

Early Sexual Maturity Among Pumé Foragers of Venezuela: Fitness Implications of Teen Motherhood

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ABSTRACT Because humans have slow life histories, discussions of the optimal age at first birth have stressed the benefits of delayed reproduction. However, given the diversity of ecological, fertility, and mortality environments in which humans live, reproductive maturity is expected to be highly variable. This article uses reproductive histories to examine a pattern of early menarche and first birth among the Pume, a group of South American foragers. Age at menarche and first birth are constructed using both retrospective and cross-sectional data for females over the age of 10 ($n = 83$). The objectives are first to define these patterns and then discuss their reproductive consequences. On average, Pume girls reach menarche at age 12.9, and give birth to their first child at age 15.3–15.5 (retrospective

and cross-sectional data, respectively). This populational average falls several years prior to what often is considered the human norm. Two questions are then considered. What are the infant mortality costs across a mother's reproductive career? How does surviving fertility vary with age at first birth? Results indicate that the youngest of first-time mothers (<14) are four times more likely to lose their first-borns than older first-time mothers (≥ 17). Given parity-specific mortality rates, the optimal strategy to minimize infant mortality and maximize reproductive span is to initiate childbearing in the midteens. Women gain no additional advantage in surviving fertility by delaying childbearing until their late teens. *Am J Phys Anthropol* 000:000–000, 2008. ©2008 Wiley-Liss, Inc.

Age at first birth is tied to one of life history's central tradeoff—the timing of sexual maturity and the tradeoff between adult production, which increases with body size, and the probability of surviving, which decreases with time spent growing (Charnov, 1989; Kozlowski, 1992; Roff, 1992). The pace of maturation and age at first birth affect an individual's potential life-time reproductive success, which has important implications as a force of selection. The slow maturation of primates generally and humans specifically presents a challenging life history problem since delayed reproduction carries a potentially expensive fitness cost.

Empirical evidence for the relatively late age of human maturity has traditionally been drawn from a few well-documented groups of modern foragers [the Hadza, (Blurton et al., 1992); the !Kung, (Howell, 2000 [1979]); the Ache, (Hill and Hurtado, 1996); the Hiwi, (Hurtado and Hill, 1987)]. Demographic data from these groups place the human mean age at first birth between 17.3 and 19.7 (Hawkes et al., 1998; Blurton Jones et al., 1999; Kaplan and Lancaster, 2000). Although these groups are widely cited as representative of the human norm, population and individual variation within different societies is considerable. When a broader ecological range of foragers and natural fertility populations for whom demographic data are now available is considered, mean ages at first birth vary from 16.2 to 25.7 (Walker et al., 2006).

This article uses reproductive history data to examine a pattern of early menarche and first birth among a group of South American foragers. After first situating the problem of early reproduction in the relevant reproductive biology literature on teen pregnancy, objectives are to first to describe these patterns and then discuss their fitness consequences. The purpose of this article is

not to define modal human characteristics, but to address two questions focused on constraints and variability in age at first birth. What are the infant mortality costs for women who reproduce at an early age? What are the age-specific fitness implications for women who reproduce at a young age under natural fertility, pretransitional conditions?

TEENAGE PREGNANCY AND CONSTRAINTS ON AGE AT FIRST BIRTH

Life history explanations for late human sexual maturation have stressed the importance of body size, production rates, and adult mortality (Stearns and Koella, 1986; Charnov and Berrigan, 1993; Hawkes et al., 1998), body size and fertility (Hill, 1993; Hill and Hurtado, 1996), brain size and metabolic factors (Leigh, 2004), and the interaction between investment in skill acquisition, adult production and mortality (Kaplan et al., 2000). Teen pregnancy studies from the reproductive ecology literature provide the complementary empirical

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data on the biological costs and benefits of early and delayed first birth.

Teen pregnancy is often associated with increased maternal risks of anemia, hypertension, obstetrical complications, as well as fetal, neonatal, and postneonatal mortality (Friede et al., 1987; Jolly et al., 2000; Lenders et al., 2000). The elevated incidence of infant mortality among teens is primarily attributed to low birthweight, either due to preterm birth or intrauterine growth retardation (Akinbami et al., 2000; Kramer et al., 2000). Debate over the causes of poor pregnancy outcomes among teens has largely centered on two factors: biological immaturity and socioeconomic conditions associated with being young (overview in King, 2003).

A growing mother is posed with an allocation trade-off—whether to invest in her own growth or that of her fetus. Nutrient partitioning has its greatest effect on compromised infant weight (Frisancho, 1981; Naeye, 1981; Scholl et al., 1990). In well-fed U.S. populations, pregnancy among still growing girls has been shown to lead to an energetic impasse where the metabolic needs of both the mother and fetus cannot simultaneously be met. Growing teens have significantly lower infant birth weights than fully grown adolescents and mature women (Scholl et al., 1994). Recent research suggests that maternal/fetal competition results in reduced placental mass, restricted uterine, and umbilical blood delivery, limited placental nutrient transfer and smaller offspring (Wallace et al., 2004). Although why still-growing mothers and fetuses compete for intrauterine resources when resources are abundant is not fully understood, it suggests that humans are metabolically designed to keep growing at the expense of a fetus, even when energetic constraints are relaxed.

Teen pregnancy is not only associated with adverse biological consequences, but teen mothers are also less likely to seek prenatal care or to be married, and more likely to be primiparous and socioeconomically disadvantaged. These factors have negative maternal and child health consequences irrespective of maternal age. When these confounding factors are controlled for, research results are mixed. Some studies find that the adverse age effects of teen pregnancy are greatly diminished, and maternal age has little residual effect on labor and delivery outcomes (Makinson, 1985; Geronimus, 1987; Lee et al., 1988). Low birthweight, for example, has been found to be almost entirely due to prenatal care after adjusting for confounding factors (Mahfouz et al., 1995). Other studies come to the opposite conclusion. In these cases teen pregnancy has been found to increase the risk of negative outcomes independently of known confounders (Fraser et al., 1995; Olausson et al., 1999; Jolly et al., 2000; Phipps et al., 2002; Chen et al., 2007) Although the literature is divided on this point, accumulated evidence suggests that poor pregnancy outcomes cannot be explained by socioeconomic factors alone (King, 2003).

Uncertainty in the magnitude of age-related effects that are independent of socioeconomic factors may in part reflect that older and younger teens are at very different points in their development. However, they are often treated as one group. Because rapid changes occur during adolescent growth, test results may be guided by the definition of age groups. A closer look at this debate reveals several points pertinent to applying the reproductive biology literature to address questions about the implications of early reproduction in natural fertility populations.

