Market integration improves traditional Hadza male childhood health with no effect on females

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While market integration sometimes benefits one sex or disadvantages the other, its impact on hunter-gatherer populations with subtle pre-existing sex-based dynamics remains understudied. We examined linear enamel hypoplasias, a biomarker of developmental stress in teeth, using time series analysis spanning 40 years in a sample of 81 bush-living Hadza. Results show that Hadza men born after the mid-1970s) experienced less early childhood stress than women and older generations. Few of the traditional explanations for health disparity explained the result, which is counter to most archaeological and contemporary studies of populations in transition. The turning point for men's childhood health coincided with an increasing supply of tourist goods and currency in the bush, remote market integration. Early and remote integration into the market economy may have had subtle health impacts on health not previously uncovered due to methodological differences and approaches. Remote market economy to bush-living Hadza appears to have disproportionately benefitted men's early childhood health and may be tied to an external signal of men's activities having higher value that exacerbated existing sex-based dynamics. The broader implications are that external forces associated with market integration can favor males over females, even in hunter-gatherer societies with traditional sex-based divisions of labor.

market integration, hunter-gatherer, childhood health, SDG 3: good health and well-being, SDG 5: gender equality, SDG 10: reduced inequalities

Introduction

The study of human health across populations and through time relies on distinct yet complementary approaches from bioarchaeology and human biology, each possessing unique strengths and limitations. Human biology data offer direct measures of mental and physical health and a nuanced understanding of how biology intricately relates to socio-economic, environmental, and even psychological factors present at the time of data collection (Stinson *et al.*, 2012). Capacity for long-term diachronic analysis, however, is inherently limited by researcher lifespans, logistical and ethical challenges, and the rapid pace of external changes. Conversely, bioarchaeology offers unparallelled ability to access information from individuals spanning millennia providing insights into the impact of major societal and environmental shifts and long-term health trends through skeletal and dental remains (Brown and Brown, 2011; Buikstra and Beck, 2009; Buikstra and Ubelaker, 1994; Steckel and Rose, 2002). These insights, however, are limited to indirect proxies for more general aspects of health, as snapshots of health in adults at the time of death or during developmental windows, and data collection is constrained by logistical and ethical challenges. Applying bioarchaeological methods to living populations (here, bush-living Hadza of Tanzania) who have been studied for decades allows us to establish baselines of past health for comparison to diachronic snapshots recorded in dental enamel relative to cultural and economic changes.

The analysis of enamel defects provides a unique, retrospective window into early life health for the Hadza across decades before researchers were studying the Hadza. The approach offers a complement to the rich body of existing literature on Hadza (Alvarado *et al.*, 2019; Apicella, 2014; Barnicot *et al.*, 1972, 1972; Bennett *et al.*, 1970, 1973; Fedurek *et al.*, 2020, 2021, 2022, 2023, 2024; Raichlen *et al.*, 2017). Roughly 85% of Hadza live in sedentary villages where they are integrated into a market economy and/or engage in small-scale agriculture (Marlowe, 2010; Pollom *et al.*, 2020; Yatsuka, 2015). Our focus is on the approximately 150 individuals who were maintaining traditional foraging lifestyles in remote bush camps and consuming mostly wild foods at the time of data collection.

The transition from foraging to other types of subsistence in the bioarchaeological literature is characterized by increased health burdens in most areas of the globe throughout history (Armelagos, 1990; Cohen, 1977). Status in egalitarian groups is subtler than in hierarchical systems (Fedurek *et al.*, 2020; Mattison *et al.*, 2016; Woodburn, 1982, 2005) and largely constrained to a sex-based division of labor (Marlowe, 2007) that starts in early infancy with social learning (Lew-Levy *et al.*, 2017, 2020, 2021). The generally egalitarian nature of hunter-gatherer societies like the Hadza (Marlowe, 2007) is not immediately compatible with the societal inequality that emerges with sedentism and agriculture (Mattison *et al.*, 2016; Price and Feinman, 1995).

While past subsistence transitions were often driven by ecological pressures, contemporary ones are largely shaped by external socio-political forces (Goodman and Leatherman, 1998), occurring rapidly rather than over millennia (Page *et al.*, 2018). Contemporary transitions to market-integrated lifestyles are also characterized by health challenges (Lew-Levy *et al.*, 2021; Page *et al.*, 2018), sometimes more pronounced than those seen in the past (Goodman, 1988; Goodman and Armelagos, 1989). While some groups have experienced benefits

(Kramer and Greaves, 2007), many hunter-gatherers find themselves marginalized in new economic hierarchies (Dounias and Froment, 2011), often accompanied by increased sex-based health disparities (Caruso *et al.*, 2015; Khera *et al.*, 2014; Osmani and Sen, 2003), with the latter potentially stemming from the initial gendered division of labor that persists in a different form in a new setting. The increased visibility of sex-based health differences in contemporary societies compared to past societies may be attributable to the fact that archaeological assemblages are very unlikely to contain information about year of birth that allows a diachronic analysis. Bioarchaeological observations of health surrounding transitions tend to be static, lacking the longitudinal depth of contemporary studies that capture gradual changes and specific disease loads. Identifying the drivers of past transitions is challenging, but assessing their impact on health is feasible.

Long-term trends in childhood stress were examined using linear enamel hypoplasias, permanent defects in dental enamel that serve as a reliable biomarker of physiological stress during growth and development (Goodman *et al.*, 1988). Defects can be timed to the specific years in which each tooth commonly develops, such as between 4.5 months to age 5.5 for the anterior maxillary teeth used in this study (AlQahtani *et al.*, 2014; Goodman and Martin, 2002). Exploratory analysis identified a sex-based trend over time in declining hypoplasia rates in men, suggesting improved childhood health over time. While many Hadza are integrated into village market economies, the market is brought to the bush-living Hadza by researchers and tourists who offer goods and currency in exchange for services, referred to here as remote market integration. Developmental stress appeared to decline in males after remote market integration. The use of enamel defects as a biomarker for health provides a unique, retrospective view of long-term trends in childhood health before, during, and after remote market integration.

Materials and Methods

Materials

This study focuses on the approximately 150 Hadza individuals living primarily in remote mobile bush camps around Lake Eyasi, a seasonal salt lake on the floor of the Great Rift Valley in Arusha, northern Tanzania. They live in mobile bush camps of ~30 individuals that relocate every few months (Marlowe, 2010, 2006). Camp membership is fluid with people moving in and out of camps frequently (Blurton Jones, 2015; Blurton Jones *et al.*, 2005). Hadza have a binary understanding of gender linked to biological sex (Marlowe, 2006) and are referred to as men and women in this study. Daily foraging practices vary by sex (Marlowe, 2006). Men typically forage alone eating berries and baobab fruit while hunting birds and mammals using bows and arrows—the latter may be poisoned arrows for hunting larger game—and they may also carry axes to access honey, a preferred food (Marlowe *et al.*, 2014; Marlowe and Berbesque, 2009). While they eat much of the honey they find, they bring roughly half their haul of medium-to-large game and baobab back to camp (Berbesque *et al.*, 2016). Women typically forage in groups of 3-8 adults plus infants, unweaned toddlers, and possible older children (Crittenden and Marlowe, 2013) and gather baobab, berries, and several species of tubers using simple, fire-hardened, sharpened branches as digging sticks. Like the men, they eat some of their foraged foods, especially roasted tubers, but take the remainder back to camp along (Marlowe, 2006; Marlowe and Berbesque, 2009).

Methods

Data Collection Methods

This research was approved by Florida State University IRB (IRB00000446) and the ethics review board of the Tanzania Commission for Science and Technology (COSTECH). Verbal informed consent was obtained, as the majority of Hadza people do not read or write.

Data were collected (JCB) on the ~150 adult Hadza individuals who, at the time of data collection (2007, 2007) obtained an estimated 90% of their daily calories from foraging (Marlowe *et al.*, 2014) and lived in six remote mobile bush camps. A total of 101 adults consented to dental assessment of anterior maxillary teeth (central incisors, lateral incisors, canines), which represent the developmental period of 4.5 months to age 5.5 (AlQahtani *et al.*, 2014; Goodman and Armelagos, 1985). Teeth were visually inspected under LED light to identify features obscuring the crown surface (e.g., chips, stains, excessive wear). Particularly, teeth with dental wear exceeding 50% were excluded to avoid skewing hypoplasia assessment (Reid and Dean, 2006). The final sample after exclusions was 81 individuals with data consisting of a count of linear enamel hypoplastic defects per tooth and the total number of anterior teeth observed. While the sample is slightly more than half the bush-living Hadza population, it represents a substantially larger part of the *adult* subset and provides sufficient statistical power for detecting even small effect sizes.

Hadza women have more dental wear from diet and using their teeth as tools for tasks like processing string and hides (Berbesque *et al.*, 2012). Despite more women being excluded due to wear, there were still more women than men, which may reflect differences in subsistence activities that take men away from camp for longer periods or greater longevity in women (**Table 1**). The sample spans 62 years with the mean age of 37 years (median = 33), with a mean birth year of 1971 (median = 1974) and a 62-year range. The period of infant and childhood health captured is as early as 1929 and as recent as 1991.

Table 1: Sample demographic data summary

Variables	Group	n	Median	Mean	StDev	StErr
Age	All	81	33.00	36.84	14.08	1.56
	Women	48	33.00	36.42	15.56	2.25
	Men	33	35.00	37.45	11.79	2.05
Year of Birth	All	81	1974	1971	13.85	1.54
	Women	48	1975	1971	15.23	2.20
	Men	33	1973	1970	11.76	2.05

* Year of birth and/or age was determined from long-standing demographic data from Nicholas Blurton-Jones and then Frank W. Marlowe.

Statistical Analytical Methods

Data analysis was completed by KCH in R 4.4.3 (R Core Team, 2021) and Python (Python Software Foundation, 2025) in Posit/R Studio 2024.12.1 (RStudio Team, 2020). Exploratory data visualization (Kassambara, 2020; Wickham, 2016) was used to examine the distribution of hypoplasia rate, calculated by the total count of defects observed per individual across all teeth present divided by the total number of teeth present (anterior dentition: central incisors, lateral incisors, canines), among the

Hadza and also compare Hadza men and women. The visualization generated the hypothesis that there were distinct sex-based temporal trends in hypoplasia rate.

Linear mixed-effects model (LMM). Data distributions were analyzed prior to selecting an appropriate model. The hypothesis was testing via a LMM using the lme4 package (Bates *et al.*, 2015) with hypoplasia rate as the dependent variable, year of birth and sex as fixed effects, and a random intercept for individuals to account for the non-independence of multiple measurements within individuals (hypoplasia on different teeth). A tooth offset (log[totalTeeth / 12]) was used to standardize hypoplasia rate across individuals with varying numbers of teeth observed, ensuring each individual rate contributed proportionally to the analysis of underlying developmental stress (i.e., the proportional contribution of someone with seven hypoplasias on one tooth is the same as someone with seven hypoplasias on 12 teeth). Because male hypoplasia rates stabilized around 1975, that date was used to center year of birth (yob - 1975) so that the model's intercept represented the estimated average hypoplasia rate for both sexes around this biologically relevant year (see Supplemental Materials **Section 2**). The model formula was specified as:

```
lmer_model <- lme4::lmer(hypoplasiaRate ~ yob_centered_1975 * sex +
offset(tooth_offset) + (1 | id), data = hadza)
```

Significance testing for the fixed effects was conducted using the lmerTest package. Effect sizes for the fixed effects were estimated using the effectsize package (Ben-Shachar *et al.*, 2020) and the interaction between year of birth and sex was visualized using the effects package (Fox and Hong, 2009). Model fit was assessed by residual analysis using the car (Fox and Weisberg, 2011) and lattice packages (Sarkar, 2008). Sensitivity analyses were conducted by comparing model results with and without identified outliers to assess the robustness of the findings.

Bayesian Confirmation (brms). The brms package (Bürkner, 2017, 2018; Stadler, 2017) was used to provide a direct summary of the uncertainty in the estimated parameters via posterior distributions. Bayes models allow assessment of whether the findings from an approach assuming a real-world representative sample are robust when considering a universe of resampled possibilities.

