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The Fitness Effects of Men's Family Investments

A Test of Three Pathways in a Single Population

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Abstract Men's investments in parenting and long-term reproductive relationships are a hallmark feature of human reproduction and life history. The uniqueness of such male involvement among catarrhines has driven an extensive debate surrounding the selective pressures that led to and maintain such capacities in men. Three major pathways have been proposed through which men's involvement might confer fitness benefits: enhancing child well-being, increasing couple fertility, and decreasing likelihood of partner desertion. Previous research has explored the impact of father involvement on these factors individually, but here we present novel research that explores all three pathways within the same population, the Mayangna/Miskito horticulturalists of Nicaragua. Furthermore, we expand the traditional dichotomous measure of father presence/absence by using a continuous measure of overall male investment, as well as two continuous measures of its subcomponents: direct care and wealth. We find that men's investments are associated with children's growth and possibly with wife's marital satisfaction; however, they are not associated with couple fertility.

Keywords Parental investment · Paternal investment · Marriage · Pair-bonds

Men's investments in parenting and long-term reproductive relationships are a hallmark feature of human reproduction and life history. Even in societies in which fathers do not appear culturally important, recent research suggests that men still invest in their children (Mattison et al. 2014). The uniqueness of such male involvement among catarrhines (Old World monkeys, apes, and humans) has driven an extensive debate surrounding the selective pressures that led to and maintain such capacities in men

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(Chapais 2008; Gray and Anderson 2010; Gurven and Hill 2009; Hawkes et al. 2010; Lancaster and Lancaster 1987; Lovejoy 1981). Although the two major components of this reproductive profile—long-term reproductive relationships and paternal investment—are independent phenomena, they are often explored in tandem since they typically co-occur and are mutually reinforcing. Indeed, in humans, there is often little distinction between parental support and spousal support (e.g., home construction, food production, etc.). Here, we explore the impacts of men's familial investments among a Mayangna/Miskito population in eastern Nicaragua. In order to more fully explore the function of such investments, we include multiple measures of investment and test for effects along multiple fitness pathways. Ultimately, understanding the importance of these functional pathways can inform the debate surrounding the evolutionary origins of humans' peculiar reproductive patterns.

The phylogenetic timing of the emergence of long-term reproductive relationships and paternal care is still undetermined. The evolutionary sequence is important because selection pressures for each can be influenced by the other. All other things being equal, paternal care is more likely to evolve after monogamy has been established because the payoffs to paternal care are heavily dependent on paternity confidence and an ability to invest after reproduction, both of which tend to be lower in non-monogamous systems (Brotherton and Komers 2003; Komers and Brotherton 1997; Lukas and Clutton-Brock 2013). With this in mind, a number of researchers have posited pathways by which longer reproductive associations between men and women might have first been selected. The leveling hypothesis suggests that the development of projectile weapons decreased variance in men's abilities to defend multiple females (Chapais 2013), something which should have decreased sexual selection for intensive mating-effort strategies in men (Kokko and Jennions 2008). An alternative model suggests that the benefits of male-male cooperation (e.g., group hunting, defense) made sexual competition more costly because it impeded the functioning of cooperative groups (Chapais 2013; Mesnick 1997).

Although returns to paternal care may be unlikely to drive monogamy in general, a number of peculiar aspects of the human story make it more likely for such returns to have played an important role. The potential for facultative polymorphic strategies in males, as well as female choice for male care, alters many of the predictions of theoretical models concerning the evolution of reproductive roles (Gavrilets 2012; Hoelzer 1989; Kokko and Jennions 2008). The ancestral state prior to long-term reproductive pair-bonding in humans was likely a multi-male/multi-female promiscuous group. In similar non-human primate groupings, males of some species have been observed establishing consortships with preferential mating access to specific females (Smuts and Gubernick 1992), as well as somehow recognizing and paternally investing in offspring (Buchan et al. 2003; Lehmann et al. 2006). Thus, it is possible that males varied in their willingness to offer parental assistance, and females varied in their weighting of parental assistance relative to other aspects of a potential mate's value. If exogenous factors altered the relative returns to focusing on a male's willingness to invest compared with other aspects, then it is possible for changes in the returns to biparental care to drive the selective pressure for pair-bonds. The important point is that in multi-male/multi-female groups, such variance in male and female strategies is more likely to already exist and be available for selection to act upon it.

Still others have emphasized the importance of alloparents other than the father in influencing the evolution of human life history patterns, suggesting that human

reproductive patterns are more accurately characterized as cooperative breeding rather than biparental (Hawkes et al. 1998; Hrdy 2005). Most research on the evolution of cooperative breeding systems suggests that monogamy tends to precede such systems (Cornwallis et al. 2010; Hughes et al. 2008; Lukas and Clutton-Brock 2012), although this needn't be the case (Kramer and Russell 2015). Alloparental investment provides another possible pathway through which greater offspring dependence might have been allowed to evolve. Once the greater need existed, returns to investment in children would have had a higher upper limit, making the selection for paternal care more likely.

Finally, it is entirely feasible that these selective pathways played out in concert, as motivations for forming long-term reproductive relationships, paternal investment, and alloparental investment coevolved. Regardless of the timing and sequence, however, it is clear that men do not simply follow or guard their reproductive partners, as some males do in other monogamous species. Men invest in their wives and in their children. Even if the returns to paternal investment did not provide the impetus for the development of long-term reproductive relationships, the subsequent evolution and maintenance of male investment must be explained.