Studies that distinguish reproductive outcomes in early versus later adolescence find that adverse outcomes are far more pronounced for very young mothers (Lancaster and Hamburg, 1986; Forrest, 1993; Satin et al., 1994; Fraser et al., 1995; Olausson et al., 1999) and very early maturers (Scholl et al., 1989). Rates of infant mortality, very low birthweight and preterm delivery are significantly greater among mothers 15 and younger compared to older teens. The incidence of these risks plateaus among older teens, whose risk levels more closely resemble those of adults (Phipps et al., 2002; Phipps and Sowers, 2002). Very early maturers, defined as girls who reach menarche before age 11, are at increased risk of ectopic pregnancy (Sandler et al., 1984), intrauterine fetal growth retardation (Scholl et al., 1989) and miscarriage (Martin et al., 1983). Because these negative outcomes also may be prevalent among late maturers, it is unclear whether risk is concentrated among young maturers because of their developmental immaturity or because of different underlying hormonal profiles.

Although negative biological and social consequences are associated with very young mothers and very early maturers, several questions remain unanswered. First, in life history terms sexual maturation marks a shift in investment of surplus energy from growth to reproduction. However, this is a protracted process that takes 10 or more years to complete in humans. Girls in their mid teens may not be fully grown, but have accomplished most of their growth. Negative biological consequences are associated with early reproduction not because of chronological maternal age per se, but because of relative developmental immaturity (Altmann, 1986). If teen mothers are within the range of normal in terms of age at menarche and are developmentally mature, or mostly mature, is early reproduction constrained by high infant mortality?

Second, most of what is known about the biological and social costs of teen pregnancy has been studied in urban, acculturated populations with low mortality and fertility demographic regimes. We know relatively little about these costs in predemographic transition environments of high child mortality and high fertility, conditions more akin to the human evolutionary reproductive milieu. Concern with early reproduction has focused largely on adverse effects to teen mothers and their infants. However, fitness, a theoretic measure of differential survival and reproduction, is mediated through both life-time mortality and fertility. To evaluate the adaptive significance of early reproduction, the cost across a mother's reproductive career, not just to mothers in their teens, needs to be considered. For example, while poor infant and fetal outcomes are greatest for the youngest of mothers, these risk factors are as high or higher among older mothers (Garn et al., 1986). What then are the fitness costs of early reproduction to mothers across their reproductive careers?

This article addresses these questions using data from a natural fertility population of South American foragers. The Pumé are an ideal population to observe the consequences of early reproduction for several reasons. While the delay between physical maturity and exposure to conception may be considerable in many human populations, among the Pumé, girls initiate conjugal relations soon after menarche and do not have access to contraception. Teenage marriage and pregnancy is sanctioned, often encouraged and not associated with negative social

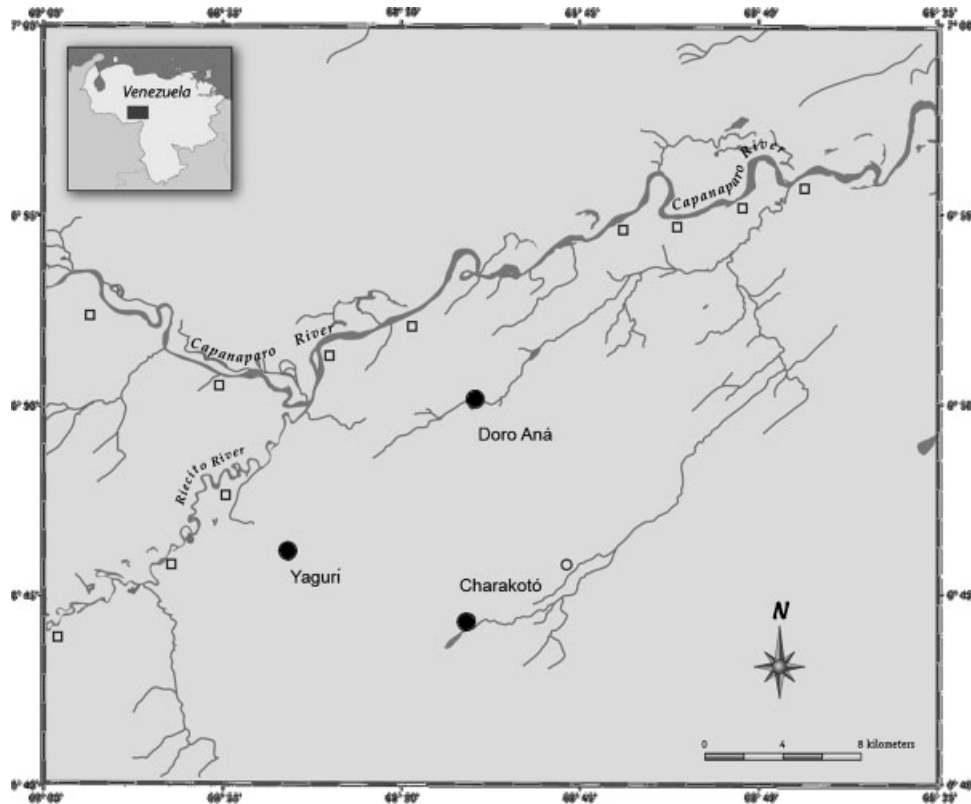


Fig. 1. Savanna Pumé study communities.

consequences. Because Pumé teen mothers are not stratified by identified confounding socioeconomic factors such as individual differences in education, marital, and wealth status, and do not have access to health care or prenatal care, the biological costs of early reproduction can be more clearly observed.

MATERIALS AND METHODS

Study population: Pumé foragers

The Pumé (Yaruro) inhabit the savannas (*llanos*) of southwest Venezuela. The Pumé economy is distinguished by geographic differences in habitation and subsistence. The river Pumé, who live along tributaries of the Orinoco River, reside in permanent villages and have a mixed subsistence economy of fish, manioc cultivation, animal husbandry, and occasional wage labor (Petrullo, 1939; Leeds, 1961; Leeds, 1964). In contrast, the savanna Pumé, who are the focus of this paper, live between these major river courses and are mobile foragers. The first detailed studies of savanna Pumé occurred in the 1980s (Gragson, 1989) and in the 1990s (Greaves, 1997; Hilton and Greaves, 2004; Greaves, 2006). The following describes the savanna Pumé of Dora Aná, Yagurí, and Charakotó as they were living during the 2005–2006 study (see Fig. 1).

The savanna Pumé move several times throughout the year between dry and wet season camps in response to hyperseasonal fluctuations in rainfall. Although inter-annually variable, six main camps were documented for Dora Aná during the 2005 annual seasonal round. During the six-month dry season, subsistence centers on

fish, which are concentrated in restricted pools and small segments of streams, and on mangos collected from wild groves not under cultivation. Related clusters of nuclear families live in ephemeral brush-shade camps located adjacent to streams and lagoons to take advantage of water and proximity to fishing locations.

