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Health, attractiveness, and marriageability among Aka hunter-gatherers and Ngandu farmer adolescents and young adults in the Central African Republic

Bonnie Hewlett [a,*], Harshita Agrawal [b], Barry Hewlett [a]

[a] Department of Anthropology, Washington State University, 14204 NE Salmon Creek Avenue, Vancouver, WA 98686-9600, United States of America
[b] Department of Mathematics and Statistics, Washington State University, Pullman, WA 99164, USA

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ABSTRACT

This study investigates how adolescents from two culturally distinct Central African communities—the Aka hunter-gatherers and Ngandu farmers—perceive health, attractiveness, and marriageability, focusing on how local socio-ecological contexts shape perceptions of health, attraction, and mate preferences. The research examines how body mass index and parasite load relate to perceived health and attractiveness. Seventy-five adolescents (39 Aka and 36 Ngandu) evaluated photographs of peers for health, attractiveness, and marriagability, while physical health was objectively measured using anthropometric and parasitological data. Regression analyses revealed that BMI was a consistent and significant predictor of both perceived health and attractiveness, whereas total parasite load did not significantly influence either outcome. Notably, perceptions of health strongly predicted attractiveness and marriageability, but not vice versa. Ethnic and gender differences in perception were also found: Aka adolescents prioritized social traits like kindness and cooperation, while Ngandu participants emphasized physical cleanliness and robustness. Male raters showed more variability and stricter standards, particularly when evaluating females. These findings underscore the role of robust phenotypic features, such as BMI, in determining how health, beauty, and reproductive value are interpreted. This research contributes to understanding how evolutionarily evolved preferences and cultural contexts shape perceptions of health, attraction, and marriageability.

1. Introduction

Human mate selection is a complex process influenced by a dynamic interplay of biological, cultural, and ecological factors. Evolutionary theories posit that mate selection corresponds to fitness-related facets of physical attraction, where physical cues serve as honest signals of mate quality. These cues include physiological health, genetic robustness, and overall fitness value, highlighting traits that indicate reproductive potential (Buss, 1988, Buss, 1989,Buss, 1994, Buss & Schmitt, 2017; Symons, 1979). Such preferences suggest that "good genes," manifesting in observable physical traits, may signal pathogen resistance, efficient energy allocation, and overall health (Thornhill & Gangestad, 1993; Thornhill & Gangestad, 1994; Thornhill & Gangestad, 1996; Thornhill & Gangestad, 1999). In this framework, physical attractiveness not only reflects health status but also correlates with fecundity, strength, and pathogen resistance (Shackelford et al., 2005; Thornhill, 1998). Mate selection may, therefore, be influenced by preferences for physical attractiveness, which can signal overall health and heritable differences in disease resistance (Buss & Barnes, 1986; Gangestad & Buss, 1993; see also Kokko et al., 2003).

The evolutionary importance of sexual selection was initially articulated by Charles Darwin (1859, 1871), who emphasized that mate choice—especially female choice—could favor elaborate traits even when they reduced survival prospects. Darwin argued that such traits, like the peacock's tail, may evolve because they are esthetically attractive, not only because they signal utilitarian benefits. In contrast, Alfred Russel Wallace took a more functionalist stance, viewing sexual dimorphism primarily as an outcome of natural selection for vigor and viability. Recent work highlights this distinction, noting that Darwin's aesthetic view has often been overshadowed by Wallace's utilitarian interpretation (Davis & Arnocky, 2022). These traits, despite impairing survivability, enhance mate attraction. The more selective sex, typically

* Corresponding author.
E-mail addresses: hewlettb@wsu.edu (B. Hewlett), harshita.agrawal@wsu.edu (H. Agrawal), hewlett@wsu.edu (B. Hewlett).

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females, must be capable of distinguishing between high-quality and low-quality mates, as making an incorrect choice can impact reproductive success and overall fitness (Trivers, 1972; but see Gomes & Cardoso, 2018).

Zahavi's (1975) "handicap principle" later expanded on this idea, proposing that only organisms capable of bearing the cost of such signals can display them, ensuring their reliability as indicators of quality. Similarly, the Hamilton–Zuk hypothesis (Hamilton & Zuk, 1982) proposed that across species, higher levels of chronic parasite load are associated with the evolution of more elaborate mating displays, whereas within species, individuals with lower parasite burdens are expected to produce stronger sexual signals (Hamilton & Poulin, 1997). In support of this hypothesis, comparative studies have shown that species with elaborate mating rituals tend to be less prone to parasitic infection (but see Balenger & Zuk, 2014). Thus, the Hamilton–Zuk hypothesis attempts to explain the parasite-driven evolution of costly ornaments or displays, such as the peacock's tail or bird song, as well as less extravagant traits (e.g., fur thickness, skin coloration) signifying disease resistance (Balenger & Zuk, 2014; Jacobs & Zuk, 2019; Møller, 1990; Møller et al., 1999). However, subsequent theoretical refinements suggest that the relationship between parasite burden and signaling may not be uniformly negative. (Getty, 2002; Getty, 2006) demonstrated that in some signaling systems, fitter individuals may not necessarily exhibit lower parasite loads, as equilibrium conditions can produce weak, null, or even positive correlations between fitness and parasite burden. Additionally, while Zahavi's handicap principle has often been used to interpret costly traits as honest signals of underlying quality, some scholars argue that this model is a poor representation of quality signaling (Penn & Szamado, 2020).

A recent meta-analysis of 424 correlations from 142 studies examined *within-population* associations between ornament expression and parasite load. The study found a weak negative relationship, which was stronger for dynamic ornaments (e.g., behavioral displays, skin pigmentation) and for parasites transmissible during sex. Importantly, Dougherty et al. (2023) concluded that these findings are more consistent with disease-avoidance mechanisms than with indirect genetic benefits.

While there are far fewer studies on the Hamilton-Zuk hypothesis in mammals, studies have consistently shown that health-related cues, such as physical appearance, body size, skin condition, and visible signs of illness, play a significant role in how human individuals assess potential mates (Mortensen et al., 2010; Schmitt, 2023; Stephen et al., 2009; Tybur & Gangestad, 2011). Health is often associated with fertility and the ability to survive environmental challenges, which are crucial factors in mate selection across many societies (Buss, 1993, 2019a; Buss & Schmitt, 2017, 2019; Buss et al., 1990; Gangestad, 2008; Gangestad & Scheyd, 2005; Thornhill & Gangestad, 1996).

Physical traits such as facial symmetry and waist-to-hip ratio are proxies for developmental stability and health, particularly in pathogen-rich settings (Gangestad & Buss, 1993; Thornhill, 1998; Thornhill & Gangestad, 2006; Thornhill & Møller, 1998). However, cultural context significantly shapes these preferences. Cross-cultural research reveals that preferences for traits like facial dimorphism or body size vary widely. For example, the Hadza of Tanzania prefer symmetrical faces more than participants in the UK (Little et al., 2007), and urban populations often associate masculinity with aggression (Scott et al., 2014). Such variation challenges the universality of evolved mate preferences and underscores the influence of social exposure and ecological conditions.

Resource availability and disease prevalence also affect preferences. In food-insecure environments, higher BMI is often seen as attractive and indicative of fertility and resourcefulness (Brown & Konner, 1987; Swami & Tovee, 2007). Where disease is prevalent, traits reflecting immune competence, like clear skin or robust appearance, become more valued (Tybur & Gangestad, 2011).

Gender-based preferences show further cultural variation. While men tend to prioritize physical attractiveness and women resource acquisition (Andrews et al., 2017; Buss, 1989), female preferences for masculinity are shaped by trade-offs between genetic benefits and paternal investment (DeBruine et al., 2010; Thornhill & Gangestad, 1996). These preferences are more pronounced in high-pathogen environments, where indicators of health carry greater weight. However, while biological signals of health and fertility are important, cultural values deeply mediate perceptions of attractiveness (Grammer et al., 2003). A cross-cultural perspective is essential for understanding how these factors interact.

The literature on health and attractiveness acknowledges the significant role of cultural, social, and ecological factors in shaping human mating preferences. While evolutionary psychology principles suggest universal preferences, cross-cultural research has demonstrated that perceptions of attractiveness and marriageability are deeply embedded in the specific ecological and cultural contexts in which individuals live. Building upon this foundation, adolescence emerges as a pivotal phase for the development of mate preferences. This period of rapid physical and social change is marked by the navigation of emerging sexual and social roles, making it instrumental in shaping perceptions of health, attractiveness, and marriageability (Bogin, 2011; Hewlett & Hewlett, 2012). Adolescents, becoming increasingly aware of societal and cultural norms, begin to internalize the factors that influence their understanding of these traits. Examining these perceptions among adolescents in diverse cultural contexts thus provides a richer perspective on the dynamics of mate selection and highlights the intricate roles ecology and culture play in shaping reproductive decisions.

2. Ethnographic context and hypotheses

This research was conducted in the rural southern region of the Central African Republic (CAR), in and around the village of Bokoka, where approximately 300 Aka hunter-gatherers and 500 Ngandu farmers coexist in the dense tropical rainforest. Despite sharing the same environment, these groups represent distinct cultural and economic systems. Bokoka and forest trails associated with the village serve as a central points for their regular social and economic exchanges.

The Aka are mobile hunter-gatherers whose forest camps are dispersed across southwestern CAR and northeastern Republic of Congo, supporting an estimated population of at least 30,000 with extremely low population density. In the Bokoka region, three Aka bands maintain forest trails connecting their seasonal camps with the village. During the dry season, Aka families live in forest camps of 25–35 individuals and engage in cooperative net hunting. In the wet season, they relocate to village camps to work on their own or Ngandu farms, reflecting a semi-symbiotic relationship with the farmers. Aka society is marked by flexible residency, egalitarianism, and strong values of autonomy, emotional and physical intimacy, and extensive sharing. Hierarchical differentiation by age or gender is minimal (Hewlett, 1992; Hewlett, 2012; MacDonald & Hewlett, 1999).

The Ngandu are sedentary agriculturalists who reside in permanent villages structured around patriclans, with village population sizes ranging from 50 to 500 individuals. Their subsistence system revolves around cultivating crops such as manioc, corn, plantains, and peanuts. Ngandu social organization is more hierarchical than the Aka, with age and gender playing central roles in determining status and access to resources. Elders and men generally receive greater deference, respect and larger shares of food. Intracultural and intercultural conflicts are common. Cultural norms emphasize social conformity, respect for authority, and resource-sharing within the extended family to prevent social discord and accusations of jealousy or sorcery. Compared to the Aka, the Ngandu prioritize collective cohesion over autonomy (Hewlett, 1992; Hewlett, 2012).

Building on these distinct cultural foundations, the study applies sexual selection theory and evolutionary psychology to test predictions about how adolescents in each group evaluate mate-relevant traits. The

first hypothesis proposes that visible indicators of health, particularly body mass index (BMI) and physical robustness, serve as reliable cues of reproductive fitness and are positively associated with perceptions of attractiveness and marriageability. (Buss, 1989; Singh, 1993; Sugiyama, 2005; Swami & Tovee, 2005). Drawing on the Hamilton and Zuk (1982), the study further predicts that individuals with higher parasite loads will receive lower ratings of health and attractiveness, assuming parasite resistance is an honest signal of genetic quality.

