Marriage Patterns in a Mesoamerican Peasant Community are Biologically Adaptive

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ABSTRACT Differential investment in offspring by parental and progeny gender has been discussed and periodically analyzed for the past 80 years as an evolutionary adaptive strategy. Parental investment theory suggests that parents in poor condition have offspring in poor condition. Conversely, parents in good condition give rise to offspring in good condition. As formalized in the Trivers-Willard hypothesis (TWH), investment in daughters will be greater under poor conditions while sons receive greater parental investment under good conditions. Condition is ultimately equated to offspring reproductive fitness, with parents apparently using a strategy to maximize their genetic contribution to future generations. Analyses of sex ratio have been used to support parental investment theory and in many instances, though not all, results provide support for TWH. In the present investigation, economic strategies were analyzed in the context of offspring sex ratio and survival to reproductive age in a Zapotec-speaking community in the Valley of Oaxaca, southern Mexico. Growth status of children, adult stature, and agricultural resources were analyzed as proxies for parental and progeny condition in present and prior generations. Traditional marriage practice in Mesoamerican peasant communities is patrilocal postnuptial residence with investments largely favoring sons. The alternative, practiced by ~25% of parents, is matrilocal postnuptial residence which is an investment favoring daughters. Results indicated that sex ratio of offspring survival to reproductive age was related to economic strategy and differed significantly between the patrilocal and matrilocal strategies. Variance in sex ratio was affected by condition of parents and significant differences in survival to reproductive age were strongly associated with economic strategy. While the results strongly support TWH, further studies in traditional anthropological populations are needed. Am J Phys Anthropol 000:000–000, 2010.

Adaptation is a central theme in evolutionary biology with variation in sex ratio a frequent target of analysis. Variance in sex ratio versus a balanced sex ratio (1:1 male–female ratio) has been analyzed in plants, animals, and humans. Environmental stress is consistently associated with a preponderance of female offspring among reptiles and in the most extreme of conditions parthenogenesis may be induced. Similarly, poor environmental conditions are associated with an altered sex ratio favoring female offspring among mammals. Maternal malnutrition has been associated with a low sex ratio in humans (Andersson and Bergstrom, 1998) and other animals (Rosenfeld and Roberts, 2004). The human sex ratio is also altered by adverse environmental conditions such as lead or arsenic exposure, and even hypergravity (Little et al., 1987b).

Species have a tendency to invest in sons and daughters equally as the genes from each sex that contribute to the next generation must be equal because each progeny has one father and one mother (Fisher, 1930). Alternatively, in situations of high fluctuation where one sex is dominant over another among reproductive individuals, the sex of the smaller number must exceed production by the majority until the sex ratio reaches equilibrium. If one sex is less numerous, its contribution is higher and overproduction of the minority sex should increase until the primary sex ratio is balanced (Hamilton, 1967). Fisher's model was based on frequency-dependent selection and appeared to explain why 1:1 sex ratios occurred. The model also influenced adaptive sex ratio theory. Accordingly, equal investment was a stable evolutionary solution if one sex was not more expensive than the other to produce. Nonrandom departure from 1:1 sex ratios is an exception. Under such conditions, differential parental investment results in systematic departure from sex ratio equilibrium (Hamilton, 1967; Trivers and Willard, 1973).

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Differential investment in offspring where parents in good condition favored sons and those in poor condition invested in daughters to maximize transmission of genes to subsequent generations was cited as the Trivers-Willard Hypothesis (TWH). Studies in numerous taxa have supported TWH to varying degrees. Metaanalysis of 381 studies of the sex ratio in mammalian taxa weakly supported TWH. However, when focus was on periconceptional maternal condition (34% of 422 metaanalysis tests), support was unanimous for the association between good maternal condition and the production of sons and for poor maternal condition and the production of daughters (Cameron, 2004).

Investigations in human populations have yielded variable support for TWH, ranging from weak support based on breastfeeding duration (Koziel and Ulijaszek, 2001; Quinlan et al., 2003) to complete contradiction of parental investment theory and TWH (Tracer, 2009). In human groups practicing female biased parental investment, which is relatively rare (Cronk, 1989, 1991), strong support for TWH was noted in the growth status of children (Cronk, 2000). Similarly, maternal "condition" (defined by wealth) heavily influenced the body mass index (BMI) of female progeny while paternal "condition" weakly affected BMI of male progeny (Godoy et al., 2006). In a contemporary US population, about 30% of tests strongly supported TWH but 70% did not significantly support TWH (Gaulin and Robbins, 1991); of note, none of the nonsignificant tests contradicted TWH. Two important trends emerged in the literature dealing with variation in sex ratio adaptive strategies: 1) severe environmental stresses were associated with an increased magnitude of support for parental investment theory, and 2) the closer the measure of "condition" was to the time of conception, the greater the support for TWH.

The purpose of the present investigation was to analyze the effects of mating patterns and parental investment on sex ratio, number of offspring surviving to reproductive age, and stature (child and adult) in a rural, indigenous subsistence agrarian Zapotec-speaking community in the Valley of Oaxaca, southern Mexico.

MATERIALS AND METHODS

Setting

A Zapotec-speaking community located in the Etla branch of the Valley of Oaxaca about 23 km northwest of the city of Oaxaca de Juarez was the focus of the study which was approved by the appropriate institutional committee for use of human subjects at the University of Texas at Austin and by community authorities. Individual informed consent was obtained. The study was conducted in 1978 when the community had a population of 1,665 individuals and 247 households. Basic data included household demography and history (age; patrilocal, matrilocal, or neolocal), agricultural production resources, pedigree, current residence (patrilocal, matrilocal, nuclear), family socioeconomic status, and heights of children and adults (Malina et al., 1980, 1982a; Little and Malina, 2005a). About 8% of residences were not patrilocal, matrilocal, or nuclear; these households typically included elderly males or females living alone, or an elderly woman living with an unmarried daughter who had several children. These households were not included in the analysis.

