Original Research Article

Early Reproductive Maturity Among Pumé Foragers: Implications of a Pooled Energy Model to Fast Life Histories

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ABSTRACT
Life history theory places central importance on relationships between ontogeny, reproduction, and mortality. Fast human life histories have been theoretically and empirically associated with high mortality regimes. This relationship, however, poses an unanswered question about energy allocation. In epidemiologically stressful environments, a greater proportion of energy is allocated to immune function. If growth and maintenance are competing energetic expenditures, less energy should be available for growth, and the mechanism to sustain rapid maturation remains unclear. The human pattern of extended juvenile provisioning and resource sharing may provide an important source of variation in energy availability not predicted by tradeoff models that assume independence at weaning. We consider a group of South American foragers to evaluate the effects that pooled energy budgets may have on early reproduction. Despite growing up in an environment with distinct seasonal under-nutrition, harsh epidemiological conditions, and no health care, Pumé girls mature quickly and initiate childbearing in their midteens. Pooled energy budgets compensate for the low productivity of girls not only through direct food transfers but importantly by reducing energy they would otherwise expend in foraging activities to meet metabolic requirements. We suggest that pooled energy budgets affect energy availability at both extrinsic and intrinsic levels. Because energy budgets are pooled, Pumé girls and young women are buffered from environmental downturns and can maximize energy allocated to growth completion and initiate reproduction earlier than a traditional bound-energy model would predict. Am. J. Hum. Biol. 21:430–437, 2009. 

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Life history models provide important frameworks for understanding many aspects of human ontogeny and reproduction. These models are robust tools for predicting differences in how long an individual should invest in growth before initiating reproduction. This fundamental life history tradeoff builds on the principle that metabolic investments are made among alternate expenditures relative to fitness payoffs. An individual expends energy to support basic maintenance (BMR, organ function, cellular repair, and immune responses) and activity functions. Energy balance in excess of these essential metabolic expenditures can be spent on production. In an immature individual, production is allocated to growth and becomes available for reproduction at sexual maturity (Charnov, 1991; Stearns, 1992). Underlying this shift in energy allocation is the assumption that the energy available for growth and reproduction is constrained by an individual’s metabolic budget (Fig. 1a). For most mammals, maternal support ends at weaning. Following weaning, an individual’s energetic budget is limited by the ability to provide its own resource needs, and growth rates are constrained by a juvenile’s own foraging efforts. However, the assumption that an individual’s metabolic budget is bound is inconsistent with human patterns of extended juvenile provisioning and resource sharing. These human patterns provide an important source of variation in the energy available for growth and reproduction.

In all human societies, metabolic costs are distributed across social units through both direct calorie exchanges and labor transfers (Fig. 1b). Unlike other mammals, the full complement of food resources and activities necessary for human growth and reproduction is funded by multiple individuals and rarely is an individual reliant only on self-provisioning. In addition to sharing food production and processing costs, shared labor extends to many other domestic, manufacture, and childcare tasks. These food and labor transfers occur across age and sex classes within biological families and in most forager societies also between more distantly related households. Food subsidies and activity underwriting may be cross-culturally organized in many ways. Economic units that pool food and labor not only vary in size and composition but only under dire circumstances does an individual in any society grow and reproduce on his or her own. Rather than construct a model that addresses hypothetically comprehensive sharing and redistribution conditions, we delineate a simple, but flexible, model. The model considers that if the energy available for growth and reproduction is not constrained by self-provisioning, then the timing of maturity and age at first birth may vary in ways not predicted by individually bound-energy models.

