Cooperative Breeding and Adolescent Siblings

Evidence for the Ecological Constraints Model?

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In humans, alloparents are usually thought to be grandmothers and adolescent girls. Although many studies have examined the influence of grandmothers on child outcomes, fewer have explored the effect of adolescents on such outcomes. We tested the hypothesis that in a community of Ecuadorian Shuar horticulturists, adolescent girls would have a positive influence on the growth and development of younger siblings. We measured height, weight, and skin fold thicknesses of children and young adults and computed body mass indexes (BMIs). Contrary to predictions, adolescent girls had a strong, significant negative impact and boys had a positive impact on child growth and nutrition: the age-standardized BMI of children with all adolescent sisters was 1.7 SD below the age-standardized BMI of children with all adolescent brothers. In this population, adolescent girls have many mating opportunities, whereas adolescent boys do not. It is therefore possible that instead of pursuing marriage opportunities, adolescent boys might have invested in younger siblings.

Introduction

Offspring in most animal species receive resources and care only from the mother—for example, via nutrients supplied with the egg or, in viviparous species, during gestation. In mammals, offspring also receive substantial maternal resources and care during an extended juvenile period. For reasons that are still debated (e.g., Houston, Székely, and McNamara 2005; Kokko and Jennions 2003; Queller 1997; Wade and Shuster 2002), paternal investment in offspring is much less common. Nevertheless, investment in offspring by bio-

logical parents presents little challenge to Darwin's theory of natural selection.

In contrast, alloparental care, in which offspring receive investment and care from individuals other than the biological parents, continues to elude a complete and convincing Darwinian explanation. Alloparental care occurs in a diverse range of invertebrates and vertebrates. Of these species, those with the relatively rare social systems combining significant levels of alloparenting with delayed or suppressed reproduction by alloparents are termed *cooperative breeders* (the precise terminology is debated; see, e.g., Brown 1987; Sherman et al. 1995; Solomon and French 1997). In some such species—such as many ants, bees, and wasps—permanently sterile castes exist whose only function is to support the reproduction of fertile members of their communities. Because nonreproducing castes inherit unique traits that cannot, in turn, be transmitted to offspring, Darwin (1882, 228) himself recognized the "special difficulty" they posed for his theory. Almost a century would pass before the correct explanation, now termed *kin selection*, was discovered (Hamilton 1964a, 1964b). In essence, an allele can increase its frequency in the population by increasing the fitness of any organism possessing that allele. Because close relatives have a high probability of sharing alleles (via descent), strategies to invest in the reproduction of relatives at the expense of one's own reproduction can evolve under appropriate conditions. Various mechanisms ensure that members of sterile castes are very closely related to the siblings they help raise.

Initially, it was thought that kin selection would also explain the evolution of cooperative breeding in species without permanently sterile castes, which includes all examples of cooperative breeding in birds and mammals. Nonbreeding "helpers at the nest" were predicted to be especially close relatives of the breeding pair. Contrary to expectations, this did not turn out to be the case: members of noncooperatively breeding groups are about as related to one another as are members of cooperatively breeding groups, and some helpers in some species were even found to be unrelated to the young they were raising (Clutton-Brock 2002). Although a high degree of relatedness is often a precondition for cooperative breeding (Dickinson and Hatchwell 2004), animal behavioral ecologists have expended considerable effort in the search for the other essential factors.

A parallel interest in cooperative breeding has arisen in primatologists and human behavioral ecologists. Among anthropoid primate species, the degree of allocare ranges from little to none among the Cercopithecinae (e.g., macaques and baboons) and Ponginae (great apes) to fairly substantial levels among Colobinae, where infants might be held 30%–50% of the time by adult and juvenile females who are not the mother, and Callitrichinae, where the percentage of time held by nonmothers ranges from 47% to 87% (Ross and MacLarnon 2000). Callitrichids are the only nonhuman primate taxon considered to be cooperative breeders in the full sense of the

term. Intriguingly, callitrichids, in contrast to the great majority of primates, share a number of prosocial traits with humans, including food sharing, mutual interdependence, and high tolerance involving independent group members, suggesting a potential link between cooperative breeding and prosociality (Burkart et al. 2007; Clutton-Brock 2002).

Although in all known human societies mothers are the primary caregivers of young children, substantial allocare is often provided by others. In fact, the care provided by multiple individuals, such as grandparents or siblings, can, in aggregate, approach or even exceed the care provided by the mother. Among the Ye'kwana, for example, mothers spend 49% of their time in direct care of children, sisters 16%, grandmothers 11%, other relatives 16%, and fathers and brothers 3% and 2%, respectively (Hames 1988). Among Aka hunter-gatherers, Hewlett (1991) found that while in camp, 1- to 4-month-old infants were held by their mothers less than 40% of the time and had, on average, seven different caregivers during the day (see also Meehan 2005). In a Caribbean village, Flinn (1992) found that among children aged 0–4, about 45% of care interactions were with nonparents: 16.3% were with siblings, 17.6% were with grandparents, and 11.7% were with other relatives and nonrelatives. Flinn and Leone (2006, 2008) also found children's glucocorticoid stress responses to be moderated by allocare. An analysis of the 58 "traditional" societies in the standard cross-cultural sample found that the mother constituted the principal relationship for young children in about one-quarter of the sample, the mother constituted less than half of young children's relationships in about half the sample, and others constituted young children's primary relationship in the final quarter of the sample (Quinlan and Quinlan 2008). Konner (2005) reviewed the data on care of young children among the !Kung and several other hunter-gatherer societies and concluded that although mothers are the primary caregivers in all of them, nonparental caregiving is also important in all of them.