Sex ratio and number of offspring surviving to reproductive age were derived from household survey data. Estimated infant and preschool mortality in 1970–1979 was high, 181/1000 live births and 36/1000 live births, respectively, and 68% of deaths occurred in the prereproductive period, $<$15 years of age (Malina et al., 2008). The estimates for infant and preschool mortality may actually be higher since under-reporting of deaths in young children was common in rural areas of Mexico (Cordero, 1968).

Growth status of children at the time of survey in 1978 was, on average, stunted with mean heights $\leq$5th percentiles of age- and sex-specific US reference values (Malina et al., 1980). Mean adult heights were 157.1 $\pm$ 5.1 cm in males and 145.6 $\pm$ 5.2 cm in females (Malina et al., 1982a) and consistent with observations for indigenous populations in Oaxaca (Faulhaber, 1970; Kappel and Selby, Unpublished manuscript). Heights of children and adults were used as proxies for "parental" condition associated with marriage and residence patterns. *Z*-scores for heights of children were computed relative to CDC standards (EPI Info, CDC, Atlanta, GA).

Farm land and socioeconomic status (SES)

More than 90% of heads of households were full-time farmers. Land holdings were relatively small which is typical in Mesoamerican communities (Kirkby, 1973; Granskog, 1974; Dennis, 1987). The average household cultivated 1.55 almudes (1.55 $\times$ 0.25 = 0.388 hectares) or 0.96 acres of irrigated land in 1978 (Little, 1983). Irrigated land production was supplemented with cultivation of dry and communal lands. Approximately 40% of households did not own land, and were considered parents in "poor condition." Such households comprised the poorest people in the community and by inference exclusively used poorly producing communal land. Number of appliances, dry land holdings (almudes), and occupation (full time farmer, part time farmer, principal job outside the community) were used to classify household SES as low and high (Malina et al., 1985). Household SES had a significant effect on growth status (high $>$ low SES, Malina et al., 1985) and sibling correlations for growth status (Little et al., 1986). SES as computed thus appeared to be a biologically sensitive indicator of parental "condition."

Demography

The community had relatively high emigration which began about 1941 (Granskog, 1974). Among 336 schoolchildren 6–15 years surveyed in 1968, 132 were no longer resident in the community in Fall 1978 (Malina et al., 1982b); thus, about 60% of school youth resident in the community in 1968 were present in 1978, suggesting about 40% out-migration as school-aged mortality was $\sim$1–2%. Emigrants were $\geq$18 years and usually from poorer households (Little et al., 2006), but did not differ in height at school age compared to those who remained in the community (Malina et al., 1982b). "Push" factors for migration at the time of study were lack of economic and employment opportunities in the community; "pull" factors were economic and employment opportunities in major urban centers, primarily Mexico City. Money was ordinarily sent back to the family by the third year of emigration; funds were used to improve of living conditions and overall community infrastructure (Conway and Cohen, 1998; Malina et al., 2008). Emigration did not, however, impact acculturation. In 1978 more than 75% of community inhabitants spoke only Zapotec (Malina et al., 2008), >95% of heads of household were full-time farmers (Malina et al., 1985), and an estimated 3% of the population's genes were from outside the community (Little and Malina, 1989; Little et al., 2006, 2008).

Generational perspective

The subsequent analysis and discussion spans three generations: 1) parents of the prospective couple—"negotiators"; 2) the prospective couple—the children of [1] and parents of children who comprise the next generation [3]; and (3) children; progeny of the prospective couple [2] and grandchildren of the "negotiators" [1]. This provides generational time depth to analyze decision making, the effect of negotiated decisions associated with socially preferred versus not socially preferred marriage behavior on biological parameters of offspring—sex ratio, offspring survival to reproductive age, and child growth status.

Postnuptial residence and household economics

As children reach marriageable age, parents began negotiations or discussions of inheritance with potential in-laws. Negotiations involved length of a resident labor contract, i.e., working for the father or father-in-law, and size of inheritance. In virilocal (patrilocal) contracts, the choice was to retain the son in the household and negotiate to obtain a daughter-in-law. In uxorilocal (matrilocal) contracts, the negotiation was to gain a son-in-law, i.e., someone to marry the daughter and work for her parents. Spouses were essentially chosen according to a theory of comparative economic advantage which focused on successful production of children (Selby et al., Unpublished manuscript). The decision on patrilocal versus matrilocal residence was reached through complex and subtle evaluations and/or negotiations by the respective families, i.e., grandparents of the prospective progeny, that were intended to maximize economic prospects for the young couple (Nutini, 1967, 1968; Nader, 1969; Selby et al., 1982). The future bilateral inheritance of the couple, including bride wealth, was the central factor in negotiations, and focus was on maximizing the "condition" of the couple for production of grandchildren.

Social preferences for marriage and residence ostensibly did not involve economics, but were aimed at the couple being reproductively successful. Locally defined regulations included incest, fictive kinship, morality and other rules for proper sexual behavior. First-cousin marriages were considered incestuous, but second cousin marriage was acceptable. Yet, people related by god-parental ties were not acceptable (Selby, 1966; Selby et al., Unpublished manuscript). These issues provided a platform for posturing and veiled economic argumentation during marital negotiations. The social preference of residence was postnuptial patrilocality which evolves into the establishment of an independent nuclear household after several years in an extended-family residence involving a labor contract linked to land inheritance (Selby, 1966; Nutini, 1967; Nader, 1969; Selby et al., Unpublished manuscript). Patrilocal arrangements were an investment in sons, whereas matrilocal contracts were investments in daughters. Longer labor contracts were generally associated with greater inheritance (Selby et al., Unpublished manuscript). Longer, uxorilocal labor contracts would thus be expected to result in the largest inheritance.

Three composite indicators of household wealth and demography were computed using information (factor weights) from a prior factor analysis of the economy and demography of the community (Appendix 1; Little et al., 1987a). "Wealth" was quantified as primary agricultural production resources (agricultural resources—Factor 1); it was the primary object of marriage negotiations. The adult component of household size (adults—Factor 2) and child component of household size (children—Factor 3) comprised household demography. A constant was added to the standardized scores for each factor (mean = 0, standard deviation = 1.0) to eliminate negative values. Prior analysis indicated that the composite variables of wealth and household demography significantly affected growth status and increments, and sibling correlations (Little and Malina, 2005a) and provided an indication of parental "condition."