Given the assumptions of a bound-energy model, fast life histories pose a paradox in our understanding of energetic budgets and allocations. An early investment in growth and a larger body size at a younger age consigns an individual to higher maintenance costs. An individual making rapid gains in body size also is less able store reserves in the form of body fat. When immune systems are challenged or downturns in environmental conditions
occur, a juvenile must make facultative decisions among allocations to growth, maintenance and activity. If these are competing energetic expenditures, then the mechanisms responsible for assuring adequate energy to sustain a fast growing juvenile are not explained by current model parameters. We consider the ethnographic example of the Pumé, a group of South American foragers who initiate childbearing in their midteens, to investigate the effect that pooled energy budgets may have on fast female life histories. Our use of a pooled energy model is an extension of arguments about juvenile provisioning, and the fitness benefits of nonmaternal assistance (Bogin, 1999; Hawkes et al., 1997; Hrdy, 2005; Kramer, 2005a; Turke, 1988).

Young Pumé females draw extensively from pooled energy budgets and benefit from shared resource and redistributed labor costs. We distinguish a pooled energy from cooperative breeding because, in the human case, the flow of resources occurs intergenerationally in both directions. Most cooperative breeding models focus on unidirectional flows from helpers to young. However in humans, while older sexually mature individuals subsidize children, children also contribute to the energetic budgets of their siblings and to the reproductive budgets of their mothers and other adults (Kramer, 2005b).

**PUMÉ FORAGERS**

The Pumé inhabit southwestern Venezuela, a low lying, hyperseasonal plain drained by tributaries of the Orinoco River. The Pumé who live on the savannas (llanos) between these major rivers are mobile foragers. The savanna Pumé move camp five to six times a year in response to hyperseasonal rainfall variation and changes in the water table. During the six-month dry season, subsistence centers on two resources, fish and wild mangos. Related nuclear families live in ephemeral camps adjacent to streams and lagoons to be near water supplies. When the llanos flood during the wet season, camps are moved to higher ground and families aggregate into more substantial thatch houses (Gragson, 1989; Greaves, 1997a, 2006; Mitrani, 1988). Fish are dispersed and difficult to locate during the wet season and the resource base shifts to small game, wild roots, and bitter manioc (Greaves, 1997b). Low plant diversity and density and an impoverished terrestrial game contribute to the seasonally depauperate savanna Pumé diet.

During both the dry and wet seasons Pumé men’s and women’s foraging activities focus on different food resources. Of the total time that men and women allocate to dry season subsistence, males perform most fishing, and women engage in about 60% of the mango collection. During the wet season, men hunt and women forage for roots (Gragson, 1989). Because game returns are small and women’s food returns are greater and more reliable (Greaves, 1997a,b), both plant and animal resources are critical to the subsistence base and widely shared. Food availability varies considerably between the dry and wet seasons. Food is most abundant during the dry season, when fish and mango are plentiful. Nutritional stress, extreme in some years, is most pronounced during the wet season. Combined with low food returns, wet season stress is exacerbated by greater exposure to disease (Barreto and Rivas, 2007).

None of the three savanna study communities have a school, health clinic, store, electricity, well water, nor can they be reached by permanent road. The savanna Pumé are monolingual. Very few speak any Spanish and none in our sample have attended school or is literate. The savanna Pumé have access to a few nonlocal goods through trade with the river Pumé, their horticultural neighbors who live along the major rivers that are the transportation routes into the region. In the past, vaccination teams sporadically visited the savanna interior. Some older individuals have been immunized, but these visits have not occurred for some time and very few children (n = 3) in the study communities have been inoculated in the last 10 years.

Most foraging models focus on unidirectional flows from helpers to young. However in humans, while older sexually mature individuals subsidize children, children also contribute to the energetic budgets of their siblings and to the reproductive budgets of their mothers and other adults (Kramer, 2005b).
portion of marriages are polygynous. Of men and women ever married, 11% (n = 94) are currently or have been polygynously married sometime in the past. Sororal polygyny is the most common form of plural marriage.

