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Hadza Women's Time Allocation, Offspring Provisioning, and the Evolution of Long Postmenopausal Life Spans

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Extended provisioning of offspring and long postmenopausal life spans are characteristic of all modern humans but no other primates. These traits may have evolved in tandem. Analysis of relationships between women's time allocation and children's nutritional welfare among the Hadza of northern Tanzania yields results consistent with this proposition. Implications for current thought about the evolution of hominid food sharing, life history, and social organization are discussed.

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Unlike other female primates, women regularly share food with their weaned but still immature offspring. Many of the foods they share cannot be taken efficiently by children themselves. This practice broadens the range of resources and habitats potentially open to exploitation. It also creates an opportunity for women to increase their daughters' reproductive success by helping to provision grandchildren. It may have important consequences for the evolution of postmenopausal life spans, another pattern characteristic of humans but not other primates.

We support this argument by appeal to quantitative data on women's time allocation and variation in children's nutritional status among Hadza hunter-gatherers in northern Tanzania. Specifically, we document the mother's role in provisioning weaned offspring, assess the effect of a new baby on the mother's continuing support of those children, and describe the grandmother's complementary role in feeding them. The results of our analysis are consistent with the argument that patterns in female resource choice, extended provisioning of weaned offspring, and long postmenopausal life spans are interdependent traits. In subsequent discussion, we review the puzzle of menopause, show how our argument contributes to resolving it, and identify important implications for current ideas about the evolution of human social organization.

The Problem of Provisioning Weaned Offspring

Human children are notoriously dependent on adults, typically requiring substantial support, including provi-

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sioning, well into adolescence (Lancaster and Lancaster 1983). This is true even among groups like the Hadza, in which children as young as five years of age sometimes meet up to 50% of their daily subsistence requirements through their own efforts (Blurton Jones, Hawkes, and O'Connell 1989). Examples of such self-reliance notwithstanding, children everywhere must be provisioned in at least some circumstances—the younger they are, the more often and more extensively.

Among most foragers, including the Hadza, a substantial fraction of this support comes from mothers. Women meet the goal of improving their children's welfare in different ways in different ecological circumstances (Blurton Jones 1993, Hurtado et al. 1992). Often they organize their own foraging and food-processing efforts and those of their children in a manner that maximizes "team" return rates, those that they and their children earn collectively (e.g., Blurton Jones, Hawkes, and Draper 1994*a*, *b*; Hawkes, O'Connell, and Blurton Jones 1995). Sometimes this means that mother and children forage together, targeting foods that the youngsters can easily take (e.g., berries). Otherwise, the mother operates on her own or in company with other adults in work that juveniles cannot perform effectively (e.g., digging deeply buried tubers or carrying mongongo nuts from distant patches), returning to share and sometimes process food with youngsters at a central place.

The human pattern is unique among primates but has a substantial foundation in primate behavior. Among monkeys and apes, the most common and widespread food sharing is from mother to offspring, typically involving foods that infants have difficulty handling (Feistner and McGrew 1989, Silk 1979). Human mothers share more food more often and, more important, extend this sharing to *weaned* but still immature offspring.

The extended provisioning typical of humans is often seen as increasing the burden children impose on mothers, but in an important sense it also does the reverse. It releases mothers from the foraging constraints imposed by juvenile capacities. Unlike other primates, humans are not limited by the distribution of resources that weanlings can handle. We can occupy habitats in which adults earn high returns from foods that juveniles cannot exploit at life-sustaining rates. Regular food sharing has another important consequence as well: individuals other than the mother can help with provisioning, potentially lightening her workload appreciably. Such assistance should be especially important at the birth of a new baby. With predictable support, the mother should be able to wean sooner and allocate more effort to the next child. Where mothers gain from provisioning weaned offspring, mothers with helpers should gain even more in the form of shorter birth spacing, increased offspring survivorship, or both.

Though clearly beneficial to mothers, such help would evolve only if it provided sufficient fitness benefits to the helper. The most common nominee for this role, mother's mate, is usually assumed to gain by increasing her reproductive success. However, men may often have more fitness to gain or lose in competition for paternity with other men. To the extent that parenting effort trades off against mating effort, men will often be drawn away from paternal activities and into mating competition instead (Hawkes, Rogers, and Charnov 1995). As we have suggested elsewhere (Hawkes, O'Connell, and Blurton Jones 1989), the grandmother is a consistently better candidate for the role of mother's helper.

In the following sections we develop this argument in greater detail with quantitative data on time allocation among the Hadza. In particular, we seek to demonstrate that (1) children's nutritional welfare depends on the mother's foraging effort, (2) this relationship is disrupted when the mother is nursing, and (3) the grandmother's foraging makes up for the interruption in the mother's support.

The Hadza

The Hadza are a small population, numbering about 750, defined as a group by the fact that they speak a common language. They live in the rugged hill country of the Eastern Rift Valley, just south and east of Lake Eyasi in northern Tanzania. The climate of this region is warm and dry. Annual rainfall averages 300–600 mm, most of it falling in the six-to-seven-month wet season (November–May). Local plant communities are dominated by mixed savanna woodland; large game animals are abundant.

At the time of first European contact, around the beginning of this century, the Hadza reportedly had this area largely to themselves and lived entirely by hunting and gathering (Blurton Jones, Hawkes, and O'Connell 1996, Obst 1912). Local incursions by non-Hadza pastoral and agricultural groups were recorded as early as the 1920s and continue, particularly in the northern part of Hadza country, to the present (Woodburn 1988). Archaeological evidence suggests that hunters, herders, and farmers have all occupied this area, at least intermittently, for several millennia. Hunters alone have been present far longer (Mehlman 1988).

During the past 60 years (and especially since the mid-1960s), various segments of the Hadza population have been subjected to a series of government and church-sponsored settlement schemes designed to encourage them to abandon the foraging life in favor of full-time farming (Ndagala 1988). None of these projects has been successful, and in every case most of the Hadza involved have returned to the bush, usually within a few months. In each instance, some Hadza have managed to avoid settlement and continued to live as hunters.

The data reported here were obtained in the course of several periods of fieldwork in the mid-1980s among 200–300 Hadza then living in the southwestern part of their traditional territory, primarily in the 600–800-km^2

district known locally as Tli'ika.[2] At the time, members of this subpopulation were typically distributed among several short-term residential base camps, the number and location of which varied seasonally. Camps were occupied by core groups of relatively constant size and composition, but visiting between camps was continuous and real change in residence by small groups (individuals or single families) not uncommon. Core composition often changed when camps were abandoned and new ones established.

Throughout the study period, subsistence in Tli'ika was based almost entirely on wild resources, mainly meat, honey, fruit, and tubers. The relative importance of different foods varied greatly within and between seasons. Agricultural products (maize, millet, and tobacco) were occasionally acquired from villages five to six hours' walk to the south and southwest, sometimes as gifts, sometimes in exchange for dried meat. Quantities involved in these exchanges were always small.

Methods

From early September 1985 through mid-July 1986, Hawkes and O'Connell lived with a variable population of about 35–75 Hadza in a series of five residential camps collecting data on time allocation, foraging, and food sharing.

Data on time allocation were gathered by means of "instantaneous" camp scans, focal-person follows, and observations of departures and returns summarized in daily logs of residents' activities (see review of these methods in Hames 1992). "Instantaneous" camp scans were spot checks of the activities of all individuals present in a camp at selected intervals during the course of a day. The recorder walked through camp making brief descriptive notes on all individuals present as encountered, their respective locations, the activities in which they were engaged, and any tools or facilities (e.g., hearths or grinding surfaces) they were using. Subjects involved in more than one activity at the same time (e.g., food preparation and active child care) were reported as such. Residents not seen were also noted. Scans were usually completed in about five minutes. They were distributed throughout the 12 daylight hours, never more than two per hour on any given day, with an average of 13 scans per scan-day. Running totals were kept of the number of scans completed per daylight hour to ensure even distribution across the day.

Focal-person follows provide detailed records of the activities of one or more individuals accompanied by Hawkes or O'Connell on day trips away from camp. Data collected included the identities of all individuals in the party, routes followed, persons encountered en route, prey types seen and quantities taken, and a detailed time schedule (particularly for all activities involving food collecting or processing).

Summaries of the activities of all camp residents were compiled at the end of each day. Data from scans, follows, and departure/arrival observations were collated and any gaps in the records for particular individuals identified. These were sometimes filled simply by asking the persons in question what they had done that day.

This work produced a very large sample, roughly 1,700 scans, each recording the precise locations and activities of all those present in camp. The general whereabouts of residents absent during a scan but determined from daily activity summaries were then slotted into each scan time. Whenever a resident's location could not be ascertained, he or she was recorded as "not seen." This resulted in a total of more than 50,000 individual behavioral records.

For purposes of analysis, these data were organized and culled as follows:

1. The sample was divided into seven subsets, each representing a "season" defined on the basis of changes in campsite location and patterns of resource choice. Dividing the sample in this way allowed us to monitor changes in individual time allocation relative to these "seasonal" parameters. Characteristics of study-group size, campsite location, resource choice, and foraging returns for each site in each season are described below.

2. Data on daytime visitors at each site were eliminated from the sample. Our observations covered only the time they spent in the study camp, not what they were doing otherwise. No time budgets could be calculated for these people even if they were frequent visitors.

3. Observations on residents who moved to another camp were eliminated for the days on which they moved, again because our data include only what they did in the hours before they left the study camp.

4. Short-term residents (those present for only a small number of scans in a particular season) were also eliminated. Although the scans *collectively* sample all hours of the day fairly evenly, they do not do so every day. Time budgets calculated on small numbers of scan times may be distorted accordingly. This adjustment results in an underrepresentation of unmarried men, who as a class are generally unlikely to remain many days in the same camp.

5. Nursing infants were excluded from the analysis because they are usually tied to their mothers.

6. To calculate time budgets for each resident in each season, each individual scan-time entry was assigned to a single activity, with food-related behavior given highest priority, child care lowest. For example, a subject observed holding a child and grinding baobab was tallied as processing food.

The resulting sample includes 243 individual time budgets on a total of 90 different individuals, each time budget based on an average of 114 (s.d. 78, s.e. 5) obser-

2. For additional information, see Blurton Jones (1993), Blurton Jones, Hawkes, and O'Connell (1989, 1996), Blurton Jones, Hawkes, and Draper (1994*a*, *b*), Bunn (1993), Bunn, Bartram, and Kroll (1988, 1991), Hawkes (1993), Hawkes, O'Connell, and Blurton Jones (1989, 1991, 1995), Lupo (1993, 1994, 1995), O'Connell, Hawkes, and Blurton Jones (1988*a*, *b*, 1990, 1991, 1992), Vincent (1985*a*, *b*).

vations (scan times). Total observations per time budget vary because the number of scans per season varies, as does the number of days any particular subject was resident in each camp. The 90 subjects range in age from under 3 to more than 70 years. They are represented by an average of 2.7 time budgets each.[3] As it happens, exactly half the subjects are males, half females. The whole sample is used to calculate average time budgets by age and sex.[4] Data on children and childbearing-aged women are used to explore seasonal variation. Time budgets for childbearing-aged women, their weaned, coresident children, and their senior helpers are used to examine covariation between women's foraging and their children's and grandchildren's weight changes.

Relationships among individuals are an important part of these analyses. We use genealogical labels to describe them but emphasize an important qualification. Assignments of the terms "mother" and "grandmother" are based primarily on behavioral criteria. We call all the juveniles in a woman's household (i.e., those who usually eat and sleep there and move with her between camps) her children even though we lack genetic data to support the assignment. Children known *not* to have been born to the adult woman of the household are not called hers. We label senior women who consistently feed, tend, and otherwise support the children of younger women "grandmothers." In this sample, the putative genealogical relationships of these "grandmothers" include two cases of mother's mother, one of mother's mother's mother, two of mother's sister, two of father's mother, and one of a more distant relationship.

Variation in nutritional status is also important to our analyses. To monitor this, we periodically weighed residents of each camp, using a simple bathroom scale from September to January and a more accurate electronic device thereafter.

Subjects' ages are estimated from an age-ranking compiled in 1985 and whether they appeared in a 1977 census (for additional details see Blurton Jones et al. 1992). Estimates were cross-checked with additional historical markers and age-rankings done in 1988, 1990, and 1992.

Sample sizes for various analyses differ. Although we use all pertinent data available for each, our records are incomplete. No weights were collected for two of the seasons; not all subjects were weighed at the beginning and/or the end of others; not all subjects have been age-ranked.

Individual subjects contribute from one to seven seasonal time budgets each. We assume that each time budget is an independent sample but recognize the biases this can create, particularly in a small data set. For example, an unusually active (or inactive) forager in some particular age/sex category who happens to be present throughout the study period may unrealistically inflate (or depress) average foraging times for members of that category. There is no easy solution to this problem. Allowing only one (randomly selected) time budget per subject would eliminate more than half the data; calculating a single time budget from all observations on each subject would not only collapse the sample but allow seasonal differences to obscure other relationships. On balance, the eccentricities of heavily sampled subjects seem to us more likely to obscure real relationships than to create phantom ones, but the problem still qualifies our results.

