

In Poor Families, Mothers' Milk is Richer for Daughters than Sons: A Test of Trivers–Willard Hypothesis in Agropastoral Settlements in Northern Kenya

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ABSTRACT The Trivers–Willard hypothesis predicts the unequal parental investment between daughters and sons, depending on maternal condition and offspring reproductive potential. Specifically, in polygynous populations where males have higher reproductive variance than females, it predicts that mothers in good condition will invest more in sons, whereas mothers in poor condition will invest more in daughters. Previous studies testing this hypothesis focused on behavioral investment, whereas few examined biological investment. This study investigates the Trivers–Willard hypothesis on both behavioral and biological parental investment by examining breastfeeding frequencies and breast milk fat concentrations. Data from exclusively breastfeeding mothers in Northern Kenya were used to test hypotheses: Economically sufficient mothers will breastfeed sons more frequently than daughters, whereas poor mothers will breastfeed daughters more frequently than sons, and economically sufficient moth-

ers will produce breast milk with higher fat concentration for sons than daughters, whereas poor mothers will produce breast milk with higher fat concentration for daughters than sons. Linear regression models were applied, using breastfeeding frequency or log-transformed milk fat as the dependent variable, and offspring's sex (son = 1/daughter = 0), socioeconomic status (higher = 1/lower = 0), and the sex-wealth interaction as the predictors, controlling for covariates. Our results only supported the milk fat hypothesis: infant's sex and socioeconomic status interacted ($P = 0.014$, $n = 72$) in their relation with milk fat concentration. The model estimated that economically sufficient mothers produced richer milk for sons than daughters (2.8 vs. 0.6 gm/dl) while poor mothers produced richer milk for daughters than sons (2.6 vs. 2.3 gm/dl). Further research on milk constituents in relation to offspring's sex is warranted. *Am J Phys Anthropol* 149:52–59, 2012. © 2012 Wiley Periodicals, Inc.

In their 1973 article, Robert Trivers and Dan Willard proposed an important hypothesis regarding parental investment. Now referred to as the Trivers–Willard hypothesis, it predicted that natural selection should favor unequal parental investment between daughters and sons under certain maternal conditions and the reproductive potential of her offspring. The hypothesis posits that mothers in good condition should invest more in sons while mothers in poor condition should invest more in daughters (Trivers and Willard, 1973). This logic reflects the observation that in sexually dimorphic polygynous mammalian species, including humans, males tend to have higher reproductive variance than females (Trivers and Willard, 1973; Howell, 1979; Hewison and Gaillard, 1999; Hinde, 2009). Different variances originate from biologically based differential parental effort between sexes, with females devoting disproportionately more time and energy to each offspring from conception to lactation and beyond (Roth, 2004). This difference is heightened in polygynous societies because reproductive success of males with a large number of mates/spouses can further increase substantially relative to males with an exclusive single partner (Roth, 2004). Given this assumption of different reproductive potential between sexes, mothers in good condition, who can provide more resources to offspring, can achieve higher reproductive success through preferential investment in sons rather than through daughters. Conversely, mothers in poor

condition, who can provide fewer resources, attain higher reproductive success by investing more in daughters who can choose a mate of higher status, known as hypergamy, rather than sons who, without sufficient resources, will not be able to adequately compete for mates (Trivers and Willard, 1973; Dickemann, 1979a,b; Quinlan et al., 2005).

For human postnatal parental investment, the Trivers–Willard hypothesis has been tested using various kinds of parental investment given to offspring, such as the levels

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of education (e.g., Hopcroft, 2003, 2005), medical care (Cronk, 1989, 2000; Guggenheim et al., 2007; Kushunick, 2010), time investment (Keller et al., 2001), and breastfeeding practices (Cronk, 1989, 2000; Gaulin and Robbins, 1991; Bereczkei and Dunbar, 1997; Koziel and Ulijaszek, 2001; Quinlan et al., 2003; Tracer, 2009; Fujita and Roth, 2011). These studies overall provide mixed results, but most examine the Trivers–Willard hypothesis with respect to the behavioral domain of parental investment. Biological investments such as the nutritional content of breast milk have only recently been explicitly examined by a few studies (Hinde, 2009; Powe et al., 2010).

