The evolutionary ecology of early weaning in Kilimanjaro, Tanzania

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Public health recommendations promote prolonged breastfeeding of all children; however, parental investment (PI) theory predicts that breastfeeding will be allocated among a mother's offspring to maximize her reproductive success. We evaluated PI in terms of risk for weaning before age two among 283 children in Kilimanjaro, Tanzania. Results demonstrate: (i) a Trivers–Willard effect—high socioeconomic status (SES) females and low SES males were more likely to be weaned early; (ii) later-born children were less likely to be weaned early; (iii) higher birthweight children were less likely to be weaned early, and (iv) no effect of cattle (a source of supplementary milk) ownership. These associations were largely independent and remained significant in models controlling for potential confounders; however, the inverse association between early weaning and birth order lost significance in the model containing birthweight. These patterns were observed despite public health recommendations encouraging breastfeeding for at least two years.

1. Introduction

Breastfeeding is widely recognized as beneficial to infant health [1], yet departures from breastfeeding recommendations are common [2,3]. Parental investment (PI) theory hypothesizes that mothers adjust the duration and intensity of breastfeeding based on the associated costs and benefits to reproductive success [4], including metabolic and energetic costs [5–7], in turn mediated by socio-ecological context. Evolutionary theorists have sought to inform public health policy by identifying factors that support or impede breastfeeding [2,3,8].

In comparative perspective, human mothers allocate little time to breastfeeding [3,9,10], which, given interference with resumption of reproductive cycling [7,11,12], may help explain our relatively rapid reproduction [13]. Humans are also the only primate to wean before children can forage independently [3]. Given its energetic costs to mothers, it is unsurprising that human lactation is flexible [3], mobilizing body stores, increasing energy intake and reducing physical activity to sustain lactation [14,15]. Research using an evolutionary perspective has shown that human breastfeeding is allocated according to children's expected contributions to household economy [16], kin assistance in childrearing [17], access to market and supplemental foods [6], socioeconomic status (SES) [18], sex differences in expected fitness [18,19] and factors affecting mother or child reproductive value [4]. These factors all affect the context-specific metabolic, energetic and/or opportunity costs of breastfeeding, and shed light on why human mothers often curtail, rather than extend, breastfeeding [13,17]. Yet, research using an evolutionary perspective constitutes a small fraction of the literature investigating human breastfeeding behaviour [3,15,20]. We explored several evolutionary hypotheses to explain early weaning among children in Kilimanjaro, Tanzania. In particular, we evaluate the probability of early weaning with respect to child's sex and SES (the Trivers–Willard hypothesis (TWH)), mother's residual reproductive value, child's reproductive value, and the availability of supplementary foods.

(a) Trivers–Willard hypothesis

A mother's condition affects her ability to sustain the costs of lactation [20]. TWH predicts sex-biased PI, mediated by parental condition (i.e. SES in humans) [21]:
If males have higher reproductive variance than females, and if children’s reproductive success is sensitive to PI [16], then parents with plentiful resources stand to gain more from investing in sons, whereas parents with fewer resources may achieve the highest fitness gains investing in daughters. If breastfeeding is reflective of overall PI [22,23], TWH predicts that high SES females and low SES males will be weaned earlier than their opposite-sex counterparts.

TWH has inconsistently been found to predict aspects of breastfeeding among humans. At the population level, two relatively impoverished and stigmatized groups (the Mukogodo of East Africa and Gypsies of Hungary) show evidence of later weaning of daughters, consistent with TWH [24–26]. Fujita et al. [18,19] demonstrated among the Rendille in East Africa a preference for daughters in breastfeeding frequency among poorly nourished mothers and in breastmilk fat concentration among economically impoverished mothers. Koziel & Ulijaszek [27] showed a weak TW effect dependent on paternal status in Poland, and Gaulin & Robbins [28] found patterns in likelihood and duration of breastfeeding consistent with TWH in the USA. However, age at weaning exhibited no TW effect in a matrifocal community in Dominica [29], nor did suckling duration in Papua New Guinea (PNG) [4]. No differences in the decision to breastfeed or the duration of breastfeeding by wealth or infant sex were observed in another US sample [30]. Finally, the Hutterites’ apparent preference for daughters was not explained by TWH [23].