Profiles of the Seven Seasons

The data analyzed here were, as indicated above, gathered over seven "seasons" in five different residential base camps. We describe seasonal conditions because they affect patterns in time allocation and children's nutritional status.

Season 1 was the late dry. The study population was camped at a site called Tsipitibe from a few weeks prior to our arrival in early September through the end of October. Its core included 45–60 individuals distributed among seven to nine households. Men and teenage boys hunted with bow and arrow at night from blinds located along heavily used game trails or over water, all within about an hour's walk (5 km) from camp. During daylight, they slept, encounter-hunted on their own, accompanied women's foraging parties, or visited other camps. Away from their own camp, they were inevitably armed and alert to hunting and scavenging opportunities (Hawkes, O'Connell, and Blurton Jones 1991; O'Connell, Hawkes, and Blurton Jones 1988*a*, *b*). Over 47 days of observation, they acquired 27 large animal carcasses. Women and children spent most days in large groups digging tubers (primarily *Vigna frutescens* [Hadza *//ekwa*]), again close by, usually within an hour's walk (Hawkes, O'Connell, and Blurton Jones 1989). Baobab (*Adansonia digitata* [Hadza *no'babe*]) was taken occasionally, but the crop was poor.

Early in November the rains began (season 2). Surface waters became widely available, eliminating opportunities for intercept hunting. Berries (*Salvadora persica* [Hadza *tafabe*] and *Cordia* sp. [Hadza *ondishibe*]) ripened; bees (*Apis melifera*) began to accumulate large quantities of honey. Tsipitibe and other camps near perennial water sources were abandoned as people moved to locations intermediate between berry patches and potential honey-collecting areas. Many from Tsipitibe (40 individuals, seven households) shifted about 2 km north to a place called Mugendeda. Once there, men divided their subsistence effort between encounter hunting and honey collecting. Hunters were almost always solitary; honey collecting usually involved small, single-family parties. Localities searched lay mainly east, south, and

3. Subjects were observed for an average of two to three seasons, each season yielding an average of 114 observations over nine scan-days per subject.

4. Cross-tabulations show no association of age or sex with season (age-category by season [d.f. 36], chi-square = 13.64, $p = 0.999$; sex by season [d.f. 6], chi-square = 2.50, $p = 0.869$).

southwest, some up to three hours' walk (15 km) from camp. Hunting success was limited: only one impala was taken during 18 days of observation. Women and children also foraged in large groups at berry patches 4–6 km northwest. *Ondishibe* were the primary target, *tafabe* having been ruined (after their initial promise) by a few days of unusually heavy rainfall. On alternate days, smaller parties of women sought tubers (mainly *//ekwa*) in patches closer to camp.

Early in December (season 3), Mugendeda was temporarily abandoned, probably because returns from berries and honey within easy foraging distance had fallen. Reconnaissance indicated that honey was abundant 10–20 km to the east. All moved to this area, most to a site called Mbea (locality A). Camp residents numbered about 40, grouped in six to seven households. Returns from honey collecting were good at first but soon fell sharply. Hunting was fair throughout. Over nine days of observation, men made two kills (eland and impala), and children scavenged small amounts of meat and fat from a decaying elephant. No weights were taken to bracket this period, so it is omitted from any analyses that require them.

The end of the month brought word that *Cordia* berries were again ripe at Mugendeda, prompting the group to return there (season 4). The camp population was essentially the same as it had been before, about 45 people in seven households. Our observation period covered only a few days. Hunters took nothing. Time budgets were developed for this period, but no weights were taken; therefore data from this camp are eliminated from some analyses.

We were out of the field from early January through mid-March. On returning, we found that most of the group we had left at Mugendeda had gone back to Mbea, making camp about 1 km west of the spot occupied in December (locality B). Rain was intermittent at this time and surface water widely available (season 5). Over the next 60 days, camp size remained relatively stable, about 35 people in six to seven households. Men's subsistence effort was devoted primarily to honey collecting, usually with their wives and children. Families typically foraged alone, sometimes in pairs. Trips were long, up to three hours just in travel (12–15 km) from camp. Hunting returns were fair; over 14 days, men from Mbea took only one adult impala, but all residents shared meat from a giraffe killed by hunters in a nearby camp. Women and children not collecting honey with men foraged in large parties for berries (*Grewia bicolor* [Hadza *kongorobe*]), usually within one to one-and-a-half hours' walk. Tubers were collected less often in this season than in any other.

In mid-April, while still at Mbea, women stopped collecting *kongorobe,* turning instead to another species of *Grewia* berry (Hadza *embiribe*) found closer to camp. Tubers were taken more often as well. These changes in foraging tactics led us to distinguish this period as a separate "season" (6). Honey collecting continued to be important. Hunting success remained constant; over 15 days, two impala (one heavily ravaged by hyenas) were taken by men from our camp, and giraffe meat was acquired from a kill made by hunters in the same nearby camp.

By mid-May, the rains had diminished and the country had begun to dry out (season 7). People from Mbea moved to a site called Dubenkela, 4 km to the south. The reason for the move was unclear but may have been related to honey-collecting success. Camp size remained the same: 35–40 people in six to seven households. Over the next two months, families foraged for honey, men hunted by encounter, and women dug tubers and collected *embiribe* and baobab. Hunting returns improved slightly. Over 36 days, hunters from Dubenkela killed two zebra and scavenged meat from another as well as from two giraffe.

Patterns in Time Allocation and Children's Weight Changes

Relationships between women's time allocation and children's nutritional status, the main target of our analysis, may be complicated by variation in subjects' age and sex as well as in seasonal conditions.

VARIATION IN TIME ALLOCATION BY SEX AND AGE

Table 1 provides a general summary across the entire study period. Time spent on food acquisition includes all time devoted to any activity routinely associated with foraging away from camp, including travel, search, pursuit, extraction or collection, and processing at or near the site of acquisition, as well as eating, attending to children, and resting between foraging bouts. Food processing counts all processing carried out at or near camp. Household maintenance includes building and remodeling shelters, collecting water and firewood, tending fires, and sweeping and cleaning household areas. Manufacture and repair counts the making and mending of clothing, decorative items, and other implements.

For women and girls (fig. 1), time devoted to all activities except food processing initially increases with age. Time spent on household maintenance peaks before adulthood and declines thereafter. Time given to manufacturing and repair tops out later, during childbearing years. All but the youngest girls spend more time acquiring food than in any other activity. Unlike that allocated to all other categories, time allocated to food acquisition continues to increase with age beyond menopause. Older women spend significantly more time foraging than females in any other age-category. Most of the extra effort is devoted to tuber collecting; time allocation to other resources does not differ from that of younger women (Hawkes, O'Connell, and Blurton Jones 1989). The difference in foraging effort between adolescent girls and women of childbearing age

TABLE 1
Hadza Time Allocation to Work (hrs./week)

		Food Acquisition Away	Food Processing at Home	Household Maintenance	Manufacture and Repair at Home	
	N	Mean ± S.E.	Mean ± S.E.	Mean ± S.E.	Mean ± S.E.	Total
Little girls (weaned–5 yrs.)	21 (8)	3.01 ± 1.01	12.01 ± 1.18	2.35 ± 0.67	0.87 ± 0.17	18.24
Bigger girls (6–13 yrs.)	17 (5)	18.26 ± 3.36	10.46 ± 1.18	5.80 ± 1.18	1.97 ± 0.34	36.49
Adolescent girls (14 yrs.–marriageable)	18 (5)	27.76 ± 3.11	6.96 ± 1.26	7.17 ± 1.43	4.05 ± 0.84	42.49
Childbearing-aged women	50 (18)	27.58 ± 2.02	8.16 ± 0.67	2.91 ± 0.34	6.23 ± 0.84	44.88
Postmenopausal women	29 (9)	36.80 ± 3.02	6.91 ± 1.09	2.47 ± 0.50	3.53 ± 0.50	49.71
Little boys (weaned–5 yrs.)	33 (13)	9.05 ± 2.02	10.17 ± 0.84	2.94 ± 3.11	1.44 ± 0.25	23.60
Bigger boys (6–13 yrs.)	17 (7)	29.91 ± 4.37	8.37 ± 1.76	2.60 ± 0.50	2.09 ± 0.59	42.97
Adolescent boys (14 yrs.–marriageable)	23 (11)	44.41 ± 2.60	4.05 ± 1.34	2.86 ± 0.76	2.33 ± 0.34	53.65
Adult men	35 (14)	28.94 ± 3.27	4.19 ± 0.67	3.22 ± 0.67	7.99 ± 1.51	44.34

NOTE: *N* is number of time budgets in the sample (number of different subjects in the sample). Age estimates are approximate.

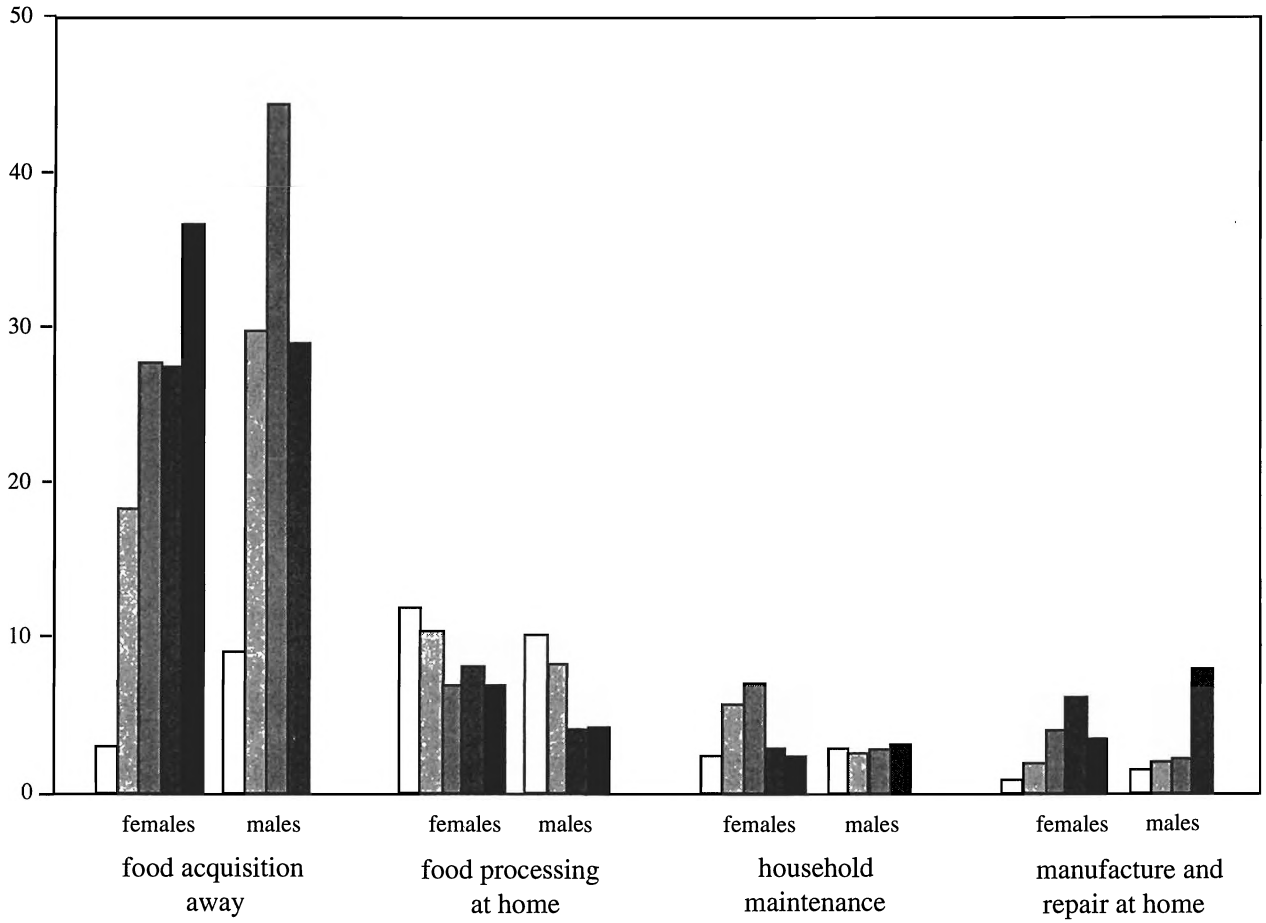

FIG. 1. *Hadza time allocation to work (hrs./week). Numbers are drawn from table 1; ages (estimated as in table 1) are approximate. Age-categories,* left to right: *weaned–5 years, 6–13 years, adolescent, childbearing aged/adult, postmenopausal.*

is not significant. There are 18 childbearing-aged women in this sample, 8 of whom had nursing infants during the study period.[5] *T*-tests show no significant differences in the mean time budgeted by nursing and nonnursing women to any of the activities listed in table 1. This contrasts with patterns found among the Ache (Hurtado 1985, Hurtado et al. 1985), where nursing women allocate less time on average to foraging.