The research also investigates whether perceived health—regardless of actual health status—predicts attractiveness and marriageability, suggesting the influence of socially constructed cues in mate evaluation. These judgments are expected to vary across groups in response to localized subsistence demands. Among the Ngandu, where physical labor, productivity, protection from aggressive others, and hierachy are emphasized, adolescents are likely to favor traits such as physical strength, health, assertiveness, and cleanliness, which signal economic potential and clan-based capital. In contrast, among the Aka, where egalitarianism, cooperation, and autonomy are culturally salient, mate preferences are expected to emphasize prosocial traits such as emotional intimacy, kindness, and sociability.

Gendered patterns of mate preferences are also considered. Following evolutionary models, male adolescents are predicted in both groups to place greater emphasis on physical attractiveness and markers of fertility, while females are expected to prioritize traits related to health, strength, and the potential for resource acquisition and provisioning the family—particularly under conditions of high pathogen exposure (Buss, 2019a,b; Buss & Schmitt, 2017, Buss & Schmitt, 2019; Gangestad, 2008; Gangestad & Simpson, 2000; Thornhill & Gangestad, 1996). The study also explores the extent to which adolescents base their perceptions of health and attractiveness on general indicators like height and weight, versus more specific measures such as parasite burden.

Together, the Aka and Ngandu provide a compelling ethnographic context for understanding how evolutionary and culturally specific models of mate evaluation emerge in response to divergent subsistence strategies and ecological pressures. This comparative framework allows for a critical examination of how adolescent mate preferences reflect adaptive responses to local challenges as well as universal evolved propensities.

3. Methods

The study employed a mixed-methods design combining quantitative and qualitative approaches to investigate how Aka and Ngandu adolescents and young adults perceive health, attractiveness, and marriageability. This approach enabled examination of how cultural norms, ecological contexts, and social structures impact mate preferences in two distinct subsistence-based societies.

3.1. Interview data

A total of 75 adolescents were recruited from two communities. Adolescents were identified using indigenous terminology referring to a life stage beginning around puberty and extending until marriage (approximately 10–20 years of age). While the indigenous terminology for this age group primarily aligns with the Western notion of adolescence, it extends to include individuals who, in developmental psychology, might be considered young adults. In this paper, the term *adolescents* is used to represent this broader indigenous category. The Aka group included 39 participants (20 females and 19 males), with mean ages of 13.50 years (SD = 3.25) and 15.05 years (SD = 2.86) for females and males, respectively. The Ngandu group comprised 36 participants (15 females and 21 males), with mean ages of 15.53 years (SD = 2.75) for females and 15.05 years (SD = 2.89) for males.

Participants completed pile-sorting tasks in which they categorized Polaroid photographs of peers based on perceived health (healthy vs. unhealthy), attractiveness (attractive vs. less attractive), and marriageability (considered suitable for marriage vs. not). Following the pile-sorting activity, participants were asked to provide free lists of traits they associated with attractiveness in the opposite gender. Subsequently, open-ended interviews were conducted to explore in greater depth the traits linked to health, attractiveness, and desirable qualities for marriage, encompassing both physical and social characteristics.

Data analysis focused on identifying shared cultural models underlying adolescents' evaluations of peers. Pile-sorting and free-listing responses provided complementary quantitative and qualitative data on perceived health, attractiveness, and marriageability. Responses were analyzed for frequency and thematic content following standard ethnographic methods (Bernard, 2017). Semi-structured interview data were coded to contextualize these patterns and to interpret how adolescents' judgments reflected collective cultural expectations. This approach highlighted that adolescents' descriptions were not simply individual preferences but reflected broader cultural frameworks tied to subsistence practices, social organization, and local values. Accordingly, Aka youth tended to emphasize sociability, vitality, and cooperative dispositions, whereas Ngandu youth placed greater emphasis on public presentation, grooming, and physical beauty—patterns consistent with culturally grounded models of attraction that shape understandings of health, competence, and marriageability.

3.2. Health evaluation and parasitological data

To assess physical health, anthropometric measurements such as height, weight, and skinfold thickness (at triceps, biceps, and subscapular sites) were collected and Body Mass Index (BMI) and body fat percentage (BF%) were calculated (Akindele et al., 2016; Jeong et al., 2023). Additional metrics like heart rate, blood pressure, respiratory rate, and dental health were also recorded but are not included in this study (see Hewlett, 2004 for results). This paper focuses on BMI as a key health measure to examine variation within and between the Aka and Ngandu populations.

Table 1
Parasitological data collected from stool samples.

Latin Name	Disease
PROTOZOA (Pathogenic)	
Entamoeba histolytica (Amoebas)	Amoebiasis, Amoebic dysentery
Dientamoeba fragilis	Dientamoebiasis
Giardia lamblia	Giardiasis
Blastocystis hominis	Blastocystosis
PROTOZOA (Nonpathogenic)	
Entamoeba coli	Nonpathogenic
Entamoeba hartmani	Nonpathogenic
Endolimax nana	Nonpathogenic
Iodamoeba butschili	Nonpathogenic
Chilomastix mesnili	Nonpathogenic
NEMATODA (Roundworms, Pathogenic)	
Trichuris trichiura (Whipworm)	Trichuriasis
Ascaris lumbricoides	Ascariasis
Ancylostoma duodenale (Hookworm)	Ankylostomiasis
Strongyloides stercoralis (Threadworm)	Strongyloidiasis

Notes
1. Blastocystis hominis is considered a yeast and is not included as a parasite but is listed because it implies exposure to fecal contamination.
2. It was not possible to distinguish between *Etamoeba histolytica* and *E. dispar*.

Health evaluation also included parasitological data collection and analysis of all adolescents in the study. Table 1 lists the 13 parasites (8 pathogenic, 5 nonpathogenic) examined. Parasitological data were collected from stool samples. Participants were asked to defecate on a piece of paper and to then transfer a portion of the stool into a Proto-fix vial which contained a parasitology fixative. The samples were then transported to the United States where they were microscopically analyzed for the prevalence (presence-absence) of the following intestinal parasites.

Because both pathogenic and commensal taxa reflect distinct aspects of ecological exposure, total parasite load (i.e., the sum of all parasite infections) was retained as a conservative overall health index. The intensity of specific parasites (i.e., the number of a specific parasite per unit measured) was not conducted on all samples. Pathogenic parasites (e.g., *Giardia lamblia*, *Ascaris lumbricoides*) can directly affect health, energy, and reproductive fitness, whereas commensal (nonpathogenic) taxa such as *Entamoeba coli* or *Endolimax nana* do not harm the host but may be useful because they indicate exposure to contaminated environments rather than infection burden. Because both types of organisms reflect different aspects of ecological exposure, total parasite load are used in most analyses as a conservative overall health index. The impact of total parasite load (pathogenic and non-pathogenic) and total pathogenic load is also considered in the analysis.

Due to the sensitive nature of the research, strict protocols were implemented. Participation was voluntary, with participants informed of the study's aims, procedures, and risks before giving consent, including parental consent for minors. Participants could skip questions or withdraw at any time without consequences. To ensure confidentiality, all data were anonymized, and no identifiable information was included. Ethical approval was obtained from local, national (CAR Ministry of Scientific Research), and Washington State Universiity institutional review board, adhering to international research guidelines. Anonymous datasets are available at doi: https://doi.org/10.5061/dryad.r4xgxd2r9. Additional figures are available in Supplemental materials.

4. Results

4.1. Descriptive statistics

The quantitative data from pile sorts and health indices were analyzed using descriptive statistics and beta regression modeling (Cribari-Neto & Zeileis, 2010) to examine factors affecting perceptions of health, attractiveness and marriageability. Key variables, including body mass index (BMI), parasite load, and perception ratings, were summarized with measures such as means, standard deviations, and extremes to provide an overview of participant characteristics in the Aka and Ngandu communities.

Aka and Ngandu measures of central tendency and variability for Body Mass Index (BMI) values are summarized in Supplementary Table 2. The overall BMI distributions indicate generally comparable anthropometric measurements between the two ethnic groups. Aka females had slightly lower average BMI values than their Ngandu counterparts (17.63 versus 18.17) but the differences were not significant. While the means in both groups fall within the World Health Organization's "normal" range, they are at the very low end of global distributions. For comparison, U.S. adolescents and young adults average considerably higher BMIs, with the Aka and Ngandu means often falling below the 5th percentile of U.S. samples (Silverman et al., 2022). Even the maximum values observed in this study remain well below U.S. averages, highlighting the distinct nutritional and ecological contexts in which these populations live. Anthropological and evolutionary research indicates that low anthropometric or physiological values among tropical forest subsistence populations likely reflect a combination of chronic infectious disease exposure, limited caloric and nutritional intake, and high energetic demands associated with active foraging and mobility in forest environments (Alt et al., 2022; Dounias & Froment, 2011). The results of this study must be interpreted in relation to this context. In low-BMI populations, small differences in body mass may serve as salient indicators of nutritional adequacy and robustness, whereas in high-BMI, industrialized settings, positive evaluations of higher BMI often decline beyond certain thresholds due to associations with obesity-related morbidity (Brown & Konner, 1987; Swami & Tovee, 2007). Thus, statistical relationships considered here may carry different cultural and biological meanings depending on the underlying population distribution.

Differences in attractiveness and health ratings between the two ethnic groups are presented in Table S3. Aka males received the highest attractiveness ratings, with 76.4 % deemed attractive, while Ngandu females received the lowest ratings for both health (56.6 %) and attractiveness (56.9 %). Males in both groups consistently scored higher than females, with the largest gender gap seen among the Aka (76.4 % for males versus 68.6 % for females). The Ngandu population had more balanced but generally lower ratings overall, especially for females. Variability in ratings as measured by standard deviations is notable, particularly in health ratings for Aka males (±32.7 %) and attractiveness for Ngandu females (±29.6 %). Aka females exhibited the lowest variability between individuals (±23.1 %) possibly suggesting greater cultural consensus about Aka female attraction and health.

Moreover, the data show notable trends in health and attractiveness ratings across genders in two ethnic groups (see Table S4). Male participants received higher health ratings from both male and female raters, with Aka males rated highest (62.5 % from females, 67.5 % from males) and Ngandu females rated lowest (56.2 % from females, 56.7 % from males). Male raters generally gave slightly higher health ratings than female raters, with the smallest difference for Ngandu females (0.5 %).

For attractiveness, Aka males were viewed as most attractive by both genders (77.3 % female, 75.6 % male), while Ngandu females received the lowest scores (56.7–56.9 %). Female raters rated Aka females significantly higher than male raters (75.1 % versus 62.6 %), in contrast to the smaller discrepancies for Aka males. The Ngandu population had lower attractiveness ratings overall, but with more balanced scores.