(b) Mother’s reproductive value

Life history theory (LHT) predicts trade-offs between current and future reproduction: the longer a mother breastfeeds, the fewer somatic resources (e.g. energy stored in adipose tissue) she has available to nurture a future pregnancy or to breastfeed future offspring. As a woman progresses through her reproductive career, the nature of this trade-off changes: she has fewer potential future offspring, diminishing the cost of investing in current offspring [29]. Thus, LHT predicts higher PI—later weaning—as women advance along their reproductive trajectories [29]. Consistent with this hypothesis, Tracer [4] showed a positive association between parity and suckling frequency among the Au in PNG, and parity and/or maternal age have been positively associated with duration of breastfeeding among mothers in other Western and non-Western contexts [30–37]. Quinlan et al. [29], however, did not find a significant association between maternal age or child birth order and weaning age in Dominica.

(c) Infant’s reproductive value

PI theory predicts that mothers prefer to invest in ‘high-quality’ offspring to the extent that such offspring can better capitalize on the investment [4,30,38]. In cases of acute illness, otherwise healthy infants stand to gain more from a unit of investment [30,39]; otherwise, PI theory predicts that larger, healthier infants should receive more investment [4,39]. Smaller infants may present poor prospects, as they are more vulnerable to mortality, developmental handicaps, and congenital abnormalities than larger infants [39], and may also negatively impact a mother’s prospects for future marriage and childbearing [40].

Breastfeeding has frequently been found to conform to this expectation: normal (versus low) birthweight infants were more likely to be breastfed among a US sample [41]; low birthweight was associated with earlier supplementation among northern Thai women [34] and earlier weaning among a sample of Hungarian women [39]; and birthweight was positively associated with likelihood of breastfeeding beyond six months in US infants [33]. However, offspring physical size and suckling duration were inversely associated with breastfeeding among the Au [4].

(d) Availability of weaning foods

The availability of foods appropriate to supplement or replace breastmilk may facilitate early weaning [42]. Using data from the Human Relation Area Files, Sellen & Smay [42] found weak support for this hypothesis across cultures. Such cross-cultural comparisons may obscure patterned heterogeneity within populations, however, when individual mothers and households vary in terms of weaning food availability.

We explored patterns in early weaning (before age two years) in Kilimanjaro for evidence of: (i) a TW effect: lower risk among wealthy sons and impoverished daughters; (ii) an inverse association with birth order; (iii) an inverse association with birthweight; and (iv) a positive association with household cattle holding.

2. Material and methods

(a) Study population

This project was carried out in the Machame area of Kilimanjaro, inhabited by the Chagga ethnic group. The majority of Chagga are farmers, cultivating subsistence and cash crops, raising animals for consumption or sale, and often reliant on other sources of income (e.g. wage labor and small business). Pregnant women in the study area receive prenatal care through the Maternal–Child Health (MCH) program, and most children in Machame attend monthly MCH clinics through age five years. MCH messaging, widely assimilated by Machame mothers, promotes breastfeeding until age two years.

(b) Data collection

Data were collected in collaboration with Nshara Community Medical Centre; field assistants were local residents and medical personnel trained in data collection. A census of the study area was conducted to identify all children aged 2–7 years; approximately 400 were then randomly selected (for a target sample of 300) and invited to participate. Participating parents provided written informed consent. Procedures and data collection protocols were approved by the Institutional Review Board of the University of Washington and the Tanzanian National Institute for Medical Research. Children’s primary caregivers completed a questionnaire and were asked to make MCH clinic records available.

(c) Data analysis

We present here a secondary analysis of data collected to evaluate associations between early life experiences (e.g. early weaning) and subsequent health outcomes; early weaning (the point at which mothers are not willing or able to continue breastfeeding [16]), defined as age at weaning less than two years, was treated here as an outcome, rather than predictor, of interest. Estimates of weaning age were provided; however, as this was reported retrospectively, the potential for misreporting was high [6]. In the presence of strong messaging that breastfeeding should continue until age two years, we judged this cutoff to be meaningful and reliable [43].
Table 1. Sample characteristics (n = 283).