Savanna Pumé girls grow up and mature in an environment with distinct seasonal undernutrition, annual fluctuations in food supply, and harsh epidemiological conditions. They have no access to modern health care, supplemental food programs or immunization. Despite these conditions, Pumé girls have fast life histories. The savanna Pumé are an ideal population to consider the effects of energy availability on the timing of reproduction for three reasons. First, while the delay between physical maturity and exposure to conception is considerable in many human populations, Pumé girls engage in conjugal relations soon after menarche, have no access to contraception, and give birth on average 2.6 years after the onset of menses. While the Pumé live in a physiologically challenging environment, emotional stressors known to affect early maturity are not evident (Boyce and Ellis, 2005; Chisholm et al., 2005). Women enjoy friendly, supportive marriages and families, and autonomy in decision making. Consequently, age at first birth largely reflects fecundity rather than cultural factors regulating either delayed or precocious exposure to conception. Second, while physiologically mature, Pumé girls commonly give birth before they mature as foragers or caretakers. Young Pumé girls and young women receive a large proportion of their calories from older individual’s foraging returns. Lastly, females are not stratified by individual differences in education, marital and wealth status, or access to resources and health care. In the absence of these confounding factors known to have heterogeneous effects on the pace of maturity, we can more clearly address the potential effects of pooled energy budgets on reproductive timing.

**Female maturation patterns**

The following description of Pumé female growth and maturation events draws from data collected in three Pumé foraging villages during 2005–2007. Age at menarche and first birth are calculated from census data and retrospective reproductive history interviews. Anthropometric data were collected on 74 females aged 4–40 years (97% of the females in the three savanna communities). Stature was taken using a stadiometer and recorded to the nearest millimeter for all adults and children over the age of two. Weights were measured using a Health-o-Meter digital scale to the closest tenth of a kilogram. Young children who could not stand on their own were weighted by subtracting mother’s weight while holding the child. The cross-sectional anthropometric data presented here were collected during the 2006 dry season. Pregnant women (n = 4) are not included in weight calculations. Lactating women are included, since deleting them would eliminate the majority of adult women in the sample (Kramer, 2008; Kramer and Greaves, 2007).

Small-scale, nonliterate populations pose challenges in establishing ages and sampling constraints not encountered in large, acculturated study populations. These limitations are common among foragers and a number of methods have been developed to construct reliable age estimates under these circumstances (Hill and Hurtado, 1996; Howell, 2000 [1979]; Kramer, 2005a). All household members, not just heads of households, were interviewed. Individuals 12 and older were asked to list their siblings and children in ranked birth order. Asking multiple relatives about kin relations and birth orders provides a check for conflicting information and identifies cases needing further clarification. Children’s ages up to two years old can be reliably recalled in moon counts by Pumé parents and other community members. The Pumé use specific kin terms to reference older and younger siblings. These terms are a cross check to corroborate relative ages within sib groups. Importantly, detailed censuses were collected in the study communities several times throughout the 1980s and 1990s and are invaluable to anchor the ages of most individuals currently in their adolescence and older. Birth and maturational dates are well bracketed for girls. Greaves has worked with the Pumé since 1990 and during his field work recorded the birth dates, first menses, and first birth events of many girls in the sample. Reproductive history interviews were conducted in the Pumé language, reducing translation and interpretative mistakes. While it is ideal to have date precision to the day, this is not feasible in the absence of written birth records. Some variation in age precision across individuals exists, introducing a potential range of deviation from true age up to a year for some individuals. Despite these challenges, research among small-scale foragers is a quickly disappearing opportunity critical to expand knowledge about the range of human variation not represented in more acculturated populations.

Distance curves are constructed from cross-sectional heights and weights (n = 50). Individual values are smoothed using a nonparametric LOWESS procedure. To retain individual variation, an interpolation value of 0.3 is used. This low-resolution value avoids over-fitting the data while not obscuring age differences in growth parameters. LOWESS smoothing techniques are less sensitive to the influence of outliers than OLS regression procedures, which are based on a parameterized structure and can impose expectations about the adolescent growth spurt. These smoothing procedures follow those employed in other small sample growth studies (Johnson, 2003; Leigh, 1996; Leigh and Shea, 1996). To situate Pumé growth comparatively, height and weight are standardized for populational body size differences by expressing values as the proportion of mean adult body size (Fig. 2). We include the CDC growth reference as a basis for comparison and not for the purpose of characterizing Pumé health.