Milk synthesis is perhaps the most energetically costly component of parental investment for the mother (Sellen, 2007; Tracer, 2009; Hinde and Milligan, 2011). Yet, our evolutionary ecological understanding of variation in human milk synthesis is still limited (Hinde, 2009). Milk fat is the main source of calories, fat soluble vitamins, and fatty acids for infants, all of which are indispensable for infant growth, development (Jelliffe and Jelliffe, 1978; Lammi-Keefe and Jensen, 1984), and ultimately their survival. Despite milk fat's important role as the major energy source in human milk, it is the most variable component of breast milk (Mitoulas et al., 2002). Milk fat concentrations have been found to vary with maternal nutritional status (Bailey, 1965; Jelliffe and Jelliffe, 1978), maternal weight gains during pregnancy (Michaelsen et al., 1995), and the duration of lactation (Underwood et al., 1970; Mandel et al., 2005; Szabo et al., 2010). The amount of milk fat in human milk also fluctuates within each day (Jennes, 1979; Prentice et al., 1981) and within each nursing episode (Jennes, 1979; Saarela et al., 2005; Murase et al., 2009).

An enormous body of literature in nutrition and pediatrics documents the nutritional content of human breast milk and factors associated with variations in that nutritional content (e.g., Bailey, 1965; Underwood et al., 1970; Hanafy et al., 1972; Lindblad and Rahimtoola, 1974; Lauber and Reinhardt, 1979; Brown et al., 1986; Michaelsen et al., 1995; Mitoulas et al., 2002; Saarela et al., 2005; Kent et al., 2006; Murase et al., 2009; Szabo et al., 2010). This literature, however, is largely limited to descriptive work, although some important cross-cultural and ecological comparisons exist (e.g., Jelliffe and Jelliffe, 1978; Jennes, 1979). Furthermore, except for a small number of studies (e.g., Michaelsen et al., 1995 for milk volume consumed by boys vs. girls), this literature is devoid of information on possible variations in maternal breast milk synthesis associated with the offspring's sex.

Recent studies indicate that individual variations in milk constituents may reflect maternal and infant characteristics consistent with predictions from the evolution of parental investment strategies for feeding young (Sellen, 2007) and the evolution of life histories (Stearns, 1992; Fujita, 2008, 2011; Hinde, 2009; Powe et al., 2010; Hinde and Milligan, 2011). Particularly noteworthy are variations in milk constituents associated with offspring's sex (Hinde, 2009; Powe et al., 2010) and maternal characteristics (Fujita, 2008, 2011; Hinde, 2009).

HYPOTHESES

The study presented here investigates both human behavioral and human biological parental investments by examining variations in breastfeeding frequencies and breast milk fat concentrations using the predictions of the Trivers–Willard hypothesis. Specifically, data from exclusively breastfeeding mothers in Ariaal agropastoral

villages of Northern Kenya were used to test two hypotheses: 1) Economically sufficient mothers will breastfeed sons more frequently than daughters, whereas poor mothers will breastfeed daughters more frequently than sons, and 2) Economically sufficient mothers will produce breast milk with higher fat concentration for sons than daughters, whereas poor mothers will produce breast milk with higher fat concentration for daughters than sons.

METHODS

Sample

The sample consists of breastfeeding mothers in Ariaal agropastoral villages in Marsabit District, Kenya. Ariaal are formerly nomadic pastoralists who once subsisted predominantly on the milk of camel and cattle but are now settled in permanent villages and engage in diversified economy (Fratkin, 1998), combining dry-land maize production and livestock herding for subsistence and cash crops, supplemented with drought food distribution from the government, religious organizations, or non-governmental organizations (Fratkin, 1998; Fratkin et al., 1999; Roth and Fratkin, 2005).

Ariaal people practice polygyny and patrilineal inheritance (Fratkin and Roth, 2005). Family assets such as livestock and land are therefore transferred from fathers to sons (Fratkin, 1998). Women have low status based on the lack of asset ownership as well as a lack of decision rights in marriage, divorce, and birth control (Fratkin, 1998). Ariaal women have on average six children during the course of their reproductive span (Roth, 1994, 1999) and thus spend considerable time and energy on pregnancies, nursing, and child rearing.