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Value</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weaned early (before age two years)</td>
<td>62</td>
<td>21.91%</td>
</tr>
<tr>
<td>Male</td>
<td>132</td>
<td>46.64%</td>
</tr>
<tr>
<td>Earth home construction materials (low SES)</td>
<td>136</td>
<td>48.06%</td>
</tr>
<tr>
<td>Birth order (mean, range)</td>
<td>2.4 (1, 6)</td>
<td></td>
</tr>
<tr>
<td>Birthweight in kilograms (mean, range)</td>
<td>3.3 (1.0, 4.8)</td>
<td></td>
</tr>
<tr>
<td>Cattle-holding household</td>
<td>180</td>
<td>63.60%</td>
</tr>
<tr>
<td>Mother employed outside the home</td>
<td>58</td>
<td>20.71%</td>
</tr>
<tr>
<td>Grandparents in the household</td>
<td>72</td>
<td>25.53%</td>
</tr>
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</table>

*Available from records of 140 children.
*Reported for 280 children.
*Reported for 282 children.

Predictors of interest included: sex; SES, a binary variable in which ‘low’ indicates residence in a home constructed of earth and ‘high’ of cement; birth order (with respect to living siblings); birthweight as measured and recorded soon after birth, and household cattle holding, a binary variable categorized as any (versus no) reported cattle ownership. Control variables were mother’s employment outside the home and co-resident grandparents.

Data were analysed with Stata v. 11.2 software using logistic regression. Significance was defined as \( p \leq 0.05 \). Results are presented both as odds ratios (ORs) and predicted probabilities: regression equations were solved for \( \exp \text{logit}(\text{early weaning}) \) across the range of a variable of interest, with values for other variables in the model held constant at the most commonly reported value. Predicted probabilities were then calculated as:

\[
\frac{\exp(\text{logit(early weaning)})}{1 + \exp(\text{logit(early weaning))}}
\]

for each value of the predictor of interest, and plotted in R (v. 2.15.2). For outcomes that are not rare (e.g. greater than 10% prevalence), ORs tend to overstate the magnitude of observed associations; predicted probabilities do not. This approach also facilitates interpretation of interaction [44].

3. Results

Information was available for 283 children, described in table 1. Predictors of early weaning are described in table 2. Model 1 evaluates the predicted interaction between SES and sex in association with early weaning; Model 2 evaluates the predicted inverse association with birth order; Model 3 evaluates the predicted inverse association with birthweight; Model 4 evaluates the predicted positive association with household cattle ownership; Model 5 includes predictors from Models 1, 2 and 4, as well as potential confounding variables; Model 6 includes all predictors and potential founders. Because birthweight was unavailable for many participants, Models 3 and 6 are based on a substantially smaller sample than Models 1, 2, 4 and 5.

Associations between sex and early weaning varied significantly by SES. Female sex was associated with early weaning among high SES children; male sex was among low SES children. Figure 1 shows predicted probabilities for early weaning by sex and SES (calculated from Model 5, for a second-born child in a household with cattle, whose mother was not employed outside the home, and whose grandparents were not a part of the household). Potential alternative indicators of SES, cattle holding and coffee farming (111 households; 39.22%), were evaluated for interaction with sex; none was found.

Birth order was inversely associated with early weaning: later-born children were less likely to be weaned early. Figure 2 shows predicted probabilities for early weaning by birth order (calculated from Model 5, for a male child of a high SES household with cattle, whose mother was not employed outside the home, and whose grandparents were not a part of the household).

Birthweight was significantly inversely associated with early weaning: higher birthweight children were less likely to be weaned early. Figure 2 shows predicted probabilities for early weaning by birthweight (calculated from Model 6, for a second-born male child of a high SES household with cattle, whose mother was not employed outside the home, and whose grandparents were not a part of the household).

Household cattle holding was unassociated or inversely associated with early weaning.

Sex \( \times \) SES and birthweight were both significantly associated with early weaning in the fully adjusted model; birth order lost significance with birthweight controlled. This may be attributable to the reduction in sample size in Model 6, or to confounding of the association between birth order and early weaning by birthweight. Higher birthweights among later-born children would suggest confounding; we observed no such association (pairwise correlation: -0.0817; \( p \) 0.3205).

Results were largely consistent, although significance was lower, when duration of breastfeeding was evaluated (see electronic supplemental material).