Descriptive analysis of total pathogen load (includes both pathogenic and non-pathogenic parasites) (see Table S5) indicates there might be significant differences between groups. Overall, 72.6 % of the total parasite load was pathogenic. By ethnicity, approximately 74 % of all recorded parasites were pathogenic among Aka, and approximately 67 % among Ngandu (with mean per-person shares closely matching these aggregates), indicating that the majority of observed burden in both groups reflects pathogenic rather than non-pathogenic taxa. Ngandu males had the highest average burden (4.00), with some individuals showing extreme loads (max = 8) and others none (min = 0). Aka males followed (3.68) with less variability and no zero-load cases. Female groups had lower loads on average, with Aka females averaging 2.90 and Ngandu females at 2.67. The presence of zero values in Ngandu males indicated possible resistance or regular treatment with Western medicines. These patterns reflect interactions between sex differences in immunity and ethnic-specific environmental or genetic factors, with greater male variability suggesting higher exposure risks or diverse immune responses.

To evaluate relationships between relevant variables, we used beta regression models to accurately represent the continuous proportional nature of dependent measures. Following the established guidelines for analyzing proportional data Smithson & Verkuilen (2006), we transformed perception scores to ensure they remained within the interval (0, 1), addressing common issues of heteroscedasticity and skewness while maintaining interpretability (Ferrari & Cribari-Neto, 2010). This method supported robust inference about predictors of perceived health and attractiveness.

We developed separate regression models for perceived health and attractiveness, incorporating BMI, total parasite load, gender, and

ethnicity as independent variables. Initially, models were estimated for all participants, then stratified by rater gender to uncover any gender-specific evaluation patterns. This analytical framework allowed for comparisons of perceived traits across community and gender dimensions while adjusting for relevant covariates.

4.2. Analysis of perceived health and attraction based on BMI, gender, ethnicity, and pathogen load

We employed beta regression to analyze determinants of perceived health and attractiveness, denoted as y_i for individual i, among Aka and Ngandu adolescents. Following established practice for proportional data (Smithson & Verkuilen, 2006), we applied a transformation to ensure all observed scores strictly occupied the open interval (0,1):

$$Y_i = \frac{[y_i(N \quad 1) + 0\,5]}{N}$$

where N refers to the number of raters or the total number of individuals in each ethnic group ($N = 39$ for the Aka and $N = 36$ for the Ngandu). This preserved the ordinal properties while avoiding boundary values.

The models incorporated four key predictors: (1) gender (male/female) – individual being rated, (2) body mass index (BMI, continuous), (3) ethnicity (Aka/Ngandu), and (4) total parasite load (PathNP). The core model specification took the form:

$$\text{logit}(\mu_i) = \beta_0 + \beta_1 \text{Sex}_i + \beta_2 \text{BMI}_i + \beta_3 \text{Ethnicity}_i + \beta_4 \text{PathNP}_i$$

where $\mu_i = E(Y_i)$ represents the expected transformed perception score (health or attractiveness) for individual i with the response $Y_i \sim Beta(\mu_i\varphi, (1 \quad \mu_i)\varphi)$

To examine rater-specific effects, we estimated sex-stratified models:

1. For female raters:

$$\text{logit}\ \mu_i^{(F)}) = \beta_0^{(F)} + \beta_1^{(F)}\text{Sex}_i + \beta_2^{(F)}\text{BMI}_i + \beta_3^{(F)}\text{Ethnicity}_i + \beta_4^{(F)}\text{PathNP}_i$$

with

$$Y_i^{(F)} \sim Beta\ \mu_i^{(F)}\varphi^{(F)},\ 1 \quad \mu_i^{(F)})\varphi^{(F)})$$

2. For male raters:

$$\text{logit}\ \mu_i^{(M)}) = \beta_0^{(M)} + \beta_1^{(M)}\text{Sex}_i + \beta_2^{(M)}\text{BMI}_i + \beta_3^{(M)}\text{Ethnicity}_i + \beta_4^{(M)}\text{PathNP}_i$$

with

$$Y_i^{(M)} \sim Beta\ \mu_i^{(M)}\varphi^{(M)},\ 1 \quad \mu_i^{(M)})\varphi^{(M)})$$

All models were fit using maximum likelihood estimation with robust standard errors. The precision parameters $\varphi, \varphi^{(F)}, \varphi^{(M)})$ accounted for dispersion in each model specification. This approach enabled separate estimation of how health indices influenced perceptions when rated by female versus male observers.

4.3. Local perceptions of health and BMI

Our beta regression analyses revealed systematic patterns in health perception across evaluators. Key findings are summarized below with supporting statistics.

BMI emerged as the most significant predictor of perceived health, with each unit increase in BMI corresponding to an approximate 0.25 increase in the log-odds of perceived health across all analytical models. This was consistently observed across evaluations from both female observers ($\widehat{\beta}_2^{(F)} = 0.24$, p-value <0.001) and male observers ($\widehat{\beta}_2^{(M)} = 0.25$, p-value <0.001), as well as within the combined group ($\widehat{\beta}_2 = 0.25$, p-value <0.001). Notably, male raters demonstrated a marginally stronger association compared to their female counterparts. These findings indicated that BMI was a good predictor of how Aka and Ngandu perceived health in both males and females.

Moreover, the analysis revealed non-significant ethnic differences in health perceptions across all models. While point estimates suggested minimal variation between Aka and Ngandu ratings across different raters (coefficients ranging from $\widehat{\beta}_3 =$ 0.03 to 0), the 95 % confidence intervals for all ethnicity coefficients substantially overlapped with zero (Combined: 0.46 to 0.39; Female Raters: 0.46 to 0.46; Male Raters: 0.54 to 0.34). Contrary to initial expectations (as discussed in Table 3), we found no evidence of significant ethnic differentiation in the proportion of individuals in their ethnic groups that were perceived to be healthy, regardless of rater sex. The non-significant estimates showed inconsistent directional patterns, with female raters showing no association ($\widehat{\beta}_3^{(F)} = 0$, p-value $= 0.989$) and male raters a non-significant negative association ($\widehat{\beta}_3^{(M)} =$ 0.1, p-value $= 0.648$). This suggests that—within each ethnic group—BMI was a stronger predictor of perceived health. However, because Aka raters only evaluated other Aka and Ngandu raters only evaluated other Ngandu, we cannot assess whether raters exhibit ethnic biases when judging out-group members.

Similarly, there was no significant association between pathogen load and perceived health in any model (Combined: $\widehat{\beta}_4 =$ 0.08, p-value $= 0.246$; Female Raters: $\widehat{\beta}_4^{(F)} =$ 0.10, p-value $= 0.176$; Male Raters: $\widehat{\beta}_4^{(M)} =$ 0.07, p-value $= 0.315$), with all confidence intervals spanning zero. This consistent null effect – occurring despite robust BMI effects (all p-value <0.001) - suggested local people were (a) unable to detect pathogen-related cues, (b) did not prioritize them when assessing health in others, or (c) that the methods to measure parasite load were not sufficient to capture phenotypic changes.

The goodness-of-fit statistics in Table 2 showed robust performance across all health perception models, with comparable AIC and BIC values. The male raters' model fit best, with the lowest AIC (35.1) and BIC (21.2), highest log likelihood (23.5), and lowest deviance (47.1), suggesting BMI health indices more strongly influenced male perceptions of others in their ethnic group than females. Female raters had a deviance of 37.6, while combined raters showed 44.8. These results highlight gender-specific perceptual patterns, underscoring the need to explore demographic factors, particularly gender, in health perception analyses. (See Supplemental data Figs. S1, S2, and S3).

4.4. Local perceptions of attraction and BMI

The attractiveness models exhibited patterns like those observed in the perceived health

models, as summarized below.

The analysis revealed that BMI was a robust predictor of local perceptions of attractiveness across all models, with consistently significant positive effects (Combined: $\widehat{\beta}_2 = 0.19$, p-value <0.001; Female Raters: $\widehat{\beta}_2^{(F)} = 0.25$, p-value <0.001; Male Raters: $\widehat{\beta}_2^{(M)} = 0.14$, p-value <0.001).

Table 2
Beta regression analysis of health perception determinants and goodness-of-fit statistics of health perception determinants from beta regression analysis.

Parameter	Combined Raters			Female Raters			Male Raters		
	$\widehat{\beta}$	95 % CI	p	$\widehat{\beta}$	95 % CI	p	$\widehat{\beta}$	95 % CI	p
Intercept	3.69	(5.52, 1.86)	***	3.68	(5.63 ,-1.73)	***	3.55	(5.45, 1.64)	***
Sex									
Male (Ref)	0	–	–	0	–	–	0	–	–
Female	0.05	(0.51, 0.41)	0.822	0.02	(0.48, 0.51)	0.949	0.08	(0.56, 0.40)	0.743
BMI	0.25	(0.16, 0.34)	***	0.24	(0.15, 0.34)	***	0.25	(0.15, 0.34)	***
Ethnicity									
Aka (Ref)	0	–	–	0	–	–	0	–	–
Ngandu	0.03	(0.46, 0.39)	0.881	0	(0.46, 0.46)	0.989	0.1	(0.54, 0.34)	0.648
PathNP	0.08	(0.21, 0.05)	0.246	0.1	(0.24, 0.04)	0.176	0.07	(0.21, 0.07)	0.315
Model Fit		Combined Raters			Female Raters			Male Raters	
AIC		32.8			25.6			35.1	
BIC		18.9			11.7			21.2	
Log Likelihood		22.4			18.8			23.5	
Deviance		44.8			37.6			47.1	
φ		3.65			2.81			3.29	
Degrees of Freedom		69			69			69	

Notes: Reference categories: Male for Gender, Aka for Ethnicity. Significance: *** = ($p < .001$). φ = dispersion parameter. All models use logit link function with beta distribution.

Notably, female raters showed the strongest relationship between ratings of attraction and BMI-, suggesting gender-specific weighting of BMI health indices. These effects remained significant after controlling for ethnicity and pathogen load, demonstrating that BMI played a key role in evaluating attractiveness of others regardless of rater gender or target ethnicity.

Moreover, significant ethnic disparities in perceptions of attractiveness were seen with Ngandu consistently rating a smaller proportion of individuals than Aka as attractive across all models. This effect was most

Table 3
Beta regression analysis of attractiveness perception determinants and goodness-of-fit statistics table for attractiveness perception determinants from beta regression analysis.