Initial attempts to fit a Bayesian model like the LMM encountered convergence issues, suggesting near-zero variance for the random effect of individuals. A comparison of LMMs with and without the random intercept using a likelihood ratio test (**Supplemental Materials ST4**) revealed no significant difference in model fit ($\chi 2 = 0.46$, df = 1, p = 0.5). The use of prior distributions in the Bayesian model may explain the near-zero variance observed for the random effect in the brms that was not observed in the LMM. Despite the discrepancy and because the brms model was not significantly different with and without the random intercept, a simplified brms model without the random intercept was to test for significant differences in the fixed effects, using the model without the intercept to generate weakly informative normal priors with standard deviations equal to its standard errors. For the residual standard deviation (σ), a weakly informative half-normal prior (mean = 0, SD = 0.2, lb = 0) was implemented using prior() and stanvar() to pass the lm-derived parameters. The model and parameters were specified as:

```
brm(hypoplasiaRate ~ yob_centered_1975 * sex + offset(tooth_offset),
  data = hadza,
  prior = prior_list_fixed,
  stanvars = stanvars_list,
  control = list(adapt_delta = 0.95, max_treedepth = 12),
  iter = 10000,
  warmup = 5000)
```

Convergence was assessed by visually inspecting trace plots and examining Rhat values and effective sample sizes (Bulk_ESS and Tail_ESS) for sufficient sampling efficiency. Model fit and convergence were further evaluated using posterior predictive checks and standard MCMC diagnostics. The standard deviation of the observed hypoplasiaRate was also examined for context in interpreting the model's residual standard deviation (sigma).

Bibliometrics. Men experienced consistently healthy childhoods after 1975, a year that coincides with an increased frequency of visits to the Hadza from researchers and tourists offering goods and currency in exchange for services (Yatsuka, 2018). Integration into the remote market economy may have positively benefitted Hadza males. Researchers paved the way for tourism and may have influenced positive male bias. The bibliometrix package (Aria and Cuccurullo, 2017) was used to analyze publications retrieved from dimensions.ai that contained the search terms ‘Hadza and women not men’ and ‘Hadza and men not women’. The search was restricted to titles and abstracts because any inherent biases in research questions, methodologies, or findings related to gender are more likely to be concentrated in these shorter texts. The package ggplot2 (Wickham, 2016) was used to plot publication counts by year for each dataset. Word co-occurrences were downloaded from dimensions.ai in json format. Network plots (and their metrics) were generated using NetworkX (Hagberg *et al.*, 2008) and matplotlib (Hunter, 2007) in Python 3.13.2 (Python Software Foundation, 2025; Van Rossum and Drake Jr, 1995). Weaker co-occurrence edges were filtered out to enhance visualization.

Results

Descriptive Statistics

On average, 8.68 (median = 10) anterior teeth were observed out of the 12 targeted by the study. Missing teeth may be due to high consumption of liquid honey causing caries (with can lead to antemortem tooth loss), tobacco and marijuana use (Crittenden *et al.*, 2017; Marlowe *et al.*, 2014), or using teeth as tools (Berbesque *et al.*, 2012). While not statistically significant, women have higher mean and median values than men for hypoplasia count (t = 0.54, df = 66, p-value = 0.6; chi-squared = 0.59, df = 1, p-value = 0.4) and hypoplasia rate (t = 1.5, df = 76, p-value = 0.1; chi-squared = 1.9, df = 1, p-value = 0.2).

Table 2: Sample descriptive statistics summary

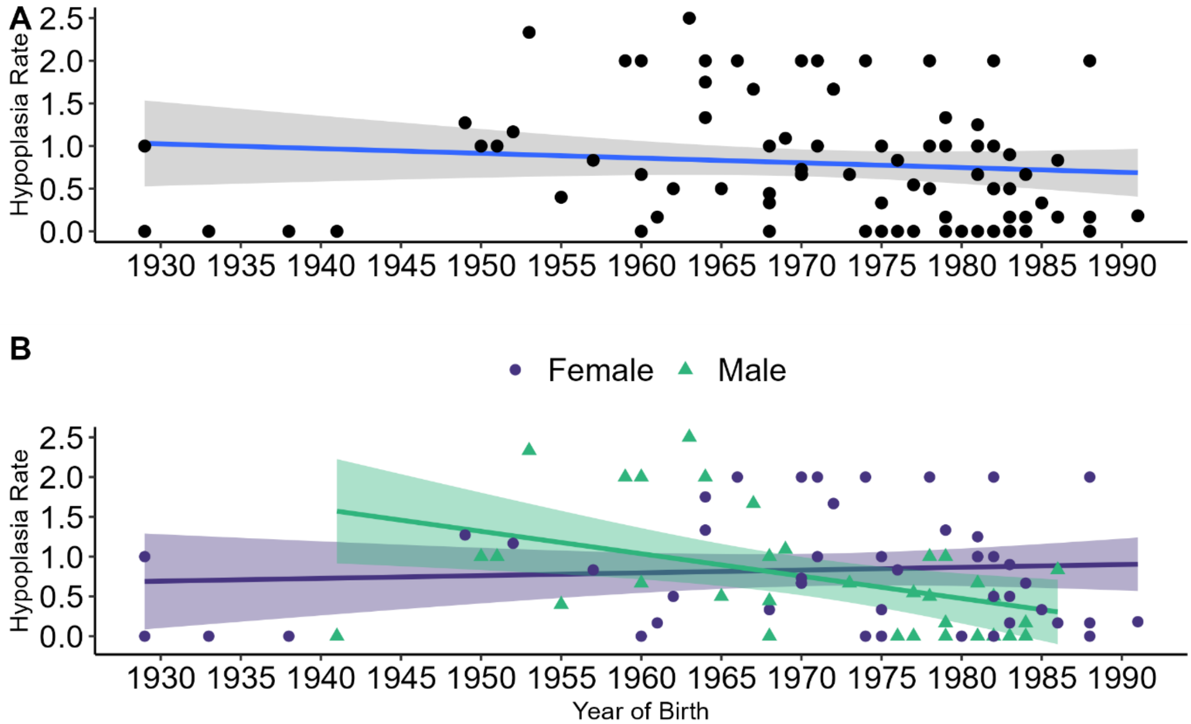
Variables	Group	n	Median	Mean	StDev	StErr
Tooth Count	All	81	10	8.68	3.35	0.37
	Women	48	11	8.83	3.42	0.49
	Men	33	9	8.45	3.29	0.57
Hypoplasia Count	All	81	6	5.89	4.82	0.54

	Women	48	6	6.54	5.12	0.74
	Men	33	4	4.94	4.24	0.74
Hypoplasia Rate	All	81	0.67	0.8	0.71	0.08
	Women	48	0.78	0.84	0.69	0.1
	Men	33	0.55	0.75	0.74	0.13

Data Visualization

Time series visualizations of hypoplasia rate revealed key patterns. First, the entire sample of bush-dwelling Hadza have a steady hypoplasia rate over time, averaging approximately one defect per tooth (**Figure 1A**). The non-significant difference between male and female rates noted above might contribute to this overall stability. When temporal trends are examined by sex, however, female rates appear flat and male line appear to slowly decrease, crossing the female line at around 1968. After this crossover, female rates diverge more from the regression line and male rates become consistently lower than females. By 1975, male rates are consistently below 0.5, with several at zero (**Figure 1B)**, suggesting a turning point in factors influencing infancy and early childhood health. Inspection of data distribution indicated a standard linear model would not be appropriate (Supplemental Materials **SF1**).

Figure 1: Scatterplot of hypoplasia rate and birth year with confidence intervals



Linear Mixed-Effects Model (LMM)

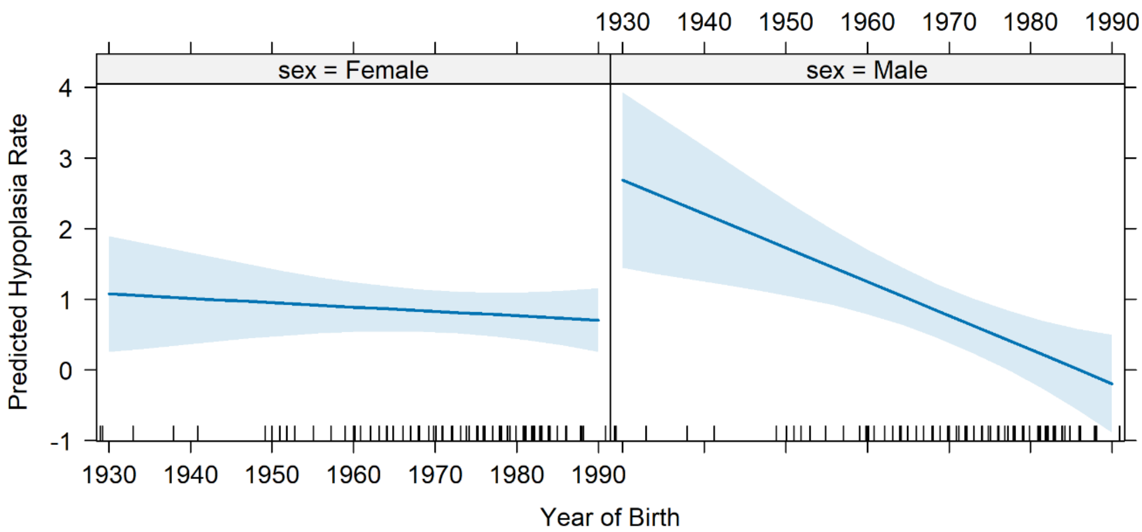
The LMM revealed a significant interaction between year of birth and sex (β = -0.04, SE = 0.02, p = 0.02), indicating temporal trends in hypoplasia rate was significantly different for men and women. The estimated hypoplasia rate for females in 1975 (the intercept) was 1.22 (SE = 0.15, $p < 0.001$). The estimated difference in hypoplasia rate between males and females in 1975 was -0.27 (SE = 0.24, $p = 0.26$).

Table 3: Linear mixed-effects model results (Year of Birth centered at 1975)

Effects	Est.	Std.Err.	df	t value	p-value	CI 5%	CI 95%
(Intercept)	1.22	0.15	76.03	8.37	**<0.001**	0.94	1.51
Year of Birth	-0.01	0.01	76.03	-0.65	0.51	-0.02	0.01
Male	-0.27	0.24	75.36	-1.14	0.26	-0.74	0.20
Interaction	-0.04	0.02	75.88	-2.37	**0.02**	-0.08	-0.01

The conditional R-squared was high (0.84) indicating that a large amount of variance was explained when accounting for fixed and random effects. The marginal R-squared, however, was low (0.12) indicating that fixed effects accounted for a limited proportion of the variance in hypoplasia rates. The remaining variability in hypoplasia rates has a standard deviation of 0.42 defects per tooth that were not accounted for by the model. **Figure 2** visualizes the LMM predicted hypoplasia rates accounting for the random effect and interaction between year of birth and sex. The trends depicted in **Figure 2** for males and females are consistent with the patterns observed in **Figure 1B**.

Figure 2: Predicted hypoplasia rates by year of birth and sex from the linear mixed-effects model (LMM)



Despite the previously noted skew in the raw data, the model diagnostics showed good agreement with normality and suggested that LMM assumptions were generally met (**Supplemental Materials SF2-8**). Sensitivity analysis was conducted by removing each of three potential outliers one at a time and re-running the model (**Supplemental Materials SF4, ST2-3**). In all cases, the significant interaction between year of birth and sex remained robust.

BRMS model

A Bayesian fixed-effects model was used to confirm the findings of the LMM using fixed effect estimates and uncertainty from the LMM *without* the random intercept to inform priors (see **Methods** and **Supplemental Materials ST4**). The final model had the formula:

hypoplasiaRate ~ yob_centered_1975 * sex + offset(tooth_offset)

The brms model was run with 4 chains, 2000 iterations per chain (1000 warm-up), resulting in 4000 post-warmup draws. Convergence diagnostics indicated good model convergence and sampling efficiency, with all Rhat values close to 1 and adequate effective sample sizes (Bulk_ESS and Tail_ESS) (**Table 4**). The brms model revealed posterior means consistent with the LMM findings (**Table 3**). The posterior mean for the residual standard deviation (sigma) was 0.88 (95% credible interval: 0.77 to 1.00), indicating the degree of unexplained variation in the hypoplasia rates after accounting for the fixed effects. While sigma is much larger than residual standard deviation of 0.42 observed in the LMM, the brms model did not include a random intercept. The credible intervals from the brms model that do not include zero appear to be slightly narrower than the confidence intervals derived from the LMM, suggesting a potentially more precise estimation of the fixed effects in the Bayesian framework for this specific model and dataset that might be attributed to the different approaches in quantifying uncertainty and the absence of the random intercept in the brms model.