Analytical methods

The hypothesis of an effect of SES (proxy for parental condition) and postnuptial residence (investment in sons or daughters) on child and adult height, offspring survival, and sex ratio were tested by modeling SES and postnuptial residence as main effects while potential confounders (maternal age, age at marriage, age at first birth, total number of live born children, household age) were modeled as covariates. Adult stature (cm) and height z-scores of children were compared by postnuptial and current residence (dependent variables) with analysis of variance (ANOVA) and while controlling for age and age-squared as covariates (MANCOVA).

Secondary sex ratio and number of offspring surviving to reproductive age (dependents) were analyzed by SES and postnuptial residence/labor contract (patrilocal vs. matrilocal—main effects) using multivariate analysis of variance (MANOVA) and multivariate analysis of covariance (MANCOVA) holding constant the following variables: maternal age, age at marriage, age at first birth, total number of children alive at birth and household age. Analyses were done using SAS V9.1

TABLE 1. Household land resources by residence pattern

		Land resources[a]					
		Irrigated land[b]		Dry land[b]		Common land[b]	
Residence pattern	n	M	SD	M	SD	M	SD
Nuclear	112	1.90	4.68	2.46	3.42	2.59	2.10
Patrilocal	53	1.31	2.11	1.76	2.59	3.19	1.89
Matrilocal	36	1.18	1.96	2.75	3.90	2.14	2.05
Anomalous	36	1.23	2.29	2.12	3.04	1.47	1.96
Total	237	1.55	3.57	2.30	3.28	2.49	2.09

[a] Raw values (not recoded); these reflect actual census figures from the 1978 household survey.
[b] Land in Almudes (0.25 hectare).

TABLE 2. Household demography by residence pattern

		Household composition									
		Household size (people)		Household age (years)		Number of producers[a]		Number of nonproducers[b]		Number of Adult units[c]	
Residence pattern	*n*	M	SD	M	SD	M	SD	M	SD	M	SD
Nuclear	112	6.09	1.96	14.53	9.89	2.85	1.04	3.24	1.65	4.47	1.33
Patrilocal	53	8.55	3.09	22.08	16.60	4.94	2.21	3.60	1.61	6.75	2.56
Matrilocal	36	7.86	2.71	22.33	17.01	4.78	1.62	3.08	1.52	6.32	2.10
Anomalous	36	4.33	3.50	25.81	17.78	3.19	2.25	1.14	1.61	3.76	2.83
Total	237	6.64	2.97	19.12	14.73	3.66	1.91	2.98	1.79	5.15	2.33

[a] Number of adults.
[b] Number of children.
[c] Producers + Nonproducers.

TABLE 3. Household livestock resources by residence pattern

		Livestock[a]									
		Cow		Pig		Goat		Oxen		Burro	
Residence pattern	*n*	M	SD	M	SD	M	SD	M	SD	M	SD
Nuclear	112	0.44	0.70	0.93	1.02	0.64	1.12	0.65	0.48	1.31	0.75
Patrilocal	53	1.17	2.78	1.17	1.09	1.06	1.26	0.74	0.45	1.52	0.78
Matrilocal	36	0.61	0.84	1.11	1.04	0.81	1.19	0.63	0.49	1.25	0.73
Anomalous	36	0.17	0.38	0.58	0.94	0.44	0.94	0.53	0.51	0.89	0.71
Total	237	0.59	1.47	0.96	1.04	0.73	1.15	0.65	0.48	1.29	0.77

[a] Raw values (not recoded); these reflect actual census figures from the 1978 Household Survey.

(SAS Institute, Cary, NC) and SPSS V.14 (SPSS, Chicago, IL).

RESULTS

Demographics

Average age at marriage in 1978 was 18 years. It indicated that the community was demographically young at the time of study, with an average age of 23.1 years. Nuclear households had more prime agricultural production resources than extended family households (Table 1), but also had the smallest average number of adults and children (Table 2). Extended family households had slightly more livestock resources than nuclear families (Table 3), while nuclear households had the lowest infant mortality and morbidity, and highest level of education (Table 4).

Postnuptial residence

Patrilocal postnuptial residence, the social preference, was violated routinely. Flow analysis of the marriage decision in the community and production of children showed that actual marriage behavior and subsequent residence pattern were not as arbitrary as being patrilocal or matrilocal (see Fig. 1). A preponderance of nuclear households evolved from a patrilocal postnuptial labor contract. Households that began as patrilocal usually became nuclear, but some were matrilocal for a period before becoming nuclear. Very few couples (6%) had enough wealth to set up a household immediately after marriage (neolocal). Wealth (agricultural resources—Factor 1) varied by residence type over time (see Fig. 2), with matrilocal households accumulating wealth early and rapidly. Numbers of adults (see Fig. 3) and children (see Fig. 4) also varied by residence type over time (i.e., with household age).

Inheritance cycle

Life histories of households, quantified by the factors, followed a curvilinear pattern of increase in agricultural resources, adults, and children in the first half of their existence, followed by a decrease in adults and children in the second half (Figs. 2–4). The pattern of increase in adults and children was more rapid over time in patrilocal households than other household types and then decreased. The nadirs or valleys in the figures mark generation change—inheritance and/or creation of a new household, while the increase following a valley indicated the succeeding generation. Through time, patrilocal households numerically reflected a continuum, patrilocal → nuclear, while nuclear and matrilocal households were essentially transitions between patrilocal household residence patterns, patrilocal → nuclear → patrilocal and matrilocal → nuclear → patrilocal. Eventually all family lines were patrilocal (investment in sons) with spikes of matrilocal (investment in daughters) and nuclear living arrangements which allowed for upward socioeconomic mobility and start-up of a new family that would very likely become patrilocal (matrilocal → nuclear → patrilocal) within a generation, i.e., when sons reach marriageable age. The trend in the community was to cycle families from being poor in one generation to well-off in the next, lower status in the third, poor in the fourth, and so on. The "negotiators" or parents of the prospective couple were thinking several generations into the future. This long-term perspective was further complicated because distribution of land by inheritance occurred more than once during a household's history and was bilateral but not equally so.