Among primates, humans exhibit relatively high levels of alloparenting (Hrdy 2005; Ross and MacLarnon 2000). The allocare of grandmothers, in particular, has been argued to have had an important impact on the evolution of human life-history traits, such as a relatively short interbirth interval and menopause (e.g., Hawkes et al. 1998; but see Reznick et al. 2006). Because postmenopausal women are permanently sterile, it has even been suggested that humans are eusocial, a type of cooperative breeding characterized by an overlap of generations and reproductive division of labor (e.g., fertile and sterile "castes"; Foster and Ratnieks 2005).

In summary, a view is emerging that cooperative breeding might help explain the evolution of several distinctive features of the human species, including our prosociality toward both kin and nonkin, longevity, long postmenopausal life spans, high fertility, and maybe even encephalization (Flinn et al. 2007; Hawkes et al. 1998; Hrdy 2005; van Schaik 2008; Voland, Chasiotis, and Schiefenhövel 2005). At the same time, alloparents include many categories of relatives other than grand-

mothers. As the data reviewed above make clear, siblings in particular often provide as much or more care than grandparents. Compared with grandmothers, however, the influence of older siblings on the growth, development, and survivorship of younger siblings has been the subject of less empirical and theoretical investigation. A recent comprehensive review of the influence of kin on child survival, for example, found that 21 of 45 studies (47%) investigated the effect of maternal or paternal grandmothers, but only six studies (13%) investigated the impact of older siblings (Sear and Mace 2008). However, adolescents typically live with younger siblings and are nonreproductive for several years. Moreover, adolescents are related to their siblings by $r = 0.5$, whereas grandmothers are related to their grandchildren by only $r = 0.25$. This high relatedness and the relative lack of their own reproductive opportunities provide incentives for older siblings to invest in younger siblings that might balance or outweigh incentives to compete with them for family resources. A somewhat similar pattern is seen in the eusocial naked mole rat, in which the helpers are young individuals, some of whom become reproductive later in life.

Hames and Draper (2004) review studies of offspring helpers at the nest and report new results for the Ju/'hoansi (!Kung). They address two questions. First, do older children have a positive effect on some aspect of parents' reproduction? Second, because, as Hames and Draper note, in many societies girls begin work at younger ages, work more hours, and are more likely to alloparent than boys, do older girls have a greater positive influence than older boys?

With some exceptions, existing studies tend to support both hypotheses. Turke (1988), Bereczkei (1998), and Kramer (2002) found evidence that older daughters had a positive impact on some facets of mothers' reproduction. Flinn (1989) found that female helpers (pre- or postmenopausal) had a positive influence on mothers' fertility but that the sex of mothers' eldest offspring had no effect (see also Kramer 2005). Crognier, Baali, and Hilali (2001) found that older offspring had a positive influence on child survivorship and mixed effects on mother's fertility, but they did not find that girls had a greater influence than boys. Hames and Draper (2004) found no positive effect of older children on mothers' fertility or child survivorship, nor did they find any significant differences in the effect of older girls versus older boys. Three additional studies included in the review of Sear and Mace (2008) found a positive effect (Beise 2005; Sear 2008; Sear, Mace, and McGregor 2000; Sear et al. 2002), and one, Hill and Hurtado (1996), found no effect.

Study Goals and Design

In general, we (and others) have found that increasing family size (i.e., more offspring) has a negative effect on individual child growth and development and, thus, plausibly, on child fitness, probably because siblings compete with one another for family resources (for review, see Hagen, Barrett, and Price

2006; Hagen et al. 2001). In our study population (see "Study Population"), for example, we found that the age-standardized height and weight of children in households with the largest consumer/producer (CP) ratio were 1.38 and 1.44 SD, respectively, below those of children in households with the smallest CP ratio (Hagen, Barrett, and Price 2006). To test the hypothesis that in contrast to the general case, adolescent siblings, specifically adolescent girls, have a positive effect on the fitness of younger siblings, we assessed the nutrition and growth of children in a Shuar village—horticulturists with kin-based social organization and a subsistence economy.