Table 4: BRMS model results using priors from LMM without random effect

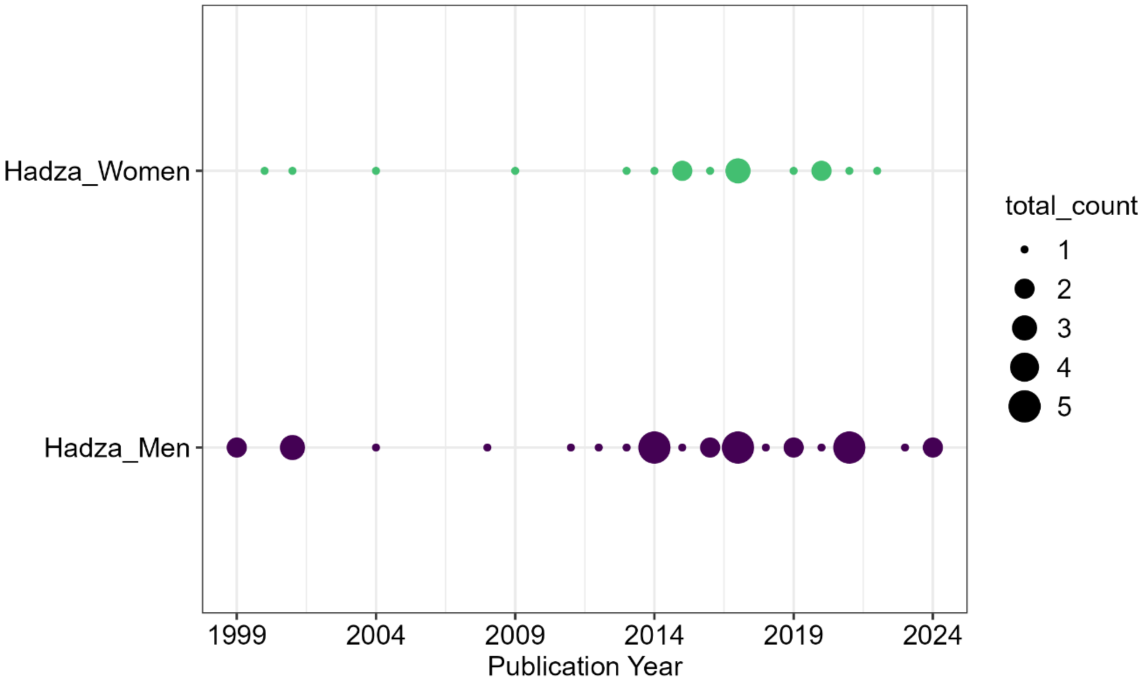
Effects	Est.	Std.Err.	CI 5%	CI 95%	Rhat	Bulk_ESS	Tail_ESS
Intercept	1.22	0.11	1.02	1.43	1	4445	3304
yob_centered_1975	-0.01	0.01	-0.02	0.01	1	4841	3067
sexMale	-0.25	0.15	-0.56	0.03	1	4516	3007
yob_centered_1975:sexMale	-0.04	0.01	-0.06	-0.02	1	4719	3257

Density overlays, histograms, and scatterplots (**Supplemental Materials SF9-11**) indicated some limitations in capturing the bimodal distribution of the observed hypoplasia rates and showed a slight tendency to overestimate the variability, but the model adequately captured the central tendency of the data and showed good fit. (**Supplemental Materials SF12-13**). The convergence and mixing of the MCMC chains were examined and visualizations of trace plots and autocorrelation plots (**Supplemental Materials SF14**) supported good chain behavior. Bivariate relationships between posterior distributions in pairs plots revealed some expected correlations between parameters but showed no indications of problematic multicollinearity (**Supplemental Materials SF15-6**). The diagnostic plots indicate generally good fit but coupled with the sigma value of 0.88, the model had some limitations in capturing the full complexity of the data distribution.

Bibliometrics

A comparison of datasets for Hadza men and Hadza women indicate a longer investment in research on Hadza men (**Figure 3**). The counts are higher overall for publications focused on men until around 2015, which coincides with the early carer research of three leading female Hadza researchers with anthropological training receiving their doctoral degrees in 2009-2010.

Figure 3: Timeline of Hadza research (excluding two early publications 1931 and 1975)



Beyond terms linked to identity and location (e.g., Hadza, Tanzania), the top terms for research on men were hunting reputation, family provision, and parental effort compared the top terms for research on women which were cortisol, rituals, and social groups (**Supplemental Materials ST5-6**). Network metrics indicate distinct patterns by sex (**Table 5**). There are more nodes (terms) in research on men. Despite having fewer nodes, the women's network has a substantial number of edges, indicating strong connections among terms, and an average degree (a measure of sparseness or connections to a node) of 28.48—almost two times greater than for men (15.45). Crucially, the density (node connectivity) of the women's network (0.89) is approximately four times greater than that of the men's network (0.21). Both networks show a high tendency to form clusters, with the women's slightly higher than men's even if the men's is sparser. While the network is sparse, the modularity metric for men indicates tight connections among terms, a sign of distinct thematic areas. In contrast, the low modularity in the denser women's network reinforces the idea of a highly interconnected web of terms without clear community divisions. The unique terms in the women's network reflect the overall interconnected focus on health, reproduction, status, and stress, whereas distinct thematic clusters in the men's network have unique focus on hunting, skills, work, and wealth (**Supplementary Materials Figures SF17-18**).

Table 5: Network Metrics for: Co-occurrences with Hadza Men and Women

Network Metric	Men	Women
Number of Nodes	73	33
Number of Edges	564	470
Average Degree	15.45	28.48

Network Density	0.21	0.89
Average Clustering Coefficient	0.90	0.99
Modularity	0.46	0.03

Discussion

This paper presents the findings of a novel application of a non-invasive developmental stress biomarker commonly used in bioarchaeology to a living population, the Hadza hunter-gatherers, thereby allowing analysis of long-term trends in childhood health in a way not possible using approaches available in human biology. Linear enamel defects are reliable biomarkers of physiological stress because they are recorded during tooth development (Goodman *et al.*, 1988) and can be timed to the specific years in which the tooth developed (Goodman and Martin, 2002). Data were collected on Hadza hunter-gatherers who followed a traditional diet and lived in remote mobile bush camps in the Arusha area of Tanzania in 2007and 2009. The anterior maxillary teeth used in this research capture the period from infancy to early childhood (4.5 months to age 5.5). The mean hypoplasia rate (total linear enamel hypoplasia count/total teeth observed) was 0.8, indicating that the average Hadza in a sample of 81 (more than half the adults in the group) experienced some interruption to growth and development during early childhood.

Studies of enamel defects in living populations indicate that higher frequencies are associated with a lower quality of living conditions during childhood and an overall lower mean age-at-death (Goodman, 1988; Goodman *et al.*, 1988; Goodman and Armelagos, 1985; Goodman and Rose, 1990). Prior research comparing enamel defect frequency suggested that Hadza health declined during the transition to sedentism in a sample of 17 bush-living Hadza (the subject of this study but using different data) and 34 village-living Hadza (Ungar *et al.*, 2017). Reduced quality of maternal diet negatively impacts development *in utero* and postpartum. Additional developmental stresses arise in villages from earlier weaning, which increases the chance of pathogen transmission to vulnerable children (Reyes-García *et al.*, 2019). Indeed, higher parasite and viral loads have been observed in Hadza spending time or living in sedentary villages compared to those living mostly in the bush (Page *et al.*, 2016) and those who spent infancy and early childhood in villages had higher frequencies of defects (Crittenden *et al.*, 2017).

A pattern of unhealthy childhoods is observed in the archaeological record during the transition to sedentism and agriculture for the same reasons, reduction in dietary breadth and early weaning (Armelagos, 1990). Sex-based health differences in enamel defects are uncommon in archaeological assemblages of hunter-gatherers and the few recorded instances have been attributed to differential parental investment in children and not inherent biological differences in buffering stress (Guatelli-Steinberg and Lukacs, 1999). The pattern is true in this study as well but with one difference. The Welch's t-test on the overall mean hypoplasia rates (**Figure 1A** discussion) found no significant difference between the sexes, but the temporal resolution offered by year of birth suggested a difference between the sexes based on year of birth.

A linear mixed-effects model (LMM) confirmed that the interaction between year of birth and sex (β = -0.04, SE = 0.02, p = 0.02) on hypoplasia rate was significant, and that finding held true when removing potential outliers (**Supplemental Materials SF3-4, ST2-3**). Bayesian analysis using brms corroborated these findings, with a posterior mean for the year of birth by sex interaction of -0.04 (95% credible interval: -0.06 to -0.02). The LMM explained a small part of the overall differences in rates among individuals (marginal R-squared = 0.12. residual standard deviation = 0.42, sigma = 0.88 (**Table 4**) but both models provided consistent evidence for a significant interaction between birth year and sex (β = -0.04, p = 0.02 in LMM; posterior mean = -0.04 in brms, **Table 4**), indicating a difference between male and female hypoplasia rates over time. Specifically, the negative coefficient suggests that the rate of these enamel defects decreased more quickly in males born after 1975 (**Figure 1B**). The fact that both types of analysis identified the same pattern strengthens confidence that this is a real trend in the data.

What may have caused the changes given that the Hadza in this study did not reside in permanent settlements like those in the studies above? A common explanation for health disparity is female neglect. The missing women hypothesis (Hesketh and Xing, 2006; Sen, 2013) has explained contemporary sex ratios that are biased towards males, particularly in Asia, and suggests that female children die at a higher rate than male children due to sex-selective abortions, female infanticide, and lower quality healthcare, and diet. The sex ratio for the continent of Africa (99.8), however, is slightly biased towards women (Hesketh and Xing, 2006) and male preference tends to occur North Africa compared to sub-Saharan Africa where the Hadza reside. In 2023, the share of women was 50.44% of the total Tanzanian population and sex ratios by age from 1950 to 2023 show a slight male bias at birth with a steady decline over the lifespan relative to females (Ritchie and Roser, 2019). The sample used for this study are aligned with the larger pattern in Tanzania that the missing women hypothesis is not likely given that females outnumber males and few to no males are as old as the older females. Female neglect has been documented in cross-cultural studies as contributing to poorer female health (Khera *et al.*, 2014), but such neglect has not been observed in the Hadza during the decades in which they have been studied and is also not likely.

Other explanations for disparity are preferential access to medical care and education. The barrier to routine and emergency medical care is the same for all Hadza. Medical care was not accessible to remote bush Hadza until 2018 with the advent of travelling medical clinics and, prior to that, visits to government clinics (starting in the 1960s) and hospitals (starting at around 2000) took several hours because they were located outside the traditional lands (Bennett *et al.*, 1973; Blurton Jones, 2015). Emergency transportation is now possible for remote Hadza via a former research vehicle repurposed as an ambulance for the critically ill (Wood, 2022). As for education, boys are preferentially sent to school (Marlowe, 2010)**: page 36)** but the nutritional benefit from school meals would not occur until after the age of five and the data presented here represented early childhood, up to 5.5 years of age. Even if younger children were brought by older siblings, of the 82% of Hadza children that attend school, none of them are children from bush camps (Pollom *et al.*, 2020).

Preferential treatment of one sex over another is another common explanation for disparity. This has not been observed in the Hadza over decades of study either. The opposite has been observed—Hadza children experience the same infancy and early childhood with mothers offering primary care during that period (Crittenden *et al.*, 2018). They are taken on daily foraging trips with their mothers until they are weaned (between 2-3), after which they are raised communally in camp and collectively forage near camp as early as three years old (Crittenden *et al.*, 2013). As they grow older, children may join larger female foraging groups but tend to continue foraging in mixed age and mixed sex parties of their peers (Crittenden *et al.*, 2013). Sex differences do not develop in middle childhood (starting at age 6) with females providing more childcare and boys almost exclusively making tools (bows and arrows) or helping with tools (sharpening knives and axes) (Froehle *et al.*, 2018). The window of development recorded by the anterior dentition used in this study is from 4.5 months to 5.5 years, before sex differentiation takes place. The role of parents in teaching Hadza children is minimal in early life (Lew-Levy *et al.*, 2021) with most learning from peers (Crittenden *et al.*, 2013) even if some same-sex observational learning occurs later in childhood (Lew-Levy *et al.*, 2021). Given the nature of Hadza childhood, there are no identifiable avenues for either sex to gain an advantage.

As noted above, **Figure 1B** showed turning point starting in 1968 with a clear pattern established after 1975 where males have few to no hypoplasias. The male rate decreased 71% after 1975 (from 1.13 to 0.33), while the female rate declined only 23% (from 0.95 to 0.73). The timing coincides with increasing participation in a remote market economy—one brought to the Hadza by researchers and tourists who pay them for services (Yatsuka, 2018). Among the primary factors that determine market participation in indigenous people (Godoy *et al.*, 2005), the Hadza are experiencing two, land encroachment and a desire for foreign goods (Crittenden, 2019; Crittenden *et al.*, 2017; Gibbons, 2018; Joachim and Zahor, 2022; Yatsuka, 2015). These are related factors because encroachment threatens food security and drives Hadza to participate in the market economy, which increases their intake of foreign goods, such as non-traditional foods, and potentially harmful substances such as alcohol, cigarettes, and marijuana (Crittenden and Blurton Jones, 2019; Gibbons, 2018). Compared to when the data for this study were collected, bush-dwelling Hadza now may acquire technologies like mobile phones, solar panels, bicycles, and manufactured goods (Crittenden, 2019).

