Hardworking Hadza grandmothers

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SUMMARY

Among Hadza hunter-gatherers in northern Tanzania, women spend a great deal of time in food acquisition, and those past child-bearing age spend more than younger women. We report this pattern of age-related work and consider explanations for it, concluding provisionally that it may be an optimal allocation of reproductive effort. We note that humans are distinguished from other primates by their capacity to extract resources with enough efficiency to regularly feed others as well as themselves. If female investments in resource acquisition compete with investments in fertility, older females may gain greater fitness by helping their adult daughters than by carrying additional, riskier pregnancies themselves. Among our hominid ancestors, this same capacity would have had profound consequences for patterns of sharing and life history strategies, including the evolution of menopause.

INTRODUCTION

Two developments in the recent literature on hunter-gatherers are of special interest here. The first is documentation of a wide range of variation in many aspects of hunter-gatherer behaviour, from sexual divisions of labour (Estioko-Griffin & Griffin 1985) through levels of work effort (Hill et al. 1985) to the complexity of political organization (Bean 1978; Marquardt 1986). The second has been the application of theory and models from evolutionary ecology to the study of this variation (see, for example, Winterhalder & Smith 1981; Hill & Kaplan 1988). These applications have been spurred by the successes gained in biology from conceptualizing patterns of behaviour as adaptations in the narrow sense (Williams 1966), that is, as strategies shaped by natural selection, and thus amenable to analysis and explanation in terms of their reproductive consequences for the individuals who display them, consequences which in turn depend on the characteristics of those individuals and their ecological context (see, for example, Krebs & Davies 1984; Stephens & Krebs 1986 for an extended discussion).

This paper is a contribution to both of these developments. More precisely, it is about women's work effort among the Hadza hunter-gatherers in northern Tanzania. In many human societies, the economic contribution of women declines

as they become grandmothers (Amoss & Harrell 1981). This is not so among the Hadza, where women work harder and procure more food as they pass from middle adulthood to their 'post-reproductive' years. Here we describe this pattern of age-related work effort, and explore some hypotheses which might account for it. We begin with a brief description of the study population, with special attention to women's foraging, then outline our methods of data collection, and report some quantitative results. Then we review some elementary components of life history theory, and in this context, identify the factors which might underlie older women's work. Evolutionary theory leads us to enquire whether the fitness-related costs and benefits of food acquisition might be key determinants of Hadza women's behaviour, and this prompts us to speculate about the role of these variables in human evolution.

THE HADZA

The Eastern Hadza are a group of 750 people who currently occupy a 2500 km² area south and east of Lake Eyasi. Much of this region is rough and hilly, and covered with mixed savannah woodland. The climate is warm and dry. Annual average rainfall is in the 300-600 mm range, most of it falling in the 6-7-month wet season (November to May) (Schultz 1971).

At the time of first European contact, around the beginning of this century, only the Hadza occupied this country (Woodburn 1964, and references therein). They apparently lived entirely by hunting and gathering. Local incursions by non-Hadza pastoral and agricultural groups are recorded in historic times as early as the 1920s (Woodburn 1964, 1986; McDowell 1981). Archaeological evidence suggests the periodic presence of farmers and pastoralists in the region for several millennia, hunter-gatherers far longer (Mehlman, personal communication). Non-Hadza settlement is now heaviest in the Mangola area, at the northern end of traditional Hadza territory, and along the western edge of the Mbulu Plateau.

During the past 50 years, various segments of the Hadza population have been subjected to a series of government and mission sponsored settlement schemes designed to encourage them to abandon the foraging life in favour of full-time farming (McDowell 1981; Ndagala 1986). None of these schemes 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 managed to avoid settlement altogether, and continued to live as full-time hunter-gatherers.

Ethnographic data on the Eastern Hadza are available in a number of short reports dating from the late nineteenth century to the mid-1960s (Baumann 1894; Obst 1912; Reche 1914; Bagshawe 1925; Bleek 1931; Cooper 1949; Fosbrooke 1956; Tomita 1966). The first comprehensive description was provided by Kohl-Larson (1958), based on field work in the 1930s. More recently, James Woodburn (1964, 1968a, 1968b, 1970, 1972, 1979, 1986; Woodburn & Hudson 1966; see also Bennett et al. 1970, 1975) has presented the results of several extended periods of local research between 1958 and 1970. Topics addressed include demography, kinship, social organization, subsistence and settlement patterns, and health and nutrition. Several projects have also been undertaken within the last decade,

primarily concerned with ecological and ethnoarchaeological issues (Smith 1980, unpublished field notes; McDowell 1981; Vincent 1985a, 1985b; O'Connell, Hawkes & Blurton Jones 1988a, 1988b; H. Bunn & E. Kroll, personal communication).

Most of the data reported here were collected over a 15-month period in 1985-86 among Hadza living in the areas known locally as Tli'ika and Han!abi. These areas are situated astride a long, narrow (50 × 15 km), north-east to southwest trending ridge, flanked on the north-west and south-east by the Eyasi and Yaeda basins, respectively. The central portion of the ridge has an average elevation of 1200-1400 m; isolated peaks exceed 1500 m. Drainage is primarily to the north-west, toward Lake Eyasi. Nearly all streams are seasonally dry, although water can be found throughout the year in isolated pools and rockholes, and in subsurface catchments in stream channels. Lake Eyasi itself is a playa, which holds water only during the wet season and for a short period thereafter.

The crest and upper slopes of the ridge are covered by thick bush (Acacia brevispica-Aloe-Dahlbergia), in which giant baobab trees (Adansonia digitata) are a common and very striking element (Schultz 1971). The lower slopes and alluvial plains on the Eyasi side are dominated by Acacia tortilis—Commiphora woodland. The Yaeda Valley is a grassland, seasonally flooded at its south-west end. Medium and large herbivores, notably elephant, giraffe, buffalo, zebra, and several species of antelope are common throughout this region (Smith 1980). Large predators, including lion, leopard, and hyaena are also present.

Since the mid-1970s, the Tli'ika/Han!abi area has been occupied by about 200—300 Hadza, all of whom have lived primarily by hunting and gathering throughout most of that period (L.C. Smith, personal communication). Also present on occasion are members of a population of Datoga, a Nilotic pastoral group, whose range includes the lower slopes of ridge on both the Eyasi and Yaeda sides (see Klima 1985 for ethnographic background). Relationships between the Datoga and Hadza are strained at best, and have in the past been punctuated by violence (Mathiesson 1972). Contact between the two groups is limited, apart from early dry-season honey trade. Datoga livestock compete with other occupants of the region for access to water during the late dry season.

Many Tli'ika/Han!abi Hadza have relatives (mainly other Hadza, or Isanzu, with whom the Hadza have intermarried to some degree; see Woodburn 1986) living in or near the villages of Yaeda, Munguli, and Mangola, located 5–15 hours' walk to the south, south-west and north-east, respectively. Some of these people are full or part-time farmers. Bush-dwelling Hadza visit them occasionally for periods of up to a week in the dry season, usually to trade dried meat for tobacco, maize, or millet. Some may stay even longer during the late wet or very early dry season in order to benefit from the harvest.

WOMEN'S FORAGING

Hadza foraging patterns vary seasonally. During the 1985 dry season, the Hadza were concentrated in five, or sometimes six relatively large camps (population

forty-five or sixty each) located near permanent water sources along the northern crest of the ridge overlooking Lake Eyasi. Camp composition was flexible with a notable tendency for married couples to live with the wife's mother (Woodburn 1968b describes this pattern as well). Parties of women foraged around these camps virtually every day. Their most common targets were tubers, most often //ekwa (Vigna frutescens). The variant called //ekwa hasa by Hadza in Mangola (Vincent 1985a) is the only type of //ekwa identified in the Tli'ika/Han!abi region. It was also taken in other seasons, usually in the same general way.

Women left camp early, sometimes by 07.00 hours, but usually between 08.00-09.00 hours. They were typically accompanied by infants under 2, children over about 6 or 7, and by armed teenage boys, or sometimes an adult man who provided protection against human strangers, most likely pastoralists who might be travelling through the area. After walking as a group from 4-60 minutes (mean = 25 ± 14 minutes for thirty-one trips), women reached their target patch for the day. They fanned out, tapping the ground around the base of the woody rootstalks with digging sticks to assess, they said, the probable presence and size of tubers in the rocky soil.

Having found a likely spot, each woman settled down to dig, usually just out of sight of other members of the party. Individuals kept track of each other with occasional calls. Periodically each woman loaded the tubers she had collected into a carrying cloth and moved on in search of another rootstalk. As she passed other women she might pause briefly to chat and check their progress. Sometimes more than one woman dug at the same rootstalk.

This was hard work. Excavations were sometimes more than a metre deep, and often involved moving large rocks through complex sequences of levering. Particularly intricate engineering problems drew the attention of several spectators. However, about three-quarters of the time spent in *lekwa* patches was devoted to active digging. Women who had carried nursing infants sometimes enlisted older children to sit with them and hold the infant, interrupting their digging periodically to nurse.

Women usually dug to just past midday, when they gathered to cook the tubers on a common high flame fire. If the party was large, more than one fire was kindled. Tubers were rubbed free of dirt and grit, piled on the fire, often to a height of 30 cm or more, roasted and turned for 5–15 minutes, pulled off, stripped by hand of their tough outer skins, and eaten. After appetites were satisfied, or the tubers all eaten, a second bout of digging began and continued through the afternoon, followed by more cooking and eating. Women then loaded the remaining cooked tubers into their carrying cloaks and returned home. Just before reaching camp, those in the lead would pause so that any stragglers might catch up. The entire group then continued, arriving in camp together, often to the accompaniment of an excited chant by the children waiting there. Children and adults who had remained at home gathered around the women, and with varying degrees of insistence, claimed a share of tubers. Although acquisition loads were routinely recorded, the total remaining to carry home after consumption was not

usually weighed during this period. Data on both acquisition totals and carryhome loads are available for a sample of 27 woman days. These indicate that 0.390 ± 0.128 of the total weight of tubers acquired was consumed in the field by the collectors, other members of the party, or by passing hunters.

Although it was the norm, women did not always go collecting as a single party. Less often, they went accompanied only by their husband. One woman who did this frequently was a topic of censurious gossip among the other women for failing to follow the proper pattern and join the women's foraging party.

During the wet season, Hadza moved camp several times, first to the lower slopes of the ridge overlooking Lake Eyasi, then later back to the crest of the ridge, roughly along the north—south drainage line. Camps were somewhat smaller throughout this period, averaging about thirty to fifty occupants. Women continued to forage for roots (especially #ekwa), but during parts of this period they spent as many as half their foraging days taking berries. Species most commonly sought were undushi (Cordia spp.), which were found in large, dense patches, hundreds of metres across, on the lower alluvium south of Lake Eyasi; and kongoro (Grewia bicolor), which were encountered in large patches at the lower elevations and in much smaller patches throughout the uplands. Berry-collecting expeditions usually involved more than an hour of travel time each way (mean = 76±37 minutes, for seven kongoro trips), some as many as 2 hours, 10 minutes.

Women intending to take berries left camp as a group, usually between 08.00-09.00 hours. Party composition was as described for root-collecting trips. Party members often stopped to snack briefly on small patches of berries encountered as they walked. On arrival at the target patch, they typically spread out over an area 30-50 m in diameter and began to collect, alternately eating and filling their carrying cloaks or whatever other containers they had brought. Undushi are juicy enough to mash easily in the folds of a cloth and so must be carried in baskets or pots. Because the ripe fruit was often densely concentrated, it was not uncommon for several women to remain within a metre or two of one another. Women carrying nursing infants would sometimes set the infant down in the care of an older child, but often a mother picked with her infant held on her back in a carrying cloth. Much talking, joking, and often singing characterized these forays. When undushi were the target, women climbed into the trees to pick, leaving infants in the care of others below. They also directed older boys or the adult man accompanying them to cut down heavily laden branches for easier picking on the ground. By about midday, women had usually filled their containers (and themselves) with the juicy berries, and started the long, hot walk back to camp. When kongoro, a much drier fruit, was the target, women usually picked well into the afternoon, and continued snacking on any fruit encountered on the way home. As on tuber-collecting trips, the party typically regrouped just before arriving at camp. At sight of the women, children who had remained at home often set up a chant about the arrival of berries, and those present in camp gathered around the women to claim shares.

The other major resources acquired by women in 1985–86 were honey and baobab fruit. While the honey of several species of insects is taken by the Hadza, especially by boys, through most of the year, only *Apis mellifera* produces large amounts of honey and this quite seasonally, first in December and again from April through early June. This honey is taken by small parties of boys, mixed groups of adolescent boys and girls, and by nuclear families. Collecting tactics of men have been described by Woodburn (Woodburn & Hudson 1966). Baobab is usually one of the main resources taken by women in the dry season, but the 1985 crop was poor and women paid little attention to it. We defer discussion of both these resources to focus on women's work during October 1985, when roots, and March—April 1986, when roots and berries were the main resources taken by women.

METHODS

Foraging time is calculated from behavioural scans in study camps. These recorded the location and activity of each individual in camp at the instant they were first seen during the scan, and the general activity (when known) of individuals sleeping in the camp, but not present at the time of the scan. Scans were evenly distributed throughout the daylight hours, from 07.00 to 19.00 hours, and occurred no more frequently than once every half hour. The number of data points available for any individual varies depending on the number of days she slept in study camps. For the individuals considered here, the range is 13–122 observations per woman for the period 13 October to 1 November 1985, and 35–160 for the period 26 March to 19 April 1986.

These figures pertain to all women (but one) living in the camp under study and old enough to show marked breast development. (The exception is one very old woman resident in the 1985 dry season study camps who never joined the other women foraging and whose own foraging was not adequately monitored.) These women are divided into three age categories: (i) unmarried girls who have not yet had a pregnancy, (ii) women of child-bearing age (this includes two women who have been married at least 2 years but have not yet had a pregnancy), and (iii) women past child-bearing (none of these women has a child under about 15, all are said to be older than any of the women in category two). For the dry season of 1985, there were four girls in the first category with a total of 488 observations in camp scans, ten women in the second category with a total of 857 camp scans, and five women in the third category with a total of 295 camp scans. For the March—April 1986 season, there were only two girls in the first category with a total of 252 camp scans, seven women in the second category with a total of 871 camp scans, and five women in the third category with a total of 668 camp scans.

Time allocation during tuber-collecting trips is calculated from focal person follows, during which minute by minute activity records were kept of a single subject. A sample of 97 hours of follows provided the figures reported here. These include 69.7 hours on five women of child-bearing age, and 27.6 hours on

two older women. Berry picking was not amenable to this method of observation because movement through and around berry bushes, or into trees made it impossible to accurately monitor picking rates, or to distinguish between picking to eat and picking to stash and carry for a single individual over a continuous period without disrupting her behaviour. Scans were used instead. At 5-minute intervals, the activity of each member of the party in sight (taken always in the same order) was described. Thirty-seven hours of berry trip scans supplied the data reported here. These covered only one girl in the first age category (175 observations total), six women in the second (1755 observations), and three women in the third (977 observations).

Return rates are reported in terms of kilograms of resource acquired per hour in patch, that is, excluding time spent walking to and from the areas of active picking or digging referred to here as 'resource patches'. For tubers, the total weight acquired was measured with a hanging spring scale for as many women as possible in a party before each cooking event. From the time women began to poke for tubers to their arrival at the cooking fire was counted as time in the patch. During the 97 hours of focal person follows tabulated here, activities other than active digging accounted for a mean of 27% of the time adult women spent in tuber patches. Travel to and from the patch and time spent cooking, eating and resting at the cooking site are counted as foraging time, but excluded from the calculation of return rates. Individual return rate averages are calculated from all occasions on which the time a woman spent in the patch and her total acquisition were measured. These are weighted by length of time in patch to calculate mean return rates for each individual as kilograms per hour in patch. The number of observed occasions from which an individual's average return rate was calculated varies from one to forty-four. The 1985 dry season means are calculated from all tuber foraging monitored from 10 September to 1 November. For the four girls in the first age category, this is a total of fifty occasions, for the ten women in the second 149 occasions and for the five women in the third 136 occasions. The March-April means are calculated from all tuber foraging monitored from 26 March to 19 April. Only one of the two girls in the first age category who was resident in the study camp was observed digging tubers during this period, and only on two occasions. Five of six women in the second category were observed on a total of twenty-eight occasions; five women in category three for thirty occasions.

Calculating acquisition rates for berries is less straightforward. Rates for the load carried home can be calculated in the same way as for roots, using weights of berries measured with a hanging spring scale divided by the time spent in the patch (Fig. 1a; Table 1, row A1). The points in Fig. 1a are calculated from nine kongoro picking occasions for the two girls in category I, 46 for the six women in category II, and 27 for the five women in category III. However, unlike tubers, berries are eaten continually during the time in patch. The load carried home is less than the total acquired. To correct for the amount eaten, we might assume an equivalent picking rate during the minutes spent eating in a patch. Since a mean of 47% as much time is spent eating as stashing, the in-patch returns might be

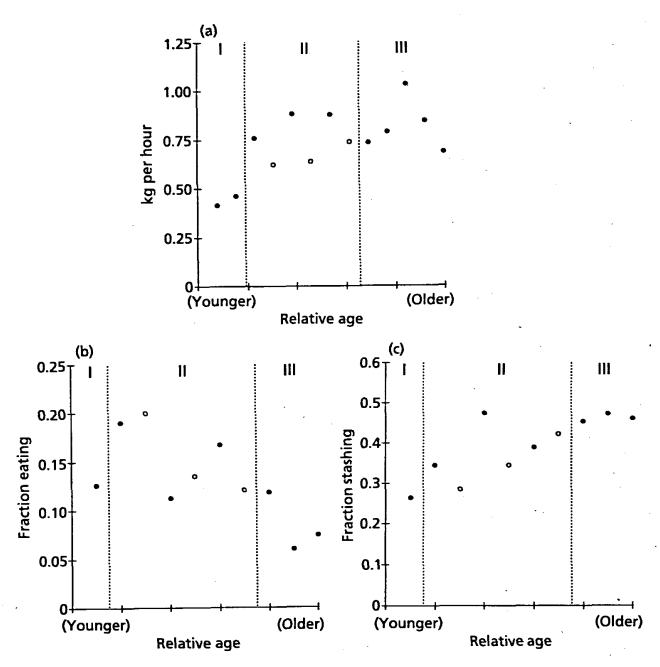


Fig. 1. Berry acquisition by relative age. Each point indicates an individual's mean carry-home rate. Individuals are ordered by relative age across the x axis from younger to older. Age categories are separated by vertical dotted lines and indicated by Roman numerals. In category I are unmarried girls with marked breast development who have not yet had a pregnancy. Category II contains child-bearing women, those who have young children or who are married and are younger than other women in this category. Category III contains women past child bearing who have no children under the age of about 15, and who are older than women in category II. Open circles represent those women who were carrying nursing infants when the observations were made. See text for description of methods. (a) Carry home rates for kongoro (kg/h in patch), 26 March—16 April 1986. (b) Time in the kongoro patch spent eating berries (fraction of in-patch scans). (c) Time in the kongoro patch spent stashing berries to carry home (fraction of in-patch scans).

categories (presented in Figs 1-4). In category I are unmarried girls with marked breast development who have not yet had a pregnancy. Category II contains child-bearing women, those who have young children or who are married and are younger than other women in this category. Category III contains women past child bearing who have TABLE 1. Age category means: women are assigned to three age categories. Age category mean values are calculated from the means for individuals in each of these no children under the age of about 15, and who are older than women in category II. See text for description of methods

	1 Un	I Unmarried girls		II Chile	II Child-bearing women	u	III	III Older women	
	Mean	S.D.	z	Mean	S.D.		Mean	S.D.	=
A Calculating kongoro rates I Carry home rate for kongoro (kg/h in patch) 26 March-19 April	0.439	0.035	พื	0.754		9	0.819	0.135	v o .
2 Eating kongoro (fraction of scans in patch) 37·3 h of scans at 5 min intervals	0.13		-	0.155	0.032	9	0.083	0.032	æ
3 Stashing kongoro (fraction of scans in patch) 37·3 h of scans at 5 min intervals	0.27		-	0.377	0.064	9	0.460	0.010	ю
B Total foraging time in two seasons I Time foraging (min/day) 26 March-19 April	238	78	8	372	103	9	454	114	'n
2 Time foraging (min/day) 13 October-1 November	141	59	4	201	88	01	389	170	v
C Return rate 1 //ekwa acquisition rate (kg/h in patch) 8 September-1 November	0.841	0.320	4	1.859	0.558	01	996-1	0.512	S
2 //ekwa acquisition rate (kg/h in patch) 26 March-19 April	1.225		-	2.313	868.0	₹	2.014	0.820	s.
3 Estimated kongoro rate (kg/h in patch) 37·3 h of scans at 5 min intervals	0.51	(a) car	I (a) carrying infant		0·13 0·09	3 6	1.033	0.257	ю
		ou (g)	no infant	1.193	0.12	m			
D Time allocation to tubers and berries 1 Time on tuber digging trips (min/day) 26 March-19 April	. 4 0	88	8	128	56	9	284	138	v.
2 Time on berry picking trips (min/day) 26 March-19 April	861	134	8	177	18	7	170	\$6	S
3 Time on tuber digging trips (min/day) 13 October-1 November	135	299	4	991	16	01	392	170	vs.

estimated at 1.47 times the carry home rate. This correction is less satisfactory when return rates by age are the topic of interest, because the proportion of time in a patch spent eating is systematically related to age (Fig. 1b; Table 1, row A2). Older women spent less time eating than did child-bearing women (one tailed t test on difference in age category means, P=0.013), and (though this need not be so since half the time in patch is spent neither eating nor stashing) older women spend more time stashing than middle adults (Fig. 1c; Table 1, row A3; difference of means, P=0.013). For purposes of this discussion, we use the smaller set of return rates which are calculated from the berry patch scans where amounts eaten can be estimated directly. Acquisition rates are calculated by assuming an individual's picking rate for the minutes she spent eating was equivalent to her mean picking rate for the minutes she spent stashing, then calculating the average total acquisition rate for each individual.

Changes in women's body weights are used as an indirect index of investment. In the 1986 dry season, these weights were measured on an industrial electronic scale with read-out to hundredths of a kilo. Subjects were weighed barefoot, wearing light clothing. During this season, foraging time is measured as the fraction of 33 observation days on which an individual spent time in food acquisition.

Difference of means tests are used throughout to compare age categories. We used independent t tests, one tailed, variances pooled or separate depending on whether there is a significant difference (P=0.05) between the two variances.

THE QUANTITATIVE PICTURE OF WOMEN'S FORAGING

Hadza women spent a surprising amount of time in food acquisition during 1985-86: an average of 4 hours (±2 hours, 22 minutes) per day in the part of the dry season, 6 hours (±2 hours, 2 minutes) per day in the part of the wet season tallied here. When roots are the target, 48% of foraging time is spent travelling to and from the patch and cooking and eating the tubers, 38% in active digging, and the remaining 14% resting, walking between rootstalks, and packing tubers for transport, all within patch. For berries, the figures are 34% travelling, 26% picking to carry home, 9% eating, and about 23% walking among the bushes in patch. The other 8% is spent attending to infants, resting, drinking at water points, and (rarely) stopping for honey. This large time investment is quite surprising, especially given common generalizations about work effort among hunters, including the Hadza (Lee 1968; Sahlins 1968; Woodburn 1968a; cf. Hawkes & O'Connell 1981).

Even more interesting is the pattern of age-related variation in work effort (Fig. 2; Table 1, section B). Older, 'post-reproductive' women foraged an average of 6 hours, 29 minutes each day in the dry season sample, and 7 hours, 34 minutes each day in the wet season sample. These figures are 22-52% higher than the averages of child-bearing women, and 90-275% higher than those of unmarried girls. The differences in means for child-bearing and 'post-reproductive' women are significant for the dry season (P=0.004), but not for the wet (P=0.122). When

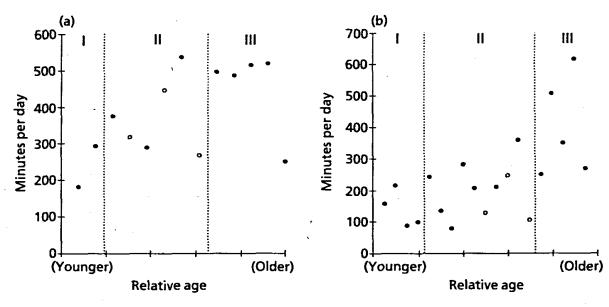


Fig. 2. Foraging time by relative age. Relative age, age categories, and nursing status as in Fig. 1. See text for description of methods. (a) Time spent foraging (min/day out of camp when the main activity was food acquisition), 26 March—19 April 1986. (b) Time spent foraging (min/day out of camp when the main activity was food acquisition), 13 October—1 November 1985.

data from the two seasons are combined, the figures are 2 hours, 53 minutes (± 76 minutes) for girls, 4 hours, 24 minutes (± 2 hours, 4 minutes) for child-bearing women, and 7 hours, 7 minutes (± 2 hours, 13 minutes) for older women (for the first pair of means, P=0.056; for the second, 0.002).

Mean individual return rates for resources which comprise the bulk of women's acquisition during the periods in question are plotted by age category in Fig. 3. Age category means appear in Table 1, section C. The return rate distributions all show the same general pattern. There is an increase in efficiency up to the age of marriage (difference between means of category 1 and 2 for the 1985 dry season, Table 1, row C1, P=0.002). After reaching adulthood, rates remain fairly constant, although women carrying nursing infants may be less efficient foragers. The difference between these women and women in the same age category who are not carrying infants is significant for kongoro (Table 1, section C, rows 3a and b, P=0.028). However, even when the two seasons for *lekwa* (for which means are not significantly different) are pooled, the difference between women carrying infants and other middle adult women does not reach significance. We are surprised at this lack of difference since nursing infants do seem to be an interference. Mothers carrying infants reduce this interference by enlisting older children or girls in age category one (whose own return rates are therefore further depressed) to sit beside them as baby sitters. Most berry picking is done standing with frequent moves among bushes. Although mothers do sometimes put their infants down to be tended by others they do this less often when berry picking than when digging tubers.

The older women, all past menopause, continue to show fairly high return rates. Because they spend more time foraging, they earn a foraging income higher

