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ORIGINAL RESEARCH ARTICLE

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Estimating impacts of the nuclear family and heritability of nutritional outcomes in a boat-dwelling community

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Abstract

Objectives: General health status is reflected in measures of height, weight, and BMI. Assessing sources of variation in these outcomes reveals population-specific variables of importance to health and nutrition. We characterize the impacts of socioeconomic variables related to the nuclear family on health outcomes of boat-dwelling Shodagor children, mothers, and fathers, and to estimate the proportion of variation in height, weight, and BMI influenced by both genetic variation and nongenetic variation among household environments.

Methods: Bayesian linear mixed models (LMMs) estimate heritability and household-effect variance components among the Shodagor. These models also assess the influences of specific socioeconomic predictor variables on different types of individuals within the household (children, mothers, and fathers).

Results: Overall, models explain 61.7% of variation in height, 59.4% in weight, and 65.8% in BMI for this sample of Shodagor. Mother's decision-making and household income have expected, positive associations with children's weight and BMI. Number of children has an unexpected positive relationship to children's height and a negative relationship to father's BMI. Genetic variation explains less than 26% of phenotypic variation for each of these traits on average.

Conclusions: Our results show that resource flows and distributions within Shodagor households account for a significant amount of variance in nutritional outcomes. Problems commonly associated with increasing market integration may lead to negative outcomes for children, while mother's autonomy may lead to positive outcomes. Our models also indicate that environmental factors account for more variation in these outcomes than expected, relative to genetics, and we discuss the implications.

1 | INTRODUCTION

General health status is reflected in measures of height, weight, and BMI, and assessing sources of variation in these outcomes reveals population-specific variables relevant to health and nutrition. This is of particular importance in societies where poor growth and health outcomes are primary concerns, such as in Bangladesh and other developing nations (e.g., Krishna, Mejia-Guevara, McGovern, Aguayo, & Subramanian, 2017), and where these issues are linked to malnutrition (de Onis et al., 2012) and chronic illness (Adair & Guilkey, 1997; Blackwell, Hayward, & Crimmins, 2001; Engeland, Bjorge, Selmer, & Tverdal, 2003). These conditions lead to increased levels of morbidity and mortality among both children and adults (Chen, Chowdhury, & Huffman, 1980; Nandy, Irving, Gordon, Subramanian, & Smith, 2005; WHO, 1995), and can lead to lowered reproductive success for adults (Blackwell et al., 2001; Martorell, Delgado, Valverde, & Klein, 1981; Sear, Allal, & Mace, 2004; Stulp, Verhulst, Pollet, & Buunk, 2012). Variation in height, weight, and BMI is influenced by a combination of genetic and environmental factors, including the amount of energy an individual consumes and the amount he or she expends. The proportions of variation in these outcomes influenced by genetics and environmental variation vary among populations, as do aspects of specific socioecology that influence how many calories come into the household, how those calories are distributed among household members, and how many calories an individual expends.

The Shodagor of Matlab, Bangladesh are a semi-nomadic community of people who live on small wooden boats, surrounded by water year-round. The Shodagor are an interesting case study for two reasons. First, they live in unique ecological circumstances that impact how resources flow into the household via parents' economic activities (Starkweather, 2017). Mothers and fathers engage in occupations that are complementary of one another and of the household's childcare needs, which are constrained by the local ecology. This results in seasonal variation in resource flow into the household and concentration of resources within the nuclear family, with sharing outside of the household rarely occurring. Also, Shodagor men's and women's occupations are associated with unusual patterns of behavior that may impact the health and nutrition of family members. Across cultures, women tend to take on work that is compatible with childcare and produces low-variance returns that are used to provision the household, while men tend to produce higher-variance returns that are shared more widely within the community (see Bliege Bird & Codding, 2015 for a review). Contrary to this trend, Shodagor women's trading is incompatible with childcare and produces higher-variance returns than men's work (Starkweather, 2016). Subsequently, many of these women's husbands spend more time in childcare than is typical for men cross-culturally (Starkweather, 2017). The second reason we examine these outcomes for the Matlab Shodagor is that no known studies on physical growth, health, or nutrition currently exist for any Shodagor or other nomadic groups in Bangladesh. Therefore, this article will be the first attempt to understand the variables that are influencing health and nutrition in this unique environment.

The purpose of this article is to parse sources of variation in health outcomes (height, weight, and BMI) by simultaneously modeling socioeconomic predictor variables and estimating heritabilities as well as the effects of shared household environments. We characterize the impacts of socioeconomic variables related to resource flows into and distributions within the nuclear family household on outcomes for Shodagor children, mothers, and fathers. Specifically, we expect variables that have been associated with these outcomes in other societies (including household income, household size, breastfeeding duration, wife's occupation, income, and autonomy) as well as socioecological variables important to Shodagor family strategies (Starkweather, 2017) to account for a substantial portion of variance in Shodagor health outcomes. We also estimate heritabilities of height, weight, and BMI using an "animal model" framework (Kruuk, 2004), incorporating complex genealogical relationships in the population to derive genetic variance components. Finally, we estimate a "household effect" variance component that captures the effects of variation between household environments on height, weight, and BMI that are not captured by the socioeconomic predictors. These results reveal the effects of genetic variation and shared household environments, and highlight socioeconomic variables of importance to health outcomes in this population. They can be used to direct future research on Shodagor health outcomes and child wellbeing as well as policy and aid campaigns focused on the Shodagor and other populations in Bangladesh.

2 | BACKGROUND

2.1 | Resource flows into the household

Food availability plays a primary role in determining how much energy is available to an individual for growth (Gunnell, Davey Smith, Ness, & Frankel, 2000; Rivera, Martorell, Ruel, Habicht, & Haas, 1995; Silventoinen, 2003). Chronic caloric deficits during childhood lead to growth stunting—or low height-for-age, which reflects a process of failure to reach linear growth potential (WHO, 1995)—while caloric deficits during adulthood and acute bouts of undernourishment during childhood are associated with low body weight relative to age (up to age 10) and height (de Onis et al., 2012). Household food supply is influenced by variables that affect the production and acquisition of resources, such as occupation or foraging strategy, income, and local ecology.

Household income has been positively correlated with child growth outcomes in a number of developing societies around the world (Black et al., 2013; Krishna et al., 2015; Mani, 2014), including Bangladesh (Foster, 1995; Perry, in press). In societies where all or the majority of food comes directly from the environment, foraging success determines the types and amounts of food people have available (Hagen, Hames, Craig, Lauer, & Price, 2001; Marlowe, 2003; Sear & Mace, 2008). In cash-based economies, the amount and types of food available to families are dependent upon household income as well as decisions regarding food expenditures (Haddad, Hoddinott, & Alderman, 1997). The Shodagor have a mixed cash-subsistence economy and diets are limited both by fishing success and household income (Starkweather, 2016). Therefore, we expect both fish availability and higher household income to have a positive impact on height for children and on weight and BMI for all family members.