Smoothed composite variables plotted over household age show the timing of different events in the household life cycle, including the periods of inheritance. Agricultural resources increased over time (see Fig. 2). Accrual of inheritance by a matrilocal household was bimodal, with an early peak at ~5 years ($P < 0.05$) and a large late peak at 20 years (see Fig. 2). In contrast, patrilocal households had peaks at ~10 ($P < 0.05$) and ~25 years ($P < 0.05$). Nuclear households inherited at their formation and when parents died and estates were settled, with a peak at ~20 years (P = ns). At 25 years, agricultural resources were significantly greater in patrilocal than matrilocal households ($P < 0.05$), and in matrilocal

TABLE 4. Household history by residence pattern

Residence pattern	*n*	Household history: Infant mortality[a] M	SD	Morbidity as cause of death[b] M	SD	Family education[c] M	SD	Bought supplemental maize[d] M	SD
Nuclear	112	0.18	0.16	0.38	0.78	2.62	1.02	0.52	0.50
Patrilocal	53	0.30	0.24	0.66	0.94	2.15	1.08	0.50	0.51
Matrilocal	36	0.41	0.24	0.78	1.10	1.75	0.84	0.50	0.51
Anomalous	36	0.31	0.27	0.39	0.55	1.47	0.91	0.67	0.48
Total	237	0.27	0.22	0.50	0.86	2.21	1.08	0.53	0.50

Raw values (not recoded); these reflect actual census figures from the 1978 household survey.
[a] Infant mortality = number of infant deaths/total number of term pregnancies.
[b] Morbidity causing death: (measles = 1; respiratory infection = 1; gastro-intestinal infection = 1; whooping cough = 1)/Number of early childhood deaths.
[c] Family education = sum of years of education of all adults divided by number of adults.
[d] Bought supplemental maize—coded as 1 = yes, 0 = no.

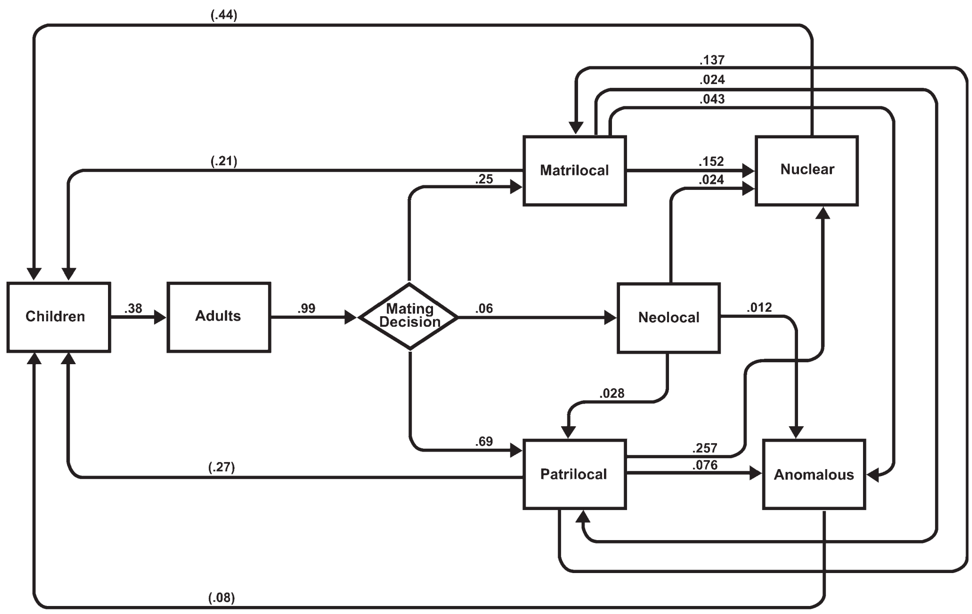

Fig. 1. Flow analysis of household residence patterns and production of children based on household census, pedigree, and interview data. Numbers in parentheses represent proportion of parous females, and other numbers are proportion of individuals (Little, 1983).

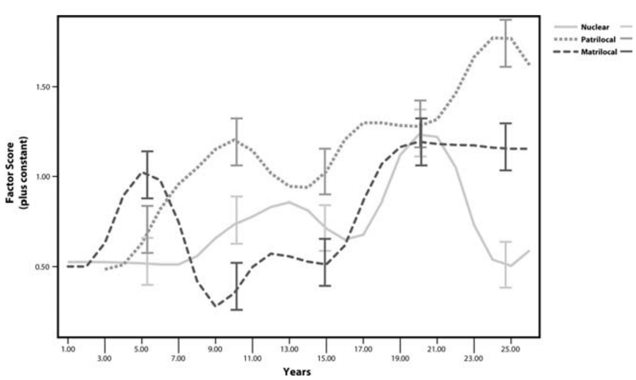

Fig. 2. Agricultural resources (irrigated land, cows, pigs, goats) by household age (Error bars are 95% confidence intervals).

than nuclear households ($P < 0.05$). The matrilocal labor contract thus resulted in socioeconomic mobility and a return to the patrilocal social preference in the next generation.

There were fewer adults (see Fig. 3) and children (see Fig. 4) in matrilocal than patrilocal households by 25 years ($P < 0.05$). Fewer adults were also present in nuclear than patrilocal households ($P < 0.05$), but the number of adults did not differ in nuclear and matrilocal (P = ns). Patrilocal households had more children than nuclear or matrilocal households by 25 years ($P < 0.01$), while nuclear households had fewer children than patrilocal ($P < 0.01$) but more than matrilocal ($P < 0.05$) households (see Fig. 4). At 25 years, therefore, matrilocal households had relatively more resources per person while patrilocal households had relatively less resources per person.