For men and boys (fig. 1) there are fewer age differences in time devoted to any activity but food acquisition. Adolescent boys and men spend less time on food processing than younger boys; household maintenance effort does not vary with age; boys of all ages spend less time on manufacture and repair than adult men. Age distribution for time spent foraging is quite different from that for females: the peak for males comes before marriage, adolescent boys spending more time foraging than members of any other age/sex-category. Married men forage no more than preteenage boys.

Between the sexes, the greatest differences are in foraging time, males of all ages except adults spending more than females of the same age-category (the same pattern is evident in other samples [Hawkes, O'Connell, and Blurton Jones 1995, Blurton Jones, Hawkes, and O'Connell 1997]). Mean time allocation to most activities is similar for childbearing-aged women and adult men, the only significant difference being that women do more food processing.

Across the sample as a whole, foraging time generally increases with subject's age while in-camp processing time decreases. Controlling for age, the pattern persists (partial correlation: d.f. 244, $r = -0.5434$, $p = 0.000$). Other activities are also inversely related with foraging time, but the correlations, though significant, account for little of the variation they themselves display (partial correlations, controlling for age-category: household maintenance, $r = -0.1649$, $p = 0.005$; manufacture and repair, $r = -0.1735$, $p = 0.003$). Variation in time devoted to the three kinds of in-camp work is uncorrelated.

SEASONAL PATTERNS AMONG WOMEN AND CHILDREN

Seasonal variation in women's and children's foraging times and children's weight changes were assessed by multiple linear regression (see appendix for details). Since age and sex contribute to variation in children's foraging times, we include them in our analysis of the seasonal patterns (see appendix table A1). They alone account for 56% of the variation (multiple regression coefficient [multiple r] = 0.746). Seasons 2 and 3 also contribute significantly. Adding these two seasons to age and sex raises multiple r to 0.821 (versus 0.839 if age, sex, and all seven of the seasons are included), accounting for 67% of the variation. Season 2 marked the beginning of a pattern of long-distance trips to collect *Cordia* (*ondishibe*) berries. Children routinely accompanied adults on these trips; their foraging times jumped sharply relative to those of the preceding late dry as a result. They foraged less in season 3 than in season 2 but more than in any other season, a pattern that may reflect continued recovery from the rigors of the late dry.

Almost all of the variation in children's weight changes is associated with seasons 1 and 2 (appendix table A2). During season 1, children lost weight. With the onset of the wet season and the related increase in their own foraging efforts (as well as those of their mothers and grandmothers), they made larger weight gains than at any other time of the year. In this sample, there is no association between weight change and child's age, a likely artifact of the lack of precision in the weights and the extreme effects of season. The regression coefficient for the variation in weight changes due to seasons 1 and 2 alone is 0.902 (versus 0.909 if age, sex, and the five seasons with weight data are all included), accounting for 81% of the variation.

Analysis of seasonal variation in women's foraging times included a binary (pre-/postmenopause) age variable because older women spend more time foraging (table 1; Hawkes, O'Connell, and Blurton Jones 1989; see appendix table A3). The correlation between women's age-category and foraging time is 0.359. Seasons 2 and 5, times when women (and children) took frequent long-distance berry-collecting trips, also contribute substantially (multiple regression coefficient for age plus these two seasons = 0.559). A multiple regression that includes age, nursing status, and all seven seasons raises the regression coefficient just slightly, to 0.613.

Covariation in Women's Foraging and Children's Weight Changes

The central focus of our analysis is the relationship between variation in mother's and grandmother's foraging returns and children's weight changes. We begin by reviewing the effects of nursing status on women's resource allocation and then outline the assumptions that underlie our use of foraging time as an index of the amount of food a woman acquires.

NURSING VERSUS NONNURSING WOMEN

Nursing affects a woman's patterns of time and resource allocation in at least two ways. First, lactation itself is expensive, costing an average of about 600 Cal/day to support (Prentice and Whitehead 1987). The in-

5. The nursing women were slightly younger on average than the nonnursing, though not significantly so, and they had significantly more coresident children. Using only the first season for each subject, eight nursing mothers had an average of 2.5 ± 0.33 children in the household and ten not nursing had 1.4 ± 0.37 ($p = 0.041$, two-tailed). Pertinent time budgets (24 for nursing women, 50 for their weaned children; 26 for nonnursing women, 39 for their children) are randomly distributed across all the seasons. (Test for association of maternal state with season [d.f. 6]: for women, chi-square = 5.35, $p = 0.499$; for children, chi-square = 9.59, $p = 0.143$).

crease in personal consumption this requires means less food available per foraging hour to share with others, including weaned offspring. Second, an infant literally comes between a woman and her work. Holding, carrying, and feeding it almost certainly interfere with her foraging efficiency, probably depressing her food acquisition rate under most circumstances and further reducing the amount of food she can gather to share.[6] A nursing woman might therefore be expected either to forage more to make up the loss in efficiency or, given a helper who can feed the children, forage less. If older children can get the same daily ration with less input from her, then the marginal benefits from her effort may be reduced to the point that she does better by allocating less time to foraging and more to other activities.

This reasoning notwithstanding, the analyses reported above show *no* differences in the *average* time budgets of nursing versus nonnursing women, even when seasonal variation is controlled by multiple regression (see appendix). One reason for this result may be that our analyses have so far treated nursing as a categorical variable, ignoring how much an infant's interference in its mother's activities varies with its age. Weaning can be noisy enough to seem quite abrupt, but it marks the end of a period in which children steadily become more competent and less dependent on mother's milk. A woman about to wean a nursling can respond to its attempted interruptions less, without penalty, than a woman with a newborn. Below we show that time allocation to foraging does in fact differ among nursing women according to infant's age: the younger the infant, the less time spent foraging.

FORAGING TIME AS A MEASURE OF FOOD ACQUIRED

We assume that acquisition rates are broadly similar within any season among nonnursing women of childbearing age and among postmenopausal women. If so, then time spent foraging is a measure of variation in the relative amounts of food women acquire. This simplification is less precarious here than it might be elsewhere. Hadza women usually target a common resource, travel to and from home as a group, and remain within earshot of each other at the resource patch (Hawkes, O'Connell, and Blurton Jones 1989, 1995). If return rates are indeed similar for any given resource and if women take the same resources within any season, then those who spend more time foraging (i.e., join the main party of women more often) will acquire more food and have more to share than those who spend less. Postmenopausal women may earn somewhat different returns per unit time than do younger nonnursing women insofar as the extra effort they devote to foraging (table 1) is directed primarily at tubers (especially *Vigna frutescens* [Hawkes, O'Connell, and Blurton Jones 1989]). For the reasons specified above, we expect nursing women's foraging efficiency to be reduced by nurslings' interference and the amounts they have to share to be further limited by their need to support their own lactation.

FORAGING TIME AND CHILDREN'S WEIGHT CHANGES

If (1) mothers' foraging and food sharing are crucial to children's welfare, (2) the cost of lactation and nurslings' interference reduce the amount of food mothers can allocate to weaned children, and (3) grandmothers' foraging provides the food required to offset the reduction in nursing mothers' support, then all these relationships should be reflected in predictable patterns of covariation between women's foraging time and children's weight changes once the potentially complicating effects of seasonal variation are removed.

The confounding problems of seasonal variation are illustrated by analysis of the relationship between children's own foraging times and weight changes. Children generally gain more weight the more time they spend foraging (table 2, row 1a), but the link could be indirect, an effect of some third seasonal variable. Children might forage more and gain more weight in some seasons not because the first causes the second but because each is due to more foraging by others in those seasons. When the large variation in weight changes associated with seasons 1 and 2 (see above and appendix table A2) is eliminated, the relationship between children's foraging times and weight changes disappears (row 1b). This result prevents us from ruling out the (unlikely) possibility that children's foraging has no direct effect on their own weight changes.

The core of our argument is the importance of maternal provisioning. Our first propositions are that (1) mother's foraging determines children's nutritional welfare and (2) her effect on that welfare is reduced by the arrival of an infant. Row 2a of table 2 shows a significant correlation between the time nonnursing mothers spend foraging and their children's weight changes, even when the strong effects of seasons 1 and 2 on those changes are controlled. For nursing mothers (again controlling for seasonal variation in children's weight changes), there is no such correlation (row 2b).

Seasonal variation in children's weight changes was controlled in this analysis in order to exclude spurious correlations. It is possible, however, that covariation with season includes a substantial direct effect of foraging time on weight changes. If so, removing those differences obscures that effect. Rows 2c and 2d of table 2 show the results of partial correlations of mother's foraging time and child's weight changes when seasonal effects are not controlled directly but the child's own foraging time (which itself varies seasonally) is controlled instead. Analyzed this way, the nutritional status of

6. Elsewhere we found no difference in foraging return rates for nursing versus nonnursing women of childbearing age (Hawkes, O'Connell, and Blurton Jones 1989). We attributed that result to sample size and expect the effect of nurslings' interference to be apparent in larger data sets.

TABLE 2
Foraging Time and Weight Changes

	Mother Nursing?	*N*	*r*	*p*
1a. Child's weight changes by own foraging time	n.a.	45	0.4164	0.002
1b. Child's weight changes by own foraging time, controlling seasons 1, 2	n.a.	41	0.0824	0.300
2a. Child's weight changes by mother's foraging time, controlling seasons 1, 2	no	6	0.6620	0.037
2b. Child's weight changes by mother's foraging time, controlling seasons 1, 2	yes	25	0.0070	0.486
2c. Child's weight changes by mother's foraging time, controlling child's own time	no	7	0.6797	0.022
2d. Child's weight changes by mother's foraging time, controlling child's own time	yes	26	0.3547	0.032
3a. Mother's foraging time by age of youngest, controlling seasons 2, 5	no	8	0.2726	0.223
3b. Mother's foraging time by age of youngest, controlling seasons 2, 5	yes	14	0.6167	0.005
4a. Grandmother's foraging time by age of youngest, controlling seasons 2, 5	yes	15	−0.7701	0.000
4b. Child's weight changes by grandmother's foraging time, controlling seasons 1, 2	yes	25	0.0019	0.496
4c. Child's weight changes by grandmother's foraging time, controlling both child's own time and mother's	yes	25	0.5139	0.003
4d. Youngest weaned child's weight changes by grandmother's foraging time, controlling mother's foraging time	yes	10	0.6829	0.007

NOTE: *N* is number of weight changes or time budgets in the sample. Rows 1a and b include weight changes of all children, regardless of mother's nursing status. Elsewhere, weight changes or time budgets are included (or not) depending on mother's nursing status.

nonnursing mothers' weaned children is still seen to be strongly dependent on mothers' foraging effort (row 2c). Weight changes among weaned children of nursing mothers are also affected by mothers' foraging, but the link is much weaker (row 2d). In these two partial correlations, nonnursing mothers' foraging time accounts for 46% of the variation in their children's weight changes, nursing mothers' 13%.

We have suggested above that nursing mothers might adjust their foraging time with age of infant. Infants can certainly be more demanding as they grow, but their increasing competence may allow mothers to be less attentive. This would raise mothers' foraging efficiency and so their marginal gains for increased foraging time. Row 3a of table 2 shows that when seasonal variation is controlled, age of youngest child has little effect on nonnursing women's foraging time. But for nursing women youngest child's age *does* make a difference: mothers initially reduce foraging time when they bear a new infant, then steadily increase it across the nursing period (row 3b, again controlling for seasonal variation). The trajectory of this change implies a reduction in maternal support for weaned children at the birth of a sibling.

Since nonnursing women's foraging time affects their children's nutritional welfare (table 2, rows 2a and c), the loss associated with the arrival of a new child (rows 2b and d) must be made up from some other source. As anticipated, grandmothers provide the required support. They show exactly the inverse pattern of nursing moth-

ers, spending the most time foraging when their infant grandchild is youngest and their weaned grandchildren are receiving least from mothers, the least when these circumstances are reversed (row 4a, controlling for seasonal variation).

We expect grandmothers' foraging time to have an effect on the weight changes of weaned children. However, if the strong seasonal variation in children's weight (that associated with seasons 1 and 2) is removed, no impact is detectable (table 2, row 4b). As noted above, the strength of the seasonal covariation may itself reflect the direct effects of foraging time on weight changes. If so, removing the seasonal differences removes the direct effect as well. When both the child's and its mother's foraging times (themselves varying seasonally), instead of season directly, are controlled, variation in children's weight changes is seen to be correlated with grandmother's foraging time (row 4c). Restricting attention to the youngest weaned children of nursing mothers—the children contributing least to their own nutrient stream—the effect of grandmothers' contribution, measured in this way, is especially strong (row 4d).