As shown in Figure 2, by the end of juvenility, at age 10, Pumé girls have reached 87% of mean adult stature (151.2 cm), and 56% of the mean adult weight (50 kg). Compared to a recent large-sample study of foragers and horticulturalists (Walker et al., 2006), Pumé juvenile girls are at the very upper end of the range of variation in height for age, and in the middle range of weight for age. Comparison with the CDC reference shows a similar pattern. Pumé girls are taller during juvenility and smaller during later adolescence relative to adult size when compared to this reference. Although the age pattern of growth differs from reference expectations, final Pumé adult stature is normal with respect to other native South Americans (Fig. 3; Diaz Ungría, 1966; Salzano and Callegari-Jacques, 1988).

Savanna Pumé girls reach menarche on average at age 12.96. Many girls become pregnant for the first time several years after menarche. Average age at first birth is 15.5
and 90% of Pume´ women have their first-born child between ages 15 and 19 (Kramer, 2008). While age at menarche is normal compared to other native South Americans, age at first birth is early. The mean age at first birth among foragers natural fertility populations is usually placed between 17.3 and 19.7 depending on groups included (Blurton Jones et al., 1999; Hawkes et al., 1998; Kaplan and Lancaster, 2000). When a greater diversity of natural fertility populations are considered, the range varies between 16.2 and 25.7 (Walker et al., 2006). While the Pume´ initiate childbearing at a relatively young age, we emphasize that their age at first birth is biologically predictable given the age at menarche, a normal period of subfecundity, and that marriage and sexual activity occur soon after menarche. Previous research showed that early childbearing is the best fitness strategy for Pume´ women to minimize the effects of high infant mortality and maximize their reproductive span (Kramer, 2008). The youngest mothers (<14) have an elevated risk of losing their first born. Mothers who initiate childbearing in their midteens, however, are no more likely to lose their first-borns than older first-time mothers. Fertility and mortality outcomes suggest that early childbearing is the optimal reproductive strategy for Pume´ girls maturing in a harsh environment.

**FAST LIFE HISTORIES**

**Limitations of extant mortality and energetic explanations**

Early age at reproductive maturity has been explained from a number of interrelated perspectives. Here we consider mortality and energetic explanations and then present a modification of the bound-energy model to explain fast Pume´ life histories.

Both theoretic life history models and empirical studies support that extrinsic mortality rates are an important indicator of age at first birth (Charnov, 1993, 2002; Hawkes and Paine, 2006; Purvis and Harvey, 1995). Although empirical studies emphasize different aspects of the mortality curve (subadult mortality, adult mortality, child mortality), it is generally agreed that when life expectancy is low or survival variable, life histories are fast and early (Chisholm, 1999; Geronimus, 1992, 2003; Migliano et al., 2007; Walker et al., 2006; Wilson and Daly, 1997). The Pume´ developmental pattern supports this association between high mortality and early reproduction.

Pume´ have a high infant mortality rate, 346 infant deaths per 1,000 live births, with 35% of newborns not surviving their first year (Kramer and Greaves, 2007). Ten percent of children who survive infancy do not reach reproductive age. This level of survival is similar to rates established for other groups of foragers. Gurven and Kaplan (2007) find that among foragers in their sample (!Kung, Ache, Hadza and Hiwi), 57% of children survive to age 15. Model life tables at appropriate levels of age distribution and birth and death rates (model east level 5) place Pume´ life expectancy at 30 (Coale and Demeny, 1983). Although early Pume´ reproductive maturity is associated with high mortality, this explanation is at odds with our current understanding of energy allocation under epidemiologically stressful conditions.