Parameter	Combined Raters			Female Raters			Male Raters		
	$\widehat{\beta}$	95 % CI	p	$\widehat{\beta}$	95 % CI	p	$\widehat{\beta}$	95 % CI	p
Intercept	2.2	(3.81,-0.58)	0.007	3.43	(5.33,-1.52)	***	1.44	(2.96,0.09)	0.066
Sex									
Male (Ref)	0	–	–	0	–	–	0	–	–
Female	0.40	(0.82,0.03)	0.066	0.09	(0.58,0.40)	0.728	0.60	(1.01,-0.19)	0.004
BMI	0.19	(0.11,0.27)	***	0.25	(0.16,0.34)	***	0.14	(0.07,0.22)	***
Ethnicity									
Aka (Ref)	0	–	–	0	–	–	0	–	–
Ngandu	0.62	(1.01,-0.23)	0.002	0.81	(1.27,-0.35)	***	0.42	(0.79,-0.04)	0.03
PathNP	0.01	(0.11,0.14)	0.839	0.03	(0.11,0.17)	0.677	0.01	(0.11,0.13)	0.886
Model Fit		Combined Raters			Female Raters			Male Raters	
AIC		47.4			52.6			45.7	
BIC		33.5			38.7			31.8	
Log Likelihood		29.7			32.3			28.9	
Deviance		59.4			64.6			57.7	
φ		4.97			3.18			5.34	
Degrees of Freedom		69			69			69	

Notes: Reference categories: Male for Gender, Aka for Ethnicity. Significance: *** = ($p < .001$). φ = dispersion parameter. All models use logit link function with beta distribution.

pronounced among female raters ($\widehat{\beta}_3^{(F)} = -0.81$, p-value <0.001), followed by the combined model ($\widehat{\beta}_3 = -0.62$, p-value = 0.002), and was still significant, albeit weaker, among male raters ($\widehat{\beta}_3^{(M)} = -0.42$, p-value = 0.03). The stronger negative coefficient for Ngandu ethnicity among female raters could indicate either: (a) Ngandu female raters were harsher in their attractiveness judgments overall, or (b) Ngandu individuals were perceived as less attractive by their raters, with this effect amplified among female observers.

Interestingly, pathogen load did not show any significant association with attractiveness ratings in any of the models. In the combined model, the effect was negligible ($\widehat{\beta}_4 = 0.01$, p-value = 0.839); for female raters ($\widehat{\beta}_4^{(F)} = 0.03$, p-value = 0.677); and for male raters ($\widehat{\beta}_4^{(M)} = 0.01$, p-value = 0.886), with all confidence intervals crossing zero. This consistent lack of effect—observed even amidst strong influences from ethnicity and BMI—highlighted that local people did not see the manifestations of parasite loads or did not consider them important especially by comparison to measures of body height and weight.

Goodness-of-fit statistics in Table 3 show strong model fits across the attractiveness perception analyses, with female raters performing best (AIC = −52.6, BIC = −38.7, log-likelihood = 32.3, deviance = −64.6), indicating more systematic standards than male raters. All models outperformed null benchmarks, with positive log-likelihoods (29.7 to 32.3) and negative deviance (−64.6 to −57.7), confirming predictor relevance. The results align with substantive findings, particularly the stronger influence of BMI and ethnicity in female raters' evaluations. (See Figs. S4, S5 and S6).

4.5. Interaction effect of ethnicity and BMI in health and attractiveness perceptions

For each outcome (health/attractiveness), we extended our original beta regression model (without interaction terms) to examine moderation effects:

$$\text{logit}(\mu_i) = \beta_0 + \beta_1 \text{Sex}_i + \beta_2 \text{BMI}_i + \beta_3 \text{Ethnicity}_i + \beta_4 \text{PathNP}_i + \beta_5 (\text{BMI}_i \times \text{Ethnicity}_i)$$

where $\mu_i = E(Y_i)$ represents the expected transformed perception score (health or attractiveness) for individual i with the response $Y_i \sim Beta(\mu_i\varphi, (1-\mu_i)\varphi)$. This builds upon our initial model specification by adding the BMI × Ethnicity interaction to test whether BMI effects differ between ethnic groups, while maintaining all other aspects of the original model structure.

The analysis revealed a significant interaction between Body Mass Index (BMI) and ethnicity in perceptions of attractiveness ($\widehat{\beta}_5 = 0.17$, 95 % CI = [0.02, 0.33], p-value = 0.029). This suggests that the relationship between BMI and attractiveness ratings varied by ethnic group. Specifically, while a higher BMI was generally linked to increased attractiveness ratings for both groups ($\widehat{\beta}_2 = 0.12$, $p = .020$), this positive relationship was notably stronger among Ngandu individuals compared to Aka individuals.

In contrast, the interaction effect was not observed for health perceptions ($\widehat{\beta}_5 = 0.09$, 95 % = CI [−0.08, 0.26], p-value = 0.287), where BMI demonstrated a consistent positive association across both ethnic groups ($\widehat{\beta}_2 = 0.21$, p-value <0.001). The differing patterns in attractiveness ratings indicate that cultural or ethnic-specific standards may influence how body size affects aesthetic judgments, with Ngandu raters being more sensitive to variations in BMI in their evaluations of attractiveness. (See Table 4 for more details).

Table 4
Parameter estimates from beta regression models examining ethnic and BMI effects on health and attractiveness ratings.

Predictor	Health Ratings			Attractiveness Ratings		
	$\widehat{\beta}$	95 % CI	p	$\widehat{\beta}$	95 % CI	p
Intercept	3.05	(−5.18, 0.91)	0.005	1	(−2.88, 0.89)	0.299
Gender (Female)	0.05	(−0.51, 0.40)	0.824	0.41	(−0.82, 0.01)	0.054
BMI	0.21	(0.10, 0.32)	***	0.12	(0.02, 0.21)	0.02
Ethnicity (Ngandu)	1.7	(−4.79, 1.39)	0.281	3.72	(−6.53, 0.91)	0.009
BMI × Ethnicity	0.09	(−0.08, 0.26)	0.287	0.17	(0.02, 0.33)	0.029
PathNP	0.07	(−0.20, 0.06)	0.311	0.03	(−0.09, 0.16)	0.595
Model Fit	AIC = −31.9, $\varphi = 3.72$			AIC = −50.2, $\varphi = 5.32$		

Notes: Significance: *** = ($p < .001$). φ = dispersion parameter. All models use logit link function with beta distribution.

4.6. Gender differences in perceptions of attraction

The analysis found that gender affects how local people perceive attractiveness. While the target's gender had little impact on health ratings (p-value >0.79), it significantly influenced attractiveness evaluations, particularly among male raters. Males showed a notable negative bias in rating female targets' attractiveness ($\widehat{\beta}_1^{(M)} = -0.64$, p-value = 0.003), while female raters did not ($\widehat{\beta}_1^{(F)} = -0.09$, p-value = 0.729). Male raters rated male peers more positively (Aka males, $\widehat{\mu} = 0.77$, Ngandu males, $\widehat{\mu} = 0.69$) than females rated their female peers (Aka females, $\widehat{\mu} = 0.75$, Ngandu females, $\widehat{\mu} = 0.58$). Additionally, males were consistently more attracted to females (Aka males rating Aka females, $\widehat{\mu} = 0.77$, Ngandu males rating Ngandu females, $\widehat{\mu} = 0.6$) than the reverse (Aka females rating Aka males, $\widehat{\mu} = 0.64$, Ngandu females rating Ngandu males, $\widehat{\mu} = 0.54$). Ethnicity also influenced ratings, with Aka individuals receiving higher scores than Ngandu, especially among female raters evaluating females (Aka, $\widehat{\mu} = 0.75$ vs Ngandu, $\widehat{\mu} = 0.58$) (See Table 5 below).

The findings indicate that attractiveness judgments vary by gender, while health perceptions remain consistent across sexes, regardless of the rater's gender. This suggests that biases in attractiveness reflect

Table 5
How gender and ethnicity impact attractiveness ratings.

Target Sex	Rater Group	Aka Rating			Ngandu Rating		
		N	$\widehat{\mu}$	95 % CI	N	$\widehat{\mu}$	95 % CI
Female	Male	19	0.77	(0.68, 0.84)	21	0.6	(0.51, 0.69)
	Female	20	0.75	(0.67, 0.82)	15	0.58	(0.47, 0.67)
Male	Male	19	0.77	(0.70, 0.83)	21	0.69	(0.61, 0.75)
	Female	20	0.64	(0.57, 0.72)	15	0.54	(0.46, 0.63)

Notes: All ratings adjusted for BMI = 18.09 and PathNP = 3.36 (population averages); $\widehat{\mu}$ = Predicted mean attractiveness score.

cultural preferences rather than health indicators, as these effects persist even after controlling for BMI and pathogen load.

4.7. Interpretation of PathNP in attraction models

Point estimates for the effect of parasite load on perceived attractiveness are near zero across all models ($\widehat{\beta}_4 = 0.01$; $\widehat{\beta}_4^{(F)} = 0.03$; $\widehat{\beta}_4^{(M)} = 0.01$). The corresponding 90 % confidence intervals are as follows: all raters, 0.090 to 0.116; female raters, 0.089 to 0.149; male raters, 0.091 to 0.108. To assess practical, rather than purely statistical relevance, we conducted an equivalence-style assessment using prespecified smallest effect sizes of interest on the log-odds scale. Using ±0.10 on the log-odds scale—which corresponds to approximately two to three percentage points change in predicted probability per one-unit increase in parasite load around the sample mean—the 90 % confidence intervals slightly exceed this band in each attractiveness model. Consequently, we cannot conclude equivalence to a negligible effect at this stricter threshold. By contrast, when using a wider band of ±0.20 on the log-odds scale—approximately four to five percentage points—the 90 % confidence intervals for all three models lie entirely within the band, which supports the conclusion that any effect of parasite load on attractiveness, if present, is at most small to moderate in magnitude.

4.8. Perceptions of health, attraction and parasite loads

The analysis revealed no association between total parasite load (PathNP) and perceptions of health or attractiveness, with all models showing non-significant coefficients. This contradicts some past research linking parasite burden to mate selection, suggesting contextual or methodological factors at play. Parasite loads might impact BMI, a crucial health indicator, while most individuals have parasites, possibly downplaying their significance. This trend persisted across health and attractiveness evaluations, indicating that specific health indicators like parasite load may be less important than broader health indices and cultural criteria. Observable traits like BMI emerged as more reliable indicators of health in social evaluations. Additionally, ethnicity influenced perceptions of attractiveness, reflecting adaptations to the local disease environment. The consistent null results across multiple models and rating contexts suggest that this pattern is a robust feature of perception in this study population rather than a measurement artifact.

4.9. Evaluation of multiple encodings of parasite burden

In this subsection we evaluated multiple, biologically informed encodings of parasite burden and compared their associations with perceived health and attractiveness outcomes. Using study fields, we defined:

Total burden (PathNP): the combined count of pathogenic and non-pathogenic parasites.
Pathogenic burden (Path): the count of pathogenic parasites only.
Ectoparasites burden (PathEct): the union of pathogenic parasites and ectoparasites.