Discussion

Although the sample of time budgets is small and of individual subjects smaller still, analysis of variation in women's foraging patterns and the covariation between women's foraging time and children's growth illustrates several points:

1. Women's foraging affects their children's nutritional welfare.
2. The arrival of a newborn reduces mother's contribution to the nutrition of her weaned children.
3. Women spend the least time foraging when their babies are youngest but increase their foraging effort across the nursing period.
4. Grandmothers offset this initial reduction in effort by nursing mothers, foraging more when the new grandchild is youngest.
5. The welfare of the weaned children of nursing mothers is affected by the foraging of their grandmothers.

The presence of these patterns among the Hadza is consistent with our expectations about relationships between resource characteristics, children's foraging capabilities, and women's foraging patterns. Previous research (Blurton Jones, Hawkes, and O'Connell 1989; Hawkes, O'Connell, and Blurton Jones 1989, 1995) has established that although Hadza children are active foragers, they earn relatively low returns from resources whose collection and processing require adult levels of physical strength and endurance. Some of these resources, notably the tuber *Vigna frutescens* (*//ekwa*), are year-round staples, available even when foods children can take efficiently are not. The relatively high returns adults can earn from such resources and the practice of regularly sharing food with children allow the occupation of habitats that would be essentially unavailable (at least seasonally) if youngsters were entirely dependent on their own foraging efforts after weaning. More generally, these features would allow hominids that possessed them to thrive in habitats marginal for pongids (Moore 1992). High returns and sharing also allow older women to support weaned grandchildren, freeing their adult daughters to allocate more effort and attention to the next baby.

IMPLICATIONS FOR LONG LIFE SPANS AND THE RIDDLE OF MENOPAUSE

This argument draws attention to two other characteristics that distinguish humans from other primates—long life spans and menopause. For large-bodied apes, maximum life span is generally estimated at no more than 50 years (Harvey and Clutton-Brock 1985). Fertility and other aspects of physiology senesce in synchrony. Among humans, maximum life span is about 100 years, yet fertility in women ends in about half that time (Pavelka and Fedigan 1991). Only human females can expect to live long beyond their last pregnancy (Caro et al. 1995).

Evolutionary theories of senescence generally assume that selection cannot favor postreproductive life because mutations that promote it would have no effect on fitness. Williams (1957) called attention to the puzzle this makes of menopause and proposed a solution in the trade-offs associated with increased investment in children already born versus continued production of new ones. In species where extended maternal care is crucial to offspring survival, aging mothers are less likely to see a new baby through to independence. Instead of bearing another child with little chance of survival, they might do better by allocating their effort to increasing the fitness of children already born. If marginal fitness gains from this strategy were sufficiently high, selection could favor earlier termination of childbearing combined with "reproductive" effort subsequently devoted to older children and even grandchildren (i.e., menopause).

Despite the appeal of this argument, long periods of juvenile dependency alone are not enough to promote early termination of fertility. Chimpanzee case studies show that extended maternal care is crucial to survival in this species. Late-born babies do confer low expected fitness benefits, as offspring born to older females often fail to live beyond their mothers' death (Goodall 1986, 1989). Nevertheless, fertility and other aspects of physiology still senesce at the same time. Moreover, chimpanzee and human reproductive spans are remarkably similar. The striking difference is our much longer adult life spans (Hill 1993, Hill and Hurtado 1991, Kaplan n.d.).

One family of theories about senescence assumes that increased "adaptive performance" at later ages exacts a cost in reproductive output earlier in life (Kirkwood and Rose 1991, Williams 1957). Greater allocation to somatic quality or maintenance may increase longev-

ity but only at the expense of reduced investment in reproduction early on. Selection results in "disposable somas" as a consequence. If the chimpanzee pattern is in equilibrium for this trade-off, then potential fitness benefits of increased longevity must be outweighed by the losses associated with reductions in earlier reproduction. The absence of a postmenopausal period in pongids, combined with the equilibrium assumption, further implies that marginal fitness benefits for bearing new offspring continue to outweigh those for investing in older children instead.

A regular pattern of mother-child food sharing could perturb this equilibrium by providing a new way for senior females to increase their fitness. The catalyst would be the adoption of a resource that yields high returns to adults but not to children. Provisioning with this resource would expand the mother's effective habitat but make weaned juveniles situationally dependent on her for food. Grandmothers could help provision these children. Mothers who enjoyed such assistance could wean their children earlier and begin another pregnancy sooner than they could without it. This division of labor would enhance grandmothers' fitness by increasing both their daughters' fertility and the survival of grandchildren by an avenue not open to other primates. Senior female chimpanzees do have important effects on the fitness of their older juvenile and even adult children. But if we assume that their pattern of senescence reflects an equilibrium, then a different and stronger effect is needed to favor longer, postmenopausal life spans. Mother-child food sharing provides the opportunity for such an effect.

This argument highlights the long life span of humans, *not* the early termination of fertility, as the derived feature that requires explanation (Kaplan n.d.). Human reproductive spans are no shorter than those of other hominoids. Fertile spans of less than three decades characterize humans, chimpanzees, and other pongids. That pattern, along with maximum life spans of about 50 years—fertility and other aspects of female physiology aging together—are the likely ancestral condition. Regular mother-child food sharing may have adjusted life span without altering age-specific declines in fertility. If food sharing allowed fitness benefits for survival (through grandmothering) to increase sufficiently, selection could have favored greater allocation to somatic effort at the expense of earlier reproductive effort. Less reproductive effort from younger mothers could have been associated, paradoxically, with higher fertility due to the compensating effects of older mothers' help. Longer life spans would have been favored accordingly.

IMPLICATIONS FOR SOCIAL ORGANIZATION

The changes in resource use that form the core of this hypothesis may also be connected with shifts in other social arrangements. If older juveniles are increasingly efficient at extracting high-return resources, then mothers should benefit from enlisting their help in supporting younger siblings (Blurton Jones et al. n.d.). Giving that help will serve older children's fitness.[7] Consistent use of high-return resources requiring skill or strength to exploit would increase the benefits for mothers and daughters remaining together. A mother still bearing offspring could use her daughter's help; a childbearing daughter would benefit from the assistance of her postmenopausal mother. In addition, within-group feeding competition would be reduced if extraction effort rather than abundance limited the acquisition of important foods. If such competition were the main limit on group size (Janson 1992, van Schaik 1989), then larger female groups might be expected, with further consequences for male strategies.

This scenario runs counter to an array of arguments about the likely pervasiveness of female dispersal and male philopatry in hominid evolution (Foley and Lee 1989, Giglieri 1987, Rodseth et al. 1991, Wrangham 1987). The frequency with which patrilocal residence is reported ethnographically and the fact that female chimpanzees (unlike the females of most primate species) tend to leave their natal groups have together stimulated arguments about the continuity of female dispersal in all descendants of our common ancestor. Advantages to males in forming kin-based alliances are assumed to have shaped the social organization of our entire clade. The evolutionary arguments of this paper focus on the advantages of proximity for *matrilineally related females* when mother-child food sharing is important.

Common chimpanzees and bonobos differ in patterns of sociality not only from humans but from each other. Common chimpanzee females are much less social toward each other than are males (Wrangham, Clark, and Isabirye-Basuta 1992). Among bonobos, where feeding competition appears much reduced, females are extremely social, and close female associations may allow mothers to affect the mating opportunities of their sons (Kano 1996, White 1996). In both species, females at maturity typically leave their natal groups. We argue that daughters would have an incentive to stay with their mothers if resources that young juveniles cannot manage were in regular use. This pattern is not found in either chimpanzee species, with one striking exception. Common chimpanzees in the Taï Forest (Ivory Coast) reportedly rely on hard-shelled nuts as a major resource during several months of the year (Boesch and Boesch 1984). Young juveniles cannot handle these nuts and depend on shares from mothers and older siblings. This is just the circumstance in which we would expect advantages for mothers and daughters remaining together to outweigh advantages for daughters leaving. Daughters in other populations of common chimpanzees do sometimes stay with their mothers (Goodall 1986). When the advantages for doing so increase, as they would with

7. Only up to a point: if siblings are likely to have different fathers, then, other things being equal, females reaching the age of maturity will gain twice as much fitness from bearing offspring themselves as from supporting a new half-sibling.

regular food sharing from *both* mother's and daughter's point of view, we expect the patterns of female sociability and sex-biased dispersal to be altered as a consequence. Female chimpanzees at Taï are more social than elsewhere (Boesch 1996). More details on patterns of chimpanzee nut use and social organization at Taï should allow us both to clarify and to test our expectations.

Emphasis on evolutionary links between food sharing and female foraging strategies also represents a departure from the long-standing focus on hunting as the key to human food sharing. Most nonhuman primates do not hunt vertebrate prey, but among those that do sharing game is a striking practice (Feistner and McGrew 1989). Food sharing is common in only one mammalian order, the Carnivora, a pattern contributing to the view that hunting and food sharing are causally linked (e.g., Kleiman 1977, Orians 1969). Since males do most of the hunting among ethnographically known humans and other primates, it is usually assumed that they did so in the past as well. The most influential hypothesis has been that hunting allowed males to provision mates and offspring, making food sharing, a sexual division of labor, and nuclear families a coevolutionary set (e.g., Alexander 1990, Isaac 1978, Lancaster and Lancaster 1983, Washburn and Lancaster 1968).

Elsewhere (e.g., Hawkes, O'Connell, and Blurton Jones 1991, Hawkes 1993) we have challenged this argument, showing that men's foraging choices are often inconsistent with family provisioning. Large-mammal hunting is an unreliable strategy for feeding dependents in arid African savanna habitats like those envisioned in conventional models. Even in areas where large prey are relatively common, hunters armed with bows and poisoned arrows are unable to provide a dependable daily flow of nutrients.[8] They would be even less effective without such weapons. In short, and whatever its other advantages, hunting cannot cover the day-to-day nutritional requirements of weaned offspring among contemporary savanna foragers and seems even less likely to have done so in the distant past. The assumption that nuclear families are fundamental *economic* units among modern human foragers, let alone ancestral hominids, is due for revision.

THE MODERN HADZA AND OUR EVOLUTIONARY PAST

The facts of the Hadza case fit the hypothesis offered here. This should not be surprising: it was the obvious industry of postmenopausal Hadza women that stimulated our attention to grandmothers in the first place (Hawkes, O'Connell, and Blurton Jones 1989). Having developed the argument on that basis, the key question now is this: Are the foraging opportunities and constraints affecting Hadza women's time allocation likely to be of general importance? Phrased in terms of resource costs and benefits and the variability these display as a function of differences in juvenile foraging capability, we expect them to be quite general and to vary in predictable fashion. Mothers' foraging should have even larger effects on children's nutrition, with consequent increases in the importance of grandmothers, where hunters supply less meat than do Hadza men. It should have been especially important in the distant past, prior to the development of projectile weapons like those used by the Hadza. Conversely, where men's contribution to local group subsistence is greater than it is among the modern Hadza, the effects of mothers' foraging in general and of grandmothers' contribution in particular should be less.

THE "GRANDMOTHER HYPOTHESIS" AND THE ACHE

The relative importance of men's contribution to the diet may be partly responsible for the results of a recent test of the "grandmother hypothesis." Hill and Hurtado (1991, 1996) collected exhaustive genealogies among the Ache of eastern Paraguay and built a set of marital, reproductive, and mortality histories spanning the period from 1890 to 1970, when the Ache lived entirely by foraging. Over that period, survivorship of juveniles and fertility of adults were found to be higher among those who had living postmenopausal mothers/grandmothers than among those who did not. But the differences were small—too small to be statistically significant. Using the measured differences to estimate the inclusive-fitness benefits of investing in older children (and grandchildren) instead of continuing to bear more offspring, Hill and Hurtado found that the "grandmother hypothesis" could not account for the timing of menopause among the Ache.

The Hadza picture and the evolutionary argument developed here highlight three important aspects of the Ache patterns. First, men's contribution to total Ache diet is extremely high. Quantitative observations in the 1980s indicate they provided > 85% of total caloric intake (Hill et al. 1987). If this figure is roughly typical of the entire period covered by Hill and Hurtado's demographic records, then even though Ache women reduce the time they spend foraging with the arrival of a newborn (Hurtado 1985, Hurtado et al. 1985), the absence of a grandmother would have a much smaller effect on a weanling's nutrition than where women's contribution to the diet is greater.

Second, increases in daughters' fertility and the survival of their offspring are identified in our argument as the main pathways by which grandmothers enhance their own fitness. Hill and Hurtado look for a difference between the survivorship/fertility of those with living postmenopausal grandmothers/mothers and those without, but the Hadza sample indicates a more diverse set of relationships between mothers and their senior helpers. In only two of the eight cases in our sample were women actually assisting childbearing daughters. In the other six, two were helping sister's daughters,

8. In the sample reported here children *lost* weight during season 1, the time when hunters were most successful, and *gained* weight during season 2, when hunting success was near its annual low.

one a daughter's daughter, two sons' wives, and one a more distant relative. Stochastic effects on sex ratios and mortalities have large effects on the investment opportunities for older women. Some will have no living daughters, some more than one, and some will die before their children reach adulthood. Nevertheless, in the Hadza sample *no nursing woman lacks a postmenopausal helper.*[9] If such patterns are common, as we think they must be, then comparing the fertilities of women with surviving mothers with those of women without will *always underestimate* the effects of help.