In immunologically challenging environments, a greater proportion of an individual’s maintenance budget is allocated to immune function. In a variety of animals,
immune activity has been shown to raise metabolic rates and energy expenditure (Martin II et al., 2003; Ots et al., 2001). Mounting even a mild immune response can incur a significant energetic cost and a reduction in energy available for alternate expenditures (Derting and COMPTON, 2003). Immune defense, especially fevers, are potentially costly with every one degree increase in body temperature estimated to raise BMR by 7–15% (DuBois, 1937; Elia, 1992; Roe and Kinney, 1965; Stettler and others 1992). Among the Tsimane in Amazonian Bolivia, children with elevated levels of immune defense have lower short-term gains in stature (McDADE et al., 2008). If growth and maintenance are competing energetic expenditures, all else being equal, immune stress, which raises maintenance are competing energetic expenditures, all else being equal, immune stress, which raises maintenance costs, should decrease energy available for growth.

Pumé girls grow up in an environment with high immunological stress, seasonal undernutrition, chronic intestinal parasite loads, nominal access to market foods, and no access to health care or immunization (Barreto and RIVAS, 2007). Cause of death is primarily opportunistic infections, gastro-intestinal disease, malaria, and complications resulting from undernutrition. While we do not know the direct energetic costs of immune function expenditures, given the assumptions of a bound-energy model, Pumé girls would be expected to have less energy available for growth, to grow slowly and delay reproductive maturity. Because they do not, it raises a question about the mechanisms that sustain fast life histories.

Foraging returns and implications of a pooled energy budget

To explain Pumé early reproductive maturity, we propose that energetic constraints imposed by a food limited and immunologically challenging environment are offset through pooled energy budgets (see Fig. 1b). We use time allocation data to consider return rates for two principle female food sources. Roots and mangos are a substantial portion of the overall diet, represent the majority of female caloric contributions to the diet, and are produced almost exclusively by Pumé girls and women. Mangos are gathered in large quantities during the dry season, when they are a critical calorie source, comprising an estimated 60% of the diet. Roots are available throughout the year but are collected in much greater quantities during the wet season when they comprise approximately 40% of the diet (Greaves, 1997a). Return rates are drawn from 200 root collection trips and 149 mango collection trips. Return rates are calculated as the amount of time spent foraging divided by the weight of the resource collected (Fig. 5). Compared to prereproductive girls, older women produce 1.7–6 times the amount of food per unit time, depending on resource and age group. Compared to young women who are initiating reproduction for the first time, older Pumé women produce 1.1–2 times as much food per unit time depending on resource and age group. This age pattern is not surprising and has been documented for other foragers (HAWKES et al., 1997; HURTADO et al., 1992). We present foraging returns here to illustrate two important points with respect to energy availability and the traditional bound-energy model.

First, individual foraging effort is not proportional to individual metabolic requirements. While a range of variables may explain variation in return rates, the focus here is on the relationship between energy input and body mass. In a bound-energy model, an individual must fund any change in body size or reproductive status through an increase in energy input by that individual’s own efforts. While efficiency may vary with age and some down-regulation in basal metabolic rates may occur, for example, during the early stages of pregnancy, the only means available to a self-provisioning animal to increase energy input is to spend more time in the activities that produce food. Given the assumptions of a bound-energy model, Pumé return rates should correlate with body mass. However, body mass is a poor predictor of foraging effort among Pumé females (Table 1), suggesting that some females underproduce and some overproduce relative to their metabolic requirements. Foraging returns of both older women and men far exceed the level of their own consumption and are shared out to other members of their community. Girls and young women benefit from the overproduction of others, not only through direct transfers of food, but importantly by reducing the time and energy that they would otherwise expend in foraging activities to meet their own metabolic requirements.

Second, any downward adjustment in activity levels increases the energy available for alternate expenditures. A relatively large proportion of an individual’s total daily metabolic costs is expended in activity. In a sample of rural subsistence populations, for example, 35–58% of total daily caloric expenditure is spent in physical activity (Leonard, 2003). Other research has shown that Pumé girls allocate very little time to economic activities compared to other populations for whom time allocation data are available for children (Kramer and Greaves, 2008).