Fitness Pathways

In addition to exploring the evolutionary history and adaptive pathways by which these behaviors evolved, a related but separate question concerns how they currently function and are maintained in extant populations. Some researchers have argued that men's provisioning should not be characterized as familial investments because they seem to function more as costly signals (Bleige Bird et al. 2001; Hawkes 1991). Although this body of research has illuminated the important ways in which even direct investment can function as a signal, subsequent empirical tests have validated that men's care appears patterned to enhance the well-being of families (Anderson et al. 1999; Gurven and Hill 2009; Marlowe 1999, 2003; Winking et al. 2009; Wood and Marlowe 2013). The question of the degree to which men's investments translate into fitness benefits along these alternative avenues, however, remains.

Paternal investment in humans today is intricately tied to the practice of forming long-term reproductive pair-bonds. In many ways, paternal investment and spousal investment can be conceptualized as the singular practice of subsidizing the reproduction of individual women. Three major pathways have been suggested through which men might experience fitness benefits from this familial investment. These pathways are not mutually exclusive and likely play roles of varying importance in maintaining familial investment, depending on socioecological variables.

Child Well-Being

The first pathway is the impact of men's familial investments on child well-being. This pathway has the longest history and largest body of research dedicated to it. From an evolutionary perspective, the primary importance of this pathway appears sensible. Human reproductive patterns differ from those of other primates in a number of important ways that make paternal investment in offspring well-being more worthwhile. Children are born extremely altricial, presenting a greater encumbrance to

women's foraging efforts (Hurtado et al. 1992; Martin 1983). Children remain nutritionally dependent for an extended period of time (Kaplan and Lancaster 2003), and finally, women give birth long before previously born children are independent (Bogin 1997). Thus, children require a higher level of investment, they require investment for a longer period of time, and often multiple children require investment at the same time. In primates, high levels of maternal investment can generally be assumed, and returns to paternal investment are essentially those experienced by investing beyond this level. Paternal investment may therefore provide considerable returns only in species in which the needs of offspring exceed the capacities of mothers to invest.

Despite the clarity of this prediction, results from numerous studies paint a complex and variable picture (Sear and Mace 2008; Winking 2006). Men's familial investments are often measured dichotomously (presence/absence), although some studies use continuous measures (e.g., time spent, food produced). Additionally, measured outcomes range from a very gross level (child mortality) to a wide variety of continuous measures of well-being. In Western populations, the presence of fathers is associated with a suite of measures linked to social well-being (e.g., psychological well-being, academic success) (Lamb 1997), although how such measures relate to fitness is unknown. Numerous studies focusing on more direct measures of fitness (e.g., mortality, growth, and fertility) among natural-fertility, subsistence-level populations suggest that the impacts of fathers tend to be weak and are extremely variable. Only around a third of such studies reported a significant effect of fathers on child mortality, despite the fact that roughly 80% of studies found such an effect for maternal grandmothers and all found such effects for mothers (Sear and Mace 2008). Far fewer studies have explored the associations between continuous measures of men's investments and child well-being among subsistence-level populations. Children's heights and weights were not associated with father presence among horticultural populations in the Amazon or West Africa (Hames et al. 2005; Sear et al. 2000), although seasonal hunting success was associated with weight gain among Hadza children (Hawkes 1993a).

Of the many studies that focus on the impact of father presence on later reproductive outcomes of children, most are tests of psychosocial stress effects—in other words, that father absence leads to accelerated sexual and reproductive outcomes (Belsky et al. 1991; Ellis 2004). However, some have explored more general measures of the well-being of adult children. In Western populations, being raised without a father is associated with lower financial outcomes (Lang and Zagorsky 2001; McLanahan and Sandefur 1994; Powell and Parcel 1997). Two studies exploring natural-fertility populations found fatherlessness to be negatively associated with later reproductive outcomes (Flinn 1988; Scelza 2010), but one did not (Winking et al. 2011).

The overall picture that emerges is one of great variability. It is clear that men's investments can positively influence children's well-being, but under many circumstances, women appear able to raise children equally as well without help from their children's fathers.

Couple Fertility

The second major pathway by which men's familial investment might result in fitness benefits is by augmenting their partner's fertility. Even direct investments in children might result in higher fertility rates if they allow mothers to reduce their own parental

investments and divert more resources to reproduction. In fact, if women (and maternal kin) do adjust their own levels of investment relative to the father's, children may experience comparable levels of investment regardless of father involvement, possibly explaining the weak effects of men's investments on children's well-being.

The dichotomous measure of paternal absence/presence seems to bear out the major predictions of this pathway. A great deal of cross-cultural variation in post-divorce custody norms exists; however, in settings where children tend to stay with mothers, husband loss is associated with an increase in the investment of mothers and maternal kin (Parker and Skoufias n.d.; Peterson 1989; Winking 2006). This suggests that the presence of paternal investment allows women to maintain lower levels of investment, freeing resources that could be shifted to fertility. This leads to the more direct prediction that women without husbands should have lower fertility than those with husbands. This prediction, however, is so self-evident in most populations that it is rarely tested or even considered. However, this is a very meaningful observation. Being unmarried is not necessarily an impediment to pregnancy in many populations, yet women regularly exhibit a preference for reproduction within long-term relationships.

Few studies have explored associations between continuous measures of men's familial investments and couple fertility; however, there is some evidence in support of such an effect. Cross-culturally, men's overall contribution to diet is positively associated with population total-fertility rates, but not juvenile mortality (Marlowe 2001). In a number of populations, men's hunting abilities are associated with men's fertility (Smith 2004), which is likely at least in part due to the effects of men's hunting on couple fertility (Gurven and von Rueden 2006).