When the llanos flood during the wet season, the Pumé move their camps to higher ground and families aggregate into more substantial thatch houses (Mitrani, 1988; Gragson, 1989; Greaves, 1997, 2006). Fish are dispersed and difficult to locate during the wet season, and the resource base shifts to small game, wild roots, and manioc. Garden foods are consumed during part of the wet season, when they supply about 35–40% of daily calories. Gardens are small and bitter manioc is the only successfully cultivated plant food. Substantial amounts of wild roots are collected throughout the wet season. Poor agricultural soils, low resource density, and diversity contribute to the generally impoverished savanna Pumé diet. Nutritional stress, extreme in some years, is most pronounced during the wet season when protein and fat are in short supply.

None of the three study communities has a school, health clinic, store, electricity, well water, or can be reached by permanent road. The savanna Pumé are monolingual, and very few individuals speak any Spanish. No savanna Pumé has attended school or is literate. They have access to a few nonlocal goods through a trade with the more acculturated river Pumé, who live along the navigable rivers that are the major transportation routes into the region. A trade network between the savanna and river Pumé has likely been in place since they have lived in the region. Axes, machetes, knives,

and clothing, which are well-worn when they are brought into the savanna interior by visiting river Pumé, are exchanged for arrowcane, fiber, resin, weaving materials, and finished arrows. Periodically when the government distributes rice and pasta in the river communities, these market foods may make their way into the exchange system.

Health care workers occasionally come into the region, but these visits are limited to the more accessible river communities. Vaccination teams visited the savanna interior in the past, but children have not been inoculated for the past 10 years. Children grow up, mature and begin to reproduce in an environment with no access to modern health care and few market foods.

Reproductive environment

Pumé girls marry at a young age, with 95% of girls having been married by age 14. The teen birth rate is 195 births/1,000 women ages 15–19. This compares to 110 per 1,000 teens in Bangladesh, which has one of the highest reported teen birth rates at the national level, to 90/1,000 in Venezuela (Population Reference Bureau, 2007), and 41.1/1,000 in the U.S. (Center for Disease Control, 2007). Marriage prior to the onset of menses is not uncommon. These early marriages are often brittle, and either partner can instigate divorce. Serial monogamy is the predominate marriage pattern, although a small proportion of adults (11%) marry polygamously. Matrilocality is common, and no out-marriage with non-Pumé was reported.

The savanna Pumé period total fertility rate of 7.41 is within the range of other natural fertility populations (Bentley et al., 1993; Campbell and Wood, 1988). The high Pumé TFR suggests that although the Pumé experience seasonal undernutrition, dry season resources are sufficiently abundant to support relatively rapid reproduction. Cohort fertility rates show a similar pattern, with women 40 and older having a completed fertility of 7.40 (Kramer and Greaves, 2007). The similarity in the period and cohort fertility rates suggests that mortality and the age pattern of childbearing has been stable over recent decades (Preston et al., 2001).

Infant mortality also is markedly high among the savanna Pumé. The infant mortality rate of 34.6% recorded in 2000–2005 (Kramer and Greaves, 2007) corroborates with previously documented high levels among the Pumé (Barreto et al., 1991). Of the few groups of mobile foragers for whom infant mortality has been reported, the Pumé rate is higher than that for the Hadza, !Kung and Ache, but similar to rates reported for the Agta, Asmat and Mbuti (Hewlett, 1991; Pennington, 2001). Of Pumé mothers 15–25, 40% experience at least one infant death by their second child, and all mothers have had a child die in infancy by their fifth parity. While young nursing infants are buffered to some extent from disease and malnutrition, after supplemental foods are introduced at six months, maternal condition affects infant health and well-being (Brown, 2003). Lactation under suboptimal dietary conditions, which savanna women can count on for half of each year, can have long terms effects on infant health (Little et al., 1992; Sellen, 2000). Maternal energy depletion during the wet season, when women lose up to 8% of their body weight, coupled with high pathogen loads, no doubt contribute to infant stress and mortality. Infanticide has never been noted in the Pumé ethnographic or demographic literature. Nor

have any cases occurred since the 1990s studies by Greaves (unpublished data).

Data collection

Reproductive histories were collected in three Pumé foraging villages in 2005 and recollected for updates and verification in 2006. All households in each of the study communities participated in the interviews, which were conducted in the Pumé language. This study builds on data collected in the 1990s (Greaves, 1997), which provides a baseline to track longitudinal information on age, births, marriages, deaths, and growth patterns.

Small-scale, nonliterate societies pose certain methodological challenges and sampling constraints not encountered in large, acculturated study populations. Forager communities, and thus sample sizes, are often small. The lack of vital records and counting systems precludes obtaining event dates or age by calendar day, month and year. Kin relationships are often reckoned in terms that do not necessarily distinguish biological from classificatory relatives. These problems are ameliorated to some extent by repetitive questioning, age-ranking techniques, and utilizing past censuses and longitudinal information.

Despite limitations, research among small-scale populations is critical to expand knowledge of the range of human biological variation not otherwise represented in urban and industrialized populations. The study of small-scale forager societies is a rapidly disappearing opportunity to observe life histories under fertility, mortality, and energetic conditions that more closely resemble the ancestral past than low fertility, low mortality, contraceptive populations.

Females ages 10 and older ($n = 83$) were interviewed and asked about their age, when their first menses occurred, their marital status, to list their siblings, parents, spouses and children from each marriage, the ages of these individuals and whether they were living or deceased. Mothers can accurately report the ages of young children up to four years by season or moon counts. Several methods are used to ascertain ages of older children and adults (Howell, 2000 [1979]; Pennington and Harpending, 1993; Hill and Hurtado, 1996; Kramer, 2005a).¹

In addition to collecting reproductive histories from mothers, all village members old enough to respond (~10 and older) were interviewed and asked about their parents, and to list their siblings and children in ranked birth order. Asking multiple relatives about kin relations provides a check for information consistency and whether further questioning was needed (Fricke, 1994; Howell, 2000 [1979]). Because the Pumé use specific kin terms to reference older and younger siblings, this provided a means to corroborate relative and absolute ages. Importantly, detailed censuses (name, age, sex, and kin affiliation) were collected in the study communities several times throughout the 1980s and 1990s (Lizarralde unpublished data; Greaves unpublished data). These provide an invaluable baseline to anchor the age of most individuals over the age of 12.

Multiple questioning and birth rank responses were also a useful check to verify that a woman's reproductive history included a complete count of her children. Past

¹A few older individuals were issued national identity cards in the 1970s. The birthdates given on these cards appear to be guesses and are often clearly incorrect.