Specific characteristics of local ecology also influence the amount and variety of foods available. For example, market integration is often associated with increased consumption of animal products as well as the purchase of more high-fat and high-sugar foods, all of which are linked to obesity

(Bermudez & Tucker, 2003). However, market integration may also result in access to a greater variety of micronutrients and exposure to ideas about healthy feeding practices, which can result in more optimal heights, weights, and BMIs (Blackwell, Pryor, Pozo, Tiwia, & Sugiyama, 2009). Broad ecological differences are also linked to growth as correlates of differential resource access, subsistence strategies and occupations, and pathogen exposure across cultures (Walker et al., 2006). Two salient features of the Shodagor ecology that play a role in seasonal work strategies for men and women (Starkweather, 2017) and determine both variety of food and amount of food (including fish) available are major markets and the Meghna River, respectively. We predict that living closer to a major market town and living closer to the Meghna River will both have positive effects on height for children and weight and BMI for all family members.

2.2 | Resource distribution within the household

The number of calories an individual consumes is also influenced by how resources are distributed once they reach the household. When family resources are limited, the allocation of food among individuals can be crucial to growth (Haaga & Mason, 1987). Factors like the size of the household influence the number of people among whom resources need to be divided (Downey, 1995), while parents' education (Alom, Quddus, & Islam, 2012; Semba et al., 2008) and women's autonomy within the household (Hoddinott & Haddad, 1991; Phipps & Burton, 1998) can affect how decisions are made regarding the types of food purchased and the distribution of the food to individual family members.

Generally, larger family or household sizes have a negative impact on the growth and body size of individuals. As the number of people in a family increases, resources must be spread across more people and the resources allocated per person generally decreases (Downey, 1995). This is especially true for families who are already resource-stressed, as is often the case in small-scale societies or developing nations. While there is evidence to suggest that some family members may be allocated fewer resources than others (Pitt, Rosenzweig, & Hassan, 1990) and that factors like sex (Chen, Emdadul, & D'souza, 1981), age (Hagen et al., 2001), and birth order (Aerts, Drachler, & Giugliani, 2004) can predict differential allocation, the negative relationships between household size (or number of children) and body size has been found across cultures (Forman et al., 1995; Hagen et al., 2001; Kramer, Veile, & Otarola-Castillo, 2016; Pelto et al., 1991). We predict that number of children will be associated with lower height, weight, and BMI for children and lower weight and BMI for parents.

Women's autonomy seems to influence both the types of resources brought into the household as well as distribution of resources among family members and is positively associated with child growth (Engle, 1991; Folbre, 1986; Hoddinott & Haddad, 1991; Phipps & Burton, 1998; Rouf, 2011; Reiger, 2016). Case studies across cultures have found that men, compared to women, disproportionately spend their income on goods for personal consumption while women are more likely to spend on basic family needs (Folbre, 1986; Guyer & Peters, 1987; Guyer, 1980). Also, when women have control over income, household allocations toward food, nutrition, health, and education increase (Gummerson & Schneider, 2013; Quisumbing, 2003). Income-earning and decision-making authority are two commonly used measures of female autonomy worldwide (Balk, 1997; Blumberg, Estrada de Batres, & Xuya Cuxil, 1994) and are also linked to better child growth outcomes, independent of overall household income (Engle, 1991; Folbre, 1986; Hoddinott & Haddad, 1991). Mother's education is also often used as a measure of autonomy and is associated with health-promoting childcare behaviors (Semba et al., 2008). Mother's education seems to have a similar impact on child growth, improving height (e.g., Rieger & Trommlerova, 2016; Semba et al., 2008; Thomas, Strauss, & Henriques, 1990) and BMI (e.g., Ahmed, Adams, Chowdhury, & Bhuiya, 1998), however father's education may also positively affect child growth (e.g., Alom et al., 2012). We predict that measures of female autonomy—percentage of household income and decision-making authority—as well as parents' education will have positive impacts on child height, weight, and BMI and adult weight and BMI.

2.3 | Inheritance of body size

Variation in height, weight, and BMI is known to result from a combination of genetic and environmental variation, and the proportion of phenotypic variation in these traits that can be attributed to genetic variation varies among populations, throughout the lifespan, and across growth measures (Visscher, 2008). Published studies report heritabilities that range from 60% to 90% for height (e.g., Macgregor, Cornes, Martin, & Visscher, 2006; Silventoinen, 2003; Yang et al., 2015), 40%-85% for weight (e.g., Dubois et al., 2012), and 30%-90% for BMI (e.g., Maes, Neale, & Eaves, 1997; Nan et al., 2012; Yang et al., 2015). Quantifying the proportion of variation in height, weight, and BMI attributed to genetic variation among the Shodagor is informative of the relative impacts of genetic and environmental variables on these health outcomes in this unique population.

Environmental quality should have a predictable impact on the heritability of growth (Silventoinen, 2003). Poorer-quality environments are also more variable, and there are more factors that could negatively impact growth and a higher probability that one aspect or another of the environment will affect various individuals within a population. As the environment improves and there is less variation across individuals, genetic contributions should account for relatively more variance (Hoffmann & Merila, 1999). Therefore, environmental factors may account for more variance in growth measures than genes in poorer environments (Roberts, Billewicz, & McGregor, 1978; Silventoinen, 2003). Most of the available heritability estimates for height, weight, and BMI come from the developed world (but see Luke et al., 2001; Roberts et al, 1978). A study of twin cohorts across eight affluent Western societies showed that, in general, there are only minor differences between populations in terms of how much influence genetics have on variation in height (Silventoinen et al., 2003). However, there is some evidence from the animal literature to suggest that more variability would be found in nonindustrialized societies (Charmantier & Garant, 2005).

Height, weight, and BMI are differentially susceptible to environmental influence throughout the lifespan, leading to more or less variability in additive genetic effects. Height is a long-term measure that reflects a process of additive effects throughout childhood and adolescence that are the result of continuous states of optimal or suboptimal health and/or nutritional conditions (WHO, 1995). Growth in height is generally finished for all individuals by the age of 19 (de Onis et al., 2007), although boys may grow slower and for a longer amount of time under poor conditions, but stunting in growth can occur due to acute bouts of poor health or malnutrition at any time during childhood. While catch-up growth may occur once the cause for stunting is removed, if the cause becomes chronic, short stature will result and cannot be reversed once a child reaches puberty (Prader, 1978).

In as much as weight is strongly correlated with height, it may serve as a general reflection of the past growth of an individual. However, since it also reflects changes in body mass, this measure also reflects recent and concurrent health and nutritional status (WHO, 1995). Weight can be a complex trait to interpret because, for example, low body weight-for-age measures fail to distinguish between short people of adequate body weight and tall, thin people (WHO, 1995). However, by nature of its components, weight is more susceptible to environmental influences throughout the lifespan than height.

Unlike independent measures of height and weight, changes in BMI primarily indicate short-term nutritional fluctuations (Rahman, Chowdhury, & Hossain, 2009), and should be more sensitive to environmental changes than either height or weight, particularly for adults. Cross-cultural heritability estimates that range from 30% to 90% reflect the nature of this measure (e.g., Maes et al., 1997; Nan et al., 2012; Yang et al., 2015). We expect genes to explain the most variance in height given its additive nature and relatively low response to short-term environmental fluctuations. Weight and BMI should have lower heritability estimates due to the flexibility of these traits in their ability to respond to changes in the environment.