It is clear in the Hadza case and necessary to the evolutionary argument that senior women do not help indiscriminately. A helper's inclusive-fitness benefits from assistance decay geometrically with kinship distance. Help given to a niece or granddaughter (other things being equal) has half the fitness value of that given to a daughter. But a woman may have no daughter to help. Aiding a daughter who is not nursing may have little effect either on her fertility or on the survival of her children, yet the same assistance could have large effects on the fertility of a nursing niece. Deploying help flexibly increases the fitness payoff for survival past menopause. An evolutionary history of variation in opportunities to help should sharpen the tendency to distribute that help according to probable marginal fitness gains. Motherless women would receive help from their aunts and grandmothers but have lower priority for assistance than closer relatives of the helpers.

This points to a third issue: the particular grandmother hypothesis that Hill and Hurtado choose to test. They focus on a trade-off between continued childbearing and effort spent on children already born. Assuming continued survival, they model menopause as "early" termination of fertility. Other modelers do the same (e.g., Rogers 1993, Peccei 1995). Here we highlight the likely importance of a different trade-off. If termination of fertility at about age 50 is assumed, then long life span after menopause becomes the pattern to be explained. Attention is directed to the trade-off between reproductive effort earlier in life and somatic effort toward increased survivorship later. We pose the problem this way because the apparent similarities in reproductive physiology and fertile span of humans and great apes make the added life span in humans the obviously derived trait. Much longer fertile spans do occur in some other mammals, indicating that mammalian reproductive physiology is not an insurmountable phylogenetic constraint (for review see Hill and Hurtado 1991, 1996). But the similarities between humans and apes suggest that adjustments may be costly. Characterizing menopause as "premature reproductive senescence" implies that modern humans and apes have converged on similar fertile spans after divergence at some earlier date. This requires longer life spans with extended fertility to evolve among (some) hominids first, followed by selection for menopause reducing the human fertile span to (coincidentally) ape proportions. Conservation of the length of the fertile span with the evolution of postmenopausal life spans in humans is a simpler scenario.

9. Our sample includes only four time budgets on postmenopausal women *not* helping a nursing relative. Three of these are from one subject whose opportunities for helping are unusually limited. She bore no children herself, and three of her (also postmenopausal) sisters are vigorous helpers of their own offspring.

OTHER LINES OF INQUIRY

Considering different trade-offs is especially timely in light of recent developments in life-history theory. Although patterned relationships among adult life spans, age at maturity, and reproductive rates have long been matters of attention (e.g., Harvey 1990, Stearns 1992), recent work points to unexpectedly strong regularities. Charnov's (1991, 1993; Charnov and Berrigan 1993) "dimensionless approach" reveals that relationships among a few central life-history features take characteristic values for similar taxa. This provides a framework for comparing human life histories with wider primate patterns in new ways (Hill 1993, Hill and Hurtado 1996). Elsewhere (Hawkes et al. 1997) we have shown that a combination of the grandmother hypothesis outlined here and Charnov's life-history model provides explanatory links between long human life spans with menopause and three other features that distinguish human life histories from those of other primates: late maturity, early weaning, and remarkably high fertility.

Comparative analyses like this can also be carried into the past. If some life-history characteristics are strong predictors of others, then attention to developmental markers preserved in hominid fossils might enable us to test an unexpectedly broad range of hypotheses about the lives of various hominids (see Bromage 1990, Conroy and Kuyenkendall 1995, Smith 1992). The apelike features of australopithecine life histories may be read to suggest that the cluster of patterns discussed here evolved later, perhaps with the appearance of genus *Homo.* Some interpretations of Neanderthal life history imply that it might be restricted to anatomically modern *sapiens* (Trinkaus and Tompkins 1990). Better understanding of links among life-history traits could guide the use of skeletal features to decide between these (or other) possibilities. Ongoing research on the connections between diet and bone chemistry (e.g., Schoeninger 1995) may ultimately enable us to relate changes in life history to features of local ecology.

The Hadza patterns reported above are consistent with a grandmother hypothesis that, if correct, makes the appearance of mother-child food sharing an especially important development in human evolution. Further exploration of modern human forager behavior, including the strategic adjustments grandmothers make in distributing help, is clearly in order. Recent expanding interest in the behavior of juvenile primates should enrich the data sets required to assess the constraints of age-specific foraging capacities and their consequences for social behavior and life histories among nonhuman primates (e.g., Janson and van Schaik 1993).

Charnov's identification of apparently invariant relationships among key life-history traits suggests new perspectives on the variation among living primates (Martin and MacLarnon 1990) and in fossil taxa as well. Several different lines of inquiry about variation in both living and fossil taxa can thus contribute to the evaluation and modification of the arguments presented here and give us an array of new hypotheses to take to the past.

Appendix: Seasonal Patterns in Foraging Times and Weight Changes

Multiple linear regressions were used to explore seasonal differences in women's and children's foraging times and children's weight changes. To construct the regressions, we defined dummy variables for each season, assigning the value 1 to all time budgets compiled in that season, 0 to those compiled in the other six. We then ran an array of multiple regressions, using each of the seasons in turn as a baseline (Pedhazur 1982:chap. 9; Aiken and West 1991:chap. 7). The standardized regression coefficient (β) is the slope of the least-squares line calculated when the variables have been standardized as *Z* scores. For dummy variables, β is an estimate of the difference between the mean values of the *Y* variable for each value of *X*. In a multiple regression, β values are the partial regression coefficients for the independent variables—the standardized correlation between the *X* and the *Y* variables when all the other independent variables included in the model are controlled. Inspection of the pattern of β coefficients in the array of regressions shows the overall variation among the seasons.

Table A1 reports the results with respect to children's foraging times. Since we know that age and sex contribute to the variation, these variables are included in the model as well. Column 1 shows the contribution of each independent variable to variation in children's foraging time when season 1 is the baseline, column 2 the contribution of each other variable when season 2 is the baseline, and so on. Reading across the first row, all cells show the variation contributed by age when the variation contributed by sex and season is controlled. The seasonal variation is of primary interest here. The signs of the β coefficients show whether foraging time is higher or lower in the season defining the row than in the baseline season. Seasons 2 and 3 are the only ones that contribute much to variation in children's foraging time. The significant positive values of all the standardized partial coefficients for season 2 when each of the other seasons is used (sequentially) as a baseline indicate higher foraging times for children in this season than in any other. Results for season 3 show more variation, including significant or borderline-significant differences between means for this season and several others. The first cell in this row shows that foraging time in season 3 is significantly higher than in season 1, and the next cell shows that it is significantly lower than in season 2. Continuing across the row, foraging time in season 3 is high compared with that in season 4. It is also high compared with foraging time in seasons 5 and 6, but differences between the mean for season 3 and the means of 5 and 6 are not significant. The final cell in the row shows that foraging time in season 3 is higher than in season 7 at just borderline significance.

Table A2 reports seasonal patterns in children's weight changes. The same exercise just described is repeated here (omitting seasons 3 and 4 because we lack the necessary data on weights). Age and sex are included

TABLE A1
Children's Foraging Time

	Baseline Season						
	1	2	3	4	5	6	7
Age	.6246**	.6246**	.6246**	.6246**	.6246**	.6246**	.6246**
Sex	.1700**	.1700**	.1700**	.1700**	.1700**	.1700**	.1700**
Season 1	–	−.3740**	−.1653*	.0140	−.0338	−.0560	−.0094
Season 2	.4037**	–	.2253**	.4188**	.3672**	.3432**	.3935**
Season 3	.1721*	−.2173**	–	.1867**	.1369	.1137	.1623*
Season 4	−.0127	−.3520**	−.1627*	–	−.0434	−.0635	−.0213
Season 5	.0323	−.3250**	−.1256	.0457	–	−.0212	.0234
Season 6	.0667	−.3843**	−.1320	.0847	.0269	–	.0564
Season 7	.0105	−.4066**	−.1738*	.0261	−.0272	−.0520	–

NOTE: Each column reports the β values for a multiple regression of children's foraging time on age, sex, and season with a different baseline season. The regression has 8 degrees of freedom, the residual 70; multiple $r = 0.839$.
**$p < 0.05$.
*$p < 0.06$.

TABLE A2
Children's Weight Changes

	Baseline Season				
	1	2	5	6	7
Age	−.0444	−.0444	−.0444	−.0444	−.0444
Sex	.0571	.0571	.0571	.0571	.0571
Season 1	–	−1.1318**	−.4418**	−.4613**	−.4278**
Season 2	1.1318**	–	.6899**	.6705**	.7040**
Season 5	.4418**	−.6899**	–	−.0195	.0140
Season 6	.5172**	−.7517**	.0218	–	.0376
Season 7	.4278**	−.7040**	−.0140	−.0335	–

NOTE: Each column reports the β values for a multiple regression of children's weight changes on age, sex, and season for a different baseline season (weight changes missing for seasons 3 and 4). The regression has 6 degrees of freedom, the residual 36; multiple $r = 0.909$.
**$p < 0.05$ (for all ** in this table, $p < 0.0001$).

to determine whether they contribute to variation in weight changes in this sample. They do not. Neither do any of the seasons except 1 and 2. All significant standardized partial coefficients (and all that are significant have $p < 0.0001$) are in the rows (or columns) for seasons 1 and 2. These two seasons alone account for almost all the variation in children's weight changes. The mean of children's weight changes in season 1 is −1.00 kg ($N = 8$). In general, they lose weight. In season 2, the mean of their weight changes is 2.06 kg ($N = 8$). In general, they gain substantially. (The means for seasons 5, 6, and 7 are 0.11 kg [$N = 9$], 0.20 kg [$N = 12$], and 0.14 kg [$N = 8$], respectively.)

Table A3 considers seasonal patterns in women's foraging time. Since we know that women past menopause spend more time foraging than younger women, a variable for age (0 = childbearing age, 1 = past menopause) is included to control for that variation. We also include a variable for nursing status (0 = not nursing, 1 = nursing) because we are interested in the effect infants have on their mothers' foraging. Only seasons 2 and 5 differ significantly from other seasons. Mean foraging time in season 2 is significantly higher than in any season except 5. It is higher in season 5 than in any season except 2, although only the difference between seasons 5 and 4 is statistically significant.

TABLE A3
Women's Foraging Time

	Baseline Season						
	1	2	3	4	5	6	7
Postmenopause	.3254**	.3254**	.3254**	.3254**	.3254**	.3254**	.3254**
Nursing	−.0516	−.0516	−.0516	−.0516	−.0516	−.0516	−.0516
Season 1	–	−.3758**	−.0571	.2671	−.2785	−.0791	−.0270
Season 2	.3969**	–	.3366**	.6790**	.1027	.3134*	.3683**
Season 3	.0603	−.3366**	–	.3423	.2339	−.0232	−.0317
Season 4	−.2090	−.5030**	−.2536	–	−.4269**	−.2708	−.2301
Season 5	.2609	−.0911	.2074	.5111**	–	−.1868	.2356
Season 6	.0875	−.3283*	−.0243	.3830	−.2207	–	.0576
Season 7	.0270	−.3487**	−.0300	.2941	−.2515	−.0520	–

NOTE: Each column reports the β values for a multiple regression of women's foraging time on age, nursing status, and season with a different baseline season. The regression has 8 degrees of freedom, the residual 40; multiple $r = 0.613$.
**$p < 0.05$.
*$p < 0.06$.

Comments

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While we agree that hardworking "grandmothers" may adjust foraging effort to accommodate selective offspring of kin, we feel uncomfortable about some of Hawkes et al.'s conclusions. We address (*a*) the theoretical focus on only females in shaping the evolution of a long postreproductive life span, (*b*) the fitness benefits of postreproductive provisioning of kin, and (*c*) directions for future study.

Although physiological menopause occurs only in women, this does not necessarily justify the exclusive female focus in explaining its origin and maintenance. If men live to old age but do little reproduction late in the life span, the long life of men also requires explanation. Evidence among !Kung, Ache, and Yanomamo men show declines in age-specific fertility rates similar to those of women but delayed by about five years (Hill and Hurtado 1996:fig. 9.6). These declines are assumed to be driven by mate choice rather than physiology but nevertheless present a life-history dilemma similar to that illustrated with female fertility and survival data. Can male food production be construed as mating investment even when achieved male fertility approaches zero? We do not yet know whether significant male reproduction takes place in old age throughout human history.

Do grandfathers provision kin more intensively than reproductive-aged men? Or did longer life in men evolve only as a by-product of longer-living women's increasing their relative fitness by provisioning both male and female grandchildren? From the Hadza data, we should at least be able to determine if there exists a relationship between grandfathers' and fathers' foraging times and (grand)children's weight change.