TABLE 1. Age at menarche for savanna Pumé females

Sample	Age at menarche	Range
Cross-sectional data ($n = 36$)	12.75 ^a	12–14
Retrospective data		
Group 1 ($n = 7$)	13.59 (SD \forall .78)	12.6–14.9
Birth day, month and year, and menses month and year known		
Group 2 ($n = 16$) ^b	12.87 (SD \forall 1.02)	11.3–14.9
Birth year, and menses month and year known		

^a Estimated from a probit function in a logistic regression procedure modeling the probability of having reached first menses among girls ages 10–20.

^b No significant difference in mean age at menarche between Group 1 (95% CL = 12.87–14.31) and Group 2 (95% CL = 12.33–13.41).

censuses were used to confirm that mothers, especially older mothers, included children who may have died some time ago. Mothers were asked to include infants who were stillborn or who had died very young in their list of children. Because of the difficulty in obtaining consistent information about miscarriages, a woman's reproductive history includes only full-term parturitions.

The Pumé are forthcoming in discussing children from previous marriages, and whether they are alive, living elsewhere or deceased. Parents can accurately report age at death by developmental markers such as weaning, walking, talking, tooth eruption, menses, and childbirth. Documenting specific age at death, rather than by developmental stage, is more problematic since the Pumé do not mark elapsed time in calendar dates. A young child who had died but whose parents could not give age at death in moon counts, was identified as an infant if he or she was breastfeeding but not walking. Observationally, children with known ages begin to walk at about a year old.

Women interviewed in 2005 and 2006 can recall the date of their first menses or birth of their first child by moon counts if the event occurred within several months of the interview, or by season counts if it occurred within the last several dry/wet season cycles. First menses is an important event both in a young girl's life and for the community. Greaves (1997), who worked in these study communities from 1990–1993, documented the birthdates of many of the young women who are now reaching sexual maturity and becoming first time mothers, and recorded the dates when young women first visited the menstrual hut.

A woman's birthdate, her first menses or first birth are known to the day if the event occurred during the 1990–1993 or 2005–2006 field seasons. A woman's birthdate, her first menses or first birth are known to the month if it occurred within several months, or to the season if it occurred within several dry/wet season cycles of the 1990–1993 or 2005–2006 field work. For mothers and firstborns with known ages but imprecise day or month counts, midyear maternal and child birthdates are used to bracket age at first birth, and maternal age is expressed in year intervals.

RESULTS

Age at menarche and first birth are estimated using both cross-sectional and retrospective data. During reproductive history interviews women were asked about their current reproductive status, whether they had had their first menses or had given birth. These cross-sectional data indicate, for example, what proportion of

female's ages 10–20 in the current population have reached menarche or given birth to their first child at each successive age. To take advantage of the finer-scaled date data and to increase the sample to include older women, retrospective data from the reproductive histories are used to estimate central tendency and variation in age at first birth. Because of the relatively small sample sizes, calculating age at menarche and first birth in several ways assures that the strength of the results rests on more than one estimate. All statistical analyses were performed in SAS version 9.1.3 (2002–2003 SAS Institute, Cary, NC).

Age at menarche

Menarche is an important gateway to reproductive maturity and a readily documented event. The frequency distribution from the 2006 cross-sectional sample of Pumé girls ages 10–20 ($n = 36$) shows that no girl under the age of 12 has had her first menses, 83% of 13-year-old girls have, and all girls 14 and older have had their first menses (Table 1). Median age at menarche estimated using probit transformation in a logistical regression procedure (Eveleth and Tanner, 1990) is 12.75.

Although a small sample, age at first menses is very well bracketed for young Pumé women since those who had their first menses during or shortly before the 2005–2006 survey were born during or shortly before the 1990–1993 field work. To calculate mean age at menarche from retrospective interviews, date precision is ranked in a nested hierarchy. For girls whose birthdate (year, month, and day) and first menses are known to the year, month, and/or day (Group 1, $n = 7$), mean age at menarche is 13.59 (SD = 0.78, range 12.6–14.9). For girls whose birth year, at minimum, and first menses year, month, and/or day are known (Group 2, $n = 16$), mean age at menarche is 12.87 (SD = 1.02, range 11.3–14.9). The difference in mean age at menarche between Group 1 (95% CL = 12.87–14.31) and Group 2 (95% CL = 12.33–13.41) is not significant.

Age at first birth

Cross-sectional results from the 2006 interviews of females 14–68 ($n = 50$) show that one girl under the age of 15 has given birth, 63% of females 17, and younger have given birth to their first child, and all women over the age of 18 have had their first child, except one 40-year-old woman. A logistic modeling procedure is used to model the probability that a female aged 10–25 ($n = 27$) has given birth to her first child. The fitted distribution

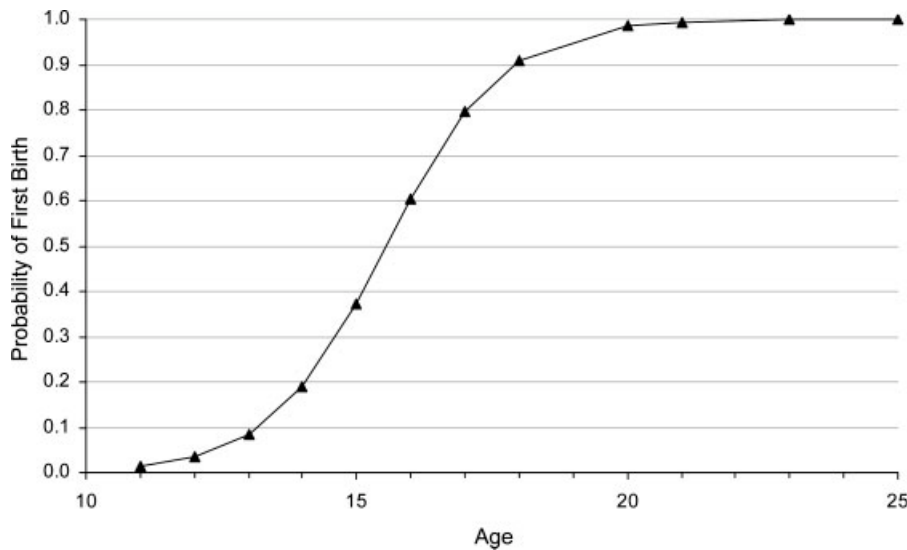


Fig. 2. Fitted distribution function for Pumé women 10 to 25 ($n = 27$) ever having given birth. Median age at first birth given at the 0.5 probability.

TABLE 2. Mean birth intervals calculated from birthrates (women-years-at-risk of pregnancy divided by the number of live births) given infant mortality experience of savanna Pumé mothers 15–25 ($n = 17$)

No of infant deaths to mothers	Birth interval (years)
0	2.62
1	2.54
2	2.07
3	1.75

function indicates that 25% of Pumé women gave birth before the age of 15, and 50% before they turn 16 (see Fig. 2). The median age at first birth taken from the 0.5 probability is 15.5.