3 | METHODS

3.1 | Study population

The Shodagor are a culturally-distinct ethnic group living on the rivers and canals in Matlab, Bangladesh (Figure 1). Matlab is a mostly rural subdistrict, located within Chandpur District, approximately 59 km southeast of the capitol city of Dhaka. Matlab consists of a few small towns and approximately one hundred forty villages and is home to approximately 200 000

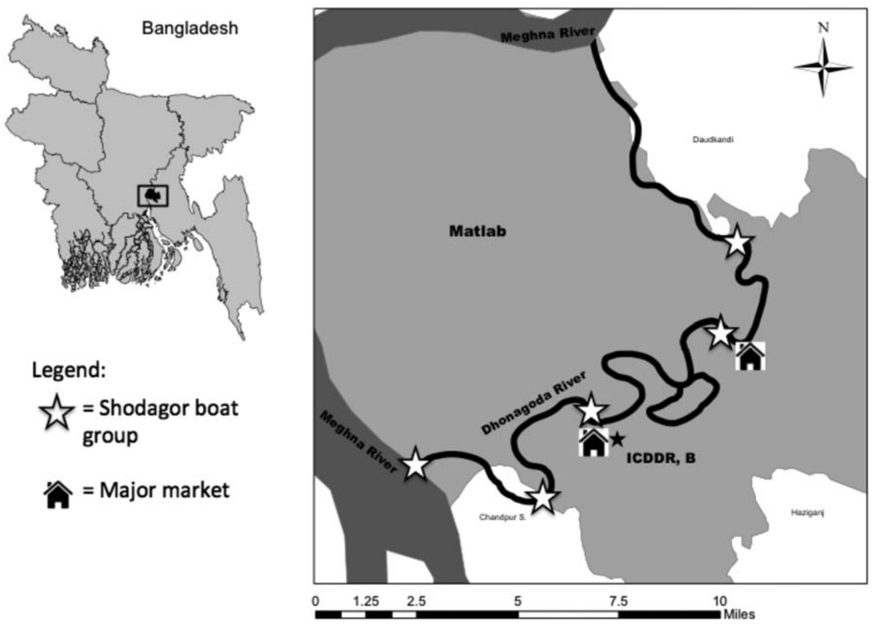

FIGURE 1 Map of Matlab, Bangladesh with stars indicating locations of 5 Shodagor bohor

people (Bangladesh Bureau of Statistics, 2010; ICDDR, B, 2014). Shodagor people live in 5 distinct groups in Matlab with group sizes ranging from 8 to 32 households (boats). Nearly all (90%) Shodagor men in Matlab fish as their primary occupation. Shodagor women either fish with their husbands (31%), work as traders, selling household goods door-to-door in the villages (44%), or stay home as housewives (25%). Some men and women change occupations seasonally as fishing becomes more profitable throughout Matlab during the rainy season, and trading is often only possible during the dry season. These occupations lead to a mixed economy in which families who fish often eat some of their catch and sell the rest for cash, and women trade goods for cash. The Shodagor diet is not only heavily reliant on fish, but also consists of rice, lentils (*daal*), and occasionally vegetables, chicken, beef, and processed market foods.

3.2 | Data collection

Interview and anthropometric data were collected over 9 months in 2014, resulting in an almost complete population sample of Matlab Shodagor. All data were collected in accordance with procedures approved by the University of Missouri's Institutional Review Board as well as the Ethical Review Committee at the International Centre for Diarrhoeal Disease Research, Bangladesh (ICDDR, B). This study includes data on 90 children from birth to age 18 as well as 36 fathers and 42 mothers for whom there were no missing data, and these individuals belong to a total of 56 households.

Anthropometric data was gathered from adults and children once during the dry season and once during the rainy season. All individuals who could stand upright independently stood on a flat surface and were measured to the nearest 0.1 cm by stretching a tape measurer from crown to the ground. Children who were unable to stand upright independently were laid on a flat surface and measured to the nearest 0.1 cm by stretching a tape measurer from heel to crown. Weights to the nearest 0.1 kg were collected using an electronic scale on a firm, flat surface. If children were too young to be weighed independently, they were weighed with their mother, whose weight was then subtracted from the combined total. Measures presented are cross-sectional.

3.3 | Analysis

We investigated heritable, environmental household, and socioecological sources of variation in health outcomes (height (cm), weight (kg), and BMI) among the Shodagor using linear mixed models (LMMs). These enabled us to estimate genetic variance components (heritabilities) as well as household effect variance components that capture household-level environmental variation. Teasing apart genetic from environmental effects can be challenging, particularly when related individuals also share an environment. Using an "animal model" framework allows us to quantify the effects of genetic variation on height, weight, and BMI for the Shodagor using complex genealogical relationships. This form of mixed model was first developed by quantitative geneticists and used for plant and animal breeding in which the explanatory terms are a mixture of fixed effects (such as age, sex) and the random effect of the genetic values of individual animals (Kruuk, 2004). This model makes use of unbalanced pedigrees (such as those found in nature rather than laboratories) and estimates genetic breeding values for trait outcomes based on proportions of shared genes between individuals in the pedigree. These breeding values are modeled as a random effect since they are inherently nonindependent (shared genes), and the variance components derived from these models measure the amount of variation in an outcome variable that is explained by that nonindependence (in this case, shared genes). Although our genealogy is limited to three generations (Table 1), this method utilizes all types of relationships among individuals, including parents, offspring, siblings, half-siblings, cousins, and so forth. Therefore, these heritability estimates are based on more complex genealogical relationships than those resulting from standard single-parent offspring regressions (or other comparable methods). There are 227 individuals in the

TABLE 1 Descriptive genealogy statistics from Pedantics (Morrissey, 2014)

Individuals	227
Maternities	222
Paternities	222
Full sibs	564
Maternal sibs	6291
Maternal half sibs	651
Paternal sibs	7214
Paternal half sibs	1574
Maternal grandmothers	107
Maternal grandfathers	107
Paternal grandmothers	99
Paternal grandfathers	99
Maximum pedigree depth	3
Mean pairwise relatedness	0.038

Values represent total relationship counts for the 227 individuals in the genealogy. For example, there are a total of 564 full sibling pairs among these 227 individuals, and so forth.

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genealogy used for deriving heritability estimates (Table 1). One hundred sisty-eight individuals were retained in the final phenotypic dataset used for running LMMs, representing 90 children, 36 fathers, and 42 mothers from 56 households. We estimate heritabilities using this model framework while also including another random effect for shared household environments to understand how much of an impact household-level environmental factors and genetic variation each have on Shodagor height, weight, and BMI. These mixed models also enable us to more precisely estimate the impacts of specific socioeconomic predictors on health outcomes by modeling these predictors and genetic/environmental random effects simultaneously, reducing confounding influences of shared genes and household environments.

Each LMM had 9 fixed effects (socioeconomic variables) and 2 random effects: one for each individual's identity within the genealogy (to produce heritability estimates) and another for household identity. Markov chain Monte Carlo (MCMC) simulations of LMMs produced variance component posterior distributions of heritabilities and household effects, as well as regression coefficient posterior distributions for the socioeconomic predictors in each model. We modeled height, weight, and BMI outcomes for Shodagor children as well as their parents, including interaction effects for each predictor variable with a factor level variable specifying individual type (child, mother, or father). Results from these analyzes are informative as to which predictor variables are relevant to health outcomes in this population, how those socioeconomic variables influence different members of the population (i.e., how each predictor influences each outcome for children, mothers, and fathers), and the extent to which heritable variation and variation in household environments contributes to the variation in height, weight, and BMI in this population.