4. Discussion

Breastfeeding practices are often resistant to changes sought by public health recommendations [34]. Evolutionary theory provides a means to understand incentives shaping breastfeeding behaviour [3]. Patterns in weaning among children in Kilimanjaro largely conform to predictions drawn from evolutionary theories of PI: consistent with TWH, risk for early weaning was higher for girls among the wealthy and boys among the poor. Risk for early weaning decreased with birth order, as anticipated by LHT, and with birthweight, suggesting higher investment in higher reproductive value children. Some have questioned weaning as a measure of PI [29]; our analyses suggest that it is a reasonable proxy thereof.

We documented a substantial TW effect among children in Kilimanjaro—high SES males and low SES females were at significantly lower risk for early weaning than high SES females and low SES males, respectively. This finding is consistent with other evaluations of TWH and breastfeeding in East Africa. Cronk [24,25] and Fujita et al. [18,19] evaluated breastfeeding and breastmilk among pastoralists and demonstrated a preference for girls by relatively poor or unhealthy mothers. Machame residents have a long history of agriculture and inhabit a lush and productive area—a very different setting than those studied by Cronk and Fujita et al. Nonetheless, we found a similar preference for girls by poorer mothers and a preference for boys by wealthier mothers. Absence of a TW effect in breastfeeding in other settings [4,23,27,29,30] does not warrant whole-scale rejection of TWH [45]. Instead, it is likely that populations vary in the extent to which TWH assumptions are met. Particularly, the ratio of male-to-female
variation in reproductive success varies dramatically across populations [46]; where the ratio is near one, TWH is irrelevant to PI.

In two models, we found a significant effect of birth order on breastfeeding investment—later-born children were less likely to be weaned early (approx. 4% decrease in probability of early weaning for each increase in birth order). This is consistent with predictions from LHT that mothers increase investment in current offspring as future offspring become less likely. Additional support for this hypothesis is seen among the Au, where maternal age and parity were associated with delayed postpartum resumption of menses [5] and with the increased intensity of afternoon suckling seen in older Quechua mothers [6]. While contributions to household labour and subsequent fertility may motivate preference for earlier born children in other settings [47], we found no evidence of such preference among Machame children.

We found that birthweight significantly affected breastfeeding duration—children born heavier were less likely to be weaned early (approx. 2% decrease in probability of early weaning for each 0.1 kg increase in birthweight). This is consistent with the prediction that mothers invest more in ‘higher quality’—larger—offspring, which provide better prospects for long-term reproductive success [39]. This finding is not consistent with studies suggesting increased investment in ‘needy’ children [4,39], but is with studies showing poor treatment of unhealthy babies [48] and more positive behaviour towards healthy twins, compared with their unhealthy counterparts [49].

Our results are not consistent with the hypothesis that available supplemental foods facilitate early weaning [6,42]. Specifically, Machame children from cattle-holding households were significantly less likely to be weaned early.

These analyses are subject to limitations. Reliance on parents’ reporting introduced potential misclassification; particularly, early weaning may have been underreported if respondents perceived it to be undesirable. House construction materials provided only an indirect indicator of SES;
however, observations over the course of multiple visits to this community suggest that concrete home construction is a priority for Machame families: we are confident that this variable effectively distinguished those with truly limited resources, even if heterogeneity within categories remained. MCH clinic cards were unavailable for approximately half of participating children, limiting the power of models that included birthweight. In addition, birthweights were recorded by healthcare providers who were not part of this project; inconsistency in measurement techniques, instruments and timing of birthweight measurement was a likely source of error. We see no reason to suspect misreporting or error systematically biased results in ways that would reproduce our findings.

5. Conclusion
We find the degree to which early weaning in Machame conformed to predictions of PI theory striking, in the face of strong encouragement to breastfeed for two years. Evolutionary perspectives stress that mothers are adapted to exercise choice in breastfeeding practices [3,13]. The substantial opportunity and energetic costs of breastfeeding provide strong incentive for mothers to allocate breastfeeding investment carefully. Deviations from what is ‘best’ for a child are often owing to constraints on mothers [3,13] or natural conflicts between mother and child [15,50], felt more strongly by mothers with relatively few resources [17]. Public health messaging encouraging prolonged breastfeeding may have little impact when it runs counter to adaptive allocations of PI [2]. Indeed, complaints about ‘pressure’ placed on mothers to breastfeed for longer than they feel optimal reveal that resistance can be strong even in the face of perceived stigma [51]. Evolutionary studies of health behaviours such as breastfeeding should be considered alongside evidence from other disciplines to generate holistic policy recommendations [3,13].

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