Relationship Maintenance

The third pathway is the effect of men's investments on the probability of gaining and maintaining a spouse (van Schaik and Paul 1996). Even if familial investments result in higher child well-being and couple fertility, the major fitness benefit might still be conferred by a higher probability of obtaining and maintaining a relationship. Men likely balance familial investments with outside alternatives (leisure time, extramarital relationships, etc.) (Waynforth 1999; Winking et al. 2007). Women, however, should be indifferent to the opportunity costs that men incur by investing in their family and should thus perceive a higher optimal level of male investment. Therefore, even if the parental and fertility benefits to male investment are minor and not great enough to make it worthwhile for men (relative to the alternatives), women might still take such benefits into account when making relationship decisions. If these effects are substantial, the associated mating benefits (i.e., the increased likelihood of actually having a partner) might be more significant than those achieved via the alternative pathways (Winking et al. 2011).

In the U.S., husbands' unemployment, underemployment, or reckless spending appear to have a greater impact on the risk of divorce than when these factors are attributed to wives (Amato and Rogers 1997; Bumpass et al. 1991; White and Rogers 2000). No study, to our knowledge, has explored the impacts of men's family investments on the probability of future divorce among non-Western populations. However, retrospective studies have found that a lack of spousal support is a more commonly reported and/or acceptable reason for women to initiate divorce than for men in a

number of populations (Amato and Previti 2003; Betzig 1989; Cohen and Savaya 2003; Mbosowo 1994).

Objectives and Hypotheses

Although abundant research has been conducted to explore the strength of these pathways, no research to our knowledge has explored these three pathways within a single population. This is important because failure to do so could result in the conclusion that men's investments are unimportant when in fact such investments might actually be resulting in effects along alternative pathways. This is particularly true given that the importance of each pathway will undoubtedly vary within and across populations. Knowing the frequency by which any pathway dominates among populations, as well as socioecological covariates of such patterns, would undoubtedly inform debates surrounding the evolution of men's familial investments. Furthermore, it is important for explorations of the impacts of men's investments to move beyond a father presence/absence model. Such approaches, while valuable for exploring some questions, are inherently limited by issues of self-selection (e.g., personality factors associated with divorce) and omitted variables (e.g., others' investments). It is also impossible to test certain pathways using a presence/absence approach, such as the effect of men's investments on women's fertility.

With these issues in mind, we explore here the hypothesized pathways outlined above among Mayangna/Miskito horticulturalists in Nicaragua. Specifically, we test whether levels of men's familial investment are positively associated with child well-being (H1), couple fertility (H2), and a lower likelihood of spousal desertion (H3). Since this initial study is cross-sectional, we use children's height and weight, number of children by number of years married, and the wife's reported marital commitment and satisfaction as proxies for these variables. Furthermore, we employ a continuous measure of overall male investment, as well as two continuous measures of its subcomponents: direct care and wealth.

Methods

Population

The Miskito and Mayangna are related indigenous populations that reside along the eastern coast of Central America. The Miskito are much more numerous, numbering over 100,000, and have a longer history of contact with colonizing populations, as well as a history of encroaching on traditional Mayangna lands (Helms 1971). The Mayangna are a smaller population and have had less reproductive and cultural admixture with Western groups. Despite a history of conflict between the two populations, trade and intermarriage are very common (Koster 2007). The current study took place within two villages located in the Bosawas Reserve in northern Nicaragua. The two villages are approximately a 15-min walk/canoe ride from each other and total about 350 individuals combined. Members of the two villages regularly interact and commonly intermarry. Although each village has a mixture of self-identifying Miskito and Mayangna inhabitants, the larger village is culturally Mayangna, with no dual-

Miskito couples, while the smaller community is culturally Miskito. Miskito and Mayangna languages are not mutually intelligible, although Miskito is understood by most and is the lingua franca within these communities. In addition to these two languages, approximately 25% can speak Spanish.

The majority of the community members practice subsistence-level horticulture, animal husbandry, and hunting/gathering mixed with varying levels of wage labor and trade (Koster and Leckie 2014). Wealth is mostly concentrated in those with official government-funded positions, primarily schoolteachers, and those who have established local stores. Cash cropping and gold panning are also used by men to earn money.

Life is mainly centered around the nuclear family. These families are often large, as contraception is rarely used and the total fertility rate is greater than eight births (McSweeney 2002). Women are largely responsible for childcare, cooking, and domestic chores within the family, while men spend more time engaged in moneymaking activities, agricultural work, and hunting (Koster et al. 2013). However, it is not uncommon to see men engaged in direct care with their small children or grandchildren.

Young individuals begin forming relationships in their late teens. While there is a clear expectation that sex should be restricted to long-term relationships, particularly among young women, the culture is relatively tolerant of casual sex (Koster 2011; McSweeney 2002). Early stages of courtship occur in public settings, often on the front porches of the houses of young women. During this time, parents and relatives often make their opinions known about the budding relationships and impose varying levels of control, but the young men and women ultimately have the final say. Marriage in these populations is typically not marked by any major ceremony and is largely defined by the woman's first pregnancy. Men will often reside with the wife's family until around the time of the second child. Afterwards, there are no clear postmarital residence rules, although most couples build their houses near one set of in-laws.

Single motherhood occurs with some frequency and carries only minor stigma. Such women almost universally reside with their parents. Given the lack of formality in the marriage process, it is difficult to determine whether such children are the product of failed marriages, courtships, or short-term relationships. While less common after the birth of many children, divorce can also occur well into marriages. Forty percent of women over the age of 22 have children from two or more fathers (Koster 2011). Upon such divorces, young children almost always reside with the mother. In the current sample, four families included dependent stepchildren (all with stepfathers) out of 27 families in which the couple had married in the past 15 years (none of the older marriages have dependent stepchildren).