Body mass index (BMI) was calculated using the igrowup package (WHO, 2007) for children ages 0–5 years and the WHO 2007 reference tables for children ages 5–19

TABLE 2 Descriptive statistics for age, height, weight, and BMI among Shodagor adults (age > 19 years)

	Min	Q1	Median	Q3	Max	Mean	SD
Males (n = 36)							
Age (year)	20.0	27.0	34.5	45.0	70.0	36.9	12.9
Height (cm)	148.0	154.0	159.0	162.0	172.0	158.8	5.6
Weight (kg)	33.6	44.7	50.9	56.5	69.6	50.5	9.0
BMI	12.8	17.5	20.0	22.2	30.5	20.1	4.0
Females (n=36)							
Age (year)	20.0	22.8	29.0	37.0	49.0	30.6	8.2
Height (cm)	132.0	141.0	145.5	147.9	163.0	146.1	6.9
Weight (kg)	27.7	40.7	47.8	55.5	72.1	48.4	11.1
BMI	12.8	18.8	22.2	24.9	33.1	22.2	4.9

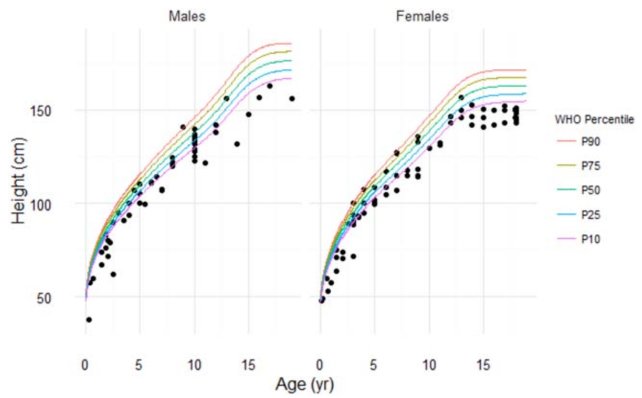

FIGURE 2 Height-for-age of children, mothers, and fathers (top panels, n = 168) and z-scored residuals from LMS curves used as outcomes in LMMs (bottom panels). Age was truncated at 30 years prior to transformation

years (de Onis et al., 2007) in R v. 3.3.1 (R Core Team, 2016). Adult BMI was calculated using the standard BMI equation (height (kg)/weight (m)^2). Outliers were removed following visual inspection of data points that were flagged implausible by WHO cutoffs (± 6 standard deviations). Height (cm), weight (kg), and BMI were transformed to account for changing means and variances across age using Lambda-Mu-Sigma (LMS) curves. LMS curves provide normalized centile standards for this population from which to calculate z-scores for all children and adults. LMS curves are often used to produce growth curves when repeated measures are available for a set of individuals (Cole, 1990), and they also allow us to obtain centile standards for the Shodagor using cross-sectional data by fitting curves through trends in the trait means and variances across age. We fit LMS curves to each outcome variable separately for males and females, accounting for both the effects of sex and age on the outcome variables (Figures 2–4) (Cole, 1990). To maintain reliable fit of LMS curves at older ages with few data points, we truncated age for the height variable at 30 years in a

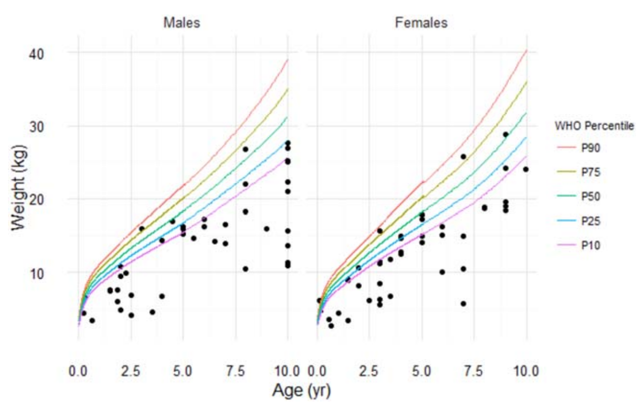

FIGURE 3 Weight-for-age of children, mothers, and fathers (top panels, n = 168) and zscored residuals from LMS curves used as outcomes in LMMs (bottom panels). Age was truncated at 50 years prior to transformation

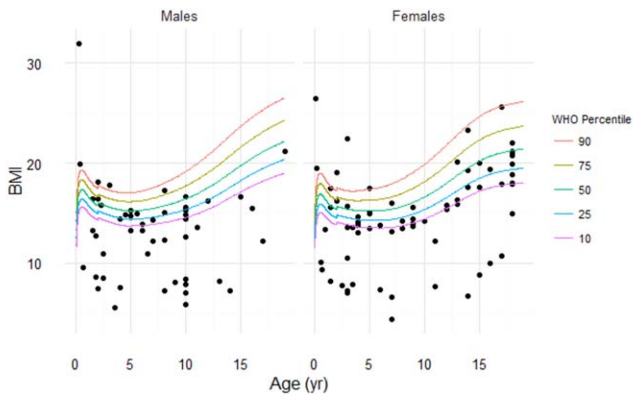

FIGURE 4 BMI-for-age of children, mothers, and fathers (top panels, $n = 168$) and zscored residuals from LMS curves used as outcomes in LMMs (bottom panels). Age was truncated at 50 years prior to transformation

winsorized fashion. Age was truncated at 50 years for weight and BMI. We fit LMS curves across ages 0–30 years for height, and 0–50 years for weight and BMI within sex using the GAMLSS package in R (Rigby & Stasinopoulos, 2005). We then z-scored the residuals of each outcome variable from its respective LMS curve to account for the effects of age and sex on height, weight, and BMI. These z-scores were then used as the outcome variables in the LMMs, eliminating the need to include age and sex as fixed effects.

We assessed the impacts of 9 household-level socioeconomic variables (fixed effects) on height, weight, and BMI in children, mothers, and fathers: household income, access to fish, an interaction between income and fish access, travel time to the market, distance to the Meghna River, number of children, wife's income percentage, wife's decision-making authority, and parental education (Table 3). Household income, a measure of annual income, was log-transformed. Access to fish is a categorical variable indicating whether at least one member of a household fishes none of the year, half of the year, or all year. An interaction between household income and fish access was also included to reflect the importance of both in a mixed cash-subsistence economy. We believe that the interaction of these 2 variables more accurately reflects differences in resource flow into households than either measures on its own. Time to market reflects the number of minutes required to travel from the center of each Shodagor group to a major market in the village, while distance to Meghna is the number of kilometers from the center of each group to the confluence of the Meghna River. Number of children refers to the total number of individuals under age 18 living in each person's household. Wife's income percentage reflects the percentage of a household's annual income earned by the wife. Wife's decision-making and parental education are dummy variables for each household, indicating whether or not wives have any decision-making authority in the household and whether either parent has any education. All variables were standardized prior to running LMMs.

We ran three LMMs with the LMS z-scores of height, weight, and BMI as the outcome variables, fixed effects detailed above, and 2 random effects: an estimated genetic effect and household-level environmental effect for each model. These random effects produced variance components, capturing any variation in the outcome variables that can be attributed to shared genes among relatives represented by relatedness among individuals in the genealogy and by variation between nuclear family household environments respectively. Equation 1 shows the general LMM in matrix form.