Also, it is unclear why Hawkes et al. focus only on matrilines. If grandmothers provisioned their *sons'* male and female offspring, a postreproductive life span could still have evolved among hominids even with a history of patrilocality. Indeed, one-fourth of the "grandmothers" in this paper are paternal grandmothers. Although the focus on hunting and male-based cooperation has dominated the thinking within anthropology for years, it does not make sense to proceed in the opposite direction without some empirical or theoretical justification. Hawkes et al. suggest that mother-offspring sharing favors matrilocality, but we see only that it increases benefits for either sex that resides with the mother. Whether the fitness benefits of residing near kin are higher for males or females is still a wide open question (see Wrangham 1996 for a patrilocal view). An important assumption of Hawkes et al.'s explanation for the evolution of a postreproductive life span is that meat constituted only a small portion of the diet, thereby making the grandmother effect due to foraging highly influential and reducing the role men played in provisioning. We do not believe this is supported by the archaeological record, which suggests significant meat eating by hominids over the past several hundred thousand years.

While we agree that grandmothers' foraging time affects weight changes among the children they provision, it would be nice to know how these benefits actually increase their inclusive fitness. If benefits are gained by increasing daughter's fertility rather than (or in addition to) son's fertility or grandchild survivorship, it must be shown that the effect of grandmother's foraging time causes a decrease in the length of her daughter's interbirth intervals and that the length of the postmenopausal life span varies positively with daughter's completed fertility. Such information is currently lacking.

If grandmothers in other hunter-gatherer populations do not target the kinds of difficult-to-acquire resources that children cannot acquire for themselves, then we must examine alternative ways in which they improve their fitness. They could be protecting children who might otherwise be at risk of death from accidents and predation in dangerous environments. In this scenario (and especially if meat *was* an important component of early humans' diet), differences in time spent foraging between nursing and non-nursing mothers might be small and grandmothers' foraging might not be necessary. If female postmenopausal life span evolved from nonforaging-related benefits to kin, this presents another challenge to the hypothesis that female-based food sharing was the catalyst for the evolution of hominid longevity.

Hawkes et al. set the stage for many interesting questions which need answering before we can understand precisely how postreproductive females increase inclusive fitness enough to select for longevity. Coefficient of relatedness can be a useful predictor of who should receive investment from postreproductive females, but other characteristics such as reproductive value of potential kin recipients might be even more important. Since only two of the eight Hadza "grandmothers" are actually maternal grandmothers, we need to know the alternative opportunities available to all postmenopausal women. In this study, there are no data comparing the relationship between work effort and weight gain for children of various relationships to older women. Do unrelated children show a weight gain correlated to the work effort of randomly chosen "grandmothers"? What exactly is the sharing pattern between older women and other individuals? If we knew how postmenopausal women in the past distributed the foods they acquired (and the degree to which they discriminated against nonkin recipients), we could perhaps estimate the time depth necessary for longevity to have evolved.

Hawkes et al. are to be commended for their theoretical discussion of the relationships between female re-

source choice, food sharing, and menopause. We hope that this will lead to more hypothesis testing on how decreased fertility in both sexes is balanced by kin investment in the postreproductive life span among samples of diverse peoples living under different ecological conditions.

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Hawkes, O'Connell, and Blurton Jones have demonstrated that (1) mothers gain considerable assistance from their mothers or mothers-in-law in enhancing the fitness of their offspring and/or to enabling them to produce more offspring and (2), reciprocally, postmenopausal women enhance their fitness through investment in daughters' or sons' offspring. At a more general level, they deal with the phenomenon of menopause in a productive way by forcing us to view it in the context of the evolution of long life spans. Their employment of life-history theory with a simultaneous focus on longevity as a derived trait and menopause as ancestral represents an important breakthrough.

Key to the development of their model is an emphasis on long-term economic dependence of offspring on their mothers, in part a consequence of exploitation of food patches which yield high rates of return for adults but not children—who lack the physical strength, endurance, and skills to harvest such resources efficiently. They fail to note, however, that hunting also fits this model.

The main problem I have with the paper is a lack of focus on the role of men as investors in their own or kin's offspring. For example, Hurtado and Hill (1992) show that paternal loss increases offspring mortality among the Aché (although it has no significant effect among the Hiwi). They claim that compared with a father a "grandmother is a consistently better candidate for the role of mother's helper." Presumably this is so because men spend more energy "showing off" to gain additional mating opportunities (Hawkes 1993). This position challenges the standard hypothesis that biparental care, especially in the area of food provisioning, is a fundamental human adaptation that helps explain marriage. It is not a bad idea to question this hypothesis, which probably originated in observations on the nature of marriage in complex societies with socially imposed monogamy. One way to demonstrate that grandmother is a better candidate would be to document the food-getting activities of fathers and their impact on food allocation to mother and children. This Hawkes et al. have not done.

Whether their model fits male and female investment in common offspring in early hominid society is problematic. It is based on the contention that savanna hunting is "unable to provide a dependable daily flow of nutrients." For documentation, they footnote that children lose weight during the most profitable hunting season. But we need to know whether rates of return were greater for hunting than for gathering during this time period or whether pooled variance (I assume that game is widely shared among the Hadza) in hunting success subjects children to an unreliable intake. We also need to know how much men contribute through gathering activities.

Hawkes et al.'s evolutionary scenario in relation to Hadza conditions appears inconsistent. In places they seem to assume that (1) longevity evolved in a savanna environment, (2) men allocated a large amount of time to inefficient hunting when they lacked projectile weapons, and (3) men have little or no positive impact on the economic survival of their offspring either through hunting or through gathering. Later they potentially change the locale of this scenario by noting that longevity "may have evolved later in time, perhaps with the appearance of the genus *Homo*," or "might be restricted to anatomically modern *sapiens*." In reference to Aché, where men contribute 85% of the group's calories, they note that grandmothers are likely to have a much less significant effect on grandchildren's fitness. Presumably there would have been little selective value in being a hardworking grandmother if Aché-like conditions had prevailed. Since we don't know at what point in time or where the hominid evolution of long life span originated, the relevance of local Hadza conditions for highlighting the origins of increased longevity remains problematic.

It seems odd to me that the authors fail to grapple with the fact that longevity increased for males as well as females, which leads one to conclude that it evolved for the same reason. (The only other choices we have is that it evolved as a side effect of female longevity or because it solved an adaptive problem peculiar to males.)

Finally, I have two minor problems with their generally high-quality data and analytic techniques. Unless I misunderstand the analysis, there may be a problem of statistical independence with correlations between various components of time allocation data. Time allocated to nonforaging activities must be, to some extent, negatively correlated with that allocated to foraging activities. Since one cannot forage and do something else (e.g., prepare food), any increase or decrease in foraging time will be negatively or positively correlated with nonforaging activities.

Hawkes et al. assume that foraging acquisition rates of nonnursing and postmenopausal women who travel together to the same resource patch will be identical. We have known for some time that this assumption is not true for hunting because of differential expertise in encountering and pursuing game, for example. I would bet on their assumption's being correct, but I believe it is time to turn this assumption into a hypothesis and test it. Testing this assumption is especially important here because the key component of their theoretical model is that there are fundamental differences in gathering efficiency between children, adolescents, and adults based on differences in strength and endurance.

It is possible that nonstrength differences such as knowledge concerning the location of large tubers or ones that are easier to extract because of the substrate and skill in handling digging tools may differentiate returns among adults. It is also possible that some work more assiduously than others.

In conclusion, this paper is an excellent contribution to anthropology because it forces us to deal with longevity, a long-ignored derived trait that distinguishes us from our closest relatives (Kaplan n.d.), while shedding new light on the old question of menopause.

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Hawkes, O'Connell, and Blurton Jones have elaborated the "grandmother hypothesis" by arguing that long postmenopausal life spans of human females coevolved with patterns of female resource choice and extended provisioning of weaned offspring. This coevolution is facilitated only in societies with female philopatry. However, most modern foragers are considered to be patrilineal, although many of them are pragmatico-local. Moreover, in the genus *Pan,* our closest pongid relative, both chimpanzees and bonobos are patrilocal and none of the other pongids (gorillas, orangutans, and hylobatines) are matrilocal. This implies that early hominids would have had a society with female dispersal. It is therefore unlikely that the proposed coevolution, if any, played a part in the early phase of hominization, that is, from our shared ancestor with pongids to the earliest hominid.

Hawkes et al. argue that the need to share food stimulated grandmothers to help their daughters, suggesting that the exploitation of foods difficult for weaned but still immature offspring to process may have changed female dispersal to female philopatry in chimpanzees at Taï and Gombe. However, there is no sign of such a shift in chimpanzees, including those of the Taï Forest. Mother-daughter coresidence of Gombe chimpanzees is exceptional, possibly affected by the concentration of a locally closed population. In general, philopatry in nonhuman primates is considered to have resulted from selection for incest avoidance: without recognition of paternity, mating with fathers is averted by female or male group transfer. Only human adult daughters can reside regularly with their mothers and then with their fathers in patrilineal societies, since inbreeding can be avoided through sociocultural recognition of kin relations.

Not only chimpanzees but bonobos at Wamba also have some difficult-to-procure/process items, such as large *Treculia africana* and *Anonidium manni* fruits, in their dietary repertoire. Infants and weanlings obtain and consume those foods by sharing with older individuals (mostly mothers). Regular food sharing from mother to offspring is seen in a wide range of sites of chimpanzees and bonobos. The necessity of sharing food with immature offspring may have originated in a remote ancestor. Nevertheless, grandmothers' participation in this seems to be only a recent occurrence.

In most species that are known to have helpers, it is younger animals that help their elders' reproduction. In humans also, adolescent individuals are good candidates for helpers. They can procure food and care for infants/juveniles almost as effectively as adults. Regardless of philopatry, adolescent girls could benefit from helping their mothers by providing their younger siblings with food and care in at least two ways: (1) increasing their inclusive fitness and (2) acquiring practice in caretaking that will be useful for their own future reproduction. In contrast, postmenopausal women get only one benefit, "increase in inclusive fitness," by helping. The increase in inclusive fitness in the two cases has the same value because the relatedness of a daughter to her mother is the same as that of a grandmother to her daughter. Investment in the young is a cost common to both postmenopausal and adolescent helpers, but according to Hawkes et al. postmenopausal women sustain two additional types of cost: (1) early termination of fertility (menopause) and (2) greater allocation to somatic effort at the expense of earlier reproductive effort. Thus, theoretically, adolescent girls seem to be better candidates for helpers than postmenopausal women. If helping by adolescents had evolved in humans similarly as in other species, helping by postmenopausal women might not have been required. The authors provide little discussion on why postmenopausal females instead of adolescent ones were chosen as helpers during the social evolution of foragers.

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I would like to limit my discussion to the possible postreproductive life and philopatry patterns in the chimpanzee-human clade.

First, it is still debatable whether the long postmenopausal life span is a unique human pattern. At Mahale, Tanzania, there were at least five female chimpanzees that survived 8–12 years after they gave birth to their last offspring (Nishida, Takasaki, and Takahata 1990: 80–81). It is true that this is much shorter than the human postreproductive life span of 30–40 years, but it is longer than the period that female chimpanzees need to spend caring for their last surviving offspring. This fact suggests that the last common ancestor might already have evolved menopause to some extent, although more data from long-term demographic study of chimpanzees and bonobos are necessary.

Second, the male philopatry of the chimpanzee-human clade appears to make it difficult for a female to help her daughter to raise the latter's offspring. Hawkes et al. may have been impressed by Goodall's vivid ac-

counts of Flo and her three-generation family group (e.g., Goodall 1986:65), but this is not the typical picture of chimpanzee society. Virtually all the females born to the study groups of Mahale emigrate from their natal groups to one of the neighboring groups (Nishida, Takasaki, and Takahata 1990:73 and unpublished data). This is the case for bonobos, too (Kano 1990:64). It appears that many more females remain at Gombe than at Mahale, probably because young females may often fail to find a suitable new group to transfer to in the small park, which contains only three groups of chimpanzees.

Hawkes et al. appear to think that philopatry patterns can be easily modified by the presence or absence of food resources that young juveniles cannot manage. Thus, they suggest that the female chimpanzees of Taï might stay with their mothers permanently because adult daughters will profit from their old mothers' assistance in child rearing. This is unlikely to be the case. The chimpanzees of Bossou, Guinea, also depend heavily for subsistence on the processing of nuts using hammer and anvil stone (Sugiyama 1979:518). Recent evidence (Matsuzawa and Yamakoshi 1995:227) suggests, however, that the females of Bossou also immigrated from other groups. Moreover, philopatry has been molded by evolution for outbreeding; if females remained in the natal group, males would have had to emigrate, and this would have produced a totally different arrangement for human evolution.

Menopause could have evolved if an early hominid grandmother had helped the offspring of her son. However, a female chimpanzee cannot know who her son's offspring are because of promiscuous mating patterns in females. As I once wrote (Nishida, Takasaki, and Takahata 1990:95),

> the evolutionary advantage of menopause in female chimpanzees is puzzling, since they rarely, if ever, care for younger relatives such as grandchildren or nieces/nephews. Because their daughters emigrate, females have no opportunity to care for young kin unless they can recognize the offspring of their sons or transfer with their sisters to the same unit-group. As a matter of fact, aged females typically live a lonely life, although some of them are often followed by unrelated (at least through their daughters) female orphans.