In food-constrained populations, nutrition and growth indices assessed by standard anthropometry are promising proxies for fitness. Deficits in age-adjusted height and weight are risk factors for increased child morbidity, such as acute lower respiratory infections and diarrhea (Ballard and Neumann 1995; Baqui et al. 1993a, 1993b; el Samani, Willett, and Ware 1988; Zaman et al. 1996). Poor growth is also associated with impaired cognitive development, poor performance in school, and many other deficits (Martorell and Haschke 2001; Semba and Bloem 2001). Although anthropometric indicators are generally poor predictors of the death of individuals (Pelletier 1991), population deficits in height-for-age and weight-for-age are clearly associated with increased child mortality rates (Pelletier and Frongillo 2003; Pelletier, Frongillo, and Habicht 1993).

Deficits in height-for-age generally indicate long-term, cumulative inadequacies of health or nutrition, whereas deficits in weight-for-age indicate either acute or chronic inadequacies (World Health Organization 1995). The body mass index (BMI) complements these in the assessment of thinness (Cole et al. 2007). Skin fold thicknesses, which measure skin and adipose tissue, correlate well with overall body fat (de Onis et al. 2007; Lohman 1981; Sarria et al. 1998) and are thus informative indexes of nutritional status. Children's body fat reflects relatively short-term access to food provided by parents and other group members and food they forage for themselves, as well as the negative effect of diarrhea and other disease.

Nutrition inadequacies largely involve deficiencies in energy and protein intake, but there is increasing evidence that deficiencies in micronutrients also play an important role (World Health Organization 1995). For more discussion of the advantages and disadvantages of using anthropometric indexes as fitness proxies, see Hagen, Barrett, and Price (2006).

Study Population

The Shuar are a subgroup of what used to be called the Jivaroan language group, a large native South American group that also includes the Huambisa, Aguaruna, Achuar, and Shiwiar (as "Jivaro" has derogatory connotations, the name "Aents chicham" has been proposed as a possible replacement term). This Shuar village is located on the western edge of the Ecuadorian Amazon at an altitude of about 1,000 m on the lower eastern slopes of the Andes. The principal dietary staples are plantains (*Musa balbisiana*) and sweet manioc (*Manihot esculenta*) from family gardens. Women do almost all of the gardening. Men work primarily in timber and, increasingly, sugar production, but they also engage in limited hunting and fishing and in household activities such as garden clearing and house construction.

Hames and Draper (2004) argue that for children to serve as "helpers at the nest," suitable economic and ecological conditions must exist that permit them to do so (e.g., a mode of subsistence in which older children can participate and a safe working environment close to the main settlement). In our population, adolescent girls contributed mainly carbohydrates, by working in their families' nearby subsistence gardens. Adolescent boys and young men provided a limited amount of food obtained through hunting and fishing. More often, though, they contributed indirectly by assisting with the labor-intensive harvesting and transport of timber for sale (we frequently observed older boys using horses to haul timber along forest trails without assistance from adult men), by tending cattle, by assisting with their families' cash crops, or by working in nearby tea and sugarcane plantations. The cash so obtained was used to buy meat and other supplies. Thus, in this village, older boys and girls were both capable of contributing economically to their families.

During our study, the village had 306 residents in 50 households. About half lived in or very near the village center; the rest lived within a several-kilometer radius. Most households consisted of a single nuclear family, and only two men were openly polygynous.

Methods

We sampled 138 (45%) members of the village in 32 different households. The sample was an opportunity sample comprising almost all families living near the village center. Here, we focus on a subsample of 72 individuals (52% of the sample) in 21 households labeled "dependents" between the ages of 3 and 20 who were not parents, heads of household, or married.

All anthropometric measurements were obtained by a single researcher (EHH) according to World Health Organization (WHO) guidelines (World Health Organization 1995). Before measurement, participants were asked to remove their shoes and heavy articles of clothing. Height was measured to the nearest millimeter using an aluminum anthropometer; weight was measured to the nearest 50 g with a digital field scale (Seca model 770) that had been leveled on a hard, flat surface. All participants were wearing lightweight cotton clothing, and no adjustments were made for clothing weight. Two consecutive readings of triceps and abdominal skin folds were taken to the nearest 0.1 mm using Lange calipers. These measurements were then averaged.

We computed each individual's height, weight, and BMI Z

Table 1. Summary statistics for study variables

Variable	N	Range	Mean	SD
Children (age ≤10;				
19 females, 25 males):				
Age	44	3–10	6.76	2.23
BMI Z scores	43	−1.42 to 2.25	.57	.77
Weight Z scores	44	−3.78 to .28	−1.36	.97
Height Z scores	43	−4.62 to .22	−2.63	1.08
Body fat residuals	36	−2.17 to −.52	−1.41	.41
ADOLBROTHERS	44	0–4	1.02	1.09
ADOLSISTERS	44	0–3	.45	.82
No. adolescent siblings	44	0–5	1.48	1.64
Adolescents (age ≥13;				
13 females, 15 males):				
Age	28	13–19	15.2	1.66
BMI Z scores	28	−1.24 to 1.64	.08	.81
Weight Z scores[a]	28	−4.30 to .51	−1.47	1.32
Height Z scores	28	−4.77 to −.87	−2.60	.94
Body fat residuals	28	−1.90 to 6.14	.07	1.93
No. child siblings	28	1–5	3.79	1.17

Note. BMI = body mass index.