TABLE 3 Summary statistics for predictor variables ($n = 168$)

	Mean	**SD**	**Min**	**Max**
Wife's income %	39.80	29.37	0.00	100.00
Time to market (min)	30.06	38.21	5.00	120.00
Distance to Meghna (km)	6.64	4.52	0.50	19.38
Raw income	148469.80	104101.80	31257.04	420836.64
Number of children	4.13	2.58	1.00	9.00
	None	**Some**		
Wife's authority	36	132		
Parental education	139	29		
	None	**Half year**	**All year**	
Fish access	6	57	105	

All predictors are household-level variables, but are matched to individual outcomes in our mixed models; thus, reported statistics summarize these household-level predictors for all 168 individuals included in our analysis.

$$y = X\beta + Z_1u_1 + Z_2u_2 + e \tag{1}$$

y is the nx1 vector of the outcome variable (z-scores of height, weight, or BMI). X is an nxp matrix of the p fixed effects (9 socioeconomic variables) that associates height, weight, or BMI z-scores with the predictors, and β is a px1 vector of fixed effect regression coefficients. Each Z is a random effect design matrix with u as the vector of solutions for the impact of shared genes (breeding values) or household environments, and e is the residual error (Kruuk, 2004).

We ran MCMC simulations of all LMMs using the MCMCglmm package in R (Hadfield, 2010) to sample posterior distributions of genetic and household environment variance components and fixed effect results. MCMC simulations ran for 10 500 000 iterations with a burn-in of 500 000 and thin of 10 000 to retain 1000 samples from the posteriors. We used parameter expanded priors for all models to facilitate chain mixing by setting prior means to 0 (alpha. mu = 0) and prior covariance matrices to 1000 (alpha. V = 1000). Variance component distributions were used to calculate heritability ratios and household effect ratios that represent the proportion of variation in each outcome variable attributed to genetic variation (Equation 2), and proportion of variation in each outcome attributed to variation between households (Equation 3) .

$$h^2 = \frac{V_a}{V_a + V_c + V_e} \tag{2}$$

$$c = \frac{Vc}{V_a + V_c + V_e} \tag{3}$$

V_a is the vector of 1000 retained genetic effect variance components, V_c is the vector of household effect variance components, and V_e is the vector of residuals. This produced distributions of 1000 variance component ratios for each

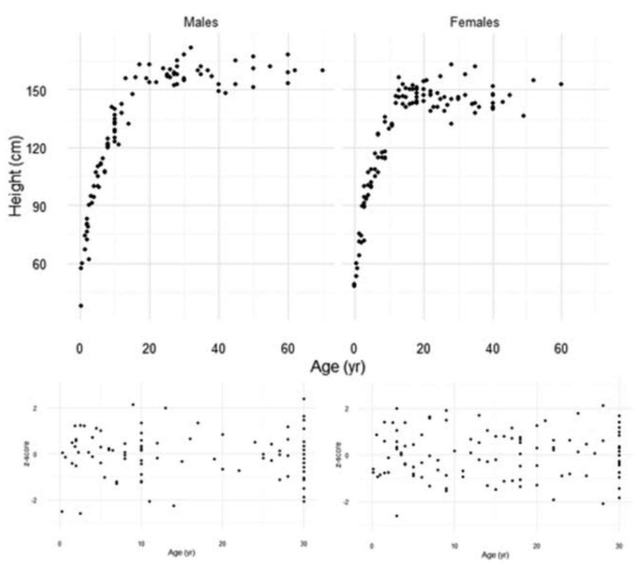

FIGURE 5 Height-for-age of 121 Shodagor children ages 0–19 years plotted with WHO percentiles for comparison (de Onis et al., 2007)

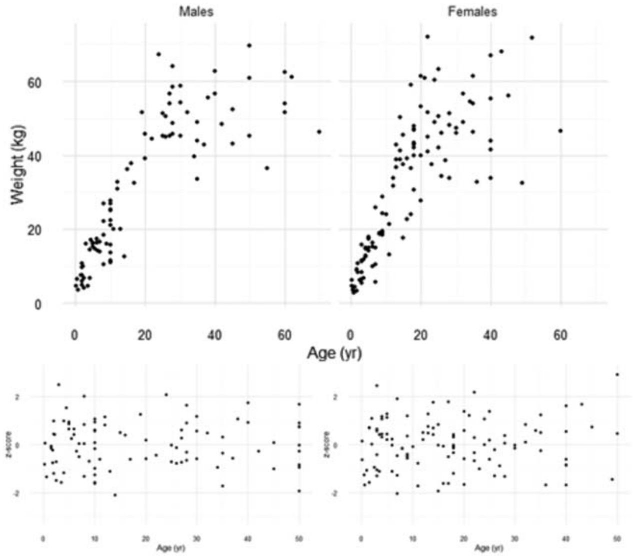

FIGURE 6 Weight-for-age of 85 Shodagor children ages 0–10 years plotted with WHO percentiles for comparison (de Onis et al., 2007)

random effect. Fixed effect coefficients produced results that show the impact of each predictor (standardized beta coefficients) on the respective outcome variable for each type of individual in the population (children, mothers, and fathers) by including interaction terms for "type" of individual with each fixed effect within the LMMs. We retained 1000 samples from these beta coefficient posterior distributions as well. MCMCglmm reported betas using type "child" as a reference category, so beta values for mothers and fathers were added to these reference distributions, and reported posterior modes and credible intervals were subsequently calculated from these distributions of 1000 samples for each individual type. Heritability and household effect estimates reflect population-wide variation for each trait (they are not specific to the "type" of individual). (R code available at https://github.com/mhkeith/AJHB_StarkweatherKeith18#ajhb_starkweatherkeith18).

4 | RESULTS

Shodagor children appear to be small relative to global populations when their height and weight is plotted with WHO percentiles (Figures 5 and 6). BMI looks to be more variable than height or weight among Shodagor children, with some overlapping WHO centiles but many falling far below global BMI-for-age measures (Figure 7). These trends are common for small-scale populations and those from the developing world (e.g., Blackwell et al., 2017; Spencer et al., 2017; Urlacher et al., 2016). Health outcomes in this population show predictable height patterns across age, with increasing variance at later ages when individuals reach adult height (Figure 2). Weight shows more variation across all ages compared to height, particularly for adults over 30 (Figure 3). Weight also appears to show more variance among females

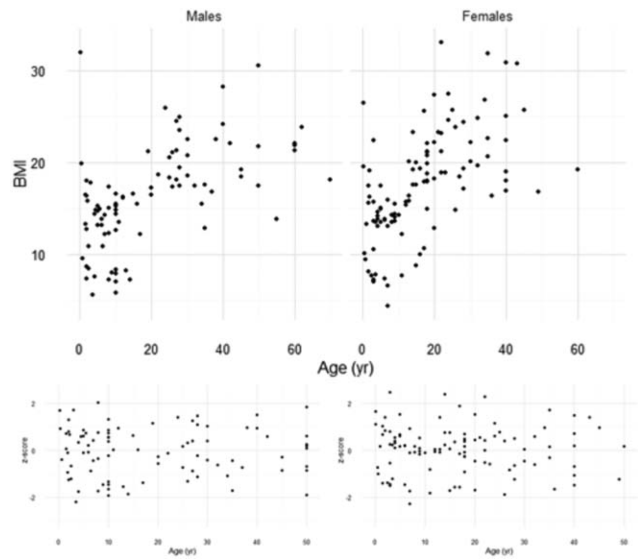

FIGURE 7 BMI-for-age of 122 Shodagor children ages 0–19 years plotted with WHO percentiles for comparison (de Onis et al., 2007)