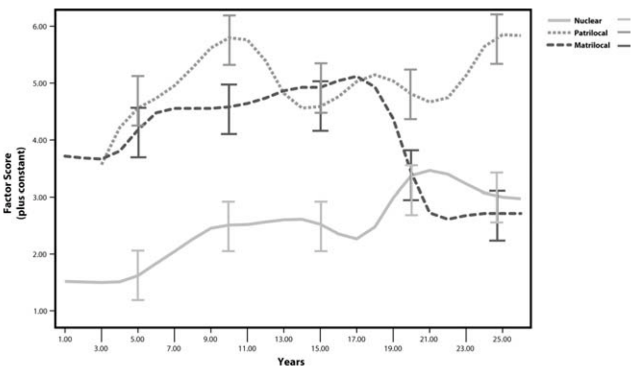

Fig. 3. Adults in household demography (number of adults, household size, family education) by household age (Error bars are 95% confidence intervals).

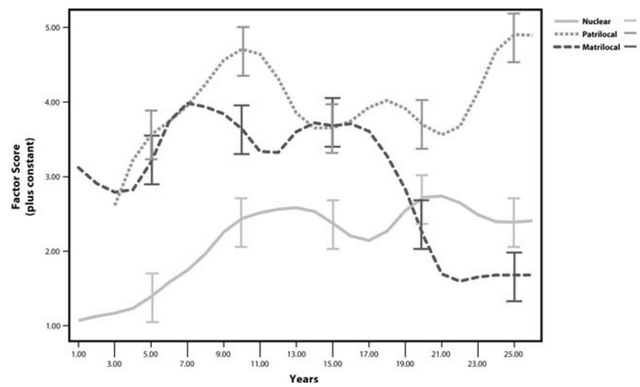

Fig. 4. Children in household demography (number of children, household size) by household age (Error bars are 95% confidence intervals).

Postnuptial residence and adult stature

Average stature was shorter among males in matrilocal (*postnuptial*) → matrilocal (*current*) (155.1 cm) households compared to males in patrilocal → patrilocal (158.5 cm, $P < 0.10$) or patrilocal → nuclear (158.0 cm, $P < 0.11$) households. Thus, the son who married into a patrilocal arrangement was in better "condition" than the son who married into a matrilocal postnuptial contract. Although the differences of 2.9–3.4 cm were biologically relevant, small sample sizes affected statistical significance (Type II statistical error). In contrast, no substantial or significant differences in statures of adult females were evident, although females in matrilocal arrangements tended to be ~1 cm taller than those in patrilocal postnuptial residence. This implied that matrilocal brides were in better "condition" than patrilocal brides, and was consistent with matrilocal residence representing an investment in daughters.

Growth status of children and residence

Z-scores for heights of children by postnuptial residence and current residence type paralleled empirical and ethnographic observations on wealth distribution (Table 5). Mean *z*-scores suggested that children in matrilocal (*postnuptial*) → patrilocal (*current*) households were significantly shorter ($z = -2.55$, $P < 0.05$) than children in patrilocal (*postnuptial*) → nuclear (*current*) households ($z = -1.94$) and patrilocal (*postnuptial*) → matrilocal (*current*) ($z = -1.61$) households. Children from matrilocal → nuclear households were also significantly taller ($z = -1.81$, $P < 0.04$) than children from matrilocal → patrilocal households ($z = -2.55$). Children from neolocal households were also slightly above average in height ($z = -1.80$, P = ns).

The growth status of children was also related to "condition" of their fathers. Matrilocal grooms were shorter (155.1 cm), i.e., in poor "condition," than patrilocal grooms (158.5 cm), i.e., good "condition," but children of matrilocal grooms were significantly taller ($z = 0.35$, $P < 0.05$) than other children in the community ($z = -1.98$), particularly children in the poorest families ($z = -2.55$; Table 5). The trend highlighted the importance of having a mother in good "condition" making investments in sons when the father was in poor "condition," i.e., matrilocal.

Sex ratio

The aggregated sex ratios of patrilocal (0.88), matrilocal (0.91) household did not significantly differ. The sex ratio was significantly reduced in low SES (0.70) compared to high SES (1.12) households ($P = 0.007$, Table 6). The sex ratio in low SES patrilocal households (mean = 0.67) indicated more females (mean = 3.5) than males (mean = 2.3), while the ratio in high SES patrilocal households (1.14) indicated more males (mean = 3.1) than females (mean = 2.7). Matrilocal households followed a similar pattern with a lower sex ratio in low SES (0.77) compared to a higher sex ratio in high SES (1.09) households.

Offspring survival

Approximately 38% of children who were born in the community survived and remained in the community to marital age; more than 50% liveborn children died before school age. After adjusting for covariates (maternal age, $P < 0.05$, age at marriage, P = ns, age at first birth, P = ns, total number of children alive at birth, $P < 0.0001$, and household age, P = ns; males adjusted $R^2 = 0.50$, females adjusted $R^2 = 0.56$), aggregated patrilocal households (investments in sons) had significantly more offspring surviving to reproductive age (mean = 5.1) than matrilocal households (investments in daughters; mean = 4.1, $P < 0.01$). Offspring survival did not differ significantly between low SES (mean = 4.7) and high SES (mean = 4.5) households, and offspring surviving to reproductive age did not differ significantly by SES in patrilocal (means: low 4.7, high 5.4) and matrilocal (means: low 4.0, high 4.2) households (Table 6).

Sex ratio and offspring survival

Number of offspring surviving to reproductive age in patrilocal households was negatively related to sex ratio, while number of offspring surviving to reproductive age in matrilocal households was positively related to sex ratio (see Fig. 5). However, regression of offspring survival on sex ratio by postnuptial residence revealed

TABLE 5. Z-scores (based on the CDC reference) for heights of children 6–14 years of age by current and postnuptial residence

	Current residence								
	Nuclear			Patrilocal			Matrilocal		
	n	M	SD	*n*	M	SD	*n*	M	SD
Postnuptial residence									
Neolocal	13	−1.80	0.99	4	−2.33	0.99	–	–	–
Patrilocal	137	−1.94	1.01[a]	72	−2.06	0.91	22	−1.61	1.01[b]
Matrilocal	47	−1.81	1.05[c]	12	−2.55	1.08[a,b,c,d]	21	−2.03	1.01

[a] Two-tailed t-test $P < 0.05$.
[b] Two-tailed t-test, $P < 0.02$.
[c] Two-tailed t-test, $P < 0.04$.
[d] Estimated mean inbreeding coefficient = 0.03; population average = 0.01 (Little and Malina, 2005b).