[a]The World Health Organization does not provide weight standards for children beyond the age of 10, so for adolescent weight Z scores, we used National Center for Health Statistics/Centers for Disease Control standards.

scores with respect to the WHO child growth standards (de Onis et al. 2007; World Health Organization Multicentre Growth Reference Study Group 2006). There are no international references for skin fold thicknesses, nor is there an appropriate reference population, so we constructed a sex- and age-adjusted "reference" based on the standardized residuals of sex-specific curves fitted to our body fat index, a sum of triceps and abdominal skin fold thicknesses of study participants. We had three measures of family socioeconomic status: family garden productivity, father status, and wealth (e.g., cattle, money). For details, see Hagen, Barrett, and Price (2006).

We wanted to avoid examining the influence of older children on siblings who were only slightly younger (e.g., the influence of 13-year-olds on 12-year-old siblings), so we selected two subpopulations of dependents that were at least 3 years apart: children (≤10 years) and adolescents (≥13 years). There were 44 children, 25 of whom had at least one adolescent sibling, and 28 adolescents.

For all children, we computed ADOLBROTHERS, the number of adolescent brothers; ADOLSISTERS, the number of adolescent sisters; and, for the 25 children with at least one adolescent sibling, FRACTIONSISTERS, the fraction of adolescent siblings that were female (a value of 0 indicated that all adolescent siblings were male; a value of 1 indicated that all adolescent siblings were female). Because children within households are not necessarily independent cases, we compared linear mixed effects (LME) models with ordinary linear regression (OLR) models to determine whether LME models using household as a grouping factor (which accounts

for within-household correlations) would better fit the data (we followed the procedures described in Pinheiro and Bates 2000). In no case was an LME model an improvement over an OLR model, so we report OLR models testing whether ADOLBROTHERS, ADOLSISTERS, and FRACTIONSISTERS predicted child anthropometry.

Results

Summary statistics for our study variables are presented in table 1. The high fraction of dependents with low weight- and height-for-age is consistent with other studies of native Amazonians (e.g., Orr, Dufour, and Patton 2001).

Our models are presented in table 2. Model A, which included all children in the sample, revealed that, controlling for the sex and age of the child, increasing numbers of adolescent sisters had a negative effect on child BMI, contrary to predictions, whereas increasing numbers of adolescent brothers had a positive effect. This model was highly significant and explained 35% of the variance in BMI Z scores. The coefficients for ADOLSISTERS and ADOLBROTHERS indicate that each adolescent sister and brother decreased or

Table 2. Four models of body mass index (BMI) and weight Z scores of children (age ≤10) as a function of the number of adolescent sisters and brothers

Model and variables	Estimate	SE	t value	P (>|t|)
BMI Z score:[a]				
Intercept	1.34	.31	4.28	.0001[***]
Sex (male)	.52	.21	2.45	.019[*]
Age	−.18	.05	−3.82	.0005[***]
ADOLSISTERS	−.33	.13	−2.57	.014[*]
ADOLBROTHERS	.33	.10	3.32	.002[**]
BMI Z score:[b]				
Intercept	1.20	.19	6.38	<.0001[***]
FRACTIONSISTERS	−1.70	.41	−4.02	.0006[***]
BMI Z score:[c]				
Intercept	1.28	.29	4.60	.0005[***]
Sex (male)	.62	.19	3.23	.003[**]
Age	−.19	.04	−4.56	.0006[***]
ADOLSISTERS	−.47	.12	−3.87	.0004[***]
ADOLBROTHERS	1.04	.23	4.51	.0006[***]
ADOLBROTHERS^2	−.26	.08	−3.34	.002[**]
Weight Z score:[d]				
Intercept	−1.43	.20	−7.27	<.0001[***]
ADOLSISTERS	−1.36	.52	−2.63	.012[*]
ADOLSISTERS^2	.36	.18	2.05	.047[*]
ADOLBROTHERS	.93	.36	2.57	.014[*]
ADOLBROTHERS^2	−.24	.11	−2.23	.032[*]

[a]RSE = residual standard error. RSE$_{38}$ = 0.62, r^2 = 0.41, adjusted r^2 = 0.35, $F_{4,38}$ = 6.64, P = 0.0004.
[b]RSE$_{22}$ = 0.67, r^2 = 0.42, adjusted r^2 = 0.40, $F_{1,22}$ = 16.18, P = 0.0006.
[c]RSE$_{37}$ = 0.55, r^2 = 0.55, adjusted r^2 = 0.49, $F_{5,37}$ = 8.96, P = 0.0001.
[d]RSE$_{39}$ = 0.91, r^2 = 0.20, adjusted r^2 = 0.12, $F_{4,39}$ = 2.51, P = 0.057.
[*]P < 0.05.
[**]P < 0.01.
[***]P < 0.001.

increased, respectively, a child's BMI by one-third of a standard deviation relative to the BMI of children with no adolescent siblings. Hence, a child with three adolescent sisters but no brothers would be predicted to have a BMI about 1.0 SD below the age- and sex-specific mean, whereas a child with three adolescents brothers but no sisters would have a BMI about 1.0 SD above the mean (but see "Diminishing Influence of Adolescent Siblings").