Land encroachment has occurred relative to population growth in Arusha, which has led to land repurposing and replacement of wildlife with livestock and bush with farms (Madsen, 2000; Redfern, 2018). Historically, the Hadza traded with neighbors such as the Datoga pastoralists, to supplement food (Marlowe, 2010), but the growth in Datoga population size and expansion of their grazing lands has caused additional hardship through loss of wildlife (traditional game), berry groves (dietary staple), availability of tubers, and honey—the latter being a large proportion of daily caloric intake (Bichell, 2009). Hadza have no individual land rights but as communities they can apply for a Certificate of Customary Right of Occupancy—even still, only 10% of their original lands have been titled to them (Redfern, 2018). Hadza have no cultural mechanisms in place to compensate for food scarcity because famine is rare in hunter-gatherers and Hadza history (Berbesque *et al.*, 2014). Conflict between Hadza and Datoga have been observed in the form of Hadza men and older boys carrying weapons to protect Hadza women when they are foraging (Wood *et al.*, 2021). Prior to the turn of the 21st century, the Hadza did not accept currency (Yatsuka, 2015). Now, Hadza camp for up to five months at a time or live on the periphery of villages semi-permanently to capitalize on tourist safaris (Marlowe, 2002, 2010), which has become their main commercial activity (Yatsuka, 2015).

Since 17% Tanzania's GDP is from tourism (Bichell, 2009), ecotourism has been proposed as a solution to challenges of land encroachment because it creates a protected cultural zone and source of community-based economic development for the Hadza (Bushozi, 2015, 2022; Moshi *et al.*, 2019). Ecotourism rose to prominence in the 1980s when governments became concerned about the damage from tourism to cultural and environmental resources (Guerrero-Moreno and Oliveira-Junior, 2024). Such protection programs can be successful pathways for indigenous integration into a market economy (Godoy *et al.*, 1998; Guest, 2002). Hadza proximity to the Ngorongoro Conservation Area, gives them access to over 400,000 tourists each year (Gibbons, 2018; Pollom *et al.*, 2020; Yatsuka, 2015), who were already known outside of academic circles by the 1970s and became famous in the 21st century following the release of BBC and PBS documentaries (Bichell, 2009). Tourists pay a $10 entry fee to communities to access remote bush locations and individual Hadza generate additional income from selling souvenirs (Yatsuka, 2018). There are over 300 safari companies that bring as many as ten tourist groups to the bush each day (Wells, 2020). Tourists bring access to agricultural products (e.g., maize, sugar, salt), textiles (e.g., clothing, blankets, mosquito nets), tools (e.g., knives, cooking pots), and electronics (e.g., radios, cell phones) (Bichell, 2009)—even if such access was less common when the data for this paper were collected. Such exposure to non-traditional technologies and resources is argued to benefit Hadza transition to a different lifestyle (Joachim and Zahor, 2022), but such arguments fail to acknowledge that external forces have imposed this transition on the Hadza. In fact, there is a wealth of evidence that tourism is not a mutually beneficial solution because it is harmful to the health and culture of the Hadza people and not aligned with what the bush-living Hadza want (Gibbons, 2018). Given the loss of cultural traditions and values exacerbated by alcohol abuse and land loss, the sustainability of a tourism-based economy is highly questionable (Bichell, 2009). African countries more broadly have struggled to keep tourism a stable industry, in part because of the impacts on traditional peoples (Yatsuka, 2018).

The external forces of visitors (tourists, missionaries, researchers, and government) and the food shortages caused by land encroachment have changed the Hadza view of themselves. The use of currency and the concept of property values have signalled that they, as a people, have monetary value to outsiders. Researchers paved the way for a clear and apparent bias towards men having prioritized men's roles and perspectives on a diversity of topics for decades compared to research on women starting in the in 2015 (**Supplemental Materials, SF 17-18, ST5-6**). The tourism industry reinforces this bias by offering two to three hour hunting trips with men and practice using their bows and arrows afterwards—only some tourists forage with women (Yatsuka, 2018). Men earn more wages which they exchange for valuable market goods including cigarettes and alcohol but also grains and other agricultural products (Pollom *et al.*, 2020). External forces may be influencing the subtle early initialization of gender roles creating tacitly permissible social inequality

(Dyble *et al.*, 2015; Kent, 1995) and wealth disparities that influenced the childhood health trends reported in this paper.

Wealth disparity is a documented side effect of tourism in other egalitarian groups (Gezon, 2014; Guenther, 2005; Wierucka, 2018). Wealth disparity, potentially influenced by the greater economic opportunities afforded to men through remote market participation, could contribute to differential resource allocation within households, possibly favoring male children. The external signal to the Hadza is that men and their activities (like hunting) have a higher value than women and their activities. Perhaps the greater leisure time afforded to men allows them to engage more with male children possibly resulting in differential access to higher quality foods, as seen in other transitioning groups. Given the same-sex passive learning structure in Hadza childhood (Lew-Levy *et al.*, 2021), Hadza men interacting exclusively with Hadza boys is a possibility. Male children themselves might participate more than girls, who are more engaged with childcare (Lew-Levy *et al.*, 2021) compared to boys who are primarily engaged with tools (Froehle *et al.*, 2018).

The research presented here has three major contributions. First, the longitudinal perspective offered through the study of dental enamel defects revealed sex-based impacts on health from remote market integration, a unique view of integration not previously considered. Second, market integration has been observed to increase female morbidity, but the opposite is true in this study. Third, the novel approach of applying a method commonly used in bioarchaeology to assess developmental stress in a living population allows analysis of long-term health trends in a group with extensive ethnographic data. The implication of the results are that gender inequality and wealth disparity may occur much earlier in the transition from egalitarianism (often hunter-gatherers) to hierarchical systems (often food producing), but retention of traditional lifestyles may buffer some effects. These subtle changes would not be visible in a bioarchaeological context due to the lack of dating accuracy in burial deposition and have not been witnessed in living transitional populations due to the lack of longitudinal health data.

The limitations of the study include the indirect nature of enamel hypoplasia as a measure of stress and the potential for other unmeasured factors (low LMM R-squared value), such as inter-individual variation (particularly for three outliers). Another limitation is that early stressors are associated with decreased longevity and the older adults in our sample may be the healthiest Hadza in this oldest age cohort because their less healthy peers have already died (Goodman, 1988; Goodman *et al.*, 1988; Goodman and Armelagos, 1985; Goodman and Rose, 1990; Yaussy *et al.*, 2016). A final limitation is that the only potential source of improvement in the health of boys during early childhood is speculative based on the timing of the dramatic shift as coincident with tourism. Several explanations from other studies were explored but none were robust relative to the sample of bush-living Hadza using for this study. Thus, there is only circumstantial evidence that the Hadza may be influenced by the strong external signal that men’s work is more valuable than women’s.

A clear future direction to build on the findings presented here is comparative data collection on indigenous populations having undergone market integration (direct or remote) in the past 2-3 generations. Even if integration is now complete, the method will capture the early childhood health status of adults before, during, and after the transition. A larger dataset following these methods will allow a re-examination of the impacts on health from subsistence and economic transition. For the Hadza specifically, data on father-son interactions in early childhood among contemporary Hadza still living in remote bush camps would provide more information to explain the findings.

In conclusion, this investigation into long-term trends in enamel hypoplasia among bush-living Hadza hunter-gatherers reveals a significant and sex-specific pattern of declining childhood stress in male children coinciding with increasing remote market participation (market brought to the bush). Specifically, the marked reduction in hypoplasia rates among males born in the mid-1970s and no change among females and older generations, indicates a gendered impact on early childhood health from evolving economic interactions. The study breaks new ground by examining market integration as a remote phenomenon, occurring even when populations have limited direct access to markets. The findings underscore the complexity of transition and highlight the need for further longitudinal and ethnographic research to elucidate the specific mechanisms driving these emerging health disparities and to inform our understanding of similar transitions in both contemporary and past populations.

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Data availability statement
https://github.com/kchoover14/HadzaMarketIntegration

Data deposition
https://github.com/kchoover14/HadzaMarketIntegration

Supplemental online material
https://github.com/kchoover14/HadzaMarketIntegration

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Supplementary Materials for: Market integration improves traditional Hadza male childhood health with no effect on females

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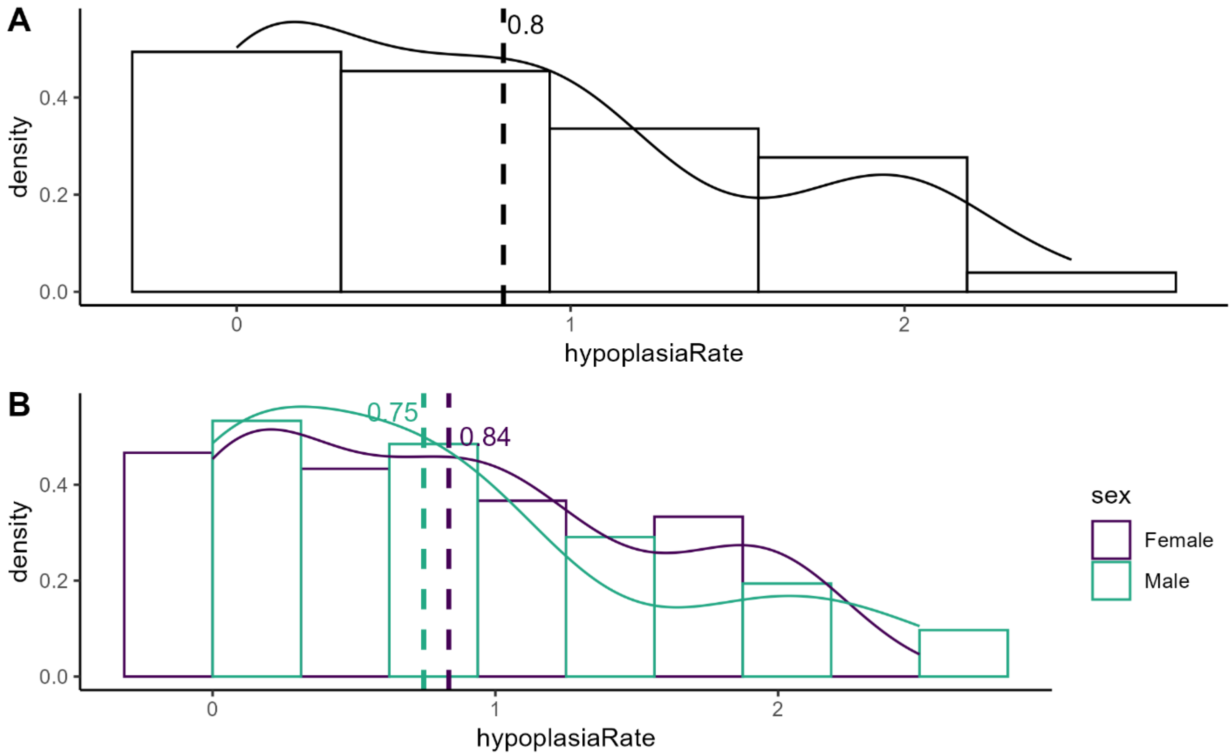
Section 1: Data Distribution

Data distributions visualized via histograms with density plots for the entire sample (**S1A**) and by sex (**S1B**). **Figure 1A** shows a clear peak in the first bin, indicating a high frequency of individuals with a hypoplasia rate around 0. The frequency decreases in subsequent bins as the hypoplasia rate increases. The density plot confirms this right-skewed distribution, with a primary mode near 0 and a tail extending towards higher hypoplasia rates. There might be a very slight secondary bump or shoulder around a hypoplasia rate of 2, but the primary concentration is at the lower end. The vertical line for the sample mean is to the right of the primary peak, consistent with a right-skewed distribution where the mean is pulled towards the tail. **Figure 1B** shows distinct distributions by sex. Both have a peak in the first bin (hypoplasia rate around 0), but the shapes differ. The female distribution appears more concentrated around 0 with a longer tail extending to higher rates. The male distribution seems to have a less pronounced peak at 0 and potentially a more noticeable secondary peak or broader distribution around a hypoplasia rate of 1-2. The density plots further illustrate these differences. The female density plot has a higher peak at 0 and a more gradual decline. The male density plot has a lower peak at 0 and a more prominent shoulder or secondary mode in the higher rate range. The female mean is slightly lower than the male mean, and both vertical mean lines are positioned to the right of the primary peak for their respective distributions. Overall, the highest frequency is at or near a hypoplasia rate of 0, indicating good developmental health for a majority of the sample. There is evidence of some individuals with higher hypoplasia rates, creating a longer tail and potentially contributing to the slight secondary mode or shoulder, particularly in the male distribution. The distribution indicates a classic linear model is not appropriate.

SF1: Distribution of data for the sample and by sex



Section 2: LLM Model Centering

Centering the mean separates the effects of predictors into within-group and between-group components and improves the interpretability of the model and significance of the effects studied. Models with different centered means for the year of birth variable were compared (mean year of birth, and two years observed as important break points in the data). Centering on mean year of birth is less meaningful than centering on a year of birth that has inherent significance in the observed patterns, which is why those results are compared to two additional years. The male slope crosses the female slope fully by 1970, and individual male values are at or below the female slope by 1975. **ST1** shows that there are no differences in the results obtained using different mean centers. Because males born after 1975 have values at or below the female slope, this year was used for centering.