We also derived composition measures that quantify mix independent of scale: the pathogenic share (the proportion of the total burden that is pathogenic) and the external parasites share (the proportion classified as pathogenic-or-ectoparasitic), with the residual constituting the non-pathogenic share. Each share is bounded in 0,1 and is set to 0 when total burden is zero to avoid undefined ratios. In the regression framework, we include both the total (z-scored) and a share term so that effects are cleanly separated: the total coefficient captures differences in overall load, whereas the share coefficient captures differences in composition holding total load fixed (i.e., a one-unit change corresponds to moving from 0 % to 100 % of the total in that category). This specification prevents a single "total count" from obscuring biologically meaningful heterogeneity in parasite type and yields coefficients with transparent interpretations (per 1 SD increase in total; per unit change in share).

4.9.1. Mathematical specification

Let $y_i \in (0,1)$ denote one transformed proportion outcome related to health or attraction for person i. Assume a beta regression with logit link:

$$y_i \sim \mathrm{Beta}(\mu_i, \varphi), \mathrm{E}(y_i) = \mu_i, \mathrm{Var}(y_i) = \mu_i(1 \quad \mu_i)/(1+\varphi)$$

$$\mathrm{logit}(\mu_i) = \eta_i = \alpha + \quad ^{\top}\mathbf{C}_i + \beta X_i,$$

where $\mathbf{C}_i = (Sex_i, BMI_i, Eth_i)$ are covariates, X_i is the parasite exposure term(s) (varying by specification), $\varphi > 0$ is the precision parameter. We consider 5 specifications per outcome:

Total count: $\eta_i = \alpha + \quad ^{\top}\mathbf{C}_i + \beta_{\mathrm{Path_NP}} Z_{\mathrm{Path_NP},i}$
Pathogenic count: $\eta_i = \alpha + \quad ^{\top}\mathbf{C}_i + \beta_{\mathrm{Path}} Z_{\mathrm{Path},i}$
Ectoparasites count: $\eta_i = \alpha + \quad ^{\top}\mathbf{C}_i + \beta_{\mathrm{PathEct}} Z_{\mathrm{PathEct},i}$
Composition A (Total pathogenic share):

$$\eta_i = \alpha + \quad ^{\top}\mathbf{C}_i + \beta_{\mathrm{Path_NP}} Z_{\mathrm{Path_NP},i} + \delta_{\mathrm{PathShare}} \mathrm{share_path}_i$$

Composition B (Total Ectoparasites share)

$$\eta_i = \alpha + \quad ^{\top}\mathbf{C}_i + \beta_{\mathrm{Path_NP}} Z_{\mathrm{Path_NP},i} + \delta_{\mathrm{EctoparasitesShare}} \mathrm{share_ectoparasites}_i$$

Here $Z_{\cdot}$ denotes the z-score of the corresponding count ($Z = \left(X \quad \bar{X}\right)/s_X$), β coefficient represents the change in log-odds of the mean outcome per 1 standard deviation increase in the count, δ coefficients are the change in log-odds per 1 unit increase in the share (from 0 to 1), holding the total constant—a composition effect, not a scale effect.

4.9.2. Results

Table 11 summarizes coefficient estimates (β), standard errors, Wald 95 % confidence intervals, p values, and AIC/BIC for each burden encoding across perceived health and attractiveness outcomes. Across outcomes, models including **PathNP, Path, or PathEct** counts alone did not yield statistically reliable associations (all p value > 14; AIC/BIC differences were small). In contrast, some composition models that included total burden (PathNP, z-scored) plus the pathogenic fraction (Path/PathNP, set to 0 when total = 0) highlighted a consistent pattern for perceived health: a higher pathogenic share of a given total was associated with higher male-perceived health (MhealT; $\beta \approx 1\ 12, SE \approx 0\ 46, z \approx 2\ 40, p$ value $\approx 0\ 016$), with a similar but marginal association for perceived health by everyone (PhealT; $\beta \approx 0\ 897, SE \approx 0\ 464, z \approx 1\ 943, p$ value $\approx 0\ 052$). Composition models using the ectoparasites share did not improve fit or produce significant effects. Attractiveness outcomes were insensitive to burden definition. Exposure effects were uniformly small and non-significant. Including PathNP together with the pathogenic fraction does not double-count pathogenic parasites; it separates two effects: (i) a scale effect of overall parasite load (captured by PathNP) and (ii) a composition effect of *how much of that load is pathogenic* (captured by the fraction). Thus, effects are interpreted "holding total constant" for the share term. In practical terms, two individuals with the same total count can differ in perceived health if one has a higher proportion of pathogenic parasites (e.g., a 10-percentage-point increase in pathogenic share corresponds to about 0 11 units on Mheal, given $\beta \approx 1\ 12$ in Table 6 below). The absence of effects for attractiveness suggests that mate-preference ratings in this dataset are not strongly coupled to parasite burden, at least within the observed ranges.

These results indicate that the composition of a person's parasite profile—specifically, the fraction that is pathogenic—matters more for perceived health than raw totals or the broader ectoparasites definition.

Table 6
Analysis of parasite burden for health and attractiveness outcomes.

Model_Pheal	Term	β	SE	z	p	95 % CI	AIC	BIC
Total	Z_{Path_NP}	0.136	0.117	1.161	0.246	(0.366, 0.094)	32.78	18.871
Pathogenic	Z_{Path}	0.012	0.117	0.1	0.921	(0.242, 0.218)	31.45	17.546
Ectoparasites	$Z_{PathEct}$	0.061	0.118	0.516	0.606	(0.292, 0.170)	31.71	17.801
comp_path	Z_{Path_NP}	0.158	0.116	1.362	0.173	(0.384, 0.069)	34.47	18.247
comp_path	share_path	0.879	0.453	1.94	0.052	(0.009, 1.767)	34.47	18.247
comp_ectoparasites	Z_{Path_NP}	0.157	0.117	1.349	0.177	(0.386, 0.071)	32.99	16.769
comp_ectoparasites	share_ectoparasites	0.678	0.453	1.497	0.134	(0.209, 1.565)	32.99	16.769
Model_Fheal	Term	β	SE	z	p	95 % CI	AIC	BIC
Total	Z_{Path_NP}	0.17	0.125	1.353	0.176	(0.416, 0.076)	25.56	11.658
Pathogenic	Z_{Path}	0.067	0.125	0.531	0.595	(0.313, 0.179)	24.03	10.128
Ectoparasites	$Z_{PathEct}$	0.115	0.126	0.917	0.359	(0.361, 0.131)	24.59	10.681
comp_path	Z_{Path_NP}	0.185	0.125	1.482	0.138	(0.431, 0.060)	24.99	8.763
comp_path	share_path	0.591	0.494	1.197	0.231	(0.377, 1.558)	24.99	8.763
comp_ectoparasites	Z_{Path_NP}	0.184	0.126	1.461	0.144	(0.431, 0.063)	24.26	8.038
comp_ectoparasites	share_ectoparasites	0.413	0.493	0.837	0.403	(0.554, 1.380)	24.26	8.038
Model_Mheal	Term	β	SE	z	p	95 % CI	AIC	BIC
Total	Z_{Path_NP}	0.122	0.121	1.005	0.315	(0.359, 0.116)	35.06	21.152
Pathogenic	Z_{Path}	0.024	0.122	0.197	0.844	(0.216, 0.264)	34.09	20.187
Ectoparasites	$Z_{PathEct}$	0.028	0.123	0.228	0.82	(0.268, 0.212)	34.11	20.2
comp_path	Z_{Path_NP}	0.145	0.119	1.22	0.222	(0.377, 0.088)	38.69	22.467
comp_path	share_path	1.117	0.46	2.404	0.016	(0.206, 2.027)	38.69	22.467
comp_ectoparasites	Z_{Path_NP}	0.146	0.12	1.22	0.222	(0.380, 0.088)	36.73	20.511
comp_ectoparasites	share_ectoparasites	0.897	0.464	1.943	0.052	(0.012, 1.805)	36.73	20.511
Model_Pattr	Term	β	SE	z	p	95 % CI	AIC	BIC
Total	Z_{Path_NP}	0.022	0.108	0.203	0.839	(0.190, 0.234)	47.37	33.467
Pathogenic	Z_{Path}	0.027	0.105	0.256	0.798	(0.179, 0.233)	47.4	33.491
Ectoparasites	$Z_{PathEct}$	0.03	0.107	0.28	0.779	(0.179, 0.239)	47.41	33.504
comp_path	Z_{Path_NP}	0.029	0.109	0.263	0.793	(0.186, 0.243)	45.55	29.326
comp_path	share_path	0.177	0.421	0.42	0.675	(1.002, 0.648)	45.55	29.326
comp_ectoparasites	Z_{Path_NP}	0.028	0.11	0.251	0.802	(0.188, 0.243)	45.46	29.237
comp_ectoparasites	share_ectoparasites	0.123	0.414	0.297	0.767	(0.935, 0.689)	45.46	29.237
Model_Fattr	Term	β	SE	z	p	95 % CI	AIC	BIC
Total	Z_{Path_NP}	0.052	0.125	0.417	0.677	(0.193, 0.297)	52.6	38.69
Pathogenic	Z_{Path}	0.052	0.122	0.426	0.67	(0.187, 0.291)	52.6	38.698
Ectoparasites	$Z_{PathEct}$	0.058	0.124	0.47	0.639	(0.185, 0.302)	52.64	38.737
comp_path	Z_{Path_NP}	0.062	0.126	0.492	0.622	(0.186, 0.310)	50.86	34.635
comp_path	share_path	0.246	0.48	0.512	0.609	(1.187, 0.695)	50.86	34.635
comp_ectoparasites	Z_{Path_NP}	0.061	0.127	0.482	0.629	(0.188, 0.310)	50.76	34.537
comp_ectoparasites	share_ectoparasites	0.192	0.474	0.406	0.685	(1.120, 0.736)	50.76	34.537
Model_Mattr	Term	β	SE	z	p	95 % CI	AIC	BIC
Total	Z_{Path_NP}	0.015	0.105	0.144	0.886	(0.190, 0.220)	45.73	31.827
Pathogenic	Z_{Path}	0.02	0.101	0.202	0.84	(0.178, 0.219)	45.75	31.848
Ectoparasites	$Z_{PathEct}$	0.021	0.103	0.205	0.838	(0.180, 0.223)	45.75	31.849
comp_path	Z_{Path_NP}	0.019	0.106	0.178	0.859	(0.189, 0.226)	43.79	27.569
comp_path	share_path	0.101	0.412	0.244	0.807	(0.909, 0.708)	43.79	27.569
comp_ectoparasites	Z_{Path_NP}	0.017	0.106	0.164	0.87	(0.191, 0.226)	43.75	27.527
comp_ectoparasites	share_ectoparasites	0.053	0.406	0.131	0.896	(0.848, 0.742)	43.75	27.527

Table 7
Statistical analysis of BMI and PathNP relationship.

Parameter	Value	Interpretation
Correlation coefficient (r)	0.2	Weak negative association between BMI and parasite load
t-statistic	1.75	Moderate deviation from null hypothesis (no correlation)
Degrees of freedom (df)	73	Based on 73 valid case pairs in the data
p-value	0.085	Marginally non-significant (p-value >0.05), but suggests a potential trend
95 % Confidence Interval	[0.41, 0.03]	Range includes zero, indicating statistically nonsignificant
Effect size (R^2)	4 % (r^2 = 0.04)	BMI explains ~4 % of the variability in PathNP

In practical terms, two individuals with the same total count can differ in perceived health if one has a higher proportion of pathogenic parasites. The absence of effects for attractiveness suggests that mate-preference ratings in this dataset are not strongly coupled to parasite burden, at least within the observed ranges.