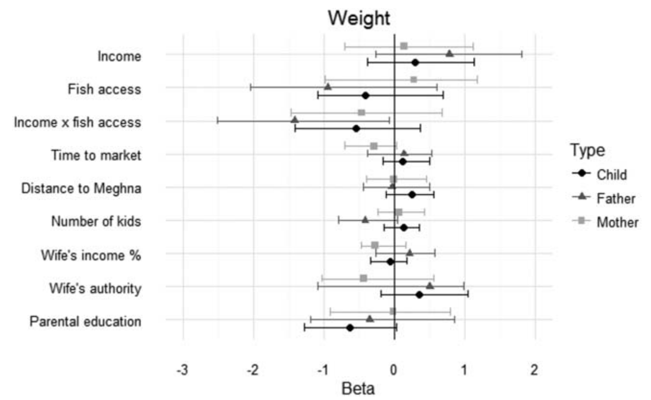

FIGURE 9 Posterior modes and 90% credible intervals summarize 1000 retained beta samples for the weight model predictors, showing the relationship of each variable with weight for children, mothers, and fathers in the population

than males, particularly at younger ages. BMI displays the most variation in young children, as we would expect from such a composite measure, and continues to exhibit relatively large variance across all ages, but fewer adults over age 20 have very low BMI compared with children (Figure 4). Stunting may produce higher BMI measures in individuals who have experienced malnutrition earlier in life but then gain access to adequate nutrition such that weight increases but height does not in older individuals.

The effects of 9 household-level socioeconomic variables were partitioned by individual type, revealing their differential impacts on children, mothers, and fathers in this population. The beta coefficients for these fixed effects are independent of any confounding genetic or other household environmental influence because genetic variance and household-level environmental variance are simultaneously modeled as random effects in these LMMs. Figures 8–10 show posterior modes and 90% credible intervals from each posterior distribution of beta coefficients. These standardized coefficients measure change in standard deviation units in the outcome variables such that a beta of 1.0 indicates that an increase of 1 standard deviation in a predictor variable results in a 1 standard deviation increase in the outcome. 90% credible intervals capture the range of 900 out of 1000 samples from each posterior distribution, revealing beta coefficient trends for each predictor in this population.

Income and fish access independently show negative associations with child height, while the interaction between the two has a positive association with child height (Figure 8). Number of children also has a positive relationship with child height. Travel time to the market and distance from the Meghna River both have negative relationships with child height, indicating that children who live closer to a market or the river grow taller. In each of these cases, the credible intervals span zero, indicating that the direction of the relationship is not always consistent. However, the majority of the posteriors lie in the indicated directions, therefore, we

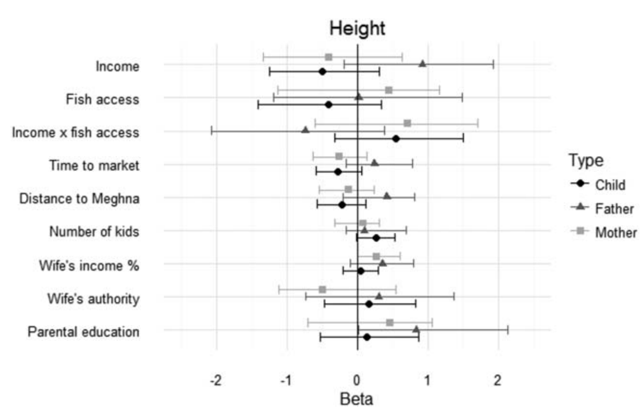

FIGURE 8 Posterior modes and 90% credible intervals summarize 1000 retained beta samples for the height model predictors, showing the relationship of each variable with height for children, fathers, and mothers in the population

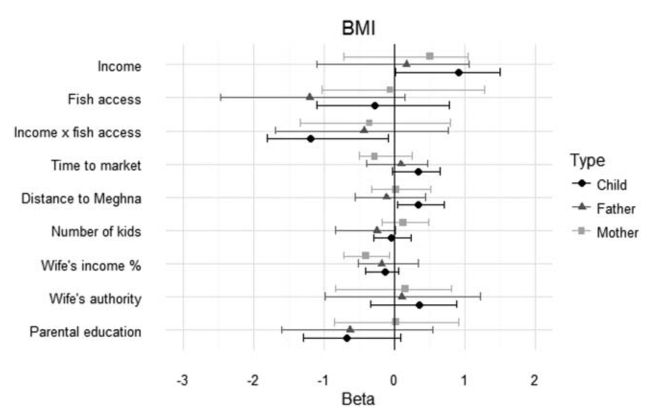

FIGURE 10 Posterior modes and 90% credible intervals summarize 1000 retained beta samples for the BMI model predictors, showing the relationship of each variable with BMI for children, mothers, and fathers in the population

TABLE 4 Variance component posterior modes with 90% credible intervals (V_A and V_C), variance component ratio posterior modes with 90% credible intervals (Heritability and Household Effect), and fit statistics from MCMC models

	Height	Weight	BMI
V_A	0.521 (0.112, 0.965)	0.450 (0.082, 0.821)	0.379 (0.098, 0.683)
Heritability	0.258 (0.091, 0.551)	0.218 (0.087, 0.506)	0.172 (0.078, 0.436)
V_C	0.271 (0.095, 0.461)	0.309 (0.111, 0.514)	0.377 (0.149, 0.587)
Household Effect	0.159 (0.066, 0.300)	0.166 (0.069, 0.329)	0.267 (0.115, 0.391)
R^2_m	0.202 (0.133, 0.280)	0.201 (0.139, 0.276)	0.214 (0.145, 0.291)
R^2_c	0.617 (0.463, 0.773)	0.594 (0.477, 0.766)	0.658 (0.491, 0.745)

Heritabilities represent the proportion of variation in each outcome variable explained by relatedness among individuals. Household effects represent the proportion of variation in each outcome variable explained by nongenetic similarities within households (shared environment). R^2_m measures the proportion of variation explained by only the fixed effects of each model, and R^2_c is that explained by both the model fixed and random effects.

can be reasonably confident in our interpretations of these trends. Height is also positively associated with parents' education for fathers, but this relationship is unlikely to be informative of the current environment. Marginal R^2 values indicate that all of the fixed effect socioeconomic variables account for approximately 20.2% of the variation in height among the Shodagor, and between 13.3% and 28.0% of the variation in 90% of cases (Table 4) (Nakagawa & Scheilzeth, 2013). Random effect results reveal an overall heritability of 25.8% and household environmental effect of 15.9% for height in this population (Table 4). Credible intervals for both heritability and household effect span wide 90% ranges (0.091-0.551 and 0.066-0.300 respectively), indicating that there is considerable variability in these effects among the Shodagor, although large credible intervals are also likely a result of the small size of this population for these quantitative genetic analyzes. Together, all modeled fixed and random effects explain approximately 61.7% of the total variation in height (Table 4), as measured by the conditional R^2 distribution (Nakagawa & Scheilzeth, 2013).