Familial Investment

In order to assess the level of men's investments in their families, we employed a photograph ranking method. This commonly used method relies on the collective knowledge of communities rather than observational measures (Escasa et al. 2010; Koster 2011; von Rueden et al. 2008). In this method, participants rank photographs of known individuals along some variable of interest. Measures of overall ranks (e.g., averages) are then assigned to each individual. Such approaches have certain advantages and disadvantages in relation to an observational approach. Observational

assessments of investment are often hampered by low external validity and a high potential for within-individual sampling error. Low external validity results when the activities being recorded (e.g., daily food production) do not account for the major sources of variation in investment (e.g., social capital). However, external validity issues are not limited to observational methods. Rankings can be influenced by social relationships and reputations concerning other characteristics, such as kindness, adding noise to the link between individual rankings and the trait on which they are being ranked. Within-individual sampling often presents the greater challenge to observational approaches, particularly when investment varies substantially from day-to-day. For instance, while simulating the accumulation of their expansive hunting dataset, Hill and Kintigh (2009) found that the middle tertile of Ache hunters (ranked by return rates) were not significantly different from the top or bottom tertiles until the accumulation of at least 100 sample days per person. In populations that engage in large-game hunting or annual harvests, even longer sampling periods might be necessary to ensure that single events do not overly sway the estimates. Those who have employed both methods, however, have found that informant rankings tend to correlate with observed measures—among four studies exploring hunting returns, including one involving the population on which this paper focuses, all reported a significant association with a median correlation of 0.6 (Blurton Jones et al. 1997; Hill and Hurtado 1996; Koster 2010; Marlowe 1999).

All men within the two villages who were living with a partner and had co-resident dependent children age 15 and under were photographed using a mini instant camera by JW, who also conducted the rankings. Adult men and women took part in ranking the photographs, which totaled 33 male and 37 female rankers in the large village and 11 male and 13 female rankers in the small village. These numbers represent all the adults in the villages who were available to participate. The photograph of the ranker was removed if he was included in the sample of fathers. The photographs were shuffled and then arranged into four rows of approximately ten photographs (maximum n of 40) on a small table (for the small village, two rows of approximately five were used for the maximum n of 11). A blind was erected to ensure the translator (who was from one of the communities) was not able to see the ranker's decisions. The participant was told that we were "interested in the ways in which men invest in their families—a man can invest by making money, providing food, providing clothes, with his labor, by taking care of children, and many other ways." We then asked the participant to choose the three men who invested the most in their families. From the remaining photographs, participants were then asked to choose the three who invested the least, then the three who invested the most, then the three who invested the least, etc. This method ensured that the participant was able to select from the tails inward, reducing the likelihood of giving up during the more challenging middle portion of the distribution. Selecting in groups of three was deemed to be the ideal balance between maximizing precision and minimizing participant fatigue. For the smaller community, photographs were selected one at a time. If the participant suggested that the photos that remained were indistinguishable, the process ended, and the remaining photographs received the same ranking.

The rankings were then translated into within-ranker percentiles to control for the fact that participants did not always have the same number of men to rank (some men returned to the village after the rankings had begun, were photographed, and used for subsequent rankings), and some participants used different groupings (e.g., those who

declared remaining photos to be indistinguishable). These percentiles were analyzed using the informal cultural consensus model (Romney et al. 1987), as implemented in UCINET 6.523 (Borgatti et al. 2002; Romney et al. 1987). Like consensus analysis more generally, the informal consensus model employs a factor analysis approach to determine if there is a unidimensional pattern of agreement among the informants' responses. Consensus is generally inferred if the first factor accounts for more than three times the variance than the second factor. The first factor loadings assign a value to each ranker and are often conceptualized as the individual's "competence" because it is a measure of the degree to which his or her rankings agree with those of other rankers. For each ranked individual, a first factor score is calculated as the average of the rankings, weighted by each ranker's competence—this is often referred to as the "answer key" (Weller 2007). Analyses were run for each community independently, and these first factor scores are used as the primary independent variable, Investment Score.

To explore the components that contribute to Investment Score, wealth and men's direct care investments were also explored. Material wealth measures were based on data from the previous year (2013). They were based on the cumulative value of an inventory of household possessions as determined from a focus group's estimates of the average value of key items, such as livestock, portable radios, and rifles.

A similar method to that described above for Investment Score was carried out to explore men's direct care. Participants were asked to rank men based on the degree to which they invest in the direct care of their children. Participants were told we were "interested in the manner in which men directly care for their children—men can hold their children, teach their children, play with their children, comfort them when they cry, as well as many other ways." They were then asked to rank men's photographs in the manner described above. Because of time constraints, Direct Care was only measured in the Mayangna community. Five men and seven women took part as rankers.

For the current study, we assume that current investment levels are indicative of past levels, during which time men's families grew, their children developed, and their wives formed their opinions concerning their relationships. Future research will hopefully allow for a more powerful prospective approach so that we can determine if ongoing investment levels impact future fertility, growth, and likelihood of divorce.

Anthropometry

As a measure of child well-being, children's height and weight were measured using a Seca portable stadiometer and Tanita BF679W weigh scale, respectively. Heights and weights of adults were also recorded to account for parental body size. Heights and weights were transformed into Center for Disease Control (CDC) 2000 age-controlled *Z*-scores using Epi Info 3.5.4. Although body size is highly heritable in Western populations, it is less so in energy-stressed populations where nutritional factors and pathogen stress play larger roles (Silventoinen et al. 2000).