4.10. Association of BMI with pathogen load

We next tested whether overall parasite burden relates to BMI, the results are shown in Table 7 below.

4.10.1. Bivariate association

The analysis suggests a possible inverse relationship between Body Mass Index (BMI) and parasite load (PathNP). A higher BMI is associated with a lower parasite load; however, the confidence interval includes zero, and the effect is not statistically significant at 5 % level of significance. This modest negative correlation may reflect improved nutrition reducing susceptibility to parasites, or it may result from sampling variation due to the limited sample size (see Fig. S7).

4.10.2. Power and interpretive limitations

The sample size was modest ($N = 75$). For a two-sided correlation test at $\alpha = 0\ 05$, power is approximately 40 % to detect $|\rho| = 0\ 20$ and 25 % for $|\rho| = 0\ 15$ With limited power, distinguishing between significant and non-significant results is unreliable for small effects. Therefore, emphasis is placed on effect sizes and confidence intervals. The wide 95 % CI [0.41, 0.03] is consistent with small to moderate negative effects or no effect, indicating inconclusive evidence for very

small associations. The 90 % CI for r does not fall entirely within a practically null band (e.g., ±0.20 or ±0.15), so the effect cannot be considered negligible. Larger samples are needed to narrow confidence intervals around the smallest effects of interest.

4.10.3. Correlation versus independence and model assumptions

The beta regression analyses require independence of observations or appropriate modeling of clustering, correct mean-variance specification, and exogenous predictors. Mutual independence among predictors is not required. The observed BMI–PathNP correlation ($r =$ 0 20) is well below common multicollinearity thresholds ($|r|$ approximately 0.7), indicating minimal linear dependence.

4.10.4. Multicollinearity diagnostics

Sensitivity checks indicated negligible collinearity across models.

Attractiveness models. Variance inflation factors (VIFs) ranged from approximately 1.02 to 1.25 overall (BMI: 1.05–1.08; PathNP: 1.21–1.25), with tolerances between 0.80 and 0.98.

Health models. VIFs ranged from approximately 1.01 to 1.18 overall (BMI: 1.05–1.07; PathNP: 1.17–1.18), with tolerances between 0.85 and 0.99.

All values are well below standard thresholds of concern, such as VIF < 5, indicating that multicollinearity is unlikely to bias the coefficient estimates.

4.10.5. Implications and next steps

Given the limited power and wide confidence intervals, strong claims are not made for non-significant results regarding PathNP. Emphasis is placed on estimated effects and their associated uncertainty. The consistent finding that BMI, but not parasite load, predicts perceived health and attractiveness suggests that visible body condition may be more salient to adolescents than underlying pathogen burden. However, this inference remains provisional until replicated with larger samples and measures of intensity rather than prevalence of parasitic infection. Future research should increase sample size to narrow confidence intervals and directly assess the smallest effects of interest, such as $|\rho| =$ 0 15 0 20. Additionally, partial or conditional relationships, such as those mediated by nutrition or immune function, should be examined to distinguish direct from indirect pathways. Where feasible, environmental exposures and immune markers should be incorporated.

4.11. Gender differences in parasite burden

Let $Q_i \in \{0, 1, 2, \ldots\}$ denote the total parasite count (PathNP) for an individual i. Each i has sex $S_i \in \{\mathrm{F}, \mathrm{M}\}$ and ethnicity $E_i \in \{\mathrm{Aka}, \mathrm{Ngandu}\}$. We model counts with a Negative–Binomial GLM:

$$Q_i|\mu_i, \theta \sim \mathrm{NegBin}(\mu_i, \theta), \text{with } \mathrm{Var}(Q_i|\mu_i, \theta) = \mu_i + \mu_i^2/\theta, \text{and}$$

$$\log\mu_i = \beta_0 + \beta_1 \mathbf{1}\{S_i = \mathrm{Male}\} + \beta_2 \mathbf{1}\{E_i = \mathrm{Ngandu}\} + \beta_3 \mathbf{1}\{S_i = \mathrm{Male}\}\mathbf{1}\{E_i = \mathrm{Ngandu}\}$$

Incidence–rate ratios (IRR) are $\exp(\cdot)$ of linear contrasts on the log-mean scale. Define the sex contrasts within each ethnicity:

$$\Delta_{\mathrm{Aka}} \equiv \log\left(\frac{\mu_{\mathrm{M,Aka}}}{\mu_{\mathrm{F,Aka}}}\right) = \beta_1, \Delta_{\mathrm{Ngandu}} \equiv \log\left(\frac{\mu_{\mathrm{M,Ngandu}}}{\mu_{\mathrm{F,Ngandu}}}\right) = \beta_1 + \beta_3,$$

with corresponding $IRR_{\mathrm{Aka}} = \exp(\beta_1)$ and $IRR_{\mathrm{Ngandu}} = \exp(\beta_1 + \beta_3)$. Averaging over ethnicities (marginal gender effect) yields the population-averaged IRR, computed via estimated marginal means on the response scale; denote this $\mathrm{IRR}_{\mathrm{marg}}$.

Hypotheses and Tests:

1. Interaction: $H_0 : \beta_3 = 0$ (no ethnicity-specific shift in the gender gap)
2. Within-ethnicity gender gaps: $H_0 : \Delta_{\mathrm{Aka}} = 0$ and $H_0 : \Delta_{\mathrm{Ngandu}} = 0$.

Marginal sex gap : $H_0 : \log\ \mathrm{IRR}_{\mathrm{marg}}) = 0$

With $\widehat{\theta}$ the Negative Binomial shape estimate and $\widehat{\phi}$ the dispersion ratio, the overdispersion test evaluates $H_0 : \phi = 1$. We obtain $\widehat{\phi} = 0\ 804$ with p *value* $= 0\ 272$, indicating no evidence of overdispersion; $\widehat{\theta} \approx 67,443$ implies the fit is close to Poisson.

Estimates and inference (reported as Female/Male IRR, i.e., exp( )):

1. Interaction: $H_0 : \beta_3 = 0$ not rejected; p *value* $= 0\ 525$.
2. Within-ethnicity gender gaps:

$$\mathrm{IRR}_{\mathrm{Aka}}^{\mathrm{F/M}} = \exp(\ \ \beta_1) = 0\ 787, z = \ \ 1\ 35, p \ \ \textit{value} = 0\ 178;$$

$$\mathrm{IRR}_{\mathrm{Ngandu}}^{\mathrm{F/M}} = \exp(\ \ (\beta_1 + \beta_3)\ ) = 0\ 667, z = \ \ 2\ 11, p \ \ \textit{value} = 0\ 0348$$

4.12. Marginal gender gap (averaged over ethnicities)

$$\mathrm{IRR}_{\mathrm{marg}}^{\mathrm{F/M}} = 0\ 724, z = \ \ 2\ 47, p \ \ \textit{value} = 0\ 0137$$

Within Aka, females have an estimated 1 0 787 = 21 3% lower mean count than males (not statistically significant at conventional levels). Within Ngandu, females have an estimated 1 0 667 = 33 3% lower mean count than males (statistically significant). Marginally across ethnicities, females have 1 0 724 = 27 6% lower mean counts than males (statistically significant). The non-significant interaction supports a broadly similar male–female gap across both groups.

4.12.1. Statistical analysis of marriageability based on BMI, ethnicity, and pathogen load

To analyze the bounded proportion data of perceived marriageability (where $y_i \in [0, 1]$ represents raw rating proportion), we applied the (Smithson & Verkuilen, 2006) transformation to avoid boundary issues:

$$Y_i = \frac{[y_i(N \ \ 1) + 0\ 5]}{N}$$

where:

- N= Number of opposite-sex raters within each group (specific to male/female models)
- Y_i= Transformed score, now $Y_i \in [0, 1]$

Cross-Gender Rating Models:

1. Female Marriageability (Rated by Males):

$$\text{logit}\ \mu_i^{(F)}\ ) = \beta_0^{(F)} + \beta_1^{(F)}\mathrm{BMI}_i + \beta_2^{(F)}\mathrm{Ethnicity}_i + \beta_3^{(F)}\mathrm{PathNP}_i$$

with

$$Y_i^{(F)} \sim \textit{Beta}\ \mu_i^{(F)}\varphi^{(F)},\ \ 1 \ \ \mu_i^{(F)}\ )\varphi^{(F)}\ )$$

1. Male Marriageability (Rated by Females):

$$\text{logit}\ \mu_i^{(M)}\ ) = \beta_0^{(M)} + \beta_1^{(M)}\mathrm{BMI}_i + \beta_2^{(M)}\mathrm{Ethnicity}_i + \beta_3^{(M)}\mathrm{PathNP}_i$$

Table 8
Beta regression analysis of marriage perception determinants and goodness-of-fit statistics of marriage perception determinants from beta regression analysis.

Parameter	Female Marriageability Rated By Males			Male Marriageability Rated By Females		
	$\widehat{\beta}$	[95 % CI]	p	$\widehat{\beta}$	[95 % CI]	p
Intercept	2.26	[3.91, 0.61]	0.007	2.95	[4.59, 1.31]	***
BMI	0.07	[0.01, 0.15]	0.093	0.11	[0.03, 0.18]	0.007
Ethnicity						
Aka (Ref)	–	–	–	–	–	–
Ngandu	0.26	[0.74, 0.23]	0.306	0.49	[0.83, 0.16]	0.004
PathNP	0.02	[0.22, 0.19]	0.884	0.09	[0.18, 0.01]	0.076
Model Fit	Female Marriageability Rated By Males			Male Marriageability Rated By Females		
AIC	35.2			90.4		
BIC	27.5			81.9		
Log Likelihood	22.6			50.2		
Deviance	45.2			100.4		
φ	8.45			22.9		
Degrees of Freedom	30			35		

Notes: Reference categories: Aka for Ethnicity. Significance: *** = (p < .001). φ = dispersion parameter. All models use logit link function with beta distribution.

with

$$Y_i^{(M)} \sim Beta\ \mu_i^{(M)}\varphi^{(M)},\ 1\quad \mu_i^{(M)})\varphi^{(M)})$$

4.12.2. Analysis of marriageability determinants. The beta regression analysis revealed significant gender differences in predictors of marriageability (Table 8).