Unexpectedly, time to market and distance to the Meghna show a positive relationship with weight among children, indicating that children who live closer to a market or the river weigh less. However, time to market has a negative relationship with mothers' weight, indicating that mothers who live closer to a market weigh more, as expected. The interaction between income and fish access is associated with lower weights for children while mother's decision-making authority and household income show positive relationships between weight in children and fathers, respectively (Figure 9). Variation in weight appears to be slightly less heritable than height (21.8%), and household environments account for between 6.9% and 32.9% of weight variation for 90% of this population (Table 4). Socioeconomic predictors account for approximately 20.1% of the variation in weight on their own, and the combination of modeled fixed and random effects explains 59.4% of the variation in this outcome (Table 4).

Increases in income percentage earned by women result in consistently decreased BMI for women and their children, but not for fathers (Figure 10). This relationship for women is probably due to a positive association between women's income percentage and their height. More access to fish and a higher number of children are associated with lower BMI for fathers, but not mothers or children. Again, these relationships likely reflect the fact that fathers in families with more fish access and more children are also taller. Household income and mother's decision-making authority result in higher BMIs for children, while parents' education, higher interaction between income and fish, and living closer to a market or the Meghna River are associated with lower BMIs for children. BMI shows the lowest heritability of any outcome variable (between 7.8% and 43.6%), and variation among household environments accounts for between 11.5% and 39.1% of BMI variation. Socioeconomic predictors explain between 14.5% and 29.1% of this outcome, and a combination of the predictors, genetic variation, and household environments accounts for 49.1%-74.5% of observed variation in BMI for 90% of this population (Table 4).

5 | DISCUSSION

The purpose of this article was two-fold. First, we aimed to tease apart the impacts of genes, shared household environments, and predictor variables related to resource flows and distributions within the household in regard to height, weight, and BMI among the Shodagor of Matlab, Bangladesh. Second, we sought to understand the differential impact of those predictor variables on these outcomes among mothers, fathers, and children. We expected measures of mother's autonomy, ecological features, and measures of household income to have positive relationships with nutritional outcomes for all family members, and the number of children in a household to have a negative relationship with nutritional outcomes. We also expected heritability estimates to be low, and environmental factors captured in the random effect of shared households as well as the fixed effects to explain the majority of variation in these nutritional outcome variables.

Our results indicate that factors influencing the flow of resources into a household and the distribution of those resources among household members have complex relationships to nutritional outcomes for children and their parents. These complexities are not unusual given the plasticity of human growth and the variety of social and ecological factors that can influence it (Bogin, 1999; Bogin & Loucky, 1997; Godoy et al., 2008; Schell & Knutsen, 2002), and call for more detailed studies of the influence of behavior and the environment on Shodagor health and nutrition.

6 | CHILD OUTCOMES

6.1 | Measures of women's autonomy

One of the most interesting aspects of the Shodagor socioecology is the apparent sex-role reversal that some women and men display in economic and parenting behaviors. Due in large part to women's role within the household economy, many of the commonly-used measures of female autonomy apply to Shodagor women, such as income-earning, working outside the home, and decision-making authority. A robust literature shows positive associations between measures of women's autonomy and health outcomes for children (Engle, 1991; Folbre, 1986; Hoddinott & Haddad, 1991; Phipps & Burton, 1998; Rouf, 2011; Reiger, 2016). Therefore, we expected measures of Shodagor women's autonomy to be important predictors of positive height, weight, and BMI outcomes for children.

Our results suggest a weaker relationship than expected. While wife's decision-making authority within the household associates with positive nutritional outcomes for Shodagor children, neither the percentage of household income earned by the woman nor parents' education show such a relationship. Increasing the percentage of household income made by women also increases the proportion of the household budget spent on food and is associated with better nutritional outcomes for children in Cote d'Ivoire (Hoddinott & Haddad, 1991), Canada (Phipps & Burton, 1998), Guatemala (Engle, 1991), and Bangladesh (Rouf, 2011). However, this may not be a salient measure of autonomy in cases where women have traditionally been independent income-earners, as Shodagor women report. It may also be the case that when women earn a very high percentage of the household income, this is indicative of female-headed households or single-earner households, both of which could be linked to lower total household incomes and negative health and nutritional outcomes for children (e.g., Johnson & Rogers, 1993), particularly given the negative relationship between a mother's percentage of income earned and her own BMI as well as the positive relationship between household income and nutritional outcomes for children among the Shodagor. These results indicate that a mother's role in household decisions—and not her income or education—and overall household income are important for the nutritional well-being of Shodagor children, and future research should examine the mechanism that drives these relationships.

6.2 | Income, fish access, and ecology: Activity levels, over-nutrition, or food insecurity?

In cash economies, income is an important determinant of dietary intake and has been linked to positive growth outcomes in a number of societies (Black et al., 2013; Krishna et al., 2015; Mani, 2014). However, in mixed economies that rely on income and subsistence goods, as the Shodagor do, both should contribute to variation in height, weight, and BMI within the population. Therefore, we expected individuals in households with higher incomes and with more access to fish to be taller (children), weigh more, and have higher BMIs. Although higher income is independently related to higher weights and BMIs in fathers and children, respectively, other results suggest the relationships between these variables are more complex than expected. In families with more access to fish (indicating that at least one person in the household fishes on a regular basis) and higher incomes, children are taller and therefore less likely to be stunted than other children. However, children also have lower BMIs, indicating that they are thinner than other children. One potential explanation for this relationship is that children in families with fish access may have higher activity levels because they are fishing with their parents. In this case, children are receiving adequate nutrition to support linear growth, but not to accumulate excess body mass.

The relationship can also be reframed: in families with no fish access (and regardless of income, by nature of the calculation of the interaction term), children are shorter and also heavier than their counterparts with fish access. This indicates a different possible explanation, which is that stunting and overweight are co-occurring in children with no fish access because they eat more market foods, which tend to be high in saturated fats and sugars (e.g., Da Silva & Begossi, 2009; Popkin & Gordon-Larsen, 2004). In low-income or developing parts of the world, increased consumption of market foods can result in intake of both insufficient nutrition and excess calories—often called "over-nutrition" (Doak et al., 2000; Eckholm & Record, 1976)—and can lead to simultaneous stunting and overweight (e.g., Popkin et al., 1996; Tzioumis & Adair, 2014). This relationship has also been demonstrated in Timor-Leste, though rather than market food, seasonal food insecurity is likely influencing outcomes (Judge, Sanders, Reghupathy, Amaral, & Schmitt, 2012). Shodagor children in households without access to fish may also have high levels of food insecurity, leading to a combination of stunting and overweight (e.g., Mahmudiono et al., 2016; Tanumihardjo, 2007).

While further examination of Shodagor children's diet and activity levels is necessary to determine the pathway between income, fish access, and nutritional outcomes, these scenarios offer potential explanatory power for similar relationships between the important ecological variables for the Shodagor—time to market and distance to the Meghna River—and children's nutritional outcomes. Children who live closer to a market and those who live closer to the Meghna tend to be taller and have lower BMIs. In both cases, adequate nutrition and higher activity levels could explain the relationship. Families who live closer to the Meghna River are more likely to take children along when they fish (Starkweather, 2017). Observational data suggest that living closer to a market may result in children spending more time on land as children often accompany parents to the market or to visit nearby friends or family members who live on the land. Inadequate nutrition may also be driving this relationship, but the source of inadequacy is unlikely to be market foods, given the direction of the relationship. Rather, food insecurity is more likely for Shodagor living farther from the Meghna as well as those living farther from a major market. Detailed data on activity levels, food insecurity, and nutritional intake would inform these relationships in a meaningful way and help determine the primary risk factors for childhood nutritional challenges among the Shodagor.