ST1: Model results and anova, comparing centers

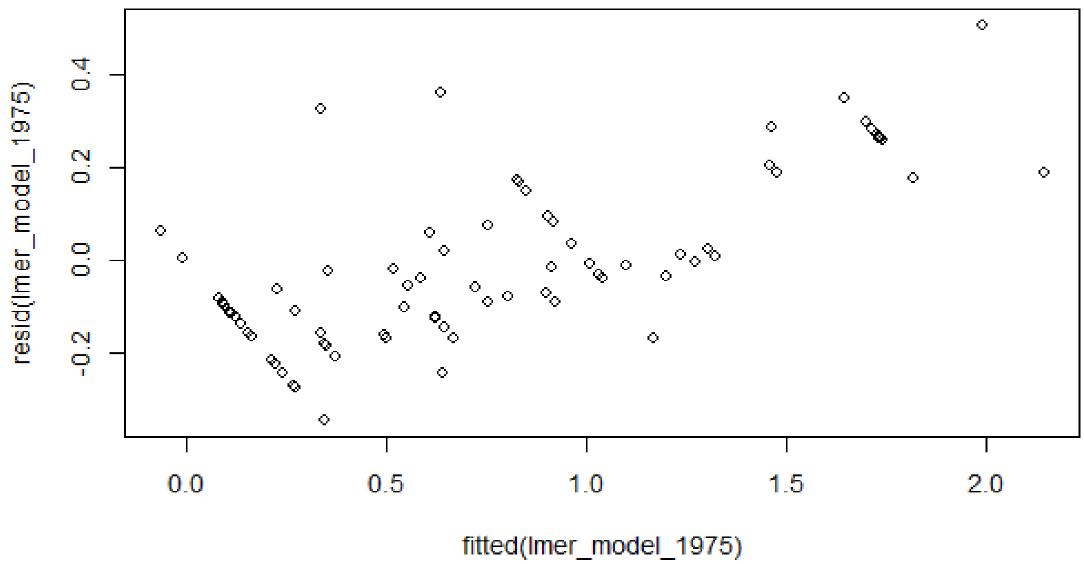
Models	Effects	Est.	Std.Err.	df	t value	p-value
Mean Centered	(Intercept)	1.25	0.14	76.03	8.82	<.01
	yob	-0.01	0.01	76.03	-0.65	0.51
	Male	-0.10	0.22	75.60	-0.43	0.67
	Intersection	-0.04	0.02	75.88	-2.37	**0.02**
1970 Centered	(Intercept)	1.25	0.14	76.03	8.83	<.01

	yob	-0.01	0.01	76.03	-0.65	0.51
	Male	-0.06	0.22	75.66	-0.28	0.78
	Intersection	-0.04	0.02	75.88	-2.37	**0.02**
1975 Centered	(Intercept)	1.22	0.15	76.03	8.37	<.01
	yob	-0.01	0.01	76.03	-0.65	0.51
	Male	-0.27	0.24	75.36	-1.14	0.26
	Intersection	-0.04	0.02	75.88	-2.37	**0.02**

Section 3: LLM Model Diagnostics

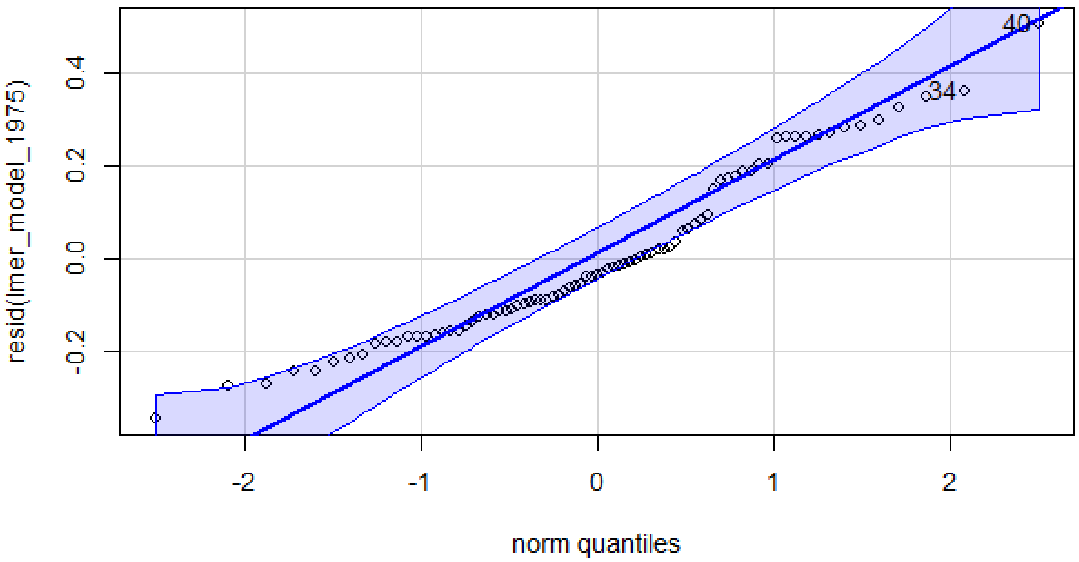
The plot of residuals versus fitted values (**SF2**) indicates the values are scattered around 0 with no obvious curvature. While the variance of residuals is slightly wider at higher fitted values (~1.5-2.0) compared to lower fitted values (~0-0.5), which suggests slight homoscedasticity. The randomness of the residuals is generally supported, suggesting the assumption of linearity is met.

SF2: Plot of residual vs. fitted values



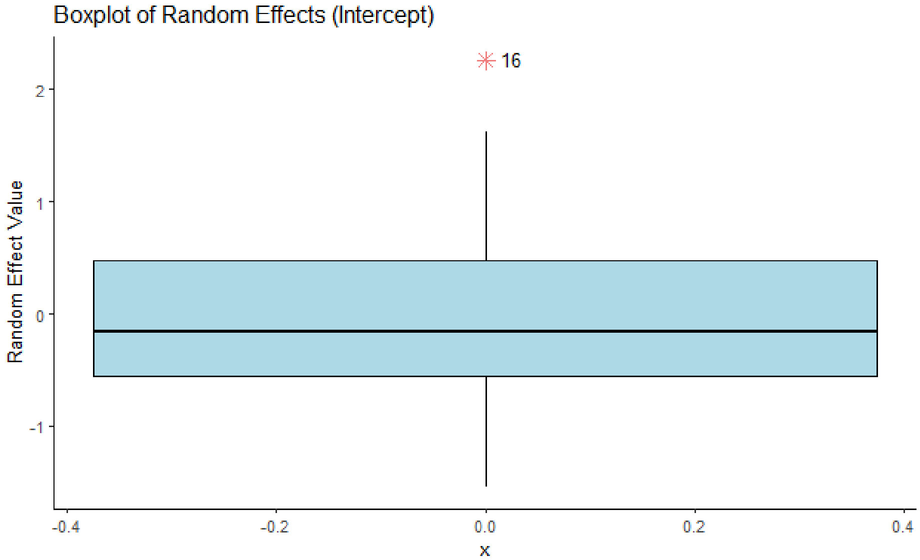
The quantile-quantile plot of the residuals (**SF3**) shows good agreement with the normal distribution line, with most points falling within the confidence interval. Overall, the distribution of residuals did not suggest a severe violation of the normality assumption, although two potential outliers were identified in the QQ-plot (Individuals 34 and 40).

SF3: QQ Plot of residuals



The boxplot summarizing the distribution of random intercepts for individual ID (**SF4**), indicates a median close to zero, and an interquartile range showing the spread of the central 50% of the individual-level deviations. There is a notable outlier at a high positive random effect value (row 16, Individual ID 861), suggesting this individual has a considerably higher baseline hypoplasia rate compared to the rest of the sample.

SF4: Boxplot of random effects (intercept)



Sensitivity testing was conducted on each of the outliers previously identified (**SF3, SF4**). These individuals impact the intercept and sex estimates, but not year of birth and interaction effects, which remain stable (**ST2**). Notably, the hypoplasia rates of these outliers align with the overall temporal trend observed in the data, with the two individuals born before 1975 (Individual 34, born 1929, rate = 1.00; Individual 40, born 1963, rate = 2.50) exhibiting much higher rates of hypoplasia compared to the individual born after 1975 (Individual 16, born 1977, rate = 0.55).

ST2: Sensitivity testing outliers (individuals: #34, #40, #16)

Models	Effects	Est.	Std. Error	t value	CI 5%	CI 95%
LLM	(Intercept)	1.22	0.15	8.37	0.94	1.51
	yob_centered_1975	-0.01	0.01	-0.65	-0.02	0.01
	sexMale	-0.27	0.24	-1.14	-0.74	0.20
	yob_centered_1975:sexMale	-0.04	0.02	-2.37	-0.08	-0.01
Minus Ind 16	(Intercept)	13.37	17.60	0.76	-21.12	47.87
(Row 40)	yob	-0.01	0.01	-0.69	-0.02	0.01
	sexMale	72.86	33.19	2.20	7.82	137.91
	yob:sexMale	-0.04	0.02	-2.20	-0.07	0.00
Minus Ind 450	(Intercept)	-5.14	19.75	-0.26	-43.85	33.58
(Row 34)	yob	0.00	0.01	0.32	-0.02	0.02
	sexMale	100.81	34.80	2.90	32.60	169.02
	yob:sexMale	-0.05	0.02	-2.90	-0.09	-0.02
Minus Ind 861	(Intercept)	13.37	18.64	0.72	-23.17	49.91
(Row 16)	yob	-0.01	0.01	-0.65	-0.02	0.01
	sexMale	81.67	35.15	2.32	12.77	150.57
	yob:sexMale	-0.04	0.02	-2.33	-0.08	-0.01

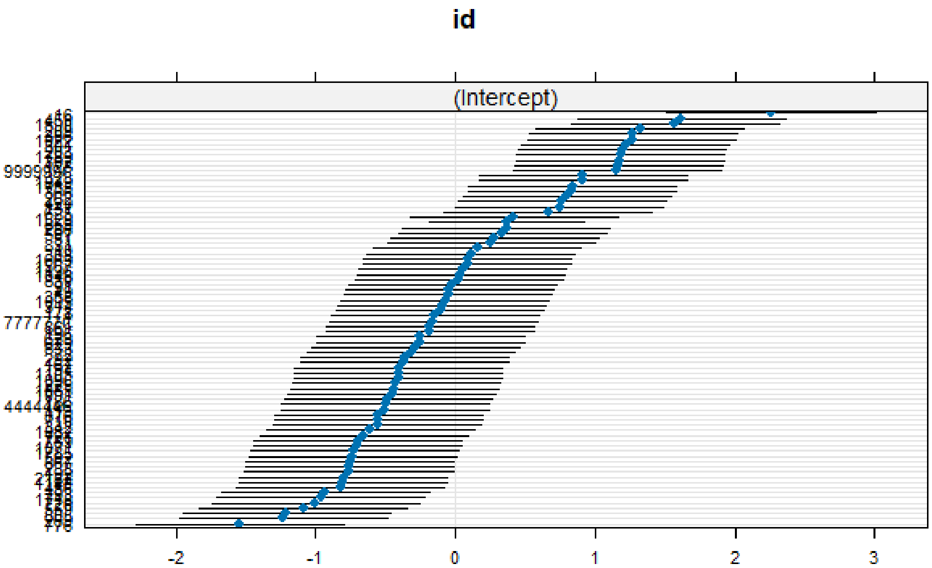
Despite their influence on the main effects (see **ST3** for individual level data), the robustness of the interaction term highlights a consistent pattern of differential change in hypoplasia rates over time between males and females, a phenomenon that warrants further consideration in the context of existing knowledge about sex-based health differences in hunter-gatherer societies.