TABLE 6. Adjusted mean[a] number of males and females, birth sex ratio, and number of offspring surviving to reproductive age by postnuptial labor contract and SES

		Birth sex ratio								Number surviving to reproductive age			
		Males			Females								
	N^b	Mean	SE	95% CI	Mean	SE	95% CI	Sex ratio	P	Mean	SE	95% CI	P
Patrilocal													
Low SES	42	2.34	0.22	1.90–2.78	3.48	0.22	3.04–3.92	0.67	0.02	5.43	0.30	4.83–6.03	NS
High SES	42	3.10	0.22	2.67–3.53	2.72	0.22	2.29–3.15	1.14		4.74	0.31	4.14–5.35	
Matrilocal													
Low SES	20	2.53	0.32	1.90–3.15	3.29	0.32	2.67–3.92	0.77	NS	4.04	0.45	3.14–4.93	NS
High SES	23	3.04	0.30	2.45–3.63	2.78	0.30	2.19–3.37	1.09		4.22	0.43	3.37–5.07	
Combined													
Patrilocal	84	2.73	0.16	2.42–3.04	3.09	0.16	2.78–3.40	0.88	NS	5.09	0.21	4.67–5.51	0.01
Matrilocal	43	2.78	0.22	2.34–3.22	3.04	0.22	2.60–3.48	0.91		4.13	0.31	3.52–4.74	
Low SES	62	2.41	0.18	2.05–2.75	3.42	0.18	3.07–3.77	0.70	0.007	4.73	0.27	4.20–5.27	NS
High SES	65	3.08	0.17	2.74–3.40	2.74	0.17	2.40–3.08	1.12		4.48	0.26	3.97–5.00	
Total	127	2.75	0.18	2.39–3.12	3.06	0.18	2.70–3.38	0.90	–	4.60	0.26	4.08–5.00	

Prereproductive mortality sex ratio 1970–1979 (n = 215): 1.13 (male excess).
[a] Adjusted means from MANOVA/MANCOVA with SES and postnuptial contract main effects holding the following covariates constant: maternal age ($P < 0.05$), age at marriage (P = NS), age at first birth (P = NS), total number of children alive at birth ($P < 0.0001$), and household age (P = NS); males adjusted $R^2 = 0.50$, females adjusted $R^2 = 0.56$.
[b] Based on reproductive history of 123 parous females and 874 children from 123 households.

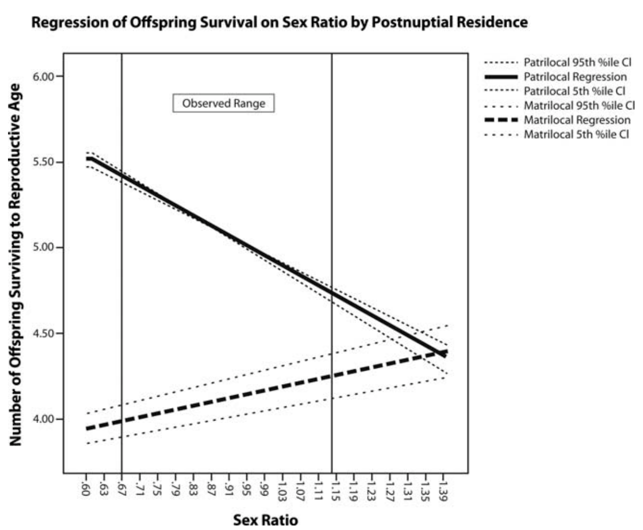

Fig. 5. Regression of offspring survival on sex ratio by type of postnuptial residence: Patrilocal (B = −1.56, SE = 0.10) vs. matrilocal (B = +0.56, SE = 0.11).

different patterns of dependency. Regression of offspring survival on sex ratio was negative, $B = -1.56$ (SE = 0.10) for patrilocal postnuptial residence (investments in sons). In contrast, the relationship between offspring survival and sex ratio was direct, $B = +0.56$ (SE = 0.11) under matrilocal conditions (investments in daughters) and differed significantly from patrilocal regressions ($P < 0.001$).

DISCUSSION

Marriage patterns and inheritance practices are proxies for parental investment as reflected in sex ratio, differential offspring survival to reproductive age and height in the Zapotec-speaking indigenous peasant community. The results link social processes with biological variation through differential parental investment in sons or daughters. Investment in daughters (matrilocal) resulted in upward mobility in ownership of wealth (irrigated land, oxen, cows, goats-Factor 1). This pattern has been noted in traditional Mesoamerican families in Guatemala that tended to cycle from being poor in one generation to rich in the next, to in between status in the third, poor in the fourth, and so on (Tax, 1952). The shortest men (reared in the poorest households) in the community fathered the tallest children (reared in the better-off households). Ownership of more wealth (agricultural resources) was associated with improved growth status during childhood, and vice versa. Socially influenced marriage behaviors thus affected investment in progeny.

Social processes (economic and marriage decisions) in the Zapotec community affected intracommunity variation in sex ratio, offspring survival to reproductive age, growth status, adult stature, and estimated inbreeding. In prior analysis, growth status, annual growth increments, and sibling correlations were significantly affected by household SES (Malina et al., 1985; Little et al., 1986, 1988). Wealth (agricultural resources) significantly affected gene–environment interaction and suppressed sibling (Little et al., 1986, 1987a, 1990) and familial correlations (Little and Malina, 2005a). A similar effect for household demography (numbers of adults and numbers of children as components of household size) was also observed presumably through gene–environment interactions. Wealth status (parent "condition") of the household significantly affected sex ratio (present study), child growth (Malina et al., 1985), and sibling correlations for growth status (Little et al., 1986). Social influences also decreased inbreeding, except among the poorest individuals (Little and Malina, 2005b). In the present analysis, sex ratio at birth (secondary sex ratio), human biological (anthropometric and genetic) variation, and differential offspring survival were affected by marriage decision.