Fertility and Ages

Demographic interviews were conducted in the winter and spring of 2013 by JK and were updated in the summer of 2014 by JW. Interviews included questions concerning the year of the participant's births and those of their parents. Ages were estimated

following the methods outlined by Gurven et al. (2007), in which multiple sources are used to estimate the most likely year of birth. These sources include direct estimates from self-reports and government-issued identification cards as well as relational information, such as sibship birth orders, estimated timing of births in relation to major events (e.g., hurricanes, the Nicaraguan Revolution), and age relative to others within the community. Birth years that could be estimated with greater accuracy (e.g., a birth in the year of Hurricane Mitch) were used as benchmarks to estimate the ages of others. When discrepancies existed among the various sources, the most accurate source was used, which was subjectively determined on a case-by-case basis. If sources that were deemed equally reliable produced different estimates, the average birth year was used.

Year of marriage was calculated in a similar manner. When this resulted in the estimated year of first birth occurring before the estimated year of marriage, the year of marriage was set to the year of first birth (this occurred for four individuals in the current sample). One couple's year of marriage was unknown and was set to 1 year prior to the first birth, which is the median years to first birth for the rest of the sample.

Relationship Scale

An ideal measure of relationship stability would be the actual risk of divorce. However, because marriages can last decades, a more immediate measure is used in the current study. All married pairs who had co-resident dependents age 15 and under were asked to complete the Investment Model Scale survey (Rusbult et al. 1998). This instrument measures one's commitment to a relationship and its three contributing elements: relationship satisfaction, quality of alternatives, and investment size. A meta-analysis of studies utilizing the Investment Model showed that these three elements jointly explain approximately 60% of the variance in commitment, which itself is highly associated with relationship dissolution at $r=-0.47$ (Le and Agnew 2003). Furthermore, the associations among the three elements and commitment do not differ across gender, ethnicity (white versus non-white), sexual orientation, relationship exclusivity, or relationship duration, suggesting that the scale is broadly applicable (Le and Agnew 2003).

A translator first translated the Spanish version of the Investment Model Scale (VanderDrift et al. 2014) into the local Mayangna and Miskito languages. A second translator then translated it back into Spanish and irregularities were discussed and corrected until both were satisfied (see Supplementary Material for the three versions and their English translations). Some elements of the scale had to be changed so as to be culturally salient. Husbands and wives were interviewed separately with the use of a translator. Since there are many levels of literacy within these communities, the questions were read aloud and respondents would point to one of five options: "Definitely No," "No," "Maybe," "Yes," and "Definitely Yes" in either Mayangna or Miskito. A screen was erected so as to obscure the participant's choices from the translator, who was from one of the communities. Five examples were given, and the options were read aloud following each question until the participant showed that they were familiar with the five options (by frequently pointing before the options could be read aloud). If the participant was completely unfamiliar with letters or expressed confusion after the examples, the "Definitely No" and "Definitely Yes" responses were covered, and only a three-point scale was used. These responses were coded identical to the five-point scale.

Two scores were calculated from the overall scale: the commitment score (sum of questions 16 through 22 with question 19 reversed) and the satisfaction score (sum of questions 1 through 5). These scores have been found to have the highest associations with relationship dissolution and sexual infidelity, respectively (Drigotas et al. 1999). In the future, we hope validate the usefulness of the scale in predicting relationship dissolution in a non-Western population.

Analyses

Bivariate correlations and general linear models were used to test hypotheses for which variables exhibited no nested structure, including the associations between Investment Score and fertility and Investment Score and relationship measures. For child anthropometry, a generalized estimating equations approach was used to account for within-family correlations. Although the data were collected separately in the two villages, the variable "Village" was not a significant predictor in any of the analyses and was excluded. All analyses were run in SPSS version 22, and all p values are reported as two-tailed.

Results

Investment Measures

Table 1 presents the descriptive statistics for the three investment measures. For both the Mayangna and Miskito communities, the ratios of the second eigenvalue to the first were sufficient to infer consensus for Investment Score (6.61 and 3.67, respectively), as well as for Direct Care (5.490). Because the distribution of Wealth is extremely positively skewed, Log Wealth is used for all subsequent analyses. The three investment measures are highly correlated, as they are with age (Table 2). A regression of the two subcomponents and age on Investment Score results in only Direct Care Score remaining a significant predictor (n=26, B=0.740, p<0.001), although only about half of the men had values for all three measures. One possible interpretation, which is

Table 1 Investment score descriptive statistics

	N	Mean number of rankings/ individual	Mean	SD	Min	Max
Investment score						
Mayangna community	40	63.90	44.69	19.48	16.55	89.56
Miskito community	11	21.09	42.74	24.19	19.36	77.73
Wealth						
Mayangna community	26	–	84,221	122,405	4900	525,931
Miskito community	8	–	32,752	21,474	11,456	80,466
Direct care score						
Mayangna community	39	11.80	45.06	20.25	13.12	86.21
Miskito community	0	–	–	–	–	–

Table 2 Correlations among investment measures and with age

	Log wealth	Direct care score	Age
Investment score	0.601	0.904	0.499
(*p*)	(<0.001)	(<0.001)	(<0.001)
Log wealth		0.727	0.372
		(<0.001)	(0.030)
Direct care score			0.495
			(0.002)

corroborated by our ethnographic impression, is that as men age, they tend to accumulate wealth, which allows them to invest more resources and time in their children.

Investment and Child Growth

The dataset includes the heights of 140 children and the weights of 146 children. Three children were excluded as high outliers, likely from age estimation errors (all were >2.5 SD for either height or weight). Although heights and weights were transformed to CDC *Z*-scores to control for growth profiles, height *Z*-scores were negatively correlated with age ($r=-0.248$, $p=0.003$), and weight *Z*-scores showed a potentially weak correlation ($r=-0.126$, $p=0.131$). This suggests that children increasingly fall below CDC standards as they age. The estimated marginal means for boys and girls, controlling for age, were −1.797 and −1.471 (standard deviations below their respective CDC means) for height and −1.103 and −0.646 for weight, respectively.