A similar analysis (table 2, model B), restricted to children with adolescent siblings, found that children with all adolescent sisters had a BMI 1.70 SD below children with all adolescent brothers. This model is plotted in figure 1, along with a line representing the sample mean BMI, again showing that brothers had a net positive effect whereas sisters had a net negative effect. This model was highly significant and explained 40% of the variance in the BMI Z scores of children with adolescent siblings. Linear models of ADOLSISTERS, ADOLBROTHERS, and FRACTIONSISTERS did not account for significant variation in weight or height Z scores or in body fat residuals (but see "Diminishing Influence of Adolescent Siblings").

Finally, models of cooperative breeding assume that allocare is costly. We therefore tested whether the number of child siblings had any effect on adolescents. We found no significant correlations between number of child siblings and adolescents' height Z scores ($r = -0.27$, $P = 0.17$), weight Z scores ($r = -0.19$, $P = 0.33$), BMI Z scores ($r = -0.14$, $P = 0.49$), or body fat residuals ($r = -0.15$, $P = 0.43$), although in each case the association trended in a negative direction. Controlling for adolescents' age and sex did not significantly alter these results (tests not reported).

Exploring Potential Confounds

Our results might be explained not by the direct effect of adolescents on their younger siblings but instead by other characteristics of children that, for whatever reason, were correlated with numbers of adolescent brothers or sisters. If children with many adolescent sisters just happened to be of a neglected sex or in a vulnerable age group, for example, our results would be better explained by the sex bias or the vulnerability of that age group rather than by the number of sisters. Another potential confound was the number of consumers in the households of children with more adolescent sisters than adolescent brothers. Perhaps children with more adolescent sisters had lower BMI Z scores because these children, for whatever reason, had more household competitors, measured as the number of child siblings and the total household consumers. If family resources were correlated with the number of adolescent brothers or sisters, they would constitute a third set of potentially confounding variables. In our previous analysis of all dependents (children and adolescents together), we found family-garden productivity to be strongly positively correlated with family size and fathers' status
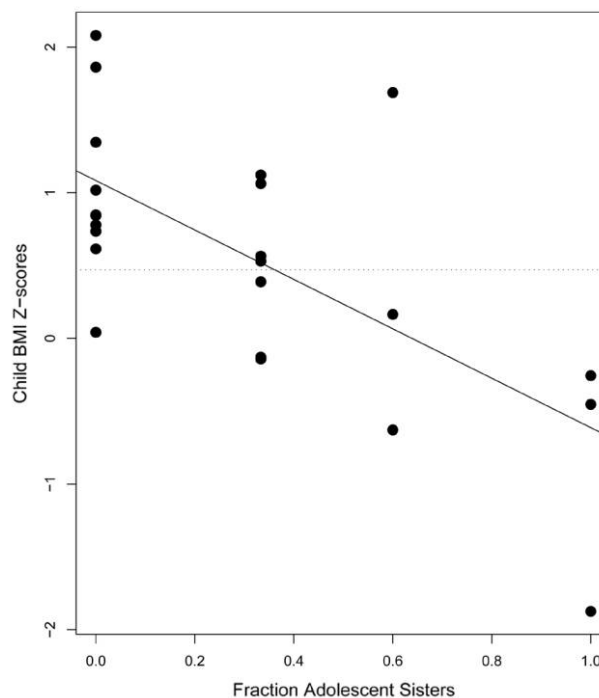

Figure 1. Body mass index (BMI) Z scores of children (age ≤10) with adolescent siblings versus the fraction of those siblings who were sisters. The horizontal dotted line is the mean BMI Z score for all children. Of children with adolescent siblings, most with a small fraction of adolescent sisters had BMI Z scores above this mean, whereas most with a large fraction of adolescent sisters had Z scores below this mean. Solid line fitted on linear regression.

strongly positively correlated with girls' (but not boys') anthropometry (Hagen, Barrett, and Price 2006).

We entered these potentially confounding variables into our models in various combinations. Model A (table 2) controlled for children's sex and age, both of which were significant, so these two factors did influence BMI Z scores (with a bias toward males and younger children), yet numbers of adolescent brothers and sisters were still significant predictors of BMI Z scores. In no model were any of the family size (i.e., number of siblings and total number of household members) or family resource variables significant, nor did any variable significantly increase model fit as measured by an increase in r^2, nor did inclusion of any of these potential confounding variables eliminate the effects of adolescent siblings (tests not reported). Hence, we conclude that potential confounds with sex, age, family size, or family resources are unlikely to account for our results.