TABLE 1. Pearson correlation coefficients and p-values for the relationship between Pumé return rates and female body mass

<table>
<thead>
<tr>
<th>Resource</th>
<th>r</th>
<th>p</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small roots</td>
<td>0.24197</td>
<td>0.0365</td>
<td>75</td>
</tr>
<tr>
<td>Large roots</td>
<td>0.12022</td>
<td>0.1928</td>
<td>119</td>
</tr>
<tr>
<td>Mangos</td>
<td>-0.12938</td>
<td>0.1052</td>
<td>158</td>
</tr>
</tbody>
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Fig. 5. Foraging return rates (mean and S.E.) for Pumé females aged 6–60 years stratified by age group and shown for small roots (n = 75 person trips), large roots (n = 125 person trips), and mangos (n = 149 person trips).
Pumé girls spend about 0.65 h per day in subsistence activities, an amount closely comparable to !Kung girls (Draper and Cashdan, 1988), known to expend little effort in foraging tasks (Hames and Draper, 2004). If Pumé girls did not receive food from others, they would have to substantially increase their foraging effort and their caloric expenditure on physical activity. Because energy budgets are pooled, Pumé girls and young women can maximize energy allocated to the completion of growth and initiate reproduction without increasing the time and energy they expend in activities that produce food.

**DISCUSSION**

Recent research points to the interesting paradox that fast life histories occur under both good and bad conditions. 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. However, evidence now supports that suboptimal prenatal and childhood conditions also can lead to early maturation (Adair, 2001; Belsky et al., 1991; Chisholm, 1993; Coall and Chisholm, 2003; Cooper et al., 1996; Ibáñez and Jankowska, 2002; Walker et al., 2006). Why exposure to suboptimal energetic, health, mortality, and emotional conditions has both accelerating and suppressing effects on female life histories poses new questions.

Young women negotiate a number of constraints to initiate childbearing. Mothers who start reproduction too young may compromise their own growth or their child’s well-being and survival. Mothers who delay first birth risk not surviving to reproductive age and having shorter reproductive spans. Since both a larger body size and early reproduction are advantageous, the timing of female sexual maturity is often modeled as a tradeoff. In the classic life history framework, energy available to parse among alternative expenditures (maintenance, activity, growth, and reproduction) is constrained by a weaned individual’s self-production. However, in human populations, the energy available for growth is not bound by a juvenile’s ability to produce energy nor is a first-time mother’s reproductive budget limited by her own resource acquisition. While this is a simple observation, it is inconsistent with the assumptions of a bound-energy model. The question we ask here is whether a modification of the traditional model is appropriate to more fully explain observed fast life histories.

Skeletal maturation is the key physiological factor determining age at menarche and the transition to final reproductive maturation (Ellison, 1981, 2001). Early investment in skeletal growth is advantageous in advancing reproductive maturity but is potentially risky. A larger body size at a younger age is achieved at the cost of fat accumulation. When environmental downturns occur or immunological stress is high, a larger juvenile is more vulnerable to low fat reserves. While adult Pumé women lose on the order of 6% of their body weight during the wet season, juvenile girls experience no decline in weight (Kramer and Greaves, 2007). This suggests younger females are buffered against seasonal fluctuations because food is preferentially shared to them and/or because of downward adjustments to their activity levels. Both supplemental feeding and reduced energy expenditure are known to have positive effects on female reproductive maturation (Gillett-Netting et al., 2004; Jasienska and Ellison, 1998; Kramer and McMillan, 2006) and growth (Gibson and Maze, 2005; Leonetti et al., 2007). Energy available for growth or reproduction can vary through two pathways: extrinsic energy harvested from the environment and through intrinsic allocations among alternate expenditures. Extrinsic energy availability is ecologically sensitive, and all animals face at least periodic shortfalls and abundances in food availability, as well as fluctuations in disease stress. Given variable environmental conditions, different intrinsic allocations are predicted based on the assumptions of a bound or pooled energy model. For a growing individual, a greater commitment to past statural growth means less energy is stored to utilize during shortfalls. When downturns in environmental conditions occur, or if immune systems are challenged, an individual makes facultative decisions about intrinsic energy allocations. Because a self-provisioning juvenile may have little recourse to offset fluctuations in environmental conditions, conservative growth rates minimize starvation risk and avail more energy for immune function. However, a juvenile who is subsidized may have other options.