Table 3 displays the results of the test for the impact of father's Investment Score on child growth. We use parental body size to account for heritable variation in children's body sizes, and we use generalized estimate equations (GEE) to account for additional, unaddressed within-family variation. Parental body size is estimated as the average of the mother's and father's CDC 2000 height-for-age *Z*-scores (with age set to 20). Height is used as the control for both the height and weight analyses because weight is more sensitive to immediate condition (i.e., a high-investor and his children might both grow heavier owing to greater access to resources). All three measures showed at least weak positive associations with weight. Although Investment Score and Direct Care were not significant predictors of child height, Log Wealth proved a strong predictor of both anthropometric measures (Fig. 1a and b). The effects are not unsubstantial—generating predictions from the regression equation for the minimum and maximum Log Wealth measures (holding all other variables at their sample mean) results in approximately a one-standard-deviation difference in weight and height. Similar calculations for Investment Score and Direct Care on weight result in differences of approximately half a standard deviation.

Investment and Couple Fertility

Table 4 presents the results of the OLS regressions of investment measures on completed fertility, controlling for the wife's age at the beginning of the marriage as

Table 3 GEE analyses of the impacts of two measures of father investments on child growth

	Investment score			Log wealth			Direct care		
	B	SE	*p*	B	SE	*p*	B	SE	*p*
Height Z[a]									
Intercept	0.030	0.431	0.944	−1.690	0.895	0.059	−0.114	0.508	0.822
Investment Measure[b]	0.003	0.005	0.601	0.445	0.177	0.012	0.001	0.006	0.882
Sex=Female	0.379	0.165	0.022	0.343	0.181	0.059	0.252	0.136	0.063
Age	−0.059	0.019	0.002	−0.066	0.020	0.001	−0.058	0.023	0.010
Avg parent Ht *Z*	0.681	0.161	<0.001	0.731	0.184	<0.001	0.592	0.205	0.004
Weight Z[c]									
Intercept	−0.570	3.771	0.160	−2.310	0.747	0.002	−0.617	0.381	0.105
Investment measure[d]	0.008	0.004	0.061	0.519	0.147	<0.001	0.008	0.004	0.066
Sex=Female	0.454	0.138	0.001	0.432	0.149	0.004	0.366	0.117	0.002
Age	−0.031	0.015	0.042	−0.037	0.017	0.028	−0.044	0.017	0.009
Avg parent Ht Z	0.307	0.168	0.068	0.383	0.172	0.026	0.235	0.190	0.217

[a] *N*=140, QIC=139.706 for Investment Score; *N*=123, QIC=119.956 for Log Wealth; *N*=104, QIC=97.824 for Direct Care

[b] Investment Measure represents either Investment Score, Log Wealth, or Direct Care depending on the column

[c] *N*=146, QIC=105.338 for Investment Score; *N*=128, QIC=93.182 for Log Wealth; *N*=107, QIC=68.443 for Direct Care

[b] Investment Measure represents either Investment Score, Log Wealth, or Direct Care depending on the column

well as years in the marriage and years in the marriage squared. Years in marriage was capped at the year in which the wife was age 45. The age of marriage for wives ranges from 11 to 25. Although girls can marry at very young ages, there is likely some error in these estimates. However, exclusion of the cases with very low age at marriage does

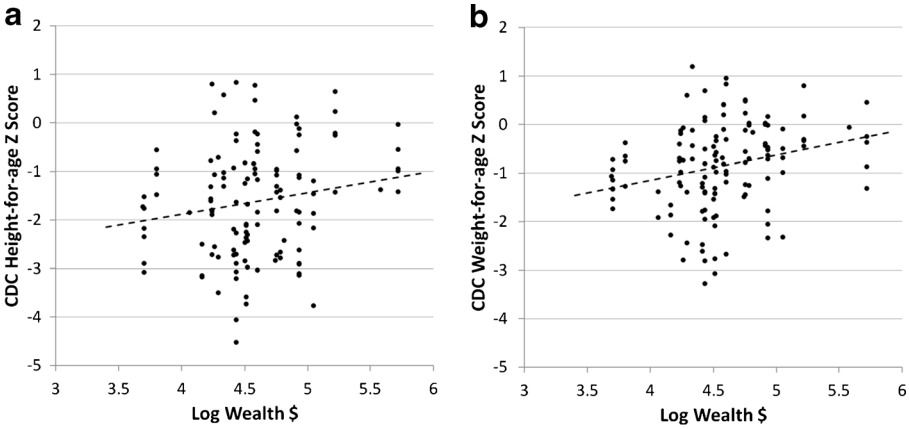

Fig. 1 Height and weight by log income. *Fitted lines* represent the GEE prediction equations with controls set to their sample means

Table 4 Ordinary Least Squares (OLS) regression analysis of the effect of Investment Score measures on fertility for length of marriage

	Investment score			Log wealth			Direct care		
	B	SE	*p*	B	SE	*p*	B	SE	*p*
Intercept	0.913	1.317	0.492	3.633	3.278	0.277	0.756	1.883	0.691
Investment score[a]	−0.004	0.012	0.765	−0.319	0.614	0.607	0.007	0.015	0.647
Wife's age at marriage	−0.053	0.070	0.451	−0.092	0.092	0.324	−0.056	0.101	0.581
Years in marriage	0.501	0.092	<0.001	0.420	0.138	0.005	0.461	0.126	0.001
Years in marriage^2	−0.005	0.003	0.085	−0.003	0.092	0.324	−0.005	0.004	0.260

N=47, R^2 =0.849 for Investment Score; N=33, R^2 =0.741 for Log Wealth; N=36, R^2 =0.817 for Direct Care

[a] Investment Measure represents either Investment Score, Log Wealth, or Direct Care depending on the column

not change the ultimate conclusions of the test, and so they are included here. One case was excluded because the man was sterile. Investment measures were not associated with completed fertility.