ST3: Raw data for outliers

Row#	IndID	Age	yob	yob_ctr	Sex	#LEH	#Teeth	hypoRate	tooth_offset
34	450	78	1929	-46	Female	1	1	1.00	-2.48
16	861	30	1977	2	Male	6	11	0.55	-0.09
40	16	45	1963	-12	Male	5	2	2.50	-1.79

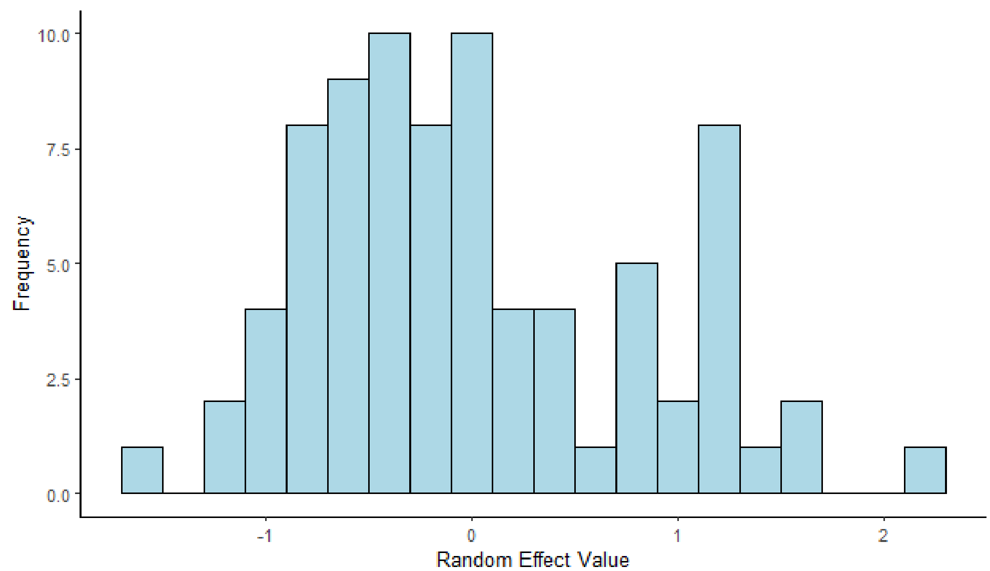
The conditional modes of the random intercepts appear symmetrically distributed around zero. Some clustering or breaks in the pattern can be observed at higher positive values suggesting groups of individuals with similarly elevated baseline hypoplasia rates (**SF5**).

SF5: Conditional Modes of Random Intercepts by Individual ID



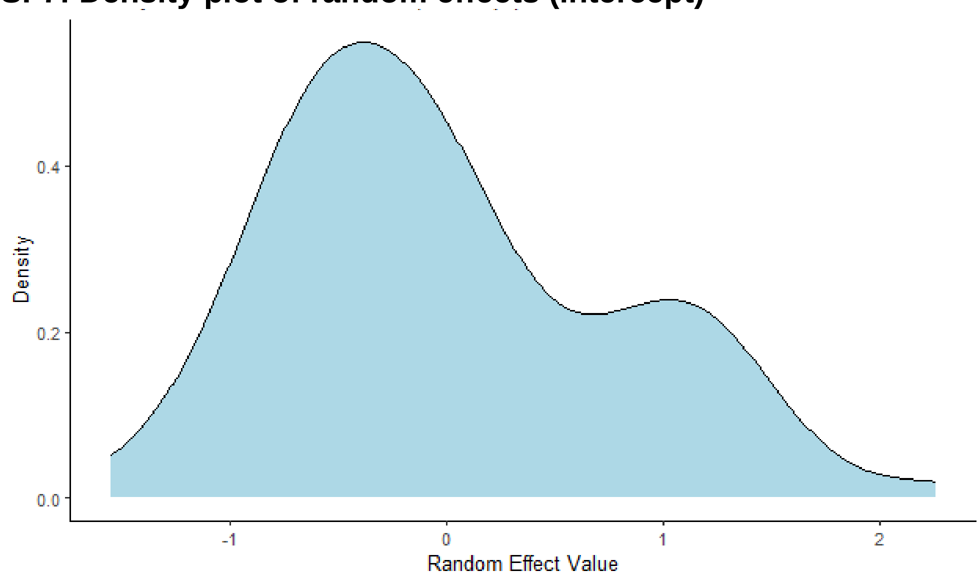
SF6 shows the distribution of the random intercepts for individual ID. While centered around zero, the histogram reveals a somewhat uneven distribution with distinct peaks around -0.25 to 0 and 0 to 0.25, suggesting potential deviations from a perfectly normal distribution of individual-level baseline hypoplasia rates.

SF6: Distribution of random effects (intercept)



SF7 presents the density plot of the random intercepts for individual ID. Consistent with the histogram, the distribution appears bimodal, with a primary peak near zero and a secondary, smaller peak around a random effect value of 1. This bimodality suggests that the individual-level deviations from the average baseline hypoplasia rate are not uniformly distributed and may reflect distinct subgroups within the population.

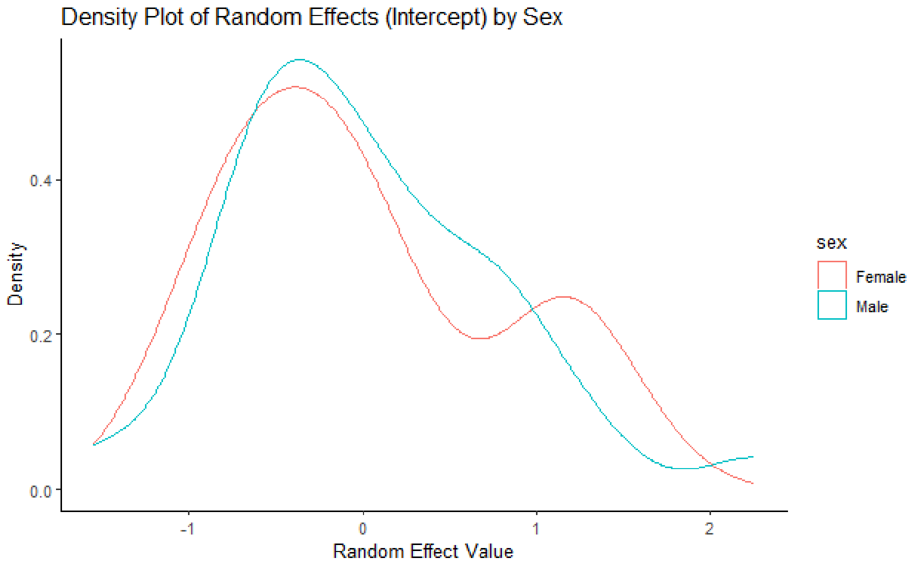
SF7: Density plot of random effects (intercept)



SF8 displays the density plots of the random intercepts for individual ID, separated by sex. The distribution for females is unimodal, centered slightly below zero. In contrast, the distribution for males exhibits a clear bimodality, with a primary peak like that of females and a distinct secondary peak around a random effect value of 1. This suggests

that the presence of a subgroup of males (born before 1975, see main paper **Figure 1B**) with higher baseline hypoplasia rates is the primary driver of the bimodality observed in the overall distribution of random intercepts.

SF8: Density plot of random effects (intercept) by sex



Section 4: Bayesian Model (brms)

LMM comparison (with and without random effect)

The LMM included a random intercept for individual ID, based on the understanding that individual-level variation might influence hypoplasia rates, but initial attempts to fit a similar Bayesian model with a random intercept encountered convergence issues, suggesting near-zero variance for this random effect. Given these challenges, we explored alternative Bayesian model specifications. We attempted to improve sampling by adjusting max_treedepth and adapt_delta, as well as increasing iterations, but convergence problems persisted. We also experimented with different weakly informative half-normal priors with varying widths (narrow, wide, and wider) for the standard deviation of the random intercept, but the near-zero variance and convergence issues remained and the posterior estimates consistently indicated near-zero variance for this random effect.

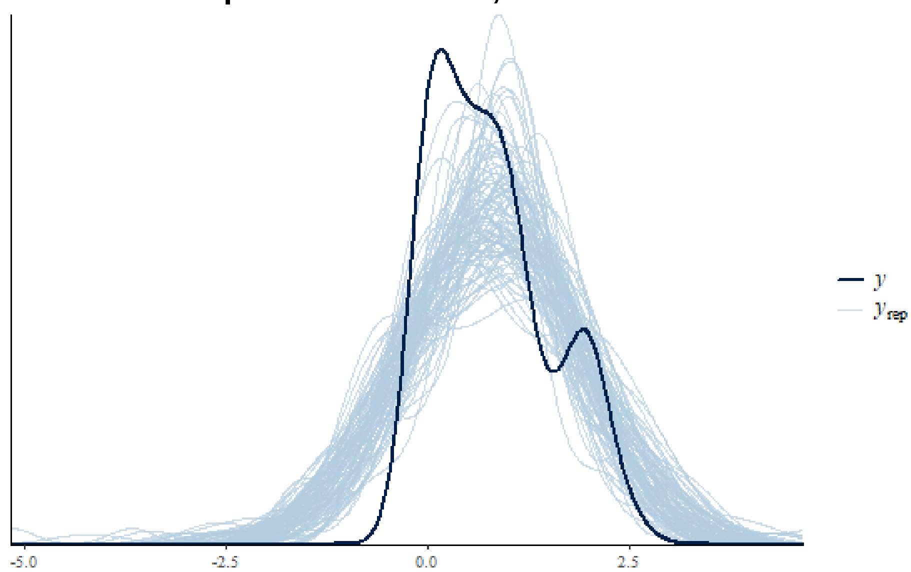
We investigated the necessity of the random intercept for individualID by comparing models with the same fixed-effect structure, the previously described and one without a random effect using lm in base R. We compared results using a likelihood ratio test in base R anova. The results of the ANOVA comparison (anova(lmer_model, lmer_model_fixed)) showed no significant difference in model fit (Chisq = 0.46, df = 1, p = 0.5). This statistical evidence supports the finding from our Bayesian attempts that the random intercept had minimal impact on explaining the variance in hypoplasia rates beyond the fixed effects of year of birth and sex.

ST4: Model comparison, with and without random effect

Models	Effects	Est.	Std. Error	t value
Random	(Intercept)	1.22	0.15	8.37
	yob_centered_1975	-0.01	0.01	-0.65
	sexMale	-0.27	0.24	-1.14
	yob_centered_1975:sexMale	-0.04	0.02	-2.37
No random	(Intercept)	1.22	0.15	8.40
	yob_centered_1975	-0.01	0.01	-0.66
	sexMale	-0.25	0.23	-1.08
	yob_centered_1975:sexMale	-0.04	0.02	-2.31

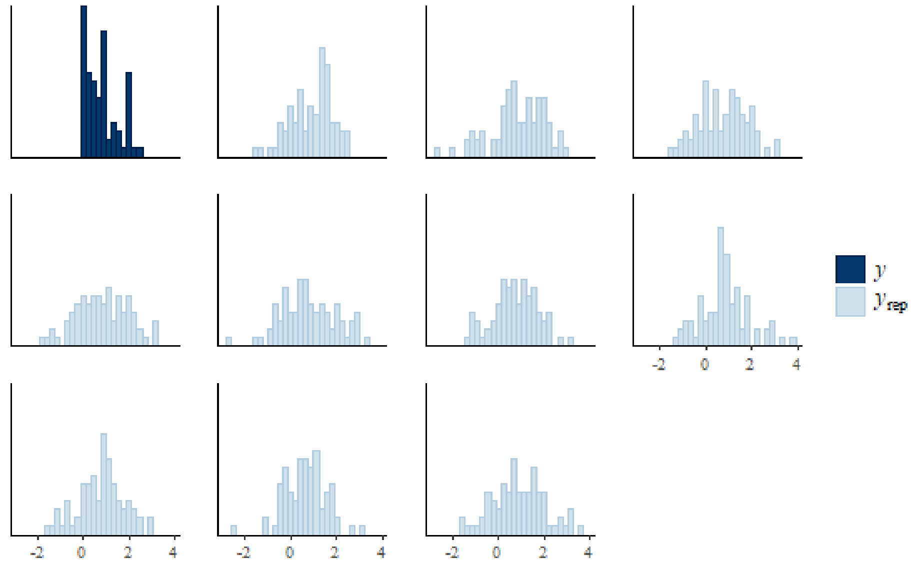
The posterior predictive checks (**SF9**) revealed some discrepancies between the observed and predicted data distributions. The density overlay indicated that while the model captured the general range of hypoplasia rates, the predicted densities tended to smooth over the observed bimodal distribution (a primary peak at zero and a secondary peak around two, driven by females). The predicted densities showed a tendency to fill in the lower values to the left of the primary peak, where the observed data had fewer observations.