To calculate age at first birth from the retrospective interview data, a subset of mothers with the highest quality reproductive history and age data was culled. Mothers were included whose birthdates were either recorded during 1990–1993 fieldwork, or whose ages are known from past censuses and whose first child's birthdate likewise is well bracketed, either as observed during previous fieldwork, or whose ages as young children were repetitively recorded in past censuses. This inclusion criteria is not expected to bias the sample toward an older or younger age at first birth. The final sample includes 26 mothers ages 14–44. For mothers whose firstborn child is living, or if deceased the child's birth year is known, age at first birth is given by subtracting the mother's and firstborn's birthdates. For mothers whose firstborn child is deceased, birth interval established from the last living child was used to estimate mother's age at first birth.

Studies in natural-fertility breastfeeding populations consistently demonstrate that birth intervals are substantially shorter following an infant death because of the positive effect that the cessation of lactation has on postpartum amenorrhea, anovulation, and subfecundity (Chowdhury et al., 1978; Grummer-Strawn et al., 1998).

TABLE 3. Age at first birth for savanna Pumé mothers

Sample	Age at first birth	Range
Cross-sectional data ($n = 27$)	15.5 ^a	14–23
Retrospective data		
Group 1 ($n = 3$)	15.07 (SD \forall 0.98)	14.3–16.2
Group 2 ($n = 20$)	14.65 (SD \forall 1.51)	11.8–17.1
Group 3 ($n = 28$) ^b	15.36 (SD \forall 2.20)	11.8–22.9

^a Estimated from fitted distribution function modeling the probability of Pumé females ages 10–25 having given birth. Median age given at the 0.5 probability.

^b No significant difference in mean age at first birth between Group 2 (95% CL = 13.94–15.36) and Group 3 (95% CL = 14.51–16.21) level data.

This relationship linking infant mortality and birth interval provides a means to adjust the length of a birth interval following an infant death based on known birth intervals when a child survives. An average birth interval is first calculated from birthrates (1/[live births within the interval/years-at-risk of pregnancy within the interval]; Neel and Weiss, 1975). Since women have most of their children in their twenties (64% of children are born by age 29), only the reproductive histories of mothers 15–25 ($n = 17$) were used to calculate birth intervals at different levels of infant death experience. Including older women inflates risk years relative to a small increase in births.² As expected, average birth intervals calculated from birthrates decrease with a mother's infant mortality experience (Table 2). When a

²Birth interval length and parity may be associated at higher parities and older ages. The sample here includes mothers 15–25, which limits it to women who have had five or less children. Sensitivity tests including mothers of different ages showed little to no difference in the IBI estimates up until about age 30. This suggests that if parity does affect IBI, it is restricted to older women. Although this cannot be formally demonstrated because of size constraints in further stratifying the sample, a parity effect is expected to be fairly minimal in Pume women 25 and younger.

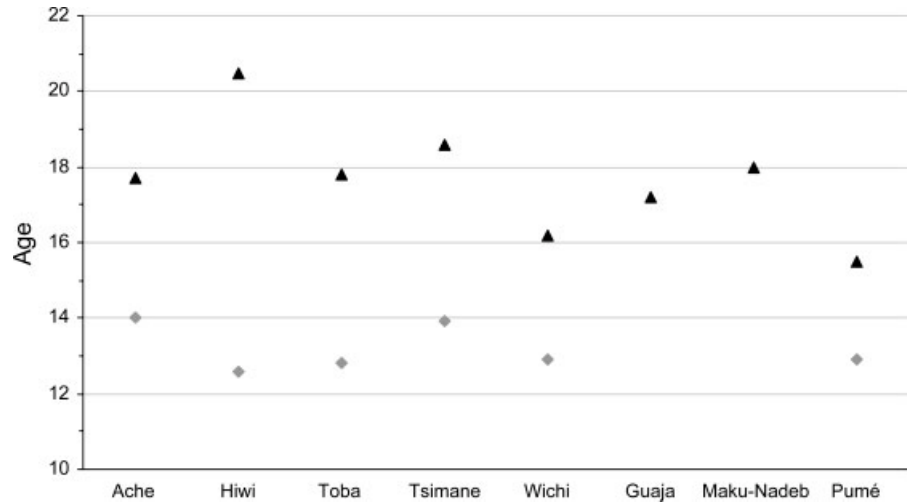


Fig. 3. Age at menarche and first birth among South American foragers. Sources: Ache (Hill and Hurtado, 1996); Hiwi, Toba, Tsimane, Wichi, Guaja, Maku-Nadeb (Walker et al., 2006: Table 2).

mother's firstborn(s) is deceased, these values are used to work back from the last living child to estimate a mother's age at first birth.

Mothers were then ranked in a nested hierarchy based on the precision of a mother's and her firstborn's birthdate. Group 1 includes mothers and firstborns whose birthdates are known to the day ($n = 3$). Group 2 includes mothers and/or firstborns whose birthdates are known to the month, at minimum ($n = 20$). Group 3 is the most inclusive and includes mothers and firstborns whose birthdates are known to the year at minimum ($n = 28$). The mean age at first birth for the few women whose birthdate and the birthdate of their firstborn are known to the day (Group 1), is 15.07 (Table 3). The mean age of first birth for the Group 2 level data is 14.65, and for Group 3 is 15.36. The difference between Group 2 (95% CL = 13.94–15.36) and Group 3 (95% CL = 14.51–16.21) is not significant.

When compared with the other groups of South American foragers, Pumé age at menarche is within the range of variation of other groups (see Fig. 3). Age at menarche varies from 14.0 among the Ache to 12.6 among the Hiwi, who live in a similar environment in close geographic proximity to the Pumé. Menarche is clinically considered precocious, often the outcome of a pathology, if it occurs much younger than age 12 (Moerman, 1982; Ibáñez et al., 2006). All but one Pumé girl was 12 or older, and the Pumé can be considered normal with respect to age at menarche. Mean age at first birth, however, is early. Pumé women on average give birth to their first child considerably younger than other native South Americans, and before their late teens, the age often cited as the human norm.

Fitness consequences of early reproduction

Two questions are considered to evaluate the adaptive implications of early Pumé reproduction. How young is too young to initiate childbearing with respect to the cost of infant mortality? And, how does fertility vary with age at first birth across a mother's reproductive career?