When the male-female sexual tie became more permanent in the hominid line, grandmothers might have begun to help their sons' wives to raise their offspring.

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Hawkes, O'Connell, and Blurton Jones's long-standing fieldwork among the Hadza has provided a wealth of information about the behavioral and evolutionary ecology of foraging peoples. This paper continues this tradition by articulating the relationship between reproductive senescence, provisioning of altricial young, and inclusive fitness. Hawkes and colleagues point out that humans differ from other primates in having an extended childhood during which mothers provision *weaned* children and a long postmenopausal life span. They demonstrate that, among the Hadza, postmenopausal females have a positive impact on the nutritional status of the weaned but dependent children of the mothers they assist. What is clear is that postreproductive Hadza females can increase their inclusive fitness through investing in grandchildren, and they do so. What is not entirely clear is that the postmenopausal life span evolved to serve this purpose.

Alternative explanations for postmenopausal longevity merit consideration. For example, it may increase females' fitness directly because of the highly altricial nature of human young. Any effort invested in dependent offspring that die after the mother dies is lost from the previous offspring. If offspring required up to 16 years of maternal investment (Lancaster and Lancaster 1983) and would not become reproductively successful without this investment, then selection would favor a postreproductive life span approximately this long. Although Hawkes et al. discuss the maximum potential life span of females, it is the actual realized life span that is important in this case. Among the Dobe !Kung, only one-third of females who reach reproductive age survive to their seventh decade (Howell 1979), and the mean observed life span is around 65 years (Trinkaus and Tompkins 1990). While the mean life span among Hadza females may be longer, in some foragers it is less (Howell 1982). Given reproductive senescence at about age 50 (see Howell 1979:129 for the !Kung), female foragers may average about 15 years of postmenopausal life in which to invest in their last-born. However, although this might explain postmenopausal life span, it does not explain why grandmothers should assist in rearing grandchildren during this time, as discussed by Hawkes et al. Furthermore, this explanation should be true of other hominoid species such as common chimpanzees, where orphaned infants rarely survive but an extended postmenopausal life span is rare. The importance of a postmenopausal life span could perhaps be addressed by looking at its duration relative to the age at which orphaned offspring are able to survive on their own in nonhuman primate species and among different human societies.

Another explanation may be that postmenopausal life span is a direct consequence of selection for other life-history traits. Williams (1966) postulated a pleiotropic positive relationship between developmental and senescence rates. This has been borne out by the strong positive relationship between reproductive age and age at death in mammals (Harvey and Zammuto 1985). Given the evolutionary conservativeness of reproductive life span, it may be that the long postmenopausal life span is simply a by-product of selection for extended childhood during human evolution.

Although these alternatives may be involved in the presence of a postmenopausal life span, they do not account for the helping behavior observed in Hadza grandmothers. Again, it will be important to examine and possibly exclude nonadaptive explanations for this behavior such as the need for older adults to offset any costs of their membership of the social group by providing services to group members. Perhaps this could be addressed by examining the fate of any nonhelping grandmothers.

In contrast, postmenopausal life span and/or provisioning behavior may be an adaptive trait, as suggested by Hawkes et al., but the mechanism of accrued inclusive fitness does not have to be confined to mother-daughter relationships. In fact, as Hawkes et al. point out, cladistic analyses suggest that this is unlikely to be the typical pattern in that the ubiquity of female transfer in apes (Foley and Lee 1989) suggests that grandmothers are unlikely to be in the same group as their mature daughters. Additional support for this is seen in human foraging societies, where only 17.3% (n = 185) have a consistent pattern of male transfer (data from Murdock 1967), again suggesting that helping by grandmothers may have evolved through the impact of this service on inclusive fitness by other routes.

We suggest that helping by grandmothers and possibly the extension of postmenopausal life may have evolved primarily by way of the benefits accrued through sons rather than daughters. We further speculate that this behavior may have aided in increasing the reproductive success of male offspring by increasing their access to females as well as their production of offspring. In fact, the range of inclusive fitness benefits that grandmothers can achieve by provisioning offspring could be used to explain the variation in relatedness of grandmother helpers in the Hadza rather than assuming that flexibility in this trait allows better adjustment to circumstances. These hypotheses are suggested by observations on the role of paternal grandmother pygmy chimpanzees. Although Hawkes et al. include data from common chimpanzees, in fact pygmy chimpanzees may be more relevant to this examination because their populations have higher frequencies of postmenopausal females; 17% of adult female pygmy chimpanzees at Lomako were considered postmenopausal (FJW, personal observation), and three of the ten E1-group females were considered old adults at Wamba (Furuichi 1989). Additionally, these postmenopausal females participate in the food sharing that occurs between females and between females and juveniles (White 1994) and have been shown at Wamba to play a crucial part in their adult sons' dominance rank and reproductive success (Furuichi 1989).

An extension of the pygmy chimpanzee example would suggest that by being in demand as a food provider to reproductive females a postmenopausal female could increase her son's reproductive success by providing him social access to proven fertile unrelated females who have transferred into the group. This currency of providing food to dependent offspring that grandmothers can use would be especially valuable to reproductive females in situations of food scarcity and would also increase the rate of reproductive output by decreasing the interbirth interval. This alternative hypothesis could explain the variability of relatedness of helping grandmothers and could be tested by examining whether helping increases the son's reproductive opportunities relative to sons without helpers. In the case presented here by Hawkes et al., all lactating females had help from grandmothers of some sort, but it is not reported whether all grandmothers helped.

The range in relatedness between Hadza grandmothers and the offspring they help illustrates various routes through which inclusive fitness can act. Because paternal certainty is always less than maternal certainty, grandmothers should invest more in their daughters' offspring if this is possible under the transferring system. Additionally, if parental investment increases with decreasing future reproductive potential, aging parents should invest more in the oldest and probably last offspring of either sex. However, in a patrilocal society, grandmothers are more likely to be in social groups with their sons, and therefore it is important to consider the inclusive fitness benefits that accrue through advantages to the sons in any evolutionary scenario.

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In this characteristically fine-grained, closely argued analysis, Hawkes and colleagues bring a rich array of data and ideas to bear on postreproductive longevity in women. The puzzle of menopause has attracted the interest of some of the best thinkers in the field (Caro et al. 1995; Hawkes et al. 1989; Hill and Hurtado 1991, 1996; Rogers 1993) and for good reason: the maintenance, if not the evolution, of this distinctively human feature of life history should be traceable to differential fitness in the present. The elusiveness of definitive empirical support for any one of the competing adaptationist accounts of menopause casts a shadow on the explanatory power of this paradigm in general and life-history theory in particular. After all, temporal patterning of reproductive effort lies at the heart of life-history theory, so its predictions should be borne out in the case of menopause. Moreover, the relative discreteness of the trait adds to its apparent analytic tractability.

On the contrary, the target article demonstrates the complexity of this problem and presents a further-refined version of the grandmother hypothesis, with a number of elegantly provocative asides concerning the assumption of the nuclear family as the fundamental economic unit among foragers and ancestral hominids, the expanded range of exploitable habitats realized through parental provisioning of juveniles, and increased postreproductive life span rather than premature reproductive senescence. The novel emphasis on

female foraging and food sharing in the evolution of prolonged postreproductive life span requires matrilocality along with low reliance on or reliability of male provisioning, and there will no doubt be debate whether these requirements are likely to have been met historically. Further, the emphasis on seasonality is salutary, as it probably was a feature characteristic of human history. Thus, whereas statistically controlling for seasonality effects was required by the question and the available sample size, one is nonetheless left wondering whether seasonal effects might actually exacerbate the feeding problem for nursing mothers and the concomitant advantage for their children. Interactions of season with paternal contributions may further open windows of food shortage at critical reproductive junctures (pregnancy, nursing). Such periods of food shortage may represent adaptive temporal bottlenecks during which grandmaternal contributions are especially critical. Pushing this logic yet farther, recent evidence for oscillating environments of human evolution (Potts 1996*a*, *b*) necessitates inclusion of instability or high variability in "the" environment of evolutionary adaptedness. Such conditions probably enhanced the potential value of juvenile provisioning for expanding exploitable habitats and of flexible expansion of the pool of potential child provisioners through grandmothering.

Hawkes et al. use an approach to coding behavior data symptomatic of a larger problem with life history that remains undiscussed. According to a central principle of life-history theory, the allocation rule, resources expended for one purpose may not be used for another. Consonant with that assumption, and for simplicity of coding, scan entries were assigned to a single activity for calculating time budgets, with child care having the lowest and food-related activities the highest priority of assignment. Yet this tactic may obscure an important feature of human behavior and thereby introduce particular difficulties for adaptationist analyses of child care. At issue is that humans rarely do one thing at a time; rather, multitasking and layering are ubiquitous strategies that people, with their mindful intentionality and other advanced cognitive capacities, routinely and strategically engage in as they pursue myriad maintenance and reproductive goals in a complex social world. Anyone who has coded behavior is familiar with the multitasking feature of ongoing activity, in which several things are going on and more than one function is served at once. This capacity may be an important adaptive feature that breaks or at least seriously bends the allocation rule. Two behavior types commonly interleaved with other tasks such as food preparation and processing, if not acquisition, are socializing and child care. Thus, the degree to which some tasks or situations restrict or preclude multitasking thereby increases their relative cost. Aspects of foraging that are behaviorally restrictive have indeed emerged as costly for nursing women because they articulate poorly with parallel child care (Hurtado et al. 1992).

The evolutionary bases of menopause have come to have more than theoretical interest as debate swirls around the appropriateness of pathologizing menopause by casting it as a historically rare condition against which selective pressure has not acted, a delayed reproductive cost rarely paid (Barrett-Connor 1993). In this scenario, menopause emerges in contemporary aging populations as a prevalent and pathogenetic artifact that requires correction through replacement therapy. Thus, presentation of menopause as epidemiologic artifact rather than evolutionary solution denaturalizes the condition and allows its recategorization as pathology meriting clinical intervention.

Why do women live so long after menopause? One can frame the question to foreground either why reproductive senescence is accelerated relative to aging in the rest of the body or why aging in the rest of the body became delayed for all but women's (not men's) reproductive function. Unless women somehow maintain reproductive value, fitness models cannot account for why women live as long as or longer than men.

Reply

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We discuss three general issues: (1) similarities between chimpanzees, bonobos, and humans in mother-child food sharing and menopause, (2) the likelihood that female dispersal is a pervasive hominoid characteristic, and (3) absent fathers. We then turn to a miscellaneous set of questions about method and argument and conclude with a final comment on the "politics" of the grandmother hypothesis.

First, several commentators note that chimpanzees and bonobos display mother-child food sharing (especially of items difficult for young juveniles to handle) and some aging individuals cease cycling in both species, yet *Pan* grandmothers do not feed weanlings. This does not counter but instead supports our argument. Given patterns like those displayed by modern chimpanzees and bonobos, individuals who lived past their own fertility could earn large fitness benefits by grandmothering *if* the food sharing became *crucial for juvenile survival.* Under those circumstances we hypothesize that selection would favor human life histories. Mother-child food sharing would have to be much more important than it is in any other living hominoid if items that weaned youngsters could not handle became a large enough fraction of their diet.

We discussed the case of nut use by chimpanzees at Taï because it appears to present an exception to the generalization that, at weaning, ape juveniles feed themselves. Boesch and Boesch (1984) attribute a very large fraction of the diet to hard-shelled nuts and report that juveniles under ten years old are not effective nut crackers—exactly the circumstances that we argue

would make help so valuable. Nishida points to chimpanzees at Bossou as another case in which nuts are used without the changes we predict, but the nut fraction of the diet at Bossou has yet to be documented. At other study sites, resources that young juveniles cannot handle comprise only a small portion of the diet. We agree with Kano that older siblings are likely helpers and noted that older juveniles share nuts with younger siblings at Taï. How often and how much remains to be reported.

Older juveniles also share food among modern human foragers (Blurton Jones, Hawkes, and Draper 1994*b*, Blurton Jones, Hawkes, and O'Connell, 1997, Hawkes, O'Connell, and Blurton Jones 1995), but, contrary to Kano's supposition, this does not obviate large grandmother effects. Younger mothers do not yet have older children. The survival of their offspring, already precarious among chimpanzees, would be more so if it depended on shared food. If maturing daughters had cooperated with their mothers to increase both the survival of younger siblings and their mothers' fertility, this would have provided conditions for continued cooperation when the daughters themselves reached childbearing age. Quantitative data on both diet composition and age-specific variation in foraging return rates for chimpanzees and bonobos will be necessary to clarify whether and how juvenile capacities affect maternal foraging strategies.