Diminishing Influence of Adolescent Siblings

Model A (table 2) shows a positive linear effect of increasing numbers of adolescent brothers. It is unlikely, however, that the benefit of adolescent brothers increases without limit. The benefit of adolescent brothers should diminish as their num-

ber increases and perhaps eventually be outweighed by the cost they impose as competitors for various family resources. Model C tests for such a curvilinear effect by adding a quadratic term to model A. The quadratic term was significant—significantly improved model fit, increasing adjusted r^2 from 0.35 to 0.49 ($P = 0.002$)—and was negative, with approximately two adolescent brothers providing the peak benefit to children's BMI.

Given the diminishing returns of adolescent brothers, it was possible that the negative effect of adolescent sisters also diminished with increasing numbers. A quadratic term in numbers of adolescent sisters was not significant in the model of BMI Z scores ($P = 0.19$), but a model with linear and quadratic terms for adolescents siblings of both sexes (table 2, model D) predicted significant variation in weight Z scores (but not height Z scores or body fat residuals). The effects are similar to the models of BMI Z scores: adolescent brothers have a strong positive effect that attenuates with increasing numbers, whereas adolescent sisters have a strong negative effect that also attenuates with increasing numbers (age and sex were not significant in this model).

Discussion and Conclusions

In contrast to many predictions and findings in the literature, we found that adolescent girls had a negative effect on the BMI of younger siblings, whereas adolescent boys had a positive effect. These effects persisted after controlling for several potential confounds, including sex, age, family size, and family resources. Models with quadratic terms revealed that the effects of adolescent siblings on BMI Z scores, as well as weight Z scores, diminished at higher numbers. Although low BMI-for-age and low weight-for-age can indicate both chronic and acute inadequacies (Cole et al. 2007; World Health Organization 1995)—because having an adolescent sibling is a transient phenomenon (e.g., early in a child's life, such a sibling is not an adolescent, and later in a child's life, such a sibling marries and moves out of the household)—the effects on BMI-for-age and weight-for-age observed for children with adolescent siblings might also be transient.

There are several limitations to our study. First, like many studies of human allocare, we tested whether the presence of particular categories of alloparents in households was correlated with child outcomes. Unfortunately, this approach cannot determine *how* potential alloparents affect outcomes, which could be via provisioning, direct care, or even some factor unrelated to care, such as the physiological cost of producing sons (e.g., Rickard, Lummaa, and Russell 2009). Similarly, such studies cannot confirm that there is any causal relationship at all. Despite our attempt to control for some obvious confounding factors, unmeasured variables might explain the association. Furthermore, our study was cross-sectional, providing only a single snapshot of children's growth and nutrition. Longitudinal investigation and inclu-

sion of additional control variables might reveal more complex and even contradictory patterns.

In addition, our sample size was relatively small. Because the variability of effect size estimates is larger in studies with small samples, this increases the risk that our effect sizes were erroneously larger than the true population effect size. Our sample might also have been biased (e.g., marriage could have removed especially economically productive adolescent women from our sample of dependents). Finally, fitness proxies such as ours ignore many factors relevant to fitness (the advantages and disadvantages of using anthropometric measures as proxies for fitness are discussed in Hagen, Barrett, and Price 2006). These limitations suggest that our results should be interpreted with caution.

We previously reported that increasing numbers of siblings had a negative effect on child anthropometry (Hagen, Barrett, and Price 2006), consistent with the view that siblings generally compete with one another for resources. It has often been proposed, however, that adolescent sisters might have a positive effect on younger siblings. But in our study population, even after controlling for number of children and adolescents in the household, adolescent sisters still had a negative effect on younger siblings. One potential explanation of this result is that whereas many previous studies focused on child survivorship or mothers' fertility, which both might be more sensitive to the availability of direct care provided by adolescent sisters, for example, we focused on child growth and development, which might be more sensitive to competition for food among siblings. Compared with males, female reproductive physiology has large energy requirements, and levels of sex hormones and other aspects of female reproductive function are more dependent on energy balance (Bribiescas 2001; Ellison 2003). As a consequence, when sufficient food is available, adolescent girls gain more body fat than adolescent boys (Frisch 1994), a pattern we also observed in our population (fig. 2). In some populations, young women have been observed to receive preferential feeding at the expense of other household members, apparently to improve fecundity and marriage prospects (for a brief review, see Gillett-Netting, Meloy, and Campbell 2004). Alternatively, young women might achieve positive energy balance by reducing activity levels (and thus productivity). If either were the case in our food-constrained study population, it could help explain the negative effect of adolescent sisters on the BMI of younger siblings.