A multivariate regression model is first constructed to observe whether the age at which women initiate child-

TABLE 4. Modeling results to predict age-specific fertility as a function of age, a quadratic term for age and age at first birth for Pumé mothers ages 14–45 ($n = 34$)

Variable	PE	SE	P-value
Age	0.58490	0.0703	<0.0001
Age 2	-0.0054	0.0010	<0.0238
Age at first birth	-0.3776	0.0589	<0.0001

Model $R^2 = 0.8896$; $P = <0.0001$.

bearing raises or lowers their potential life-time fertility. The outcome variable is age-specific fertility and predictor variables include age, a quadratic term for age and a continuous term for age at first birth ($n = 34$ women ages 14–45, $R^2 = 0.8896$, $P < 0.0001$).³ When the age terms are controlled for, age at first birth is a significant predictor of age-specific completed fertility (Table 4). This result is expected as demographers have long recognized that the age pattern of marital fertility is an important predictor of completed fertility (Coale, 1967; Dyson and Murphy, 1985; Campbell and Wood, 1988). Fitting the regression model, women who initiate childbearing at the population mean of 15.5 are predicted to have 7.56 children by the end of their reproductive careers. This corroborates with the TFR of 7.41 documented for the same communities (Kramer and Greaves, 2007).

All else being equal, women who start childbearing at younger ages should have longer reproductive careers and higher completed fertility. These advantages may also come at a cost. Although clinical studies show that young teens are at an increased risk of infant mortality, little is known about the age effects of teen motherhood in predemographic transition populations characterized by both high fertility and mortality. Using Group 2 date data, women whose firstborns die in infancy are signifi-

³Sample size analysis shows that the model is powered at 99.9% at an alpha of .05 and an n of 34. In other words there is 0.01% chance of making a type II error and accepting the null hypothesis when it is not true. The model is sufficiently powered to detect the effect of age at first birth on age-specific fertility.

TABLE 5. Odds ratios for firstborn infant mortality by age at first birth for savanna Pumé mothers

Age at First Birth ^a	N	% Infant mortality ^b	Odds ratio	95% CI	P-value
Firstborn					
Young (<14)	9	55.6	4.25	0.28–2.61	0.0152
Average (14–16)	18	22.2	0.97	–1.12 to 1.06	0.9573
Late (≥17)	15	6.7	1.00	–	–

^a Mothers stratified by those who gave birth to their firstborn one standard deviation below the mean (young), those within one standard deviation of the mean (average) and mothers one standard deviation above the mean (late).

^b Percent infant deaths per live births in each age group.

cantly younger on average (13.7, 95% CL = 12.9–14.5, $n = 9$) than women whose firstborn survives (15.4, 95% CL = 14.3–16.4, $n = 10$, $P = 0.0122$).

To further evaluate which age groups are at greatest risk of infant mortality, mothers are stratified into three groups. Mothers who gave birth to their first child within one standard deviation of the mean are ranked as average reproducers (ages 14–16). Mothers are ranked as young reproducers (younger than 14) if they gave first birth to their first child one standard deviation below the mean. Mothers whose age at first birth is greater than one standard deviation above the mean are ranked as late reproducers (17 and older). A logistic modeling procedure is used to analyze the probability of a mother's firstborn dying in infancy. Odds ratios, the exponentiated parameter estimates, indicate the relative risk of infant mortality for mothers in one age group relative to a referent group. Since mothers age 20–24 have the lowest rates of adverse outcomes, they are usually used as the referent group to evaluate the relative risks of teen pregnancy (Fraser et al., 1995). However, because so few Pumé women give birth for the first time in their 20s, late reproducers are used as the referent group. Odds ratios show that young reproducers are four times more likely to lose their firstborn, compared to late reproducers (Table 5). Average reproducers, however, are not at significantly greater risk. Mothers age 14–16 are as likely to lose their firstborn in infancy as older first-time mothers.

To test the significance of age-related differences in infant mortality through later parities, age at first birth is expressed as a categorical term and mothers are again stratified as young, average and late reproducers. The youngest of mothers are significantly more likely to lose their firstborn compared to mothers in their midteens (Table 6). While the youngest of mothers also have a high probability of losing their second borns, the difference is not significant. Infant mortality experience does not significantly vary between average and late reproducers for any parity.

If the youngest of mothers have an elevated risk of infant mortality in the first parity, how does this reticulate through her reproductive career? To take advantage of empirical parity-specific mortality probabilities, the combined effects of infant mortality and fertility are summarized in a model of surviving fertility given the level of infant mortality at each parity (see Fig. 4). Values for infant mortality of the first born are taken from Table 6. Since differences in infant mortality between first-birth age groups are not significant in subsequent parities, infant mortality rates are averaged across the three groups at each parity. These rates are as follows: parity 2 = 0.333, parity 3 = 0.324, parity 4 = 0.345, parity 5 = 0.364, parity 6 = 0.35, parity 7 = 0.40, parity

TABLE 6. Proportion infant deaths per live births by parity for savanna Pumé mothers

Parity	Age at first birth ^a		
	Young (<14)	Average (14–16)	Late (≥17)
1 ($n = 44$)	0.56 ($P = 0.0299$)	0.20 ($P = 0.3273$)	0.07
2 ($n = 39$)	0.45 ($P = 0.6489$)	0.35 ($P = 0.4971$)	0.23
3 ($n = 34$)	0.17 ($P = 0.1969$)	0.47 ($P = 0.1958$)	0.23
4 ($n = 29$)	0.40 ($P = 0.7288$)	0.31 ($P = 0.7288$)	0.36
5 ($n = 22$)	0.50 ($P = 0.8040$)	0.40 ($P = 0.8040$)	0.30

p -values compare the infant mortality experience of young and average, and average and late reproducers.

^a Mothers stratified by those who gave birth to their firstborn one standard deviation below the mean (young), those within one standard deviation of the mean (average) and mothers one standard deviation above the mean (late).

8 = 0.71, parity 9 = 0.63. The increase in later parities is expected (Fretts et al., 1995). These values then are used to calculate cumulative surviving fertility for the typical young, average and late reproducer. Young reproducers have a lower surviving fertility at each parity. After the eighth child (TFR = 7.41), mothers who initiated childbearing in their early teens have to have an additional child to catch up to mothers who started in their mid and late teens. While they may be young enough to have that additional child, few Pumé women give birth to more than eight children.