Differences in stature of adult males by postnuptial residence (2.9–3.4 cm) were approximately the magnitude of a one generation secular increase in size (Tanner, 1992), but were not statistically significant ($P < 0.11$ or 0.10) due to small sample sizes (Type II statistical error). Differences among females were smaller and consistent with the generally accepted view that heights of females were less affected by environmental stressors than heights of males (Stinson, 1985). Adult height was used as a proxy for parental investment when the adult was a child. The shortest males were reared in poor households that apparently did not invest in sons. The "neglected" sons entered into matrilocal arrangements, which benefited their children through parental investment as evident in the increased stature of children reared in matrilocal households.

Zapotec social processes resulted in statistically significant, abrupt changes in parent "condition" (agricultural resource—Factor 1) over time (see Fig. 2). When a son or son-in-law completed his labor contract he acquired wealth (ownership of irrigated and dry land) through inheritance from his father or father-in-law. Inheritance distributed to a son or son-in-law was often a significant proportion of the land owned by the extended virilocal or uxorilocal family household (see Fig. 2), and was associated with changes in adult and child components of households (Figs. 3 and 4). The result of this planned schism or evolution was the formation of a nuclear family with wealth (i.e., fulfilled labor contract). Importantly, the bride and groom continued to acquire wealth (land) throughout the household life cycle by: a) satisfying the labor contract, b) forming a nuclear family from an extended family, c) forming an extended family from a nuclear family as children mature, and d) settling estates and distributing property when each spouse's parents die. The cycle of inheritance and distribution of wealth was associated with child growth status and adult stature. Interestingly, sex ratio was significantly affected by SES and postnuptial residence independently of one another. Thus, postnuptial residence was not a simple proxy for SES; it may likely have reflected differential parental investment.

Continued residence in a patrilocal household was associated with lower than average z-scores for childhood height, while continued residence in a matrilocal household was associated with the shortest male adults (sons-in-law), i.e., poor "condition," and average-to-above average z-scores for childhood height. It is important to note that children in nuclear households (44%) had average-to-above average z-scores, regardless of post-nuptial residence. Successful transition to a nuclear household was critical for child growth, implying that intra-household competition may be involved (i.e., larger household, more sibling competition). The helpers at the nest effect may have been a factor (Crognier et al., 2001). Nuclear households had more irrigated land, on average, than other households (Table 1), especially those formed after a matrilocal labor contract. The average age of nuclear households was about 14 years (Table 4) and reflected the first peak of resource accumulation (inheritance; see Fig. 2). Although patrilocal households had more resources (Table 1) and were older, mean of 22 years (Table 4), nuclear households had more agricultural resources, specifically irrigated land (Table 1). Patrilocal households also had more people to feed than nuclear households (Figs. 3 and 4) and were more reliant on labor intensive poorer producing land (dry land) than on irrigated land (Table 1). The preceding suggests increased intra-household competition for resources in patrilocal households which tended to invest in sons. As a result, height z-scores for children in nuclear households from patrilocal postnuptial residence were -1.94, while those for children in patrilocal residence ranged from -2.06 to -2.55 (Table 4).

Using household SES as a proxy for "condition" of the mother, poor maternal conditions were associated with a markedly lower proportion of males ($P < 0.007$), paralleling TWH predictions. However, SES did not appear to be directly associated with the number of offspring surviving to reproductive age. Rather, offspring survival appeared to be directly related to type of marriage decision (patrilocal vs. matrilocal). Socially preferred marriage practices (patrilocal) were associated with birth cohorts that had a preponderance of females (low sex ratio) and a higher mean number of offspring surviving to reproductive age compared to patrilocal households with high sex ratios (preponderance of males). On the other hand, a preponderance of males (high sex ratio) in matrilocal households was associated with higher offspring survival, compared with households with low sex ratios (more females than males), which were associated with lower offspring survival (see Fig. 5). Notably, males, grandsons of the "negotiators," had the advantage when there was less competition (lower number of siblings, lower number of adults) in matrilocal households.

Marriage practices (patrilocal vs. matrilocal) exerted a direct influence on differential offspring survival (see Fig. 5) and were associated with sex ratio, child growth and a tendency to lower inbreeding in the small breeding population. Ultimately, marriage practices affected sex ratio, survival to reproductive age, stature and endogamy. Observations on variation in sex ratio by SES were similar to predictions of parental investment in sons versus daughters and multi-generational reproductive success based on the TWH (Trivers and Willard, 1973).

Marriage preferences were associated with differential offspring survival to reproductive age. Patrilocal postnuptial residence was associated with high offspring survival (mean = 5.1) compared to matrilocal postnuptial residence (mean = 4.1). The association of offspring survival to reproductive age with sex ratio was confounded by postnuptial residence. The inverse relationship between sex ratio and offspring survival in patrilocal households contrasted the direct (positive) relationship between sex ratio and offspring survival in matrilocal households (see Fig. 5). Thus, sex ratio was apparently "influenced" by environmental conditions. Extension of the analysis to offspring survival highlights a potentially important association between socially preferred marriage patterns and differential offspring survival. While the effects were observed in the sex ratio, the analysis of offspring survival indicated that socially preferred patterns of marriage and differential sex ratios interacted to produce a significant effect on natural selection. This implies that social mobility had a reproductive fitness penalty in the community, approximately one less offspring surviving to reproductive age per generation per couple for increased wealth (mainly land holdings).

Patrilocal "strategy" was to invest in sons whose wives tended to produce more female children. As the sex ratio decreased in patrilocal households, the number of offspring surviving to reproductive age increased. Conversely, matrilocal households tended to produce more offspring that survived to reproductive age with an increasing sex ratio (see Fig. 5). Prior analysis in the community showed that the marriage patterns analyzed in the present study actually practiced decreased frequency of random inbreeding by slightly more than 40% (Little and Malina, 2005a,b).