We suggest that pooled energy budgets affect energy availability at both environmental and intrinsic levels. Food subsidies raise overall energy availability and smooth fluctuations in foraging returns. If variance in energy availability is attenuated, juvenile growth rates can be set at a higher mean level without compromising energy available for maintenance and immune function. Although little is known about the priority interests of intrinsic energy allocations, any downward adjustment in activity levels should leave more energy available for growth and maintenance. Because the lower productivity of girls is compensated by food inputs from others, they work less than otherwise would be needed to meet metabolic requirements. The observed fast growth of juvenile Pumé girls (see Fig. 2), early first birth (see Fig. 4), and lower return rates of girls and young women relative to body size (see Fig. 5), suggest that fast Pumé life histories are accomplished through energy transfers.

Pooled energy budgets have several implications for the timing of first birth. Biologically humans can successfully reproduce well before they can competently support children. Menarche is cued to skeletal maturity and occurs after girls have accomplished 95% of their statural growth (Ellison, 1981, 2001). This human growth pattern delays fecundity and minimizes the probability that females will conceive before the near completion of growth. While selection has been strong against fecundity among skeletally immature juveniles, the onset of reproduction is not linked to economic maturity. Women in many traditional societies have their first-born well before they are economically independent or are competent childcare providers.

At age 15.5 young Pumé women are mature neither as foragers nor as caretakers. Pooled energy budgets offset the lower competence and productivity of young mothers and attenuate conflicts in allocating energy to reproduction and subsistence activities. Cross-culturally, young children growing up in traditional societies receive about 50% of their childcare from their mother (Goodman et al., 1985; Hames, 1988; Kramer, 2005a; Valeggia, in press). The balance comes from various nonmaternal sources of allocare. Previous research among the Maya, a group of Yucatan subsistence agriculturalists, showed that an esti-
mated 60% of the calories that the mother needs to support her children comes from individuals other than herself (Kramer, 2005b; Robinson Sullivan et al., 2008). While human age at maturity is often characterized as delayed, if young mothers were not subsidized, childbearing would be even further delayed. From that perspective, humans initiate reproduction surprisingly early compared with current model expectations.

While physical maturity is a constraint on first birth, it does not determine its timing in humans. Because first birth also is conditioned by behavioral practices that mediate a young woman's exposure to conception, age at first birth may not be a reliable indicator of the switch point in energy reallocation from growth to reproduction. It may, however, indicate the availability of allocate and dependable metabolic support for reproduction. If young Pumé mothers relied solely on their own efforts, they would have to delay childbearing until they matured as foragers and caretakers. Pooled energy budgets permit young women to reproduce before they are otherwise ready to support childrearing.

All human groups pool energy. We expect cross-cultural variation in the kinds of resources that can be harvested in excess of individual consumption needs, the age structure of overproducers, who receives surpluses, and how these factors affect activity budgets, metabolic allocations, and life history outcomes. Variability in allocations to activity is an aspect of the tradeoff model that has received little attention but is expected to have a substantial impact on the residual energy available for growth and maintenance. The Pumé case is presented as an example that lower activities levels and food subsidies can offset metabolic tradeoffs and free energy for other maintenance and growth expenditures. A pooled energy model may help explain fast life histories in challenging nutritional and epidemiological environments.

LITERATURE CITED