SF9: Posterior predictive checks, brms



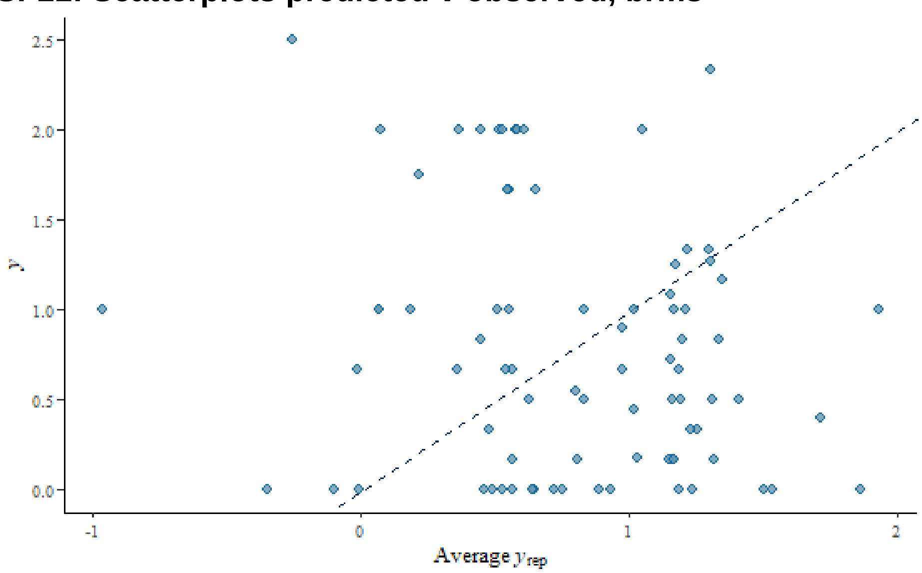
Similarly, the histograms (**SF10**) showed that while the observed data had a high frequency in the first bin (zero hypoplasias) with decreasing frequency in subsequent bins, the predicted data exhibited a more even distribution with some predictions extending to lower values than observed.

SF10: Histograms observed v predicted, brms
Predicted densities, brms



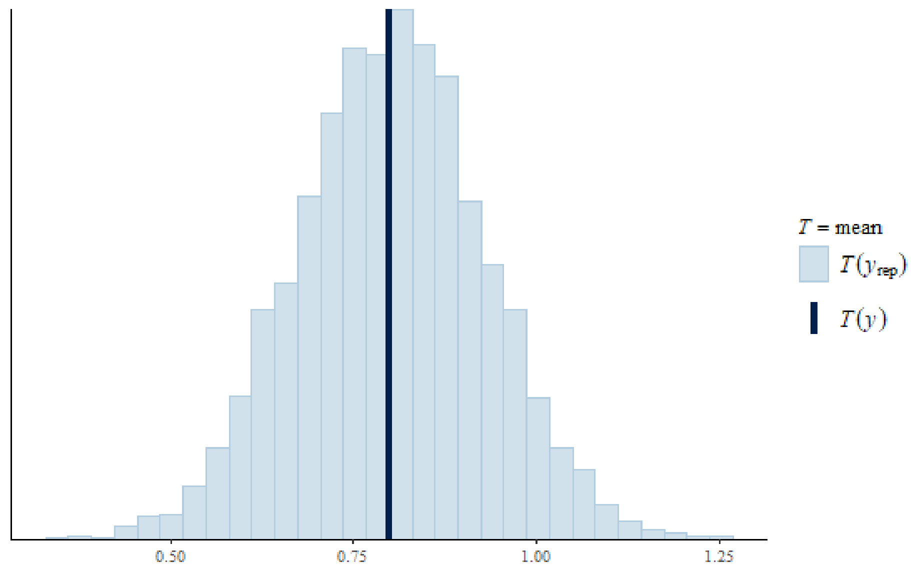
The average predicted vs. observed scatterplot showed a reasonable fit, with points scattered around the identity line, and denser areas at zero and two, reflecting the modes in the observed data (**SF11)**.

SF11: Scatterplots predicted v observed, brms



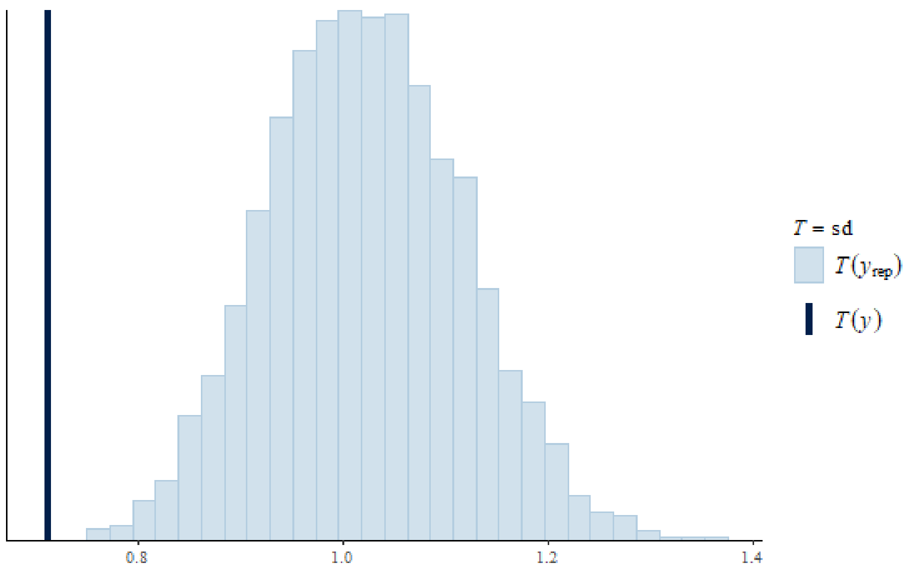
The posterior predictive checks for the mean (**SF12)** showed the mean of the observed data (0.71) lies within the distribution of the means of the predicted data, suggesting the model adequately captured the central tendency.

SF12: Posterior predictive checks for mean, brms



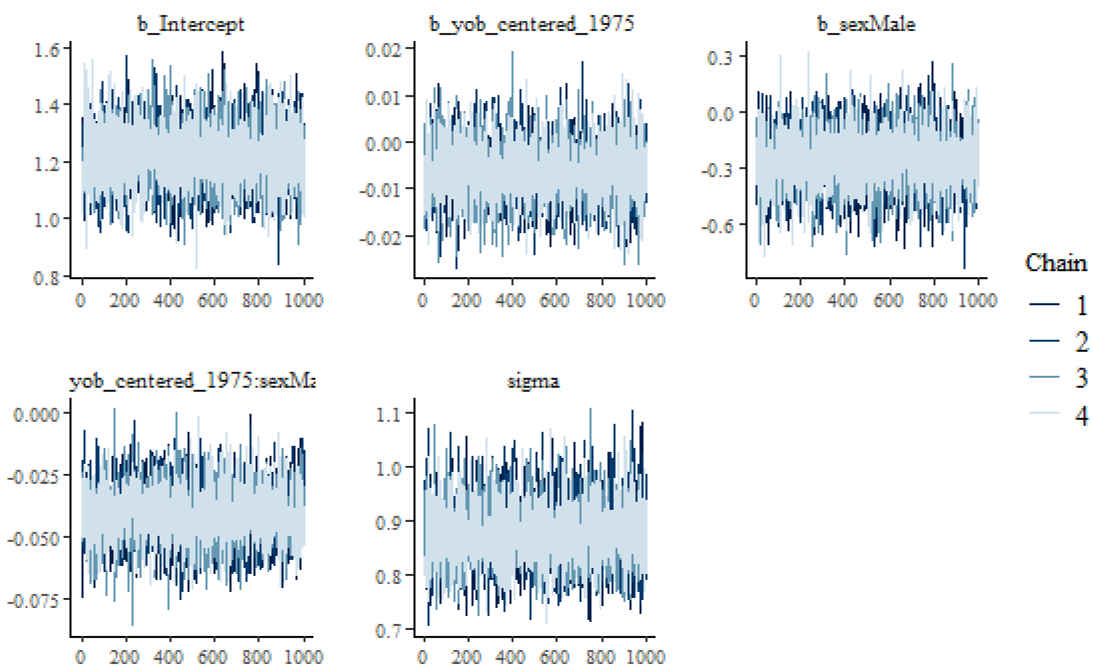
In contrast, the posterior predictive check for the standard deviation (**SF13)** indicated that the standard deviation of the observed data (0.71) was at the lower end of the distribution of the standard deviations of the predicted data, suggesting the model might be slightly overestimating the variability in the outcome.

SF13: Posterior predictive checks for std.dev., brms



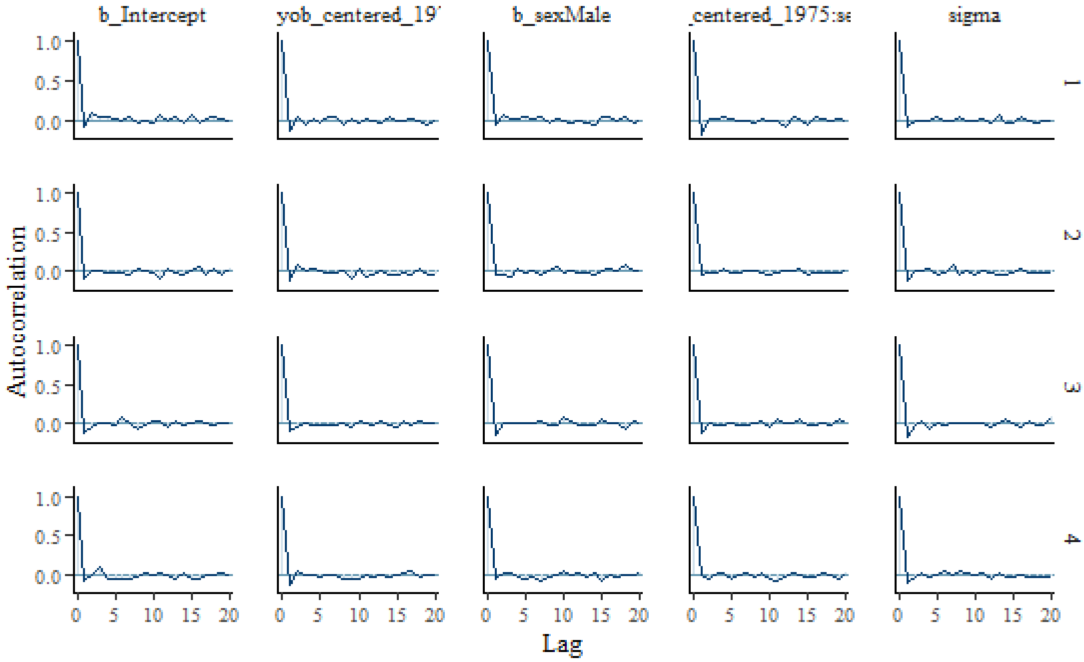
The convergence and mixing of the MCMC chains were assessed through visual inspection of trace plots and by examining Rhat values. Trace plots for all parameters (**SF14**) showed intermingling and stationarity across the four chains, further supported by Rhat values of 1.00. Effective sample sizes (Bulk_ESS and Tail_ESS) were also adequate (all above 1500, **Table 4**), indicating efficient sampling.

SF14: Trace plots, brms



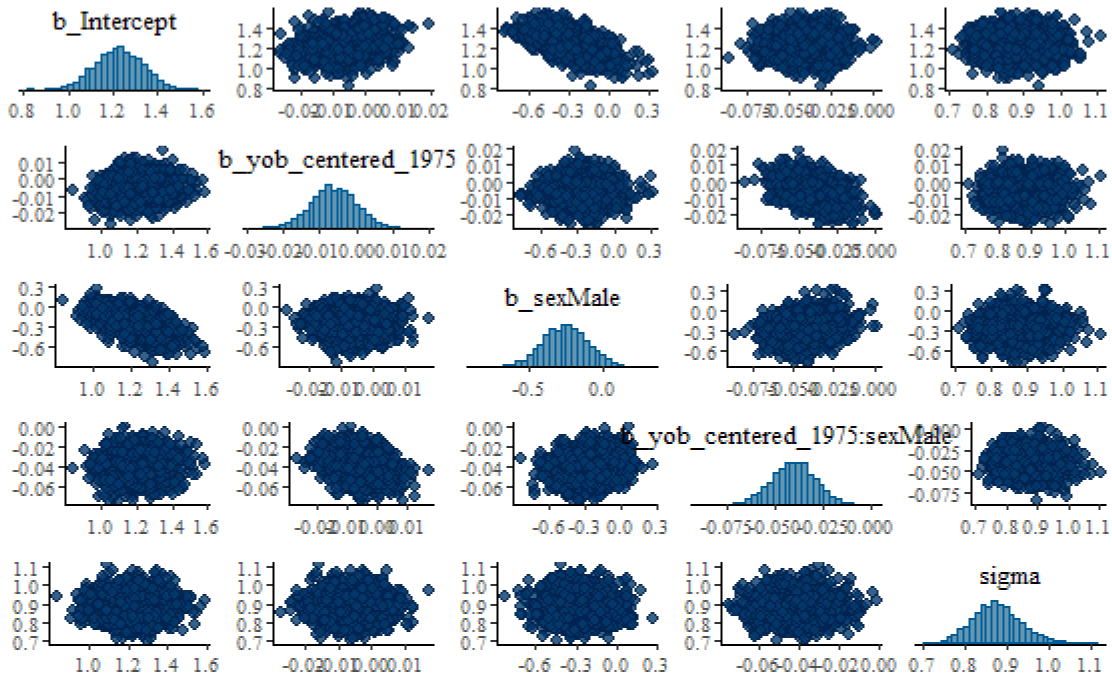
Further evaluation of the MCMC chains involved examining autocorrelation function plots for all parameters (**SF15**). These plots demonstrated a sharp decline to near zero within 1-2 lags, suggesting low autocorrelation and that the MCMC samples are largely independent, each providing new information about the posterior distribution. This efficient sampling behavior strengthens confidence in the reliability of the brms model's parameter estimates.