It is not clear, however, that among the Shuar higher levels of body fat or body mass would improve the marriage prospects of young women. As a partial test of this hypothesis, we analyzed data on the attractiveness of women in this population, which were collected at the same time as other data reported here. Attractiveness was measured by having four adult men who were members of the community rank the physical attractiveness of unmarried women over the age of 10; their rankings were then averaged (range: 0–19.25; mean = 7.9, SD = 6.5). This population of women was es-
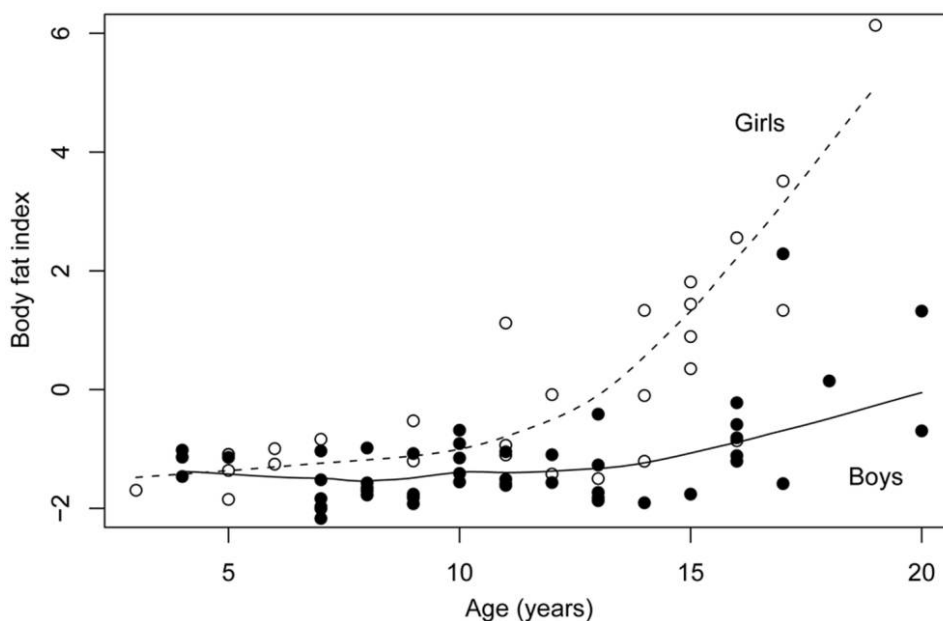
Figure 2. Body fat index of Shuar dependents versus age. Girls (*open circles, dotted line*) tend to gain more body fat during adolescence than do boys (*filled circles, solid line*; Frisch 1994), a pattern we observed in our population. The body fat index was the sum of triceps and abdominal skin fold thickness Z scores. Lines fit by locally estimated scatterplot smoothing regression.

sentially the same adolescent sibling population we reported on here except that the age range was slightly larger (11–21), and some of these women did not have younger siblings. There were strong, positive correlations between women's attractiveness and both their BMI Z scores ($r = 0.56$, $P = .01$, $N = 17$) and their body fat residuals ($r = 0.55$, $P = .01$, $N = 17$). These correlations remained significant and essentially unchanged after controlling for women's age (and there were no significant age effects; tests not reported). Although these correlations are consistent with the hypothesis that higher levels of body fat and body mass are attractive to men in this population, they are also consistent with the hypothesis that attractive girls simply receive more food and other forms of investment from their families. In the Shiwiar, however, a closely related Ecuadorian population (Sugiyama 2004), males preferred drawings of women exhibiting higher body fat within locally observed levels, which supports the first hypothesis (both hypotheses could be true, of course).

Equally interesting is the positive effect of adolescent brothers on the BMI of younger siblings, which suggests that brothers rather than sisters might be serving as "helpers at the nest." In animal behavioral ecology, several models have been proposed to explain the emergence of cooperative breeding, especially in birds. One, the influential ecological constraints model (e.g., Emlen 1982), appears to explain significant within-species variation in cooperative breeding, although it has done less well explaining between-species variation (which

in birds at least might be better explained by variation in life-history traits or by temporal environmental variability; see, e.g., Hatchwell and Komdeur 2000; Rubenstein and Lovette 2007). According to the ecological constraints model, within-species variation in cooperative breeding is a consequence of individual variation in breeding opportunities—individuals with little current opportunity to establish an independent breeding territory, for example, who are often young adult males (e.g., Hatchwell and Komdeur 2000), can do better by helping to raise siblings.

Because we are attempting to explain human variation in cooperative breeding rather than why as a species humans tend to breed cooperatively, we employ the ecological constraints model. In humans, adolescent and young adult women appear to face fewer constraints on mating than adolescent and young adult men. For example, women usually marry at younger ages than men, often in their mid- to late teens. Worldwide, United Nations data show that in the 15–19 age category, more than five times as many women are married (14.7%) as men (2.6%; Hess and Hagen 2006). In this village there were four teenaged mothers and one teenaged father. The average age of marriage in this population is 17 for women and 21 for men (E. Pillsworth, personal communication; see also Pillsworth 2008).