Investment and Wife's Perceptions of Marriage

One individual was excluded because her responses in the Investment Model Scale did not vary, suggesting she did not understand the exercise. Wife's commitment and satisfaction scores were strongly correlated (n=46, r=0.576, p<0.001), although neither was correlated with the husband's corresponding scores (respectively, n=44, r=−0.061, p=0.694; n=44, r=0.237, p=0.122). Wife's satisfaction was weakly correlated with length of marriage (n=46, r=0.288, p=0.053), but there was no association between wife's commitment and years of marriage (n=45, r=0.068, p=0.656). Years of marriage was also correlated with Investment Score (n=48, r=0.408, p=0.004) and Direct Care (n=36, r=0.468, p=0.004), but not with Log Wealth (n=34, r=0.245, p=0.162).

Wife's commitment was not associated with Investment Score (n=46, r=0.048, p=0.752), Log Wealth (n=32, r=0.056, p=0.761), or Direct Care (n=35, r=−0.122, p=0.485). Years in marriage was included as a control for tests of the effects of men's investments on women's satisfaction (Table 5). Although none of the measures proved a significant predictor, scatter plots revealed a potential threshold effect such that individuals with very low Investment Scores and Log Wealth values were more likely to report low satisfaction (satisfaction score <20) (Fig. 2). Using logistic analysis with years in marriage as a control, Investment Score (n=47, B=0.070, p=0.066) and Log Wealth (n=33, B=4.846, p=0.048) proved to be significant predictors of the probability of women reporting high satisfaction, whereas Direct Care did not (n=35, B=0.020, p=0.492).

Discussion

The research reported here was conceived to more fully explore the fitness effects of men's familial investments within a single population by examining multiple measures

Table 5 OLS regression of the impacts of father investment score on wife satisfaction score

	Investment score			Log wealth			Direct care		
	B	St. Err	*p*	B	St. Err	*p*	B	St. Err	*p*
Intercept	17.654	1.458	<0.001	11.169	6.308	0.087	18.771	1.838	<0.001
Investment measure[a]	0.025	0.031	0.424	1.860	1.424	0.201	−0.011	0.040	0.788
Years in marriage	0.097	0.065	0.141	0.063	0.074	0.408	0.121	0.085	0.165

N=46, R^2 =0.096 for Investment Score; N=33, R^2 =0.097 for Log Wealth; N=35, R^2 =0.065 for Direct Care

[a] Investment Measure represents either Investment Score, Log Wealth, or Direct Care depending on the column

of investment and multiple fitness pathways. Below we summarize these effects and evaluate potential alternative explanations given the observational nature of the research design. Finally, we explore the theoretical implications of the results and directions for future research.

The results reported above indicate that men's investments have a positive effect on children's growth (H1) and a possible effect on women's satisfaction in marriage (H3) within these communities. Although these two hypotheses received some support, there was no indication that men's investment levels were associated with within-couple fertility (H2). With regard to children's growth, the estimated effects of men's investments were not unsubstantial—the predicted changes in height and weight when going from the lowest to highest household wealth levels were both approximately an entire CDC *Z*-score. Household wealth, which is largely determined by men's wage earning, proved the strongest predictor of children's growth and wife satisfaction, suggesting that providing of resources is a major pathway by which men impact their families' well-being in this population.

The effect of men's investments on wives' satisfaction appear to be defined by a threshold effect such that women with husbands with low Investment Scores or low wealth were more likely to report low satisfaction, although there was no continued change beyond this initial increase. Although commitment scores were highly correlated with satisfaction scores, men's investments were not associated with higher levels of wife's commitment. This might be due to the fact that women's options become increasingly constrained as they have more children. There are few culturally appropriate avenues for women with many children to escape a bad marriage since children

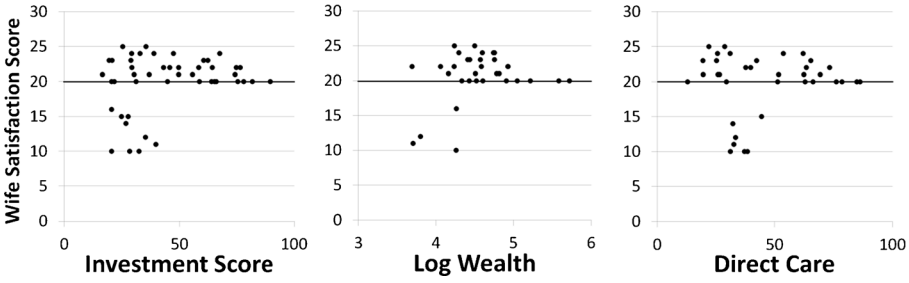

Fig. 2 Wife satisfaction score by investment measures. *Solid line* represents the Wife Satisfaction=20 cutoff

typically follow the mother. In these two communities, two large families were headed by women whose husbands had left, but none were headed by men whose wives had left. If we limit the sample to only those couples who have been married less than 10 years (i.e., those in which wives might be able to leave), Investment Score shows a more suggestive correlation with wife commitment score (n=18, r=0.425, p=0.070). As this is a post-hoc analysis with a limited sample size, however, further research is needed to validate that length of marriage mediates the effect of male investment on wife's commitment.