For female marriageability as rated by male evaluators, the model showed a significant negative intercept ($\widehat{\beta}=$ 2.26, p-value = 0.007), indicating an overall conservative rating tendency among male evaluators regardless of ethnicity. BMI exhibited a marginal positive association with female marriageability ($\widehat{\beta}=$ 0.07, p-value = 0.093). Notably, the non-significant Ngandu coefficient ($\widehat{\beta}=$ 0.26, p-value = 0.306) suggests that when rating female marriageability, Ngandu male raters did not significantly differ from Aka male raters in their evaluations, when rating women from their ethnic group. Moreover, pathogen prevalence ($\widehat{\beta}\beta=$ 0.02, p-value = 0.884) did not significantly predict male ratings of female marriageability. At the mean predicted probability (0.174), the average marginal effect was 1.24 percentage points per unit (95 % CI [2.61, 0.13]). As above, the 90 % confidence interval was not fully contained within ±0.10 log-odds but was fully contained within ±0.20, again suggesting that effects larger than small-to-moderate magnitudes are unlikely.

For male marriageability rated by female evaluators, results showed stronger and more significant effects. The negative intercept ($\widehat{\beta}=$ 2.95, p-value <0.001) indicates female raters generally preferred males with higher BMIs. BMI had a significant positive effect ($\widehat{\beta}=$ 0.11, p-value = 0.007), demonstrating that female raters from both ethnic groups used this metric in evaluating someone to marry. The significant negative coefficient for Ngandu ethnicity ($\widehat{\beta}=$ 0.49, p-value = 0.004) reveals that Ngandu women rated fewer Ngandu men as marriageable by comparison to the number of males Aka women thought were marriageable. The parasite-load coefficient was near zero ($\widehat{\beta}=$ 0.09, p-value = 0.076). At the sample's mean predicted probability (0.245), the average marginal effect was approximately 0.28 percentage points per one-unit increase in parasite load (95 % CI [4.09, 3.52]). The 90 % confidence interval was not fully contained within a strict smallest-effect band of ±0.10 log-odds, but it was fully contained within ±0.20, indicating that effects larger than small-to-moderate magnitudes are unlikely.

The goodness-of-fit statistics highlighted notable differences in rating consistency between the two models (Table 8). The male marriageability model rated by females showed superior fit, evidenced by lower AIC (90.4 vs 35.2) and BIC (81.9 vs 27.5), a higher log likelihood (50.2 vs 22.6), and greater precision (φ = 22.9 vs 8.45). This indicates that female raters considered BMI metrics more when evaluating males, suggesting either more uniform preferences among women or clearer signaling of traits by male targets. These findings may reflect fundamental gender differences in mate evaluation.

5. Cultural models of health and attraction

5.1. Freelisting and frequency of mention analysis

To explore local conceptions and cultural models of attractiveness, a semi-structured freelisting approach was used with a sample of 27 Aka and 32 Ngandu participants who were asked to spontaneously list traits or qualities they considered attractive in potential mates. Freelisting is widely used in cognitive anthropology to elicit cultural domains and to identify both salient and commonly shared concepts across informants (Weller & Romney, 1988). Freelisting analysis considers both the frequency of items mentioned by individuals and the ranking of the items, i.e., which item was mentioned first, second, and so on. The frequency and ranking of all individuals is used to calculate an average saliency of the items listed. Averages range from 0 to 1 and the higher the score means greater mental saliency and greater cultural consensus.

Table 9 summarizes the top six items of Aka males and females and shows a strong convergence between them on the importance of social and personality traits: pleasant personality, laughs a lot, and cheerfulness were highly salient in both groups. These traits were particularly salient for Aka women. Men's scores were lower on average than women's primarily because men listed more different traits than women which lowers average salience scores. Overall, prosocial temperament anchors attractiveness for both genders, with women weighing vitality and hygiene a bit more than males, and men adding sharper attention to facial features and grooming.

Among the Ngandu, patterns of trait salience reveal a clear emphasis on external and physical markers of attractiveness. Ngandu women consistently prioritized men's appearance and grooming over personality or prosocial traits, which were more salient among the Aka (see Table S10). The most salient items for Ngandu male attraction to females included wearing nice clothes (average salience = 0.32), good form or posture (0.31), health (0.31), a pleasant face (0.30), and bodily cleanliness (0.26). These items had similar average salience scores, indicating general agreement among respondents. The focus on visible presentation likely reflects the social ecology of this farming society, where diligence, respectability, and public reputation are central to social

Table 9
Top six average salience scores of Aka females and males.

Female Aka (n = 13) — traits attractive in males	Average Salience	Male Aka (n = 14) — traits attractive in females	Average Salience
pleasant personality	0.50	pleasant personality	0.23
laughs a lot, cheerful	0.37	laughs a lot, cheerful	0.18
brown skin	0.27	small nose	0.16
clean clothes	0.24	good clothes	0.15
small nose	0.21	brown skin	0.14
walks good/strong	0.13	small mouth	0.11

standing and marriage prospects. For Ngandu women, attraction to men who appeared "well-kept" and healthy may also relate to agricultural labor demands, intrasexual violence, and the symbolic link between outward presentation and personal discipline.

Ngandu men likewise emphasized external features when describing female attractiveness. Their most salient traits included beauty and nice clothing, followed by a pleasant face (0.28), good form or posture (0.20), health (0.23), and bodily cleanliness (0.19). Cultural consensus was particularly strong around beauty and dress, underscoring the importance of visible cues in evaluating desirability. For Ngandu men, "beauty" is conceptualized not only in terms of facial attractiveness but also through grooming, clothing, and public presentation—attributes that signal respectability and social competence. This consistent prioritization of overtly aesthetic qualities suggests that both male and female Ngandu adolescents conceptualize attractiveness primarily in visual and performative terms, linking desirability to how individuals present themselves in socially approved, well-maintained ways.

In addition to the freelisting method, any references to attractiveness mentioned during open-ended interviews while discussing other topics of the health and development research project (Hewlett, 2004) were noted. This study enabled one to capture unprompted comments in the flow of daily conversation. The open-ended interviews took place with 34 Aka and 38 Ngandu adolescents.

Tables 9 and S10 present the frequency and proportion of traits mentioned by Aka and Ngandu adolescents when asked to describe what they found attractive in the opposite sex. Because the number of participants differed across groups, proportions are provided to allow direct comparison. Among the Aka (18 females and 16 males), responses emphasized traits such as cleanliness, strength, skin color (explained as a lighter brown skin tone), and pleasant personality. These reflect an integration of physical appearance and social qualities tied to cooperative daily hunter-gatherer life. Among the Ngandu (13 females and 25 males), traits such as beauty, clothing, body form, and facial features were emphasized, highlighting the importance of outward presentation and public reputation in village-based social life. Together, the tables illustrate how ideals of attractiveness are impacted by culture and reveal differences in how Aka and Ngandu youth evaluate health, beauty, and marriageability. The patterns in Tables S6–8 show that Aka and Ngandu adolescents converge on valuing cleanliness, grooming, and bodily form as outward indicators of health and respectability, but they diverge in the traits they emphasize most. By presenting proportions, the tables account for differences in sample size and make visible the stronger Ngandu consensus around beauty and clothing, contrasted with the Aka's balance between physical appearance and personality traits such as pleasant temperament.

5.2. Comparative discussion: Aka and Ngandu

Across both measures, the Aka (foragers) and Ngandu (farmers) converge on the idea that attractiveness communicates competence, respectability, and social value. Where they diverge is in the weighting of cues. The Aka emphasize vitality and prosocial personalities essential to daily cooperative life, while the Ngandu place greater emphasis on appearance and public presentation embedded in village farming-based systems of status and reputation.

Cleanliness and grooming are valued in both societies. A clean body and clothing function as visible proxies for health, self-care and adherence to community norms. Physical form and bearing are also important: traits such as "walks strong" among the Aka and "good form" or "posture" among the Ngandu signal stamina, work capacity, and health. Facial evaluation, though framed differently, appears in both groups. Among the Ngandu, descriptors such as "handsome" or "beautiful" carry explicit weight in evaluations of attractiveness. In contrast, the Aka tend to situate facial features within broader clusters of assessment that also encompass temperament, cheerfulness, and subtle physical traits such as the size of the eyes, mouth, or nose—markers understood to signal overall health. As several Aka informants explained, someone with a "big mouth" might be suspected of having a dental or oral infection, while a person with "big cheeks" could be thought to suffer from an infection, throat or systemic illness.

Despite these shared emphases, systematic differences are apparent. Among the Aka, "good looks" are inseparable from temperament and vitality; pleasant personality, cheerfulness, and walking strength intertwine with appearance. By contrast, Ngandu informants tie attractiveness more tightly to public presentation—clothing, posture, grooming, and beauty are central to their evaluations. Clothing, while important for both groups, carries distinct weight: for the Aka, it sits alongside sociability and vigor, while for the Ngandu it is central, signaling economic means, diligence, and conformity to communal standards. Personality and sociability are at the heart of Aka judgments, whereas aesthetic and grooming signals dominate Ngandu assessments. That is, cultural context impacted these patterns; for Ngandu raters, health was closely linked to marriageability and potential labor capacity, while Aka evaluations were more likely to reflect communal values such as kindness and cooperation. These contrasts correspond to differences in ecology and subsistence. Ngandu agriculturalists engage in sedentary, labor-intensive farming in areas with more stable exposure to pathogens, making physical health and work capacity salient indicators of value as a spouse. By contrast, while both groups inhabit high-pathogen tropical environments, the Aka's mobility as forest foragers allows them to relocate seasonally or move from high-intensity pathogen zones. This mobility, combined with their egalitarian social structure, may lessen the selective pressure linking visible health to marriageability and instead favor preferences emphasizing social reliability and cooperation.

Gendered evaluations further illuminate these contrasts. Aka women emphasize an everyday competence profile: vitality ("walks strong"), hygiene/health ("clean clothes"), appearance (brown skin, small nose), and temperament (pleasant personality, cheerfulness). Aka men share this concern with hygiene and vitality but add morphological and reproductive cues, such as "big behind" and beauty, while still valuing agreeableness within the context of camp life. Ngandu women highlight presentation—nice clothes, posture, health, cleanliness, and handsomeness—as markers of respectability and diligence within farming contexts. Ngandu men show extremely high consensus on beauty and clothing, followed by form, health, and cleanliness, producing a more concentrated aesthetic-forward hierarchy than that found in women's evaluations.

These differences make sense when situated in ecological and social contexts. For the Aka, subsistence depends on coordination in small, mobile camps. Traits enabling extensive sharing outside of the household, intimate living, joint foraging, and conflict avoidance—good temperament, stamina, and cleanliness—can be adaptive and difficult to fake. For the Ngandu, whose settled villages are shaped by social hierarchies and reputation-based economies, visible markers of conformity and household status—such as clothing, physical appearance, and posture—serve as more effective and easily interpreted signals. In signaling terms, Aka preferences align with performance-oriented cues, while Ngandu preferences align with presentation-oriented cues. Risk, mobility, and interdependence in the forest reward compatibility and reliability, whereas agrarian settlement rewards conformity and public display.

The patterns also emerge clearly in the comparative analysis of frequency and salience. Frequency highlights how often a trait was mentioned, while salience considers both rank and frequency of mention. Ngandu men's extremely high values for beauty and clothing reveal both consensus and priority in their hierarchy of attractiveness. Among the Aka, traits such as pleasant personality and cheerfulness achieved high salience despite potential methodological biases favoring visible features, underscoring the centrality of sociability. Cleanliness and walking strength also showed strong and consistent representation across elicitation modes.