In addition, young men in many populations have low fertility compared with that of women of the same age (fig. 3). Because fecundity begins at an earlier age in males than
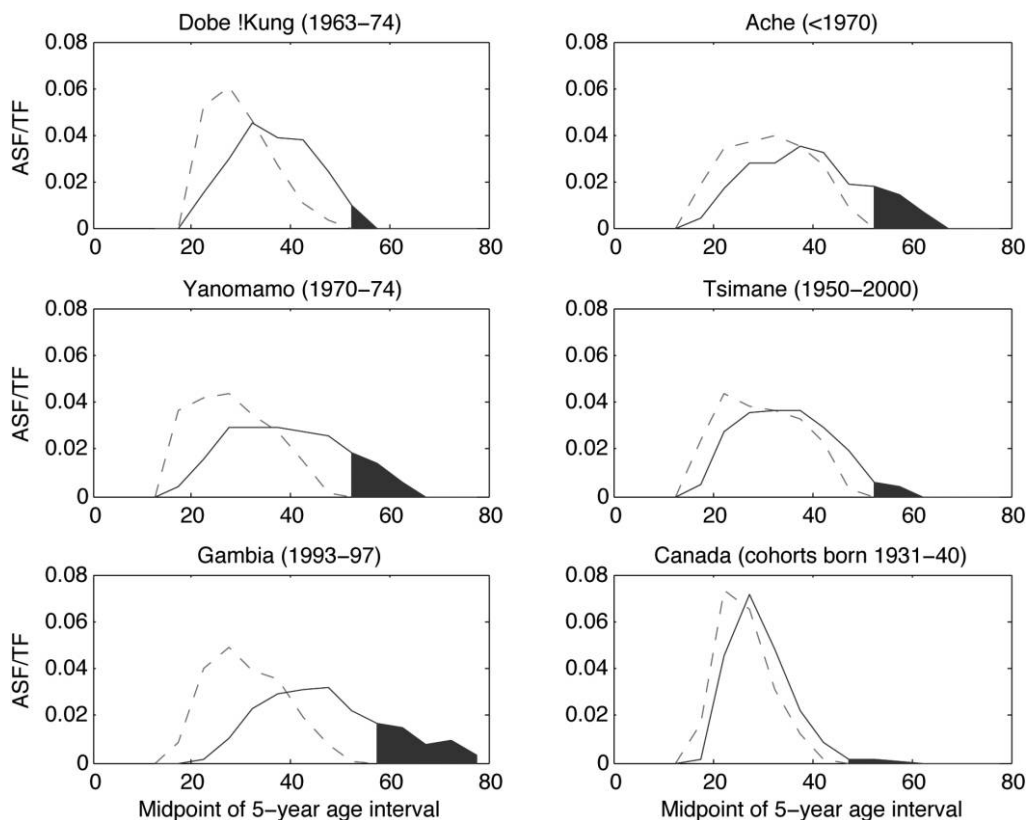
Figure 3. Age-specific fertility (*ASF*) as a fraction of total fertility (*TF*) for men (*solid line*) and women (*dotted line*) in six populations. Whereas the low fertility of older adult women relative to men and to average life span (right side of each chart) provided the inspiration for the grandmother hypothesis, the low fertility of young men relative to young women (left side of each chart) suggests an ecological constraint on male reproduction that could motivate investment in younger siblings. Figure from Tuljapurkar, Puleston, and Gurven (2007).

in females (Wood 1994), low fertility among young men, including those in this village, also suggests that they face greater constraints on mating than do young women. In our population, the major constraints on men were money and other assets (e.g., livestock) and developing a reputation for being a hard worker and a conscientious provider and family member (E. Pillsworth, personal communication). Pillsworth (2008) found that for Shuar women, but not for men, the romantic desirability of opposite sex members of their community was correlated with those members' provider qualities (when ranking traits of a hypothetical mate, however, both men and women valued resource acquisition ability).

If in most populations young men face greater constraints on mating than young women, then under the ecological constraints model, variation in helping at the nest by young men would be explained by variation in their ability to contribute economically to the family. As we discussed in "Study Population" above, adolescent boys have several avenues for earning cash. Their economic contributions might therefore

have been directed to younger siblings rather than themselves; in addition to the benefits of helping close kin, this would enhance their reputations as providers.

Application of the ecological constraints model to our population is speculative, of course, and there are many other possible explanations for the patterns found here. We caution that we do not have the data to determine the relative economic contributions of adolescent girls and boys or their levels of consumption and thus whether either are net consumers or producers. In addition, we observed that mothers usually controlled the distribution of food from the gardens and fathers controlled the sale of timber and the use of the resulting cash. The effects we observed could therefore be a consequence of the decisions of parents, not adolescent siblings. The confluences and conflicts of interest regarding food distribution within Shuar families are topics for future study.

In summary, although grandparenting has received much attention (e.g., Voland, Chasiotis, and Schiefenhövel 2005), there are also compelling theoretical reasons to investigate the

positive and negative effects of adolescents on the fitness of their parents and younger siblings. Adolescent boys in particular have been neglected in the theoretical literature on cooperative breeding in humans, probably because adolescent girls seem to provide more direct care of young siblings. Worldwide, men marry later than women, however, and often stay in their natal group. Hence, in some situations, teenaged and young men might have greater opportunities and fitness incentives to invest in younger siblings, perhaps via provisioning more than direct care, than would grandparents or teenaged and young women. Indeed, in many cooperative breeding species, it is not uncommon for young adult males to face ecological constraints on reproduction and therefore to provide much of the nonparental investment in offspring.

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