Nishida and White and Churchill note the presence of several "old," perhaps postmenopausal, females in wild populations of chimpanzees and bonobos and, on this basis, suggest that menopause need not be unique to humans. These field reports are consistent with zoo data showing that some female chimpanzees live several years past their last birth (Caro et al. 1995). More demographic data will be required to measure life expectancy at menopause in these species. We know the life expectancy and age-specific fertility of 45-year-old !Kung, Ache, and Hadza women. Neither measure can be adduced from White and Churchill's report that 17% of adult female bonobos at Lamako were considered postmenopausal or from Nishida's observation that at least five female chimpanzees lived 8–12 years after their last birth at Mahale, especially given mean interbirth intervals of 5 years. In any case, the field observations underline our larger point: what distinguishes humans from the other apes is not menopause itself but much *longer postmenopausal life spans.*

The second general issue addressed in many comments is the pervasiveness of female natal dispersal in both *Pan* and humans. If, as is widely assumed, male philopatry is a characteristic of our clade, it rules out the mother-daughter coresidence required by the grandmother effects that we hypothesize.

The influential characterization of hunter-gatherers as generally patrilocal (Radcliffe-Brown 1931, Steward 1936) was briefly overturned with *Man the Hunter* (Lee and DeVore 1968), at least in part because the best-studied cases were *not* patrilocal, but the earlier view has since been resurrected. Ember's (1978) cross-cultural tabulation showed patrilocality to be the most common residential arrangement reported for hunter-gatherers. Subsequently, the pattern of male philopatry among chimpanzees was recognized to distinguish them from most monkey species, in which males usually disperse. Combined with the generalization that hunter-gatherers are usually patrilocal, this stimulated the suggestion that female dispersal could be a characteristic of all members of the African ape clade (Wrangham 1987, Giglieri 1987, Foley and Lee 1989, Manson and Wrangham 1991, Rodseth et al. 1991).

The cross-cultural variation in hunter-gatherer residence patterns actually turns out to be more consistent with our hypothesis than current generalizations imply. Patrilocality is *less* frequent among nonequestrian, nonfishing-dependent hunters tallied in the *Ethnographic Atlas* than in the sample as a whole, which includes societies of all subsistence types (56% vs. 71%) (Ember 1978, Murdock 1967). Substantial property holding characterizes most nonforaging societies, and with wealth differences come different residence trade-offs. Among foragers the tendency toward matrilocality increases with women's relative contribution to subsistence and (separately) with increased dependence on gathering (Ember 1975). Moreover, *even in cases classified unequivocally as patrilocal,* female kin may be coresident more frequently than is generally supposed (e.g., Denham 1974; O'Connell, unpublished Alyawarra data).

Nishida says that we assume that natal dispersal patterns can be readily altered by food resources and fail to consider the role of inbreeding constraints in maintaining the status quo. If female dispersal had been the pattern in ancestral populations when ecological circumstances began to favor more mother-child food sharing, then "transition costs" would have been inevitable. Daughters who stayed with their mothers to gain the benefits allowed by food sharing could have confronted inbreeding problems. But these problems are not insurmountable. The food-sharing benefits we postulate are not available to chimpanzees at Gombe, but even without them Flo's daughter Fifi gained sufficient *net* benefits by staying with her high-ranking mother to earn the highest reproductive success ever recorded for a free-living chimpanzee (Goodall 1986).

If we consider the dispersal patterns from the male point of view, the transition problem seems more formidable. If, as in chimpanzees, a male risked death with no prospects of mating elsewhere if he left his natal group, the constraints maintaining male philopatry would remain powerful. But the strategies that pay off for males vary with female grouping and foraging strategies. If females form more cohesive, larger groups and forage over larger ranges, the payoffs for coalitions of males defending territories will collapse. Bonobo females form larger parties than common chimpanzees, and bonobo males do not display the territorial coalitions seen in chimpanzees at Gombe and Mahale. Even in common chimpanzees there is broader variability. At Bossou, the case Nishida mentions, Sugiyama and Koman (1979) concluded that male migration was more frequent than female migration. They described a visit

by stranger males that generated great excitement but no aggression in this population. In captivity chimpanzee males show remarkable facility in constructing and manipulating alliances with unrelated strangers (de Waal 1982). Changing payoffs could easily increase the frequency of events that otherwise remain rare in this species.

Some commentators suggest that pathways for grandmother effects might go through sons as well as daughters. White and Churchill, for example, reckon that a food-sharing mother might make her sons more attractive to potential mates. Exploring multiple alternatives is certainly in order, but a pathway through sons seems unlikely to be as important as the mother-daughter alternative. Mothers and daughters face similar trade-offs while sons must invest in mating competition. A food-sharing mother might attract females to her son's group, but this would not assure her son paternity of those females' offspring. His fitness would depend on his success in competing with other males. Winners of that competition would have higher reproductive success, *whether or not* their mothers contributed to the fertility of their mates. Even if a grandmother could identify her son's offspring and single out grandchildren to feed, her potential fitness gains through the increased fertility of "daughters-in-law" would be devalued by the uncertain paternity of *subsequent* children more quickly born to the mothers of those grandchildren.

The third issue raised repeatedly is the very limited attention we have given to men—this from Gurven and Hill, for example: "Although the focus on hunting and male-based cooperation has dominated the thinking within anthropology for years, it does not make sense to proceed in the opposite direction without some empirical or theoretical justification." Both empirical and theoretical justifications are ample. Consider the challenges we cited to the long-held view that hunting is the key adaptation that distinguishes humans from other apes. In that scenario, hunting allows men to feed their mates and offspring, making families fundamental economic units that can produce more, and more dependent, children. Elsewhere we have provided argument and evidence that hunters in tropical habitats are *not* provisioning their families (Hawkes 1990, 1991, 1993; Hawkes, O'Connell, and Blurton Jones 1991). In the case of the Hadza, for instance, among whom average rates of meat procurement are very high, individual hunters nevertheless fail to kill (or scavenge) large game on 97% of all hunting days (O'Connell, Hawkes, and Blurton Jones 1988*a*, Hawkes, O'Connell, and Blurton Jones 1991). Their average meat procurement rate is high because the animals they take are so large. But because prey are large most of every carcass goes to someone other than the hunter and his family. A hunter's actual *consumption* return rate (and that of his family) is but a fraction of his procurement rate. By specializing in big game, the hunter routinely forgoes opportunities to supply a steady stream of small prey to his household (Hawkes, O'Connell, and Blurton Jones 1991). If he gathered plant foods, he could provide even more calories to his own family (Hawkes 1993).

The point to underline is that by hunting large animals men are choosing *not* to pursue activities that would provide more food for their own households. The Hadza are similar in this way to the Ache: meat makes up a large portion of everyone's diet, but very little of the meat eaten by women and children is supplied by their own husbands and fathers. Hames protests the "lack of focus on the role of men as investors in their own or their kin's offspring" and asks about the food-getting activities of fathers. Hunting is the main foraging activity of men, but it is *not* a "paternal" activity. Hunters provide a substantial fraction of the average diet of women and children, but *husbands/fathers do not.* More like community defense than domestic support, hunting supplies a collective good from which all benefit *regardless* of their relationship to the hunter. It is women's foraging that differentially affects their own families' nutritional welfare.

Gurven and Hill point to Paleolithic archaeology for evidence of the ancient importance of hunting. The fact that the archaeological record begins with the appearance of stone tools in association with the bones of large animals is surely one of the main reasons that the "hunting hypothesis" has dominated thinking about human evolution for so long. But identifying the activities that created the archaeological record, let alone their frequency or importance in the lives of our ancestors and collaterals, is difficult and contentious (e.g., Binford 1981, O'Connell 1995). Moreover, even if the archaeology indicated "significant meat eating by hominids over the past several hundred thousand years," meat eating itself does not indicate paternal provisioning.

Other theoretical and empirical reasons to focus on women emerge from recent work on life histories. Charnov's (1991, 1993; Charnov and Berrigan 1991) mammal model shows that broad regularities in life-history patterns can be explained as the result of natural selection adjusting age at maturity to adult life spans. It also shows that the "slowness" of primate life histories (slow growth rates and low birth rates compared with those of other mammals of the same size) can be explained as the result of one variable: a characteristically low "production coefficient" (Charnov and Berrigan 1993). As in most of life-history theory, this model deals only with trade-offs confronted by females (Hawkes 1994). Robust regularities in female life histories are apparent across the mammals, including the primates, even though *variation in male strategies is ignored.*

Elsewhere (Hawkes et al. 1997) we have shown that, combined with Charnov's model, the grandmother hypothesis can account for several features of human life histories that distinguish us from the other apes, including our long postmenopausal life spans, late ages at maturity, short interbirth intervals, and high fecundities. Commentators observe that men as well as women have long life spans. We expect that long-lived mothers with long-lived daughters would also have long-lived sons, but males face different life-history trade-offs. Under a wide array of circumstances, they cannot avoid substantial allocation to mating competi-

tion (Hawkes, Rogers, and Charnov 1995). What men are doing is important but not in the way generally assumed. Since it is impossible to study everything at once, let alone report all results in the same paper, we hope that readers will follow our exploration of men's strategies and the evolutionary consequences of large animal hunting as reported elsewhere.

We turn now to a residual set of questions. Some are points of information; others raise general conceptual issues.

White and Churchill ask about the presence of Hadza grandmothers who were not helping. We reported the rarity of this in n. 9.

Hames queries our "assumption" that Hadza women's foraging return rates do not decline with menopause. This is empirical: data showing similar return rates for postmenopausal and childbearing women are reported in Hawkes, O'Connell, and Blurton Jones (1989).

Hames points out that more time spent foraging must leave less time for other things. But we did not include all activities in this analysis, so there is no *necessary* complementarity among the ones we report. Even very "busy" adolescent boys could devote more time to any one of the four activities (foraging, processing food in camp, working on tools, or camp maintenance) without reducing the time they spent on the others by giving up "resting" or "idle" social time.

Worthman comments on our coding of simultaneous activities to focus on "food-related/productive" tasks. This was dictated by the questions we were asking. Other questions, like those about child care, would require different coding. She suggests that it is distinctively human to carry on multiple tasks simultaneously, "an important adaptive feature that breaks or seriously bends the allocation rule"—by which she means the rule that "resources expended for one purpose may not be used for another." Whether people tend to do more things at once than other primates is an empirical question, but whatever the answer "mindful intentionality and other advanced cognitive capacities" are certainly not required for tasks to be time-shared. The degree to which activities are mutually interfering (in time, space, or requisite capacity) ranges across a complex spectrum from perfect incompatibility through reductions in efficiency in one or more depending on the combinations to perfect compatibility. This variation defines allocation problems affecting everything from the competitive exclusion that drives species divergence to the evolution of two sexes. The widely used diet-breadth model in foraging theory is an example of the way in which differential interference affects behavioral strategies. That model assumes that "optimal foragers" (of any species) time-share (perfectly) the search for all resources. The trade-off they face is between time spent searching for everything at once and time spent handling any particular resource.

White and Churchill argue that it is "important to examine and perhaps exclude nonadaptive explanations" for grandmothering. Among the problems with that position is the lack of guidance it offers for research. How shall we enumerate, let alone test, the infinite number of nonadaptive "explanations"? Which of them is worth testing? The power of an adaptationist or selectionist approach is that it provides a theoretical warrant for developing multiple, often conflicting hypotheses that *are* worth testing. That is, results of a test in one time and place extend understanding of systematic relationships among study variables and so provide reasons to expect related patterns in other times and places. The iterative process of generating theoretically warranted hypotheses, running empirical tests to rule out those that are incorrect, using theory and results to develop alternative hypotheses, testing those, and so on, is a research strategy of unmatched productivity. White and Churchill's suggestion seems the opposite of a coherent research strategy.

Hames considers us "inconsistent" in locating the cascade of grandmother effects at different points in the past. We expect them to arise when high-return resources that young juveniles cannot handle constitute an important fraction of the diet. But we gave only passing attention here to the specific location of those circumstances in our evolutionary past. Available data suggest *at least* three possible dates for the initial occurrence of regular mother-child food sharing, extended life spans, and related adjustments in life history: (1) coincident with the emergence and dispersal of *Homo erectus* (e.g., Peccei 1995, Walker and Leakey 1993, Swisher et al. 1994), (2) with the first appearance of "archaic" *Homo sapiens* (McHenry 1993), or (3) with the dispersal of fully modern *sapiens* (Klein 1995, Trinkaus and Tompkins 1990). Tests for each alternative (and any others that might be identified) are clearly in order.

Finally, Worthman's observation about the politics of menopause invites an elaboration. To the extent that menopause *is* seen as a "pathogenic artifact of contemporary longevity," the grandmother hypothesis proclaims revolution. Among the characteristics that made us "human" in the first place are our capacity to invade new habitats successfully, our long life spans and long childhoods, and the population dynamics that allowed us to displace competitors. All these features could have evolved because of grandmothers (Hawkes et al. 1997). Rather than an artifact of novel modern conditions, this makes long postmenopausal life spans a keystone adaptation in human evolution. Whether or not this is correct should not—as we are sure Worthman would agree—affect calculation of the medical pros and cons of estrogen supplementation. But surely it is a(nother) reason for critical review of favored evolutionary scenarios, setting new agendas for future work.

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