In sum, 90% of Pumé mothers have their firstborn child in their teens, with a population average in their midteens (Table 7). Infant mortality is also high. The youngest of mothers (<14) have the greatest probability of losing their first born, four times that of mothers who initiate childbearing in their late teens. Infant mortality is high across later parities for all first-birth groups, though probabilities do not significantly vary between groups. The net outcome of fertility and mortality is summarized in a model of surviving fertility as the typical young, average, and late reproducer moves through her reproductive career. Given parity-specific mortality probabilities, mothers who initiate childbearing in their early teens have lower surviving fertility at each parity compared to mothers who initiate childbearing in their mid and late teens. To recoup the elevated risk of infant mortality in the first parity, the youngest first-birth mothers must have an additional child. While they may do so, this is energetically a more costly strategy to achieve the same level of surviving fertility. Those young mothers, however, who do not lose their first born would raise their lifetime fertility. A range in age at first birth may exist because some proportion of Pumé women benefit from initiating reproduction at these very young ages. Mothers who wait until in their midteens lower their probability

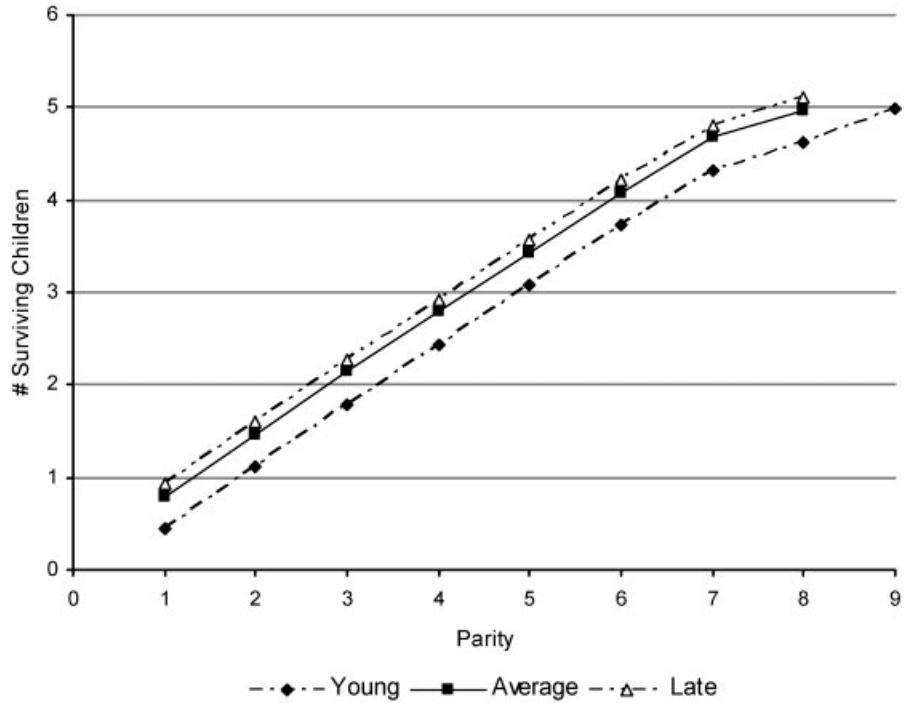


Fig. 4. Model of life time surviving fertility given level of mortality at each parity for Pumé females ($n = 44$) who initiate childbearing young (<14), on average ($14-16$) and late (≥ 17). Table gives data used in graph, showing empirical probabilities of infant mortality, infant survival and cumulative number of surviving children at each parity for young, average and late reproducers.

TABLE 7. Data supporting Figure 4

Parity	Young			Average			Late		
	Dying	Surviving	No. of children	Dying	Surviving	No. of children	Dying	Surviving	No. of children
1	0.56	0.44	0.440	0.20	0.80	0.800	0.07	0.93	0.930
2	0.33	0.67	1.107	0.33	0.67	1.467	0.33	0.67	1.597
3	0.32	0.68	1.783	0.32	0.68	2.143	0.32	0.68	2.273
4	0.35	0.65	2.438	0.35	0.65	2.798	0.35	0.65	2.928
5	0.36	0.64	3.074	0.36	0.64	3.434	0.36	0.64	3.564
6	0.35	0.65	3.724	0.35	0.65	4.084	0.35	0.65	4.214
7	0.40	0.60	4.324	0.40	0.60	4.684	0.40	0.60	4.814
8	0.71	0.29	4.614	0.71	0.29	4.974	0.71	0.29	5.104
9	.63	0.37	4.989						

of losing the first born, but they gain no advantage in surviving fertility by delaying childbearing until their late teens.

DISCUSSION

Two conditions are necessary for an individual to initiate reproduction—fecundity and exposure to conception. In many human societies, while sexual maturity is a constraint on age at first birth, it does not determine its timing. In natural fertility populations, the lapse between menarche and exposure to conception is highly variable, and may last one to two years up to over a decade (Whiting et al., 1986; Schlegel, 1995). In a recent cross cultural study of foragers and horticulturalists (Walker et al., 2006), the mean duration between menarche and first birth is 4.5 years. Among the Pumé the lapse between menarche and first birth averages 2.6 years. Several explanations may account for this short duration, the early Pumé age at first birth, and highlight directions for future research.

Biologically, age at first birth is mediated by age at menarche and the duration of subfecundity. Attention

has been paid to the onset of menarche because it is a discreet event that marks the transition from partial to full reproductive potential (Altmann, 1986). Since the secular trend in age at menarche was first recognized, good and improved childhood nutrition and health have been associated with earlier menarche, and poor childhood conditions with delayed menarche (Foster et al., 1986; Gain, 1987; Eveleth and Tanner, 1990; Riley et al., 1993; Ellis, 2004). Although this assumption is still deeply embedded in the literature on puberty, growing evidence supports that suboptimal prenatal and childhood conditions also lead to early maturation (Cooper et al., 1996; Ibáñez et al., 2000; Adair, 2001; Koziel and Jankowska, 2002; Coall and Chisholm, 2003). Many native South Americans, as the Pumé, reach menses at an age comparable to contemporary urban populations (Eveleth and Tanner, 1990: Table 10; Bentley, 1999: Table 1; Walker et al., 2006: Table 1). Although genetic determination may explain some portion of populational differences in the mean age at menarche (Towne et al., 2005), the Pumé results support findings that early menarche is not only associated with good or improved nutritional and energetic circumstances, but also occurs under marginal conditions.

Several studies indicate that girls who reach menarche early have a proportionally shorter duration of subfecundity and time to establishment of adult ovarian function. A comparison of Kikuyu (East African horticulturalists) and urban British girls found that earlier maturing girls progress more quickly through the pubertal sequence (Worthman, 1987; Worthman, 1993). Apter and Vihko (1983) find that girls who reach menarche at age 12.0–12.9 achieve 50% ovulatory cycles, which is considered normal adult function, 3.0 years after menarche. In contrast, girls who are 13.0 and older at first menses, achieve adult function 4.5 years after menarche (but see Foster et al., 1986). Mean populational differences in menarcheal age are negatively related to ovarian function as inferred from midluteal progesterone levels. Importantly, this advantage holds throughout a woman's reproductive career. In populations with a mean age at menarche less than 13, women have higher levels of midluteal progesterone during their prime reproductive years (Ellison, 1996). Early menarche, thus, may confer a negative effect on the duration of subfecundity and a positive influence on life-time fertility.