7 | PARENT OUTCOMES

7.1 | Fathers take the nutritional hit?

Outcomes for Shodagor parents mostly followed expected patterns or have clear explanations. Mothers who live closer to a market as well as fathers in families with higher incomes weigh more. Fathers with higher fish access (indicating that they fish year-round) have lower BMIs than fathers without, likely due to higher activity levels associated with more work. Mothers who earn a higher percent of the household income have lower BMIs, due to being taller but weighing less than mothers who earn a lower percent of household income. Lower body mass for these mothers may also reflect an association between earning a higher percent of the household income and more hours of work.

One of the more surprising results from our analyzes is the relationship between fathers' BMI and a family's number of children. Our results indicate that fathers in families with more children are taller, but also weigh less than fathers in families with fewer children. Given the link between maternal and child health and nutritional outcomes (e.g., Black et al., 2008) and the fact that mothers are more likely to spend money on improvements for child health and nutrition while fathers are more likely to spend on personal gains (Hoddinott & Haddad, 1991), we might expect that mothers should also be more likely than fathers to show lower body mass when a household has more individuals to divide resources among. However, neither Shodagor mothers nor children show similar negative effects of higher numbers of children. In fact, there is a small, but positive, effect of this variable on children's height. These results indicate a possibility that children benefit from having more siblings at their fathers' expense: that resources are distributed toward children and away from fathers. Unusually high levels of parenting effort demonstrated by some Shodagor fathers bolster the plausibility of this connection, although it is also possible that the effect of number of children on fathers and children are independent of one another or due to some unknown mediating variable. These findings call for detailed examination of resource distribution within the household, including an investigation into the different outcomes based on who makes decisions about distributions.

7.2 | Genetic and household-level environmental effects

Our dataset includes a number of sibling sets, many of whom lived in the same household the year this study was conducted. The random effect of the household accounts for the similarities that siblings and their parents experience within shared household environments (including maternal effects) and illuminates between-household differences in environmental and behavioral factors. This is independent of variation due to shared genes among relatives, which was also modeled as a random effect. Diet and activity level are two primary environmental drivers of body size (e.g., Gunnell et al., 2000; Rivera et al., 1995; Silventoinen, 2003), as have been discussed, and are likely underlying between-household variation for Shodagor children. While activity levels among individuals in the same household may correlate in certain circumstances, such as when entire families fish together year-round (Starkweather, 2017), diet is very likely to covary among household members and we might expect between-household variation in diet to be a primary force driving variation in height, weight, and BMI. Illness also affects growth outcomes in human populations (e.g., Adair & Guilkey, 1997; Silventoinen, 2003), and may cluster at the household level for the Shodagor in cases where the illness is communicable or where it is associated with a common environmental factor, such as water contamination—a major risk factor in Bangladesh (e.g., Rahman, Vahter, Ekstrom, & Persson, 2011).

Heritability estimates for height, weight, and BMI among the Shodagor are low relative to most published estimates from other populations, which typically range from 60% to 90% for height, 40% to 85% for weight, and 30% to 90% for BMI. The estimates for this dataset of the Matlab Shodagor fall at 25% or below for each outcome, though as expected, shared genes have the greatest explanatory power for height and less for weight or BMI. One major limitation to understanding variation in genetic influence on body size is that the majority of studies conducted so far have focused on Western or developed populations (see Min, Chiu, & Wang, 2013; Silventoinen, 2003 for reviews), though there are a few exceptions (e.g., Luke et al., 2001). This is relevant because in populations where environmental conditions are similar for most individuals, heritability estimates will be higher because the majority of phenotypic variation will be due to genetic differences (Charmantier & Garant, 2005). Given what we expect to be a poor environment for the Shodagor (compared to those in the developed world), it is not surprising that genetic variation accounts for less variation in height, weight, and BMI (or, put another way, that environmental differences account for more variation), but it is unknown whether other small-scale societies in more variable environments would show similar estimates or not. It may also be the case that the nature of this model in which we estimate variance due to shared genes simultaneously with shared environment and a set of predictor variables accounts for the low rates at which genes account for phenotypic variation.

8 | CONCLUSIONS

Overall, these analyzes account for more than 60% of the variation in height, weight, and BMI for the Matlab Shodagor in 2014. Using a multilevel model to determine the amount of variance that is attributable to shared genes, shared household environments, and individual predictor variables allows us to parse these effects and gain a more holistic understanding of the impacts each has on indicators of health and nutrition. Our results show that a wife's decision-making authority in the household, but not the percentage of household income she earns or her (or her spouse's) education, is related to positive outcomes for children's weight and BMI. Results also suggest a complex relationship between income, ecological variables, and child outcomes: the two key features of the ecology that drive Shodagor parenting and economic decisions (Starkweather, 2017) are associated with greater height, but lower weight and BMI for children. The same is true for the interaction of household income and fish access. Activity levels may be driving these outcomes in children, as appears to be the case for fathers. It is also likely that either over-nutrition or food insecurity (or both) are the culprits. Diets with high caloric but low nutritional value are of major concern in the developing world as people transition into consuming more market goods and could present health challenges for the Shodagor.

This study faces a few limitations. First, the cross-sectional nature of these data means that we are unable to address trends in growth within the society. This also results in a relatively small sample size. Data were collected on all available individual Shodagor people in Matlab, resulting in a nearly complete population sample. While a full population sample is beneficial in many ways, collecting anthropometric measures longitudinally will provide more information about Shodagor growth in general as well as the factors that influence it. Second, the use of a tape measurer to measure height may have introduced some error, relative to a more accurate instrument. Finally, this study is lacking empirical data on diet or nutritional intake. Access to fish is the only current measure of Shodagor nutrition we have, and we are unable to make specific inferences about how much fish is consumed.

In future research, activity level should be considered in terms of the difference it may have on short-term measures of weight and BMI compared to the long-term measure of height. Seasonal differences in nutritional intake and activity level are also important to characterize in light of major changes in the local environment that are correlated with changes in mothers' and fathers' occupations and parenting strategies (Starkweather, 2017). Finally, a more detailed study of women's autonomy and subsequent behaviors of fathers as they relate to acquisition and distribution of resources among household members could elucidate the roles of mothers and fathers in influencing health and nutrition outcomes for themselves and their children.

Bangladesh is a concentrated point of focus for governmental, nongovernmental, and nonprofit research and interventions that target maternal and child health and nutrition. This study shows that Shodagor behaviors within the household account for a large portion of variation in nutritional outcomes, and that problems commonly associated with increasing market integration, such as over-nutrition and food insecurity, may lead to negative outcomes for children. It also indicates that environmental factors account for more of the variation in these outcomes than expected, relative to genetics, suggesting that further research and interventions could positively impact Shodagor nutrition and health.

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AUTHOR CONTRIBUTIONS

KS and MK drafted the manuscript. MK analyzed the data. KS designed the original data collection process and collected the data.

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