SF15: Autocorrelation function plots, brms



The pairs plot of the posterior distributions (**SF16)** showed generally reasonable bivariate distributions for the model parameters, with some expected correlations (e.g., between the intercept and yob, and between sexMale and yob:sexMale) but no indications of problematic strong or unexpected relationships.

SF16: Pairs plots of posterior distributions, brms



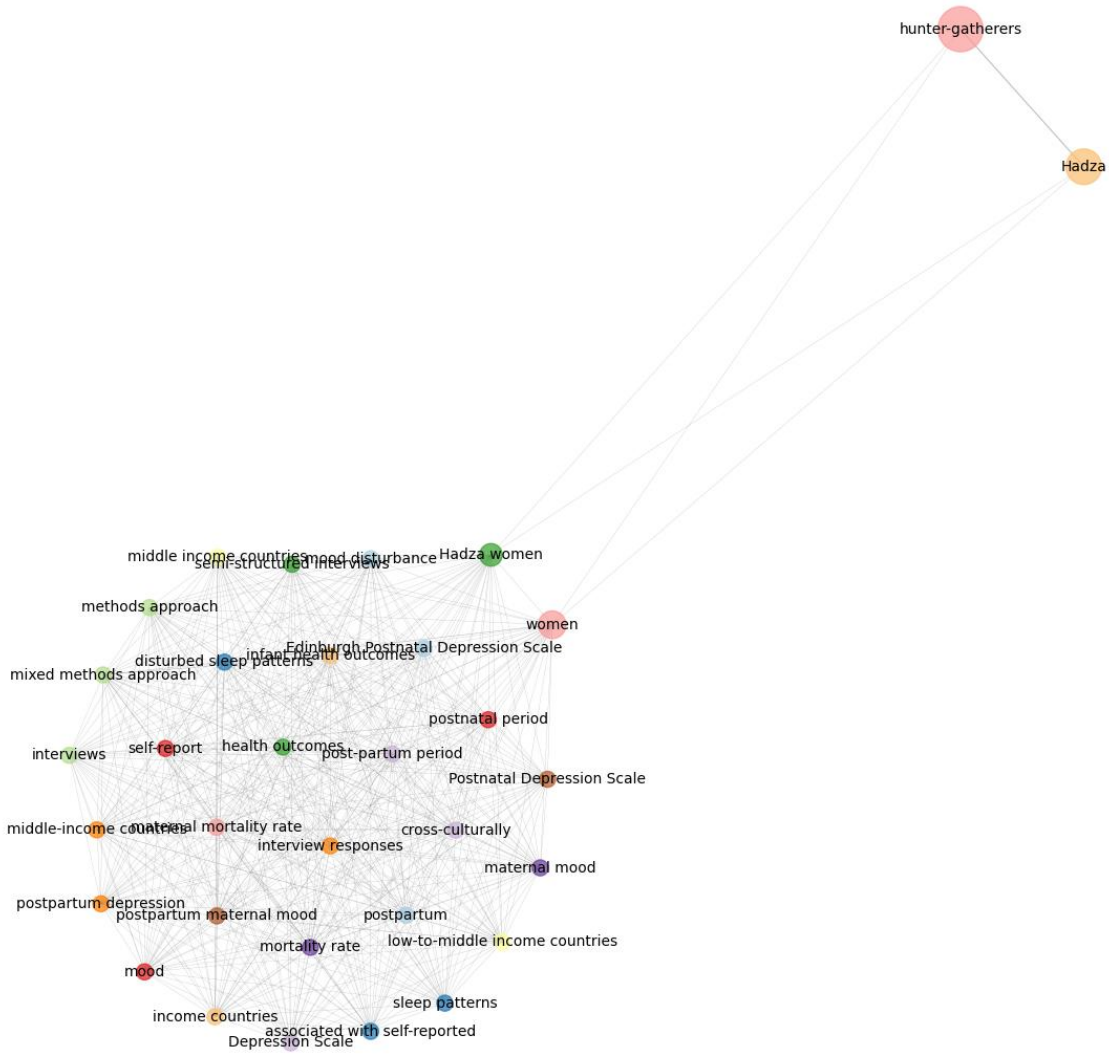
In summary, while the Bayesian model had some limitations in capturing the full bimodality of the data, the satisfactory convergence and mixing of the MCMC chains provide confidence in the reliability of the estimated fixed effects, which were consistent with the LMM results.

Section 5: Bibliometric Analysis

Bibliometric research focused on a timeline of publications and word co-occurrence/concept networks using data from dimensions.ai with the search parameters focused on ‘Hadza AND men NOT women’ or ‘Hadza AND women NOT men’. Network metrics were presented in the main paper. This section includes the network visualizations and the terms that define the network clusters.

The women’s network (**SP17**) shows a more tightly clustered and interrelated set of topics, which likely reflects the shorter time depth and interests of the collaborative networks producing the research.

SF17: Women’s Co-occurrence Network



The cluster terms (**ST5**) provide insights into main topics including demography, mental health, physical health, legal matters, childcare, and social structure.

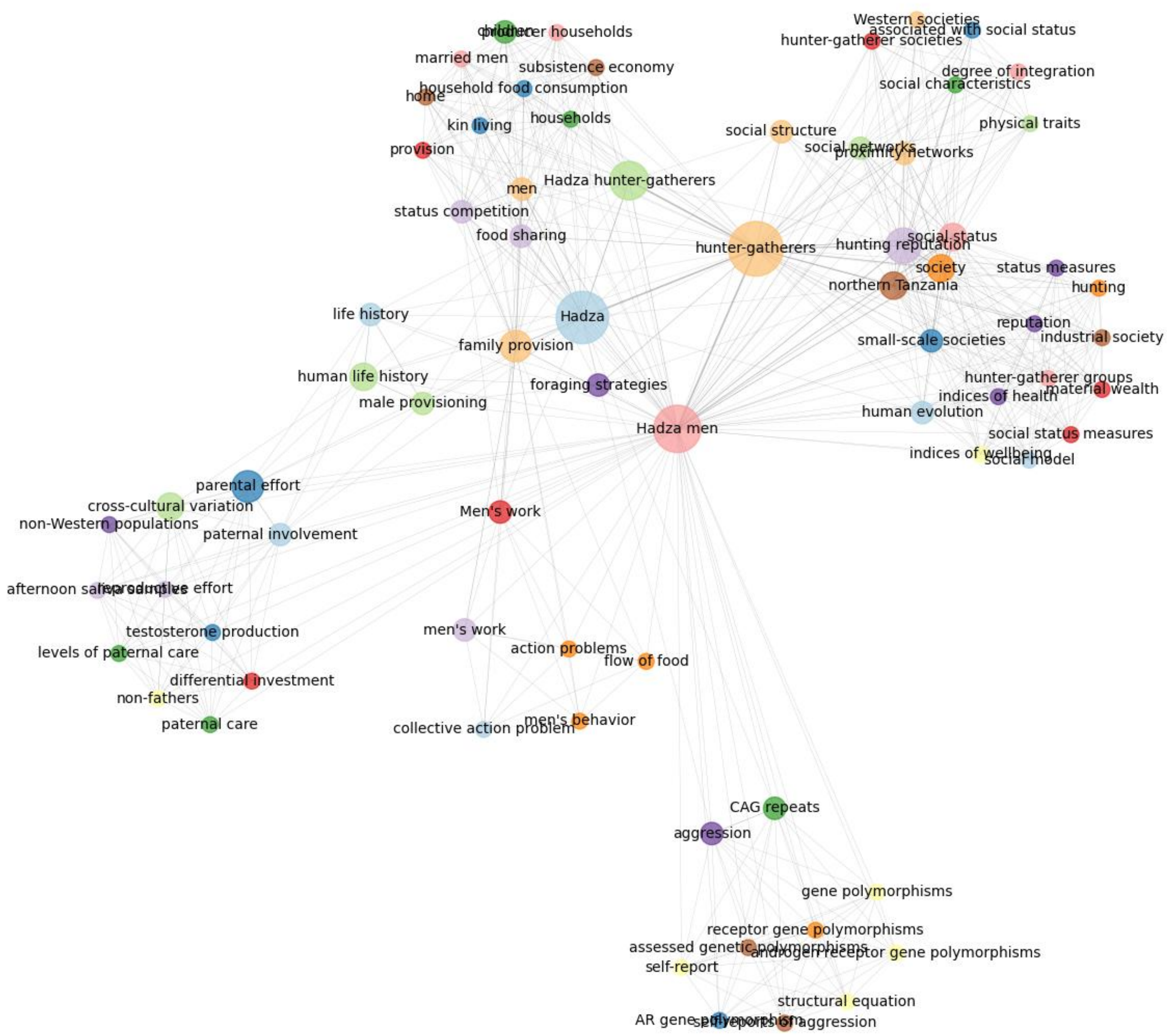
ST5: Cluster Terms for Hadza Women Network

Cluster 4	African hunter-gatherers, Hadza foragers, age of women, age structure, demographic differences, demography, estimates of age structure, higher fertility, living children, population growth rate, total population size

Cluster 1	Depression Scale, Edinburgh Postnatal Depression Scale, Hadza women, Postnatal Depression Scale, associated with self-reported, cross-culturally, disturbed sleep patterns, health outcomes, income countries, infant health outcomes, interview responses, interviews, low-to-middle income countries, maternal mood, maternal mortality rate, methods approach, middle income countries, middle-income countries, mixed methods approach, mood, mood disturbance, mortality rate, post-partum period, postnatal period, postpartum, postpartum depression, postpartum maternal mood, self-report, semi-structured interviews, sleep patterns, women
Cluster 7	East Africa, allomaternal nursing, biological kin, ethnographic reports, follower's observations
Cluster 2	Hadza, Hadza hunter-gatherers, Hadza hunter-gatherers of Tanzania, Sternberg's triangular theory, coital frequency, concept belief, fallback foods, human evolution, human evolutionary past, hunter-gatherer populations, hunter-gatherer societies, hunter-gatherers, low caloric value, people, reproductive success, rituals, women of reproductive age
Cluster 6	assault, court documents, legal problems, professional jealousy, sexual assault, sexual misconduct
Cluster 5	associated with hair cortisol concentrations, associated with higher hair cortisol concentrations, camp members, effects of social relationships, in-person, social network measures, social relationships
Cluster 3	egalitarian social structure, egalitarian society, foraging bands, hair cortisol concentrations, high social status, human evolutionary history, human society, individual social status, non-human animals, social groups, social hierarchy, social status, social structure, women's social status

The men's network (**SP17**) shows a sparse set of clusters with strong internal connections and a broader set of topics, which likely reflects the longer time depth of study, multiple generations of researchers, and broader collaborative networks producing the research.

SF18: Men’s Co-occurrence Network



The cluster terms (**ST6**) provide insights into main topics including genetics, men’s activities, subsistence, household, transition, skills, tools, status, and wealth.

ST 6: Cluster Terms for Hadza Men Network

Cluster 2	AR gene polymorphism, CAG repeats, Hadza, Hadza of Tanzania, aggression, androgen receptor gene polymorphisms, assessed genetic polymorphisms, chimpanzees, gene polymorphisms, human population, receptor gene polymorphisms, self-report, self-reports of aggression, structural equation

Cluster 1	Hadza data, Men's work, action problems, ancestral mothers, collective action problem, dependent offspring, early Homo, family provision, flow of food, hunter-gatherer ethnography, hunting hypothesis, men, men's behavior, men's work, primate males, status competition
Cluster 8	Hadza foragers, division of labor, foraging strategies, human life history, hunter-gatherers, life history, male provisioning, non-human primates, sexual division, sexual division of labor
Cluster 5	Hadza hunter-gatherers, children, food sharing, home, household food consumption, households, kin living, married men, producer households, provision, subsistence economy
Cluster 3	Hadza men, Western societies, associated with social status, degree of integration, hunter-gatherer societies, hunting reputation, northern Tanzania, physical traits, proximity networks, social characteristics, social networks, social status, social structure, society
Cluster 7	afternoon saliva samples, differential investment, levels of paternal care, male care, non-Western populations, non-fathers, parental effort, paternal care, paternal involvement, reproductive effort, testosterone production
Cluster 6	age of acquisition, cross-cultural differences, cross-cultural variation, oblique transmission, perceptions of task difficulty, ratings of teaching, social practices, subsistence skills, task difficulty, teaching labor, use of teaching
Cluster 4	human evolution, hunter-gatherer groups, hunting, indices of health, indices of wellbeing, industrial society, material wealth, reputation, small-scale societies, social model, social status measures, status measures