Caveats remain. We harmonized terminology across informants (e.g.,

"nice" recoded as "pleasant personality"), and sample sizes differed, which can affect apparent consensus. Nevertheless, directional patterns are robust, and the Aka's consistent elevation of temperament—despite methodological tendencies toward visible traits—strengthens the interpretation.

In synthesis, the Aka prioritize performance-relevant qualities—vitality, cleanliness, and cooperative temperament—that facilitate collective foraging, extensive sharing, and camp life. The Ngandu prioritize presentation-relevant qualities—beauty, clothing, posture, and grooming—that render status and respectability legible in village settings. Both models are rational, locally adaptive responses: one optimized for cooperation under mobility and mutual dependence, the other for social ordering in stratified, reputation-driven contexts.

5.3. Limitations of the freelisting and salience data

Despite the advantages of the freelisting method, it is important to note that not all informants provided lists. Some participants appeared not to fully understand the freelisting request, while others were reticent to discuss attractiveness, either in the freelist task or in open-ended interviews. As a result, the number of participants is not always balanced across groups. This variability means that the frequency and salience analyses reflect patterns drawn from a subset of participants rather than universal responses across the entire sample.

5.4. Narratives of health, attraction and marriageability

Qualitative data enhanced quantitative analysis by providing insights into perceptions of health and attractiveness among Aka and Ngandu adolescents and young adults. Their unique cultural frameworks reflected social and ecological contexts that shaped individual and community criteria for health, beauty, and mate preference (see Tables 5, S6–8).

For the Ngandu, health assessments from interviews were tied closely to physical appearance, with adolescents identifying observable features as indicators of illness or wellness. Descriptions often revolved around specific physical irregularities or markers of poor health. One 13-year-old female adolescent remarked that someone was "not attractive because they are not in good health," further elaborating, "he is skinny and has big cheeks, so he has an infection." Other adolescents associated unattractiveness with hygiene or physical deformities, with one 18-year-old male saying, "She has bad hair, fleas (here meaning sandfleas, generally on the feet) is not strong, is skinny and is in poor health," an assessment echoed by a13-year-old female "he is not healthy, he is skinny, his cheeks are swollen, he is dirty, his hair is not done well, and his clothes are not clean."

When describing attractiveness, Ngandu adolescents placed significant emphasis on cleanliness and physical robustness (see Tables 5, S6 and S8). A 13-year-old female participant explained, "He is attractive because his skin is clear and nice and black, and his clothes are clean." Similarly, a 16-year-old female said, "I like big, strong men who are healthy." Male participants highlighted attributes such as body size and facial features. As one 13-year-old male said, "I like big women with nice-shaped heads and big [not 'bulgy'] eyes with a good posture, and also if they have nice clothes and a pretty face." Cleanliness emerged as a consistent criterion across both genders, with an older 18-year-old female stating, "I like big men with a big behind who are clean and in good health and not skinny."

Mate selection among the Ngandu mirrored these criteria, with adolescents identifying physical health, cleanliness, and strength as critical factors for marriageability. One male (19-years-old) explained his preference, saying, "I would marry her because she's a big strong woman, and wears nice clean clothes." A 11-year-old male noted, "She is a good one, she is very beautiful, has clean clothes and nice hair and face." Females expressed similar sentiments, with one 19-year-old explaining, "I would marry him because he is clean and has nice clothes, his skin is clear, and he has a nice-shaped head and face." Interestingly, several females rated one particular male high in cleanliness, health and attractiveness (he also had the lowest number of parasites and a healthy BMI) but reported they did not consider him marriable as he was well known in the community as being a "sorcerer".

In contrast, the Aka adolescents emphasized behavioral and social traits alongside physical characteristics when discussing health, attractiveness, and mate preferences. Commonly mentioned illnesses included "intestinal worms, coughing, and diarrhea," but Aka adolescents were less concerned with physical imperfections or ill health than their Ngandu counterparts. When describing attractive traits, the Aka consistently valued personality and behavior (see Tables 5, S7). A 17-year-old female participant stated, "When people are nice, they are attractive," adding, "they are nice and laugh, walk well, and are clean." Another 17-year-old male adolescent remarked, "A woman who is nice and laughs a lot and has nice necklaces and a big behind" was considered attractive.

Physical attributes such as "little eyes and mouth and pointed teeth" were noted as desirable by some Aka participants, but these traits were often secondary to social behaviors. "Walking with strength" was also frequently mentioned, with one 20-year-old male explaining his preference for "Women who walk with strength and sweat," while females, as explained by one 15-year-old, noted that "men who are clean and walk with strength" were particularly attractive.

Interestingly, Aka adolescents and young adults demonstrated a higher degree of flexibility in mate selection compared to the Ngandu. Despite acknowledging unattractive features, many Aka participants expressed a willingness to marry individuals they considered less desirable in terms of health or physical appearance. As one 15-year-old male (and several others) stated, "I would marry all of them because they are all girls." Another 12-year-old male explained, "I would marry her because she is beautiful and has hair between her breasts and lots of hair on her arms and legs." Females were similarly nuanced, with one 12-year-old explaining, "I would marry him because my heart tells me he is good and handsome." A young 16-year-old female added, "I would marry all of them because they will heal if they are not well and will work hard and find honey and meat for their wife."

Taken together, the frequency and proportion data, salience patterns, and qualitative narratives provide a coherent picture of how Aka and Ngandu adolescents conceptualize attractiveness. These findings highlight both shared concerns with health and cleanliness and culturally specific emphases—temperament and vitality for the Aka, appearance and presentation for the Ngandu—that will be situated in broader theoretical and comparative perspective in the discussion that follows.

6. Discussion and conclusion

This study demonstrates a complex interaction between evolved preferences and cultural norms in shaping judgments of health, attractiveness, and marriageability. Across both groups, BMI emerged as the strongest and most consistent predictor, while gender and ethnicity introduced meaningful variation. These findings underscore the value of integrating biological, ecological, and cultural perspectives in cross-cultural mate evaluation research.

Qualitative data showed that cultural models mediate how evolved cues are interpreted. Ngandu adolescents linked attractiveness closely to cleanliness, posture, and physical robustness, while Aka youth prioritized prosocial traits such as kindness, laugh4ter, and sociability. These contrasts illustrate how universal mate choice mechanisms—attentiveness to health, fertility, and sociality—are expressed through locally adaptive values shaped by subsistence strategies and settlement contexts (DeBruine et al., 2010; Shackelford et al., 2005).

Our findings should not be read as rejecting evolutionary explanations but as highlighting their flexibility. As evolutionary psychologists emphasize, universality lies in shared underlying mechanisms, not identical behaviors across settings (Confer et al., 2010; Lewis et al.,

2017). From this perspective, the consistent role of BMI across Aka and Ngandu supports context-sensitive evolutionary models (Buss & Schmitt, 2017; Gangestad et al., 2006). In environments marked by food insecurity and parasitic infection, body condition functions as a salient proxy for health and resilience, aligning with resource availability models predicting that body size carries greater value under ecological stress (Brown & Konner, 1987; Swami & Tovee, 2007).

Parasite load, by contrast, did not predict attractiveness or health judgments. This likely reflects the near-universal presence of parasites in these communities, where visible signs are less informative than overall body condition. In such contexts, BMI appears to overshadow subtle phenotypic indicators of infection. This suggests limits to human ability to detect pathogen-related disease where parasitism is common, but infection intensity may be relatively low.

Gender and ethnicity further shaped evaluations. Male raters applied stricter standards, particularly toward females, while female raters were more even in their assessments—patterns consistent with evolutionary theory that men prioritize physical cues and women attend to broader social attributes (Andrews et al., 2017; Buss & Schmitt, 2017, 2019). Ngandu adolescents overall judged fewer peers as attractive compared to Aka, possibly reflecting their stronger emphasis on appearance, clothing, and public presentation, versus the Aka's integration of temperament and sociability.

Finally, interpreting anthropometric cues requires attention to local context. BMI values in these populations fall below the 5th percentile of U.S. distributions, underscoring the distinct ecological and nutritional contexts of these populations. In this setting, modest increases in BMI are more likely to reflect adequate energy balance and disease resistance than excess adiposity (Silverman et al., 2022). As such, BMI remains highly valued as a marker of health and resilience. This contrasts with high-income societies, where higher BMI is often stigmatized due to its association with chronic disease (Brown & Konner, 1987; Swami & Tovee, 2007). These differences underscore that body size is not a universal signal of stigma or risk but a flexible indicator whose meaning shifts with ecological pressures and cultural models of the body.

In sum, Aka and Ngandu adolescents evaluate health and attractiveness through a shared evolutionary architecture that is expressed in culturally distinctive ways. These findings reinforce the value of a biocultural approaches, showing that while universal psychological mechanisms impact mate preferences, their expression is modified by ecological constraints and cultural models, producing locally adaptive criteria of health and attractiveness. In doing so, this research highlights the unique contribution of anthropology—bridging biology, culture, and ecology to illuminate the diversity and flexibility of human mate choice.

7. Limitations and future directions

While this study is one of a few to examine relationships between parasite loads, BMI and cultural perceptions of health and attraction, certain limitations should be acknowledged. First, a more in-depth study is needed to understand the reasons influencing individual assessments. For instance, what cultural models exist regarding the specific parasites examined in this study? Which parasites are viewed as extremely harmful to health, and which are seen as a normal part of the environment? Future studies should also consider incorporating more specific health indicators—such as using intensity rather than prevalence of parasitic infection, clinical evaluations of immune function or hormonal levels—to complement the robust yet informative measures of BMI and parasite burden currently used. Additionally, it is important to recognize that the relatively small sample size ($n = 75$) limits quantitative analysis. Although the ethnographic depth and cross-cultural perspective are significant strengths, the limited number of participants—especially when divided by rater sex or ethnic group—reduces statistical power. Therefore, while the consistent role of BMI and the observed patterns related to gender and culture provide valuable insights, these findings should be interpreted with caution. Future research with larger and more balanced samples will be crucial for confirming the robustness of these patterns and for exploring whether additional health or social indicators influence judgments of attractiveness and marriageability.

The sample was limited to two cultural groups totaling 75 participants, with logistical constraints in remote fieldwork sites limiting feasible recruitment. Including a broader range of societies would allow for a deeper understanding of how diverse ecological and cultural factors shape mate selection.

Finally, while parasite load was not a significant predictor here, longitudinal research could examine how shifts in environmental or disease conditions affect preferences over time. Such studies could illuminate the evolving relationship between health, attractiveness, and reproductive decision-making in different ecological contexts.

CRediT authorship contribution statement

Bonnie Hewlett: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Harshita Agrawal:** Writing – review & editing, Formal analysis. **Barry Hewlett:** Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.evolhumbehav.2025.106815.

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