Even though women may not own assets in a legal sense, they are responsible for feeding their household using family resources (Fratkin, 1998). Living in permanent settlements has increased the importance of women's contribution to the household economy (Fratkin and Smith, 1995) and nutrition (Sell-Duncan and Obiero, 2000). In settled communities, women principally tend farms/gardens, milk livestock for household consumption, and sell surplus milk or vegetables to customers in towns for income (Roth, 1994, 1999; Smith, 1998). The cash income generated by women in such activities appears to benefit the nutrition of their children. Households in which the adult female has any discretionary resources have been reported to have higher nutritional welfare relative to other equivalent households (Shell-Duncan and Obiero, 2000). Greater levels of maternal autonomy were also found to be positively associated with the nutrition of juvenile children (3–10 years of age but not for infants; Brunson et al., 2009). However, little is known about infants' diets and nutrition in relation to age, sex, and wealth among African pastoral populations (Sellen, 2010), including the Ariaal.

Sampling and data collection

Cross-sectional data from exclusively breastfeeding mothers ($n = 83$) with complete information on breastfeeding frequency, socioeconomic status, and possible covariates (maternal age, parity, time since childbirth, dietary intake of fat, body mass index [BMI], household composition, and community membership) were used in this analysis. This dataset originates from a larger 2006 study (Fujita, 2008) featuring 241 non-pregnant, breast-

feeding mothers recruited through stratified random sampling in Karare (including Parkishon and Hulahula), Kituruni (including Ilpus) and Korr, respectively representing highland and lowland communities. The sampling strata represented five postpartum age-range strata of 0–3, 3–6, 6–9, 9–12, and 12–20 postpartum months. The major economic systems of Karare, Parkishon, and Hulahula (hereafter Karare) include dry land maize cultivation, cattle and small stock-raising, and livestock and milk marketing in Marsabit Town, the district capital. Kituruni and Ilpus (hereafter Kituruni) share the above economic systems but also produce fresh vegetables such as kale. The community of Korr represents lowland desert villages whose land is too arid to sustain cattle-raising or plant cultivation. Rather, camel herding provides important livelihoods for some, but camels are expensive and many residents make a living via wages or more opportunistic activities such as collecting and selling firewood. The institutional review boards of the University of Washington and the Kenya Medical Research Institute approved study procedures for the original study. Data collection methods for variables relevant for the current study are discussed.

Breastfeeding frequency. Nursing frequency per 24 h (1, 2, 3 . . .) was assessed through questionnaires, adopting the methodology of Lande et al. (2003). Mothers were asked to report the breastfeeding frequency during the last 24 h, and to assess if that frequency was a typical daily frequency. All but three mothers confirmed that the 24-h feeding frequency was a good approximation of usual daily frequency. For the three mothers, the reported typical frequency was used for analysis as our research question concerns the typical level of parental investment unaffected by an unusual event (such as child illness).

Milk fat concentrations. In the morning following an overnight fast, mothers manually expressed a sample of foremilk (the milk released at the beginning of the breastfeeding episode, or in this case the manual expression) of ~10 ml from whichever breast was not nursed overnight. Samples were frozen within a few h of collection and kept frozen until analysis. Milk fat concentrations were determined via the Creamatocrit method (Lucas et al., 1978 explained in detail by Wang et al., 1999) which examined the percentage of cream column over the total milk column of thawed and centrifuged milk samples. The average value of triplicate Creamatocrit measures of each milk sample was then converted to milk fat concentration (gm/dl) using the following equation for thawed breast milk (Wang et al., 1999): $Y = 0.54x + 0.39$ where x = Creamatocrit (%) and y = lipid (gm/dl). Some milk vials broke during transport in the field condition, resulting in the smaller sample size for milk fat ($n = 72$) than breastfeeding frequency analysis. As the distribution of milk fat concentrations was skewed, we used natural log values of milk fat concentrations for statistical analysis (see Supporting Information Fig. 1 for the original and transformed distributions).