The period between sexual maturity and first birth is also mediated through cultural norms that restrict exposure to conception. Pumé girls often cohabit with spouses in adolescence and begin coital relations soon after menarche. Although a behavioral trend between early menarche, and early marriage and first birth is evidenced in natural fertility populations (Urdu and Cliquet, 1982; Sandler et al., 1984; Borgerhoff Mulder, 1989; Wood, 1994), some residual variation in age at first birth cannot be explained by menarcheal age. Comparison between the Hiwi and Pumé is a case in point. The Hiwi and Pumé live in the same general environment, have similar seasonal nutritional constraints, and reach menarche at a relatively early age. However, they differ considerably in age at first birth. Average age at first birth among the Hiwi is 17.9–22.5, depending on estimate (Walker et al., 2006), compared to 15.5 among the Pumé. The extent to which the Hiwi later age at first birth is due to a longer period of subfecundity or delayed exposure to conception is unknown, but raises the question about optimal age at first birth and fitness outcomes.

Life history models emphasize the importance of body size, production rates and mortality to explain taxonomic differences in optimal age at first birth (Kozłowski, 1992; Charnov and Berrigan, 1993). Because humans have slow life histories, discussions of the optimal human age at first birth have stressed the benefits of delayed reproduction. Explanations for postponing first birth include ecological constraints associated with competitive mating environments (Boone, 1988; Clarke and Low, 1992; Strassman and Clarke, 1998; Low, 2000), enhanced skill acquisition and adult energy production (Kaplan et al., 2000), and lower adult mortality rates (Hill and Kaplan, 1999). On the other hand, early maturation is expected when survival is low or variable (Chisholm, 1999). Although researchers emphasize different aspects of the mortality curve (subadult mortality, adult mortality, child mortality), it is generally agreed that when life expectancy is low, life histories are early and fast (Geronimus, 1992, 2003; Wilson and Daly, 1997).

Here I have considered infant mortality and its effect on surviving fertility. It is unknown to what extent elevated infant mortality among the youngest of mothers is the outcome of maternal-fetal competition because of developmental immaturity. However, because infant mor-

tality is significantly lower among mothers in their mid-teens compared to mother in their early teens and only in the first parity, it suggests that biological immaturity has a threshold effect on teen pregnancy.

The optimal age to initiate reproduction also depends on age-specific maternal mortality. If young reproducers have a higher probability of dying from childbearing related causes, this clearly offsets the fertility advantage of young reproduction. In a model to predict optimal age at first reproduction among the Ache, adult forager mortality is low enough that in delayed reproduction it does not offset the more costly effects of a shortened reproductive span and reduced fertility (Hill and Hurtado, 1996). Although age-specific mortality rates for Pumé mothers are unknown, the ratio of Pumé maternal to child deaths over the past 15 years is 1:20, suggesting that in high exogenous mortality environments, child mortality plays a greater role in fitness outcomes and population growth potential.⁴ Current research is directed at developing a life table for this population.

Given the diversity of ecological, social, epidemiological, fertility, and mortality environments in which humans live, flexibility in life histories is not unexpected (Chisholm, 1996; Ellison, 2001; Bateson et al., 2004; Ellis, 2004). Research on the timing of human reproduction has primarily addressed the dynamics behind delayed reproductive development. The Pumé data indicate that variability in human reproduction includes a strategy of early first birth. As part of ongoing research, this article has focused on implications of age at first birth to fertility and infant mortality outcomes. Increased foraging productivity and maternal competence, factors that affect female reproductive success, are important benefits of delayed reproduction (Lancaster, 1986; Kaplan and Lancaster, 2000; Lancaster et al., 2000). Pumé mothers in their mid teens may be less skilled and less productive than older first-time mothers. The extent to which young mothers can rely on social support to help subsidize their dependent young is known to affect the number of children mothers can successfully raise (Hrdy, 1999; Kramer, 2005a,b). Subsequent analyses will address how the time allocation and productivity of kin, and the help mothers receive from others affect variability in age at first birth, fertility, and survival of offspring. Comparisons of Pumé women's age at first birth and the effects of allocare, matrilineal residence and the extensive food sharing observed among savanna Pumé may clarify why they initiate childbearing comparatively earlier than the few groups of other well-studied foraging populations.

CONCLUSIONS

Negative consequences are commonly associated with teen pregnancy in acculturated populations that have already passed through the demographic transition. However, teen motherhood is prevalent in many natural fertility populations and the norm among traditional agriculturalists and foragers. Even so, most Pumé girls become mothers at comparatively early ages, initiating childbearing on average at 15.5. The analysis then

⁴Using the 1992 census as a baseline population of women, 2 of 26 (7.7%) mothers under the age of 31 in 2006 died between 1992 and 2006, and 40 of their 78 children (51.3% of births) born in the same time interval did not survive.

turned to variation within the population to assess the adaptive implications of the early Pumé first birth and how Pumé females might make the best of high mortality conditions. The combined fertility and mortality outcomes (surviving fertility) across the reproductive span indicate the generational effects that different first birth strategies have on the force of selection.

Mothers negotiate a series of changing constraints over the course of their reproductive careers. Mothers who initiate reproduction too young, compromise their own and their child's survival. Mothers who delay, have a shorter reproductive spans and risk the compounded effect of negative pregnancy outcomes at older maternal ages (Hansen 1986; Fretts et al., 1995). A mother's ability to compensate for these constraints, adjust birth intervals, and thus fertility potential, is affected by the time and energetic constraints of supporting pregnancy, lactation, and provisioning older children. Women who initiate reproduction at different ages, consequently face different tradeoffs in the costs and benefits associated with infant mortality and the length of their reproductive careers.

The Pumé results concur with the reproductive biology literature that the youngest of mothers (<14) have an elevated risk of losing their firstborns. Pumé mothers who delay childbearing until their midteens, however, are no more likely to lose their firstborns compared to older first-time mothers.

When surviving fertility is modeled across a mother's reproductive career, mothers who initiate reproduction at the youngest ages, have a lower surviving fertility at each parity. Because of the higher probability of losing their first child, young reproducers can not recoup that loss, compared to late reproducers, without having an additional child over the course of their reproductive career. This is a potential energetic cost that mothers who delay childbearing until their midteens do not pay.

Two points are made from the perspective of a young Pumé woman starting her reproductive career. First, the optimal strategy to minimize infant deaths is to wait until her midteens to have her firstborn. Second, women in their midteens gain no additional advantage in significantly lowering infant mortality or raising the number of surviving children by delaying childbearing until their late teens. Both early reproduction and low infant mortality are advantageous. This tradeoff—maximizing reproductive span and minimizing infant mortality—is best resolved by delaying first birth until the midteens. Nonetheless there is heterogeneity in the timing of first birth. The extent to which this variability is due to individual differences in menarcheal age or other factors can be addressed in future research as the sample size of young Pumé girls reaching menarche and giving birth for the first time increases.

These results raise new questions: how do Pumé women adjust birth intervals under conditions of high mortality; do women who initiate reproduction earlier, have their last child at a younger age. As longitudinal study continues, we will augment our understanding of the early first birth to address these and other questions.

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