relevant to developing public health policy. Insofar as major public health organizations such as the World Health Organization (WHO) aim to promote extended breastfeeding to reduce morbidity and mortality in mothers and children, such institutions should take into account that mothers' needs for and access to allocare influence breastfeeding durations.

Lastly, the positive association between duration of breastfeeding and later-born status we observed may be indicative of 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 & Hinde, 2008). So, it seems likely that much of what we observe with respect to breastfeeding behavior reflects mothers (unconsciously) asserting their overall fitness interests. However, if the assumptions of the declining opportunity costs hypothesis are correct, duration of breastfeeding for later-born children probably reflects a convergence of maternal and offspring preferences. Paying attention to how long later-born children continue to breastfeed may inform us about the breastfeeding strategies most beneficial to infant health and wellbeing in a particular ecological context, and these patterns can potentially inform public health policy. Comparisons of breastfeeding durations between later-born children and their earlier-born sibs 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 allocations in the face of both risks and opportunities.

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NOTES ON CONTRIBUTIONS

All authors (LM, MC, RA, DS, and PN) contributed to the development of the study's aims, design, and interpretation of results, and co-authors MC, RA, and PN edited the text after it was drafted by the lead author. In addition, LM assisted with data collection and carried out the main analyses. MC assisted with field preparation and helped to develop the structure of the manuscript. RA developed methods for estimating mother's past weights, carried out robusticity analyses, and assisted with the main analyses. PN was the principal investigator for the field project.

ENDNOTES

[1] Women were asked to free-list items they preferred to give to each of their children as introductory foods. Children of mothers who listed meat, fish, eggs, beans, and/or dairy among their preferred weaning foods were coded as having a relatively high quality weanling diet, whereas children of mothers who listed only low protein density foods (e.g., mashed vegetables, fruits, tortillas, maize porridge) were coded as having a relatively low quality weanling diet.

[2] Women were asked if they held a salaried job and, if so, how much time it required. Women were also asked if they sold food, handicrafts, or other goods at market and, if so, how often they engaged in this activity. Women who had salaried jobs and/or who sold goods at market two or more times per week were coded as earners; all other women were coded as non-earners.

[3] 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 & 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' 38th birthday as later-born children.

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