Infant's sex and socioeconomic status. Sex of the infant (son = 1/daughter = 0) was reported by the mothers in questionnaires. Women were assigned socioeconomic status (SES; higher = 1/lower = 0) using household economic indicators from questionnaires. These included the respondent's self-assessment of her family as poor or not poor (poor = 1/not poor = 0), the size of the land (in acres) owned by their family, and the num-

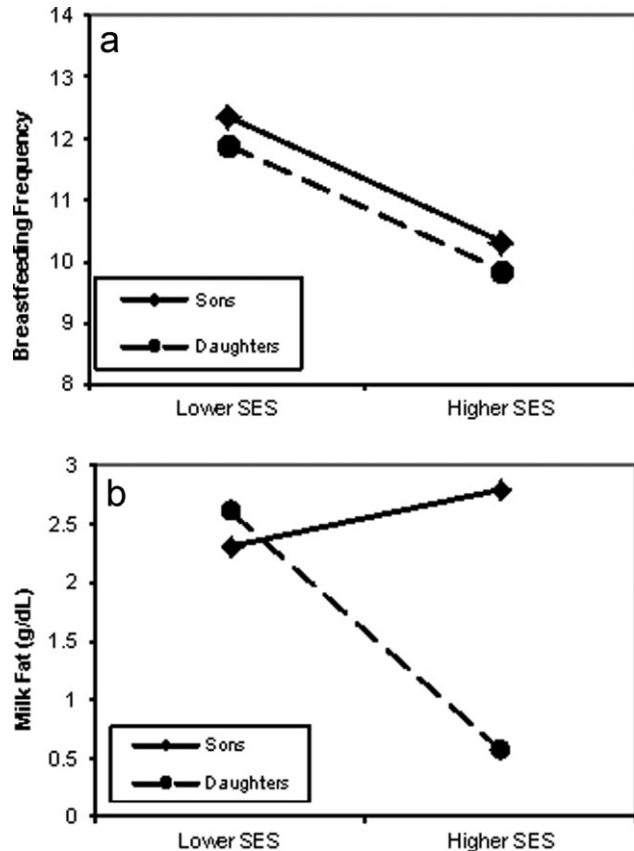


Fig. 1. Regression model predictions for breastfeeding frequencies (a) and milk fat concentrations (b) by socioeconomic (SES) status and offspring sex.

ber of milking animals (camel, cattle, goats, and sheep) held by their family, converted into the Tropical Livestock Unit (TLU) where a camel, a cattle, and a goat/sheep were, respectively, assigned the TLU value of 1, 0.8, and 0.1 to make the comparison of varying livestock compositions possible (Dahl and Hjort, 1976; Roth, 1990). Specifically, women were classified as lower SES if all of the following were true: poor = 1, their land size was <2 acres, and their TLU was ≤ 1 .

Covariates. The information on maternal age (years), parity (1, 2, 3 . . .), time since childbirth (postpartum time in days), and household composition (number of sons/daughters living at home; 1, 2, 3 . . .) were also collected using questionnaires.

Maternal daily dietary intake was estimated by a 24-h dietary recall interview. The mother was asked to report all foods consumed the previous day and estimate the amount in common household units such as cups and spoons. The resulting recall list of foods and portion sizes was converted to daily nutrient intake, using the SIGHT AND LIFE Vitamin A intake calculator (Erhardt, 2003) which estimates dietary fat intake (grams) among other nutrients.

Body weight was taken using a SECA digital scale to the nearest 100 g, and height was measured with an anthropometer to the nearest mm. Resulting measurements were used to derive BMI using the formula: $BMI = \text{weight (kg)} / (\text{height (m)})^2$ (Frisancho, 1990). Dummy variables for community memberships were created

TABLE 1. Characteristics of mothers (mean ± SD)