Because this study is observational, it is important to explore possible confounders. Whereas researchers exploring animal behavior are ethically and practically less encumbered and are able to employ well-controlled experimental research designs to reveal the impacts of males' contributions (e.g., Bart and Tornes 1989; Petrie and Williams 1993), those exploring humans must rely on observational studies. Using natural variation in the treatment variable often presents challenges related to self-selection and omitted variables. Regarding the present study, this means that unexplored factors that associate with men's investment levels might impact the hypothesized associations, obscuring or inflating observed patterns. This does not necessarily mean that the effects are not real. And despite the fact that confirmatory results may have alternative explanations, such findings still retain inferential power inasmuch as the exercise fails to refute the hypotheses.

Regarding children's growth, there are few avenues for self-selection patterns to alter the hypothesized pathway. It is possible that some heritable component allows for men to invest higher levels in their family *and* leads to larger size in children, but this pathway seems unlikely. A more likely confound concerns the hypothesis that men's investments associate with fertility. If the populations are moving through a demographic transition, then we might not expect a positive link between investment levels and couple fertility. Such transitions are marked by a reduction of fertility, particularly among the more educated and wealthy. This reverses the relationship between resource availability and fertility that is often seen among natural-fertility populations (Skirbekk 2008). Thus two effects might be acting in opposite directions: reduced resource availability might be limiting fertility for lower levels of investment, and reduced desire for a large family might be reducing fertility for higher levels. Among the two communities participating in this study, the total fertility rate was 7.6 over the past 3 years, which is comparable with other natural-fertility populations. However, there has been a reduction in fertility since 2000, so this possibility cannot be ruled out (Fig. 3).

Furthermore, the relationship between men's investments and wives' perceptions of their marriages might be complicated by the non-random pairing of husbands and wives. Assortative coupling results in the pairing of men and women who are more equally matched than chance would predict. Thus, high-investing men might have wives who have comparably high bargaining leverage, can demand more, and likely have more alternatives outside of marriage. However, the marriage pool from which individuals choose partners is substantially limited relative to Western contexts, and wealth (and investment levels) typically rises later in life, both of which likely limit the degree of assortative coupling.

Finally, the direct effects of men's investments might be obscured by the fact that it is common for younger families to reside within the households of the wife's parents.

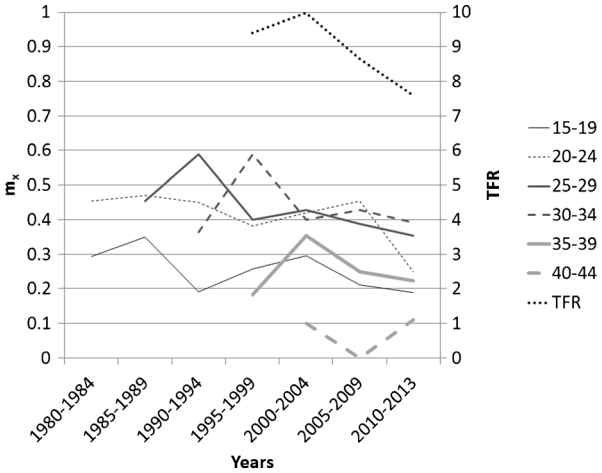

Fig. 3 Age-specific fertility rates and total fertility rate by year. The analysis is based on 328 births over 1351 risk years. The average age-specific fertility rate for ages 40 to 44 ($m_{40–44}$) was used in the calculation of the 1995–1999 Total Fertility Rate, as there were no individuals in this age/year bracket

This was true for seven families in the sample used for the current study. Conceptually, however, the effects of grandparental investment need not be taken into account because the returns to men's individual investments are defined by the effects of such investment beyond that which is being provided by others. In the current sample, eight of the 22 marriages that had lasted at least 15 years included one or more unmarried daughters with children. Comparing the 18 children of these mothers with those with present fathers reveals no difference in weight *Z*-scores (GEE with mother as repeated subject, controlling for sex and age, Father Absent, $B=0.310$, $p=0.290$).

The fact that child weight associates with investment levels suggests that children's growth is sensitive to available resources. Therefore, if father presence is not associated with children's weight, this would suggest that children raised without fathers are still receiving levels of investment comparable to those with fathers. Others must be compensating for the absent fathers (most likely maternal kin). This raises the question as to why most men choose to stay with their wives when others are willing to provide their share of investment in their absence. It is important to note that such a decision is based on the existence of some men who are willing to provide investment. If no men are willing to invest, there would be no concerned fathers-in-law either. This question is closely related to that concerning men's investment decisions among forager populations, in which food is often shared extensively (Hawkes 1993b).

One solution to this conundrum is that although men's investments might not be associated with increases in child well-being beyond that which is observed in fatherless families, investment might be an avenue through which men can increase wife's fertility. Such an effect has been suggested in previous studies (Gurven and von Rueden 2006), but no effect of men's investments on wife's fertility was found in the current study. An alternative solution to the question might lie in individuals responding to the varying substitutability of men's and maternal kin's investments. We would therefore predict that men who are married to women whose fathers are less able to invest (e.g., those born to much older fathers) are more likely to stay and invest themselves. Based on this logic, it is the flexibility of the cooperative system of human childrearing that

might allow men to exit partnerships, even when alloparental support is obligatory. Finally, women and their kin who stand to benefit the most from a man's investments might demand assurances of intent and of future investment, making philandering strategies less productive. Bride-wealth and -service may therefore function less as an economic transaction and more as honest signals of intent.

Ultimately, developing the answers to these complex questions will require an extensive body of cross-cultural data, and we add another piece to the puzzle here. As in countless other populations, it is clear that many Mayangna and Miskito men invest heavily in their families and have deep concern for the welfare of their children and their wives. The results here suggest their resource investments in the form of wealth have the largest impacts on family well-being, particularly in child growth and possibly in wife satisfaction. Future research will allow for a clearer picture to emerge as longitudinal data among this population will allow for more direct measures of the hypothesized fitness outcomes and validation of the measures used here.

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