Morbidity and mortality are consistently higher in males than in females in early life, but the underlying mechanism(s) remain unknown. The prereproductive mortality sex ratio was 1.13 in the Zapotec community, indicating a 13% male excess mortality rate. Sex differences in vulnerability early in life are usually ascribed to natural selection for optimal maternal strategies to maximize lifetime reproductive success, which is the result of differential offspring survival to age of reproduction (Wells, 2000). The child health and nutrition literature supports the premise that the ratio of male to female offspring results from differential reproductive returns on parental investment, depending on the condition of the parents, especially the mother (Wells, 2000; Rosenfeld and Roberts, 2004; Quinlan, 2007). Thus, natural selection has apparently favored maternal ability to "influence" (manipulate) offspring sex according to environmental conditions (parental "condition"), though not consciously. The association between maternal environmental conditions in early life (periconception) and variation in secondary sex ratio is an observed pattern (Cameron, 2004). By extrapolation, the same argument may apply to an extended period of parental investment, at least until weaning. The critical weakness of this line of reasoning is the lack of a biological mechanism by which these associations may operate. Several environmental stressors as diverse as undernutrition (Wells, 2000), exposure to chemicals (Amato, 1992) and hypergravity (Little et al., 1987) are associated with a preponderance of females in a birth cohort (low secondary sex ratio).

Male susceptibility to environmental stress during early life is favored by natural selection. Vulnerability of males is indicated in elevated preterm and term birth mortality rates and persistence of excess male mortality through early childhood. Chronic undernutrition per se and in synergistic interaction with infection in the preschool years may be the fundamental trigger mechanism contributing to mortality in early childhood. It is also suggested that "...whatever improvements are made in medical care, any environmental stress will affect males more severely than females in early life" (Wells, 2000). Conversely, males tend to respond more acutely to positive changes in the environment as they are a sensitive leading indicator of the secular trend (Stinson, 1985; Wells, 2000).

In summary, a system of apparently adaptive marriage practices has evolved in the Zapotec community that was associated with sex ratio, offspring survival to reproductive age and stature (child and adult). These parameters responded to environmental conditions in a predictable manner—lower SES households have relatively and absolutely more female offspring. Marriage preference as practiced in the community reduced inbreeding by slightly more than 40%. Offspring survival was higher among those who followed the socially preferred practice (patrilocal) and represented an adaptive advantage. Sex ratio responded to maternal condition with mothers in good condition producing more sons while those in poor condition producing more daughters. Biological variation (growth) and inbreeding were affected in a positive manner by the socially preferred processes and practices. Marriage practices and processes in the Zapotec-speaking community positively affected wealth distribution compared to other possibilities (widespread high inbreeding, more severe poverty for the majority). Socially preferred patrilocal residence and labor contracting is widespread in Mesoamerica. It is practiced by the Maya, Nahua, Mixtec, and Zapotec, among others (Tax, 1952; Nutini, 1961, 1967, 1968; Nader, 1964; Selby, 1974; Kellogg, 2005) and very likely predates Spanish contact (Kellogg, 2005). Further investigation of marriage practices, human biology, and genetics in indigenous communities across Mesoamerica should be conducted to validate and augment these findings.

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APPENDIX 1

Factor Analysis of Household Resources (from Little et al., 1987a)

	Environmental factors derived							
	1	2	3	4	5	6	7	C
Environmental Variable								
Lands								
Irrigated land	0.53						0.39	0.49
Dry Land							0.70	0.52
Common						0.44		0.33
Livestock								
Cow	0.59							0.41
Pig	0.49							0.27
Goat	0.48							0.30
Ox						0.62	0.20	0.47
Burro						0.49		0.34
Household								
Household size[a]		0.71	0.67					1.00
Number of adults[b]	0.21	0.86						0.80
Number of children[c]			0.91			(0.19)		0.86
Morbidity[d]				0.75				0.58
Mortality[e]				0.72				0.57
Demography								
Household age[f]	0.20				0.39			0.24
Residence[g]					0.74			0.60
Post-nuptial residence[h]	−0.27							0.11
Family Education[i]	0.25	0.25		−0.60				0.54
Supplemental Maize[j]	−0.51							0.31
Eigen value	2.83	1.72	1.31	1.05	0.72	0.63	0.51	
% Variance	32.3	19.5	15.0	12.0	8.2	7.2	5.8	

Reproduced from Little et al. (1987). **Factor 1** Primary Production Resources; **Factor 2** Household Demography; **Factor 3** Child Demography; **Factor 4** Child Mortality; **Factor 5** Residence (Nuclear vs. Extended); **Factor 6** Tertiary Production Resources; **Factor 7** Secondary Production Resources.

[a] The number of individuals in the household.

[b] The number of individuals over 15 years of age in the household.

[c] The number of individuals 15 years of age or younger.

[d] The number of individuals in the offspring cohort (birth to 15 years) who died from infectious disease (measles, gastro-intestinal, whooping cough, respiratory).

[e] The number of surviving children expressed as a percentage of the total live-born children (i.e., number of post-natal childhood mortalities + number surviving children); surviving children/live born children.

[f] Household age, the number of years the mother has been in the present household is an indicator of how far along the family unit is in the inheritance cycle, and is correlated with resources because older households tend to have more wealth.

[g] The mode of residence at the time of the survey (patrilocal-25.3%, matrilocal-13.7%, widowed-9.1%, nuclear-43.3%) indicates the stage in the traditional post-nuptial labor contract and extended family residence coded as 0 (nuclear family) or 1 (extended family).

[h] The mode of post-nuptial (patrilocal-69%, matrilocal-25%, neolocal-6%) indicates the type of residence and labor contract that was negotiated, and is associated with the distribution of wealth. Matrilocal contracts tend to be made with slightly more wealthy households, and can therefore be more rewarding in terms of inheritance and coded as 0 and 1 (patrilocal).

[i] The sum of the years of education of all members of the family divided by the number of household members six years of age or older.

[j] The amount of maize (kg) the household purchased in supplementation of the previous years harvest. This is essentially a measure of the sufficiency of production. About 51% of the households purchased supplemental grain.

C, Communalities.

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