	Combined (n = 83)	Daughter (n = 36)	Son (n = 47)	t-Test ^a , P	Higher SES ^b (n = 58)	Lower SES (n = 25)	t-Test ^c , P
Maternal age	28.0 ± 6.9	29.6 ± 7.2	26.7 ± 6.4	†	28.5 ± 7.5	26.6 ± 5.0	ns
Parity	3.7 ± 2.3	4.6 ± 2.6	3.1 ± 2.0	**	3.9 ± 2.5	3.4 ± 1.8	ns
Days since childbirth	122 ± 72	127 ± 75	117 ± 69	ns	123 ± 73	119 ± 71	ns
Breastfeeding frequency	9.7 ± 4.0	9.9 ± 3.7	9.5 ± 4.2	ns	9.4 ± 3.8	10.4 ± 4.5	ns
Height (cm)	159 ± 7.2	159 ± 7.8	159 ± 6.8	ns	159 ± 7.8	160 ± 5.4	ns
Weight (kg)	51.8 ± 8.3	51.5 ± 8.8	52.0 ± 8.0	ns	51.2 ± 7.9	53.1 ± 9.0	ns
Body mass index (kg/m ²)	20.5 ± 3.1	20.4 ± 3.1	20.6 ± 3.1	ns	20.4 ± 3.3	20.6 ± 2.7	ns
Dietary energy (Kcal)	1631 ± 627	1706 ± 730	1573 ± 537	ns	1630 ± 585	1632 ± 730	ns
Dietary fat (g)	20.2 ± 12.3	22.6 ± 16.3	18.4 ± 7.6	ns ^d	20.9 ± 13.0	18.7 ± 10.4	ns
Number of sons	1.7 ± 1.3	1.6 ± 1.6	1.7 ± 1.1	ns	1.8 ± 1.4	1.3 ± 1.1	ns
Land size ^e	2.19 ± 3.0	2.03 ± 2.5	2.31 ± 3.4	ns	3.1 ± 3.3	0.2 ± 0.3	**
Tropical livestock unit	1.76 ± 4.3	1.6 ± 3.3	1.9 ± 4.9	ns	2.4 ± 5.0	0.2 ± 0.3	*
Lower SES (%)	30.1	33.3	27.7	ns	–	–	–

^a Two-sample *t*-tests compare mothers with female infants and mothers with male infants. Chi-squared test is reported on the last line. ns: not significant.

^b SES: socioeconomic status.

^c Two-sample *t*-tests compare higher SES with lower SES.

^d For the subsample of mothers (*n* = 72) for milk fat analysis, mothers with female infants consumed a greater amount of fat (23.7 ± 17.9 g) than mothers with male infants with marginal statistical significance (18.4 ± 7.3 g; *P* < 0.1).

^e *n* = 82 for Land Size, *n* = 46 for mothers with sons, *n* = 57 for mothers classified as higher SES.

† *P* < 0.1.

* *P* < 0.05.

** *P* < 0.01.

using Korr as the reference community. Preliminary bivariate analyses were conducted using the dependent variable and each of the above covariates.

Statistical methods

To test the hypotheses, linear regression models were fitted using breastfeeding frequency or natural log breast milk fat concentration as the dependent variable, infant’s sex (son), SES, and the sex-SES interaction as the predictors. The following covariates were included in these models: maternal age (age), parity, postpartum time, BMI, dietary fat intake, sons living at home (sons at home), and the community membership. We included the number of sons because it was marginally correlated with milk fat concentration while the number of daughters was not based on our preliminary bivariate analyses. Community membership was significantly correlated with breastfeeding frequency for Karare and Kituruni and thus also included. The statistical models were as follows:

$$\begin{aligned} \text{Breastfeeding frequency} = & \beta_0 + \beta_1 \text{ SES} + \beta_2 \text{ son} \\ & + \beta_3 \text{ SES} \times \text{son} + \beta_4 \text{ age} + \beta_5 \text{ parity} + \beta_6 \text{ postpartum time} \\ & + \beta_7 \text{ BMI} + \beta_8 \text{ fat intake} + \beta_9 \text{ sons at home} + \beta_{10} \text{ Karare} \\ & + \beta_{11} \text{ Kiturutni} \end{aligned}$$

$$\begin{aligned} \text{Ln (milk fat)} = & \beta_0 + \beta_1 \text{ SES} + \beta_2 \text{ son} + \beta_3 \text{ SES} \times \text{son} \\ & + \beta_4 \text{ age} + \beta_5 \text{ parity} + \beta_6 \text{ postpartum time} + \beta_7 \text{ BMI} \\ & + \beta_8 \text{ fat intake} + \beta_9 \text{ sons at home} + \beta_{10} \text{ Karare} \\ & + \beta_{11} \text{ Kiturutni} \end{aligned}$$

The coefficient of interest was the interaction term, β_3 . This term was dropped if it was not significant.

To visually clarify the results, line graphs were drawn to examine how the relationships between the dependent var-

iables and SES varied by offspring’s sex. Statistical analysis was done using STATA version 9.2 (StataCorp, 2004-7).

RESULTS

General characteristics of the mothers (*N* = 83) are summarized in Table 1. The mean (±SD) breastfeeding frequency was 9.7 ± 4. 57% had a male infant. About 30% were classified as lower SES. Mothers with a male infant were slightly younger (26.7 ± 6 years of age, *N* = 47) than those with a female infant (29.6 ± 7 years, *N* = 36; $t_{81} = 1.884, P = 0.063$), and they also had lower parity (3.1 ± 2 births) than those with a female infant (4.6 ± 3 births; $t_{81} = 2.911, P = 0.005$). The subsample of mothers for milk fat analysis (*n* = 72) had the mean milk fat concentration of 2.3 ± 1.2 gm/dl in original value and 0.75 ± 0.47 in natural log. They shared similar general characteristics with the whole sample, except for the dietary fat intake pattern by infant’s sex. In this subsample, mothers with a male infant tended to consume slightly lower amount of dietary fats (18.4 ± 7 gm/day) compared to those with a female infant (23.7 ± 18 gm/day, $t_{70} = 1.764, P = 0.082$).

Hypothesis 1: Economically sufficient mothers will breastfeed sons more frequently than daughters while poor mothers will breastfeed daughters more frequently than sons

The statistical test for breastfeeding frequency did not support the hypothesis. Offspring’s sex and wealth did not interact (*P* = 0.99, *n* = 83) in their relation with breastfeeding frequency. In the final model without the interaction term, having higher SES ($\beta_1 = -2.079, P = 0.008, n = 83$; Table 2) was a negative predictor of the frequency (regardless of the sex of the infant; Fig. 1a). For covariates, community membership in Karare was a negative predictor ($\beta_{11} = -2.679, P = 0.016$), whereas living in Kituruni was a positive predictor ($\beta_{12} = 3.669, P = 0.003$) of the frequency.

TABLE 2. Regression models for breastfeeding frequency and milk fat concentration predicted by socioeconomic status and offspring sex

Predictor	Breastfeeding frequency		Milk fat (natural log)	
	Model ^a , β	Model ^b , β	Model ^c , β	Model ^d , β
Intercept	10.157**	10.166**	1.127*	0.844
SES ^e	-2.064†	-2.079**	-0.401*	-0.057
Son	0.467	0.447	-0.123	0.278*
SES × Son	-0.029	—	0.594*	—
Age	0.086	0.086	-0.010	-0.010
Parity	-0.219	-0.219	0.080†	0.085†
Postpartum time	0.004	0.005	0.0005	0.0003
BMI	-0.115	-0.115	-0.005	-0.002
Fat intake	0.060†	0.060†	0.004	0.003
Number of sons	0.345	0.346	-0.112†	-0.125*
Karare	-2.678*	-2.679*	-0.167	-0.128
Kituruni	3.672**	3.670**	-0.185	-0.126

^a Interaction model: $R^2 = 0.50$, Adjusted $R^2 = 0.42$, $P < 0.001$, $n = 83$.

^b No interaction model: $R^2 = 0.50$, Adjusted $R^2 = 0.43$, $P < 0.001$, $n = 83$.

^c Interaction model: $R^2 = 0.21$, Adjusted $R^2 = 0.06$, $P = 0.18$, $n = 72$.

^d No interaction model: $R^2 = 0.12$, Adjusted $R^2 = -0.02$, $P = 0.57$, $n = 72$.

^e SES: socioeconomic status.

† $P < 0.1$.

* $P < 0.05$.

** $P < 0.01$.

Hypothesis 2: Economically sufficient mothers will produce breast milk with higher milk fat concentration for sons than daughters while poor mothers will produce breast milk with higher milk fat concentration for daughters than sons

The statistical test supported the hypothesis in the milk fat model: offspring's sex and SES interacted ($\beta_3 = 0.594$, $P = 0.014$; Table 2) in their relation with milk fat concentration. Specifically, the model predicted that economically sufficient mothers would produce substantially higher fat milk for sons than daughters whereas poor mothers produce milk with higher fat concentrations for daughters than sons, controlling for covariates. These predictions are visually illustrated in Figure 1b for hypothetical mothers having mean values for covariates. The differing slopes for sons vs. daughters (in contrast to the parallel slopes for breastfeeding frequency in Fig. 1a) suggested that mothers with a daughter have a negative relationship between milk fat and SES, whereas mothers with a son have a positive relationship. This translated into the specific predictions that economically sufficient mothers will produce richer milk for sons (2.8 gm/dl) than daughters (0.6 gm/dl), whereas poor mothers will produce richer milk for daughters (2.6 gm/dl) than sons (2.3 gm/dl), again after controlling for covariates. Among covariates, the number of sons living at home was a marginally significant negative predictor of milk fat concentration ($\beta_9 = -0.112$, $P = 0.05$) while parity was a marginally significant positive predictor ($\beta_5 = 0.08$, $P = 0.09$). No other covariates were significant.

DISCUSSION

This study examined the Trivers–Willard hypothesis in terms of both behavioral and biological parental investment, measured as breastfeeding frequency and

breast milk fat content among exclusively breastfeeding mothers in Northern Kenya. What differentiates this study from previous studies are concurrent investigations of both behavioral and biological domains of parental investment. Previous research on sex-biased parental investment focused on more behavioral factors of nursing such as breastfeeding frequency and duration as parental investment indicators. The Trivers–Willard hypothesis was originally formulated by linking evolutionary theory and social behavior theory (Trivers and Willard, 1973), recognizing that parental behavior can be flexibly modified at the parents' will, making it an important possible means to adjust parental investment in a context-specific manner. Although some aspects of human biology may not have the flexibility of behavioral modification, human reproductive biology is a product of natural selection with considerable phenotypic plasticity to accommodate various ecological perturbations (Voland, 1998). Numerous studies have demonstrated that human milk composition is responsive to maternal or external conditions (e.g., Jelliffe and Jelliffe, 1978; Michaelsen et al., 1995; Saarela et al., 2005) although earlier researchers (e.g., Lauber and Reinhardt, 1979) suggested otherwise. As such, physiological traits such as milk constituents may fluctuate in manners consistent with condition-specific parental investment strategies. Parental investment theory such as the Trivers–Willard hypothesis therefore should apply to both biological investments as well as behavioral investments.

In this study, the use of breastfeeding frequency as the behavioral investment marker did not provide support for the Trivers–Willard hypothesis. This echoes previous studies of the behavioral extent of breastfeeding which also found little support for the hypothesis using breastfeeding structure (including frequency; Tracer, 2009) and breastfeeding duration (Quinlan et al., 2003) based on maternal economic condition. Our final statistical model predicted that lower SES mothers will breastfeed more often (approximately two additional times per 24 h) than economically sufficient mothers, regardless of the infant's sex. At the same time, community membership was an important predictor of feeding frequency. For example, living in Kituruni predicted more frequent feeding (three to four additional times a day) than mothers in other communities. The community of Kituruni is located on the southern slope of the Mt. Marsabit which affords relatively more diverse and robust economic production systems than other communities, and this advantage in turn may afford mothers in Kituruni either more resources and/or time with the infant, resulting in more frequent breastfeeding. This interpretation echoes previous reports that women's access to household discretionary resources and/or decision-making ability in Northern Kenya resulted in better nutritional statuses of their households (Shell-Duncan and Obiero, 2000) or their children (Brunson et al., 2009). We infer that in Northern Kenya, breastfeeding frequency is influenced by specific ecological and related contexts of the communities as well as the family's SES, regardless of the infant's sex.

The 24-h frequency of breastfeeding in our study was based on recall questions. This type of data, based on maternal recalls, has been shown to have limited reliability representing the observed suckling frequency (e.g., Vitzthum, 1994). The limitation in the quality of our data therefore may have partly contributed to the failure to confirm the hypothesis with the breastfeeding data.

In contrast to breastfeeding frequency, the use of milk fat concentrations as the biological indicator of parental investment provided results consistent with the Trivers–Willard hypothesis. Our statistical model predicted that poor Ariaal mothers produce richer milk for daughters while economically sufficient mothers produce richer milk for sons. Our findings are also consistent with a recent study on milk energy content by Powe et al. (2010), which reported that mothers of male infants produced milk having 25% greater energy content than mothers of female infants among well-nourished, relatively well-off mothers in Massachusetts.

A curious finding from our study is the near-significant negative influence of the number of sons living at home on milk fat concentrations regardless of the sex of the offspring. This highlights the potential importance of the household ecology, particularly the number and sex of older siblings on the milk synthesis. In our sample, mothers with male infants consumed slightly less dietary fats than those with female infants. It is possible that this resulted from mothers allocating more fats for sons at the expense of their dietary intake. If older sons in the household are similarly fed more fats (than older daughters) at the expense of maternal fat intake, it might lead to lower maternal milk fat concentrations, although we are not able to test this hypothesis at present.

From an evolutionary perspective, Trivers' (1974) parent-offspring conflict model posits that the interests of the parent and offspring do not coincide, and that conflict arises regarding the amount of parental investment given to each sibling since siblings must compete for their share of limited parental investment. In this framework, nutrient transfer in the mother–child dyad needs to be understood not only as maternal parental investment strategy but also in terms of sibling competition within the household. This is important in a place such as Northern Kenya where an average mother raises six children. The role of household ecology and older siblings should be examined more carefully in future studies. Nonetheless, we have statistically adjusted for the presence of older sons as well as the level of maternal dietary fat intake and still found support for the milk fat hypothesis based on the Trivers–Willard hypothesis.

Another notable finding from the milk fat model is that daughters of economically sufficient mothers have received breast milk with extremely low fat content (0.6 gm/dl or 6 gm/liter on average) and thus may be at serious risk of undernutrition. To put this value in perspective, the examples of reported median human milk fat concentrations are 24.5 gm/liter in Copenhagen ($n = 713$ foremilk samples; Michaelsen et al., 1995) and 41.1 gm/liter (with a range of 22.3–61.6) in Western Australia ($n = 71$; Kent et al., 2006). Poverty is a well-established risk factor for nutrient deficiency among infants (McLaren and Frigg, 2001) and children of poor families may receive greater attention from a nutritional intervention perspective. Our study suggests that the sex of the infant may be as important a factor as the SES for modulating the parental investment and thus health outcomes for the infant.

A limitation of our study is the lack of information on milk volume consumed by the offspring. A recent study with Rhesus macaques (Hinde, 2009) reported that while mothers biased milk energy density favoring sons more than daughters, this bias was offset by larger milk yield for daughters. Similarly, among the Chacma baboons a

possible sex-bias in milk yield may produce infant and juvenile growth patterns at odds with our findings (daughters of lower ranking mothers were smaller than daughters of higher ranking mothers while sons did not show a relationship between their growth and maternal rank; Johnson, 2003). If there is a similar bias in Ariaal mothers' milk yield offsetting the observed sex-bias in fat concentrations, our study results would provide inadequate support for the Trivers–Willard hypothesis. An inverse relationship between the mean milk fat content and the 24-h milk yield per breast has been reported from Australia although the sex of the infant had no effect on the milk fat content in that study (Kent et al., 2006).

Similarly, our study is not able to address milk fat variations potentially occurring within each nursing episode. Milk fat concentrations are generally higher in hindmilk (the milk released toward the end of a breastfeeding episode) than foremilk (Jennes, 1979; Saarela et al., 2005; Murase et al., 2009). Our samples were all foremilk samples collected in early morning from whichever breast was not nursed overnight. Although this methodology allowed us to control for milk fat variations within each nursing episode, if such variations occur in a sex-biased manner, our study design would be inadequate to address the total milk or milk fat transferred to boys vs. girls. For example, if boys tend to nurse longer each time than girls, sons would be able to tap in to more of the richer hindmilk in each nursing episode than daughters. This could potentially offset the sex bias in milk fat concentration, or perhaps contribute to the sex-biased total milk transfer despite the equivalent feeding frequencies for sons and daughters. These dimensions should be investigated in a more comprehensive future study.

The infants' growth data would provide another direct test of the Trivers–Willard hypothesis. Unfortunately, our study did not collect such data from infants. A significant positive correlation between breast milk energy and infants' growth has been previously reported by others (Dewey and Lonnerdal, 1983 for weight-for-length and weight gain for 20 infants from 1 to 6 months of age). Similarly, infant weight, weight gain, or fat gain has been found to significantly correlate with breast milk intake (Butte et al., 2007 for the first 4 months of life; Forsum and Sadurskis, 1986 for the first 10 weeks). Therefore, it is likely that infant growth would reflect milk nutrients and milk intake in this population as well. A future study should include infant growth and health data in the hypothesis tests.

This study provided tentative support for the predictions from the Trivers–Willard hypothesis on human milk fat. In addition to improving upon the above limitations, the next logical step would be to clarify possible physiological and/or behavioral pathways to the realization of this systematic milk fat variation. Future studies of milk fat and other milk constituents grounded in the evolutionary parental investment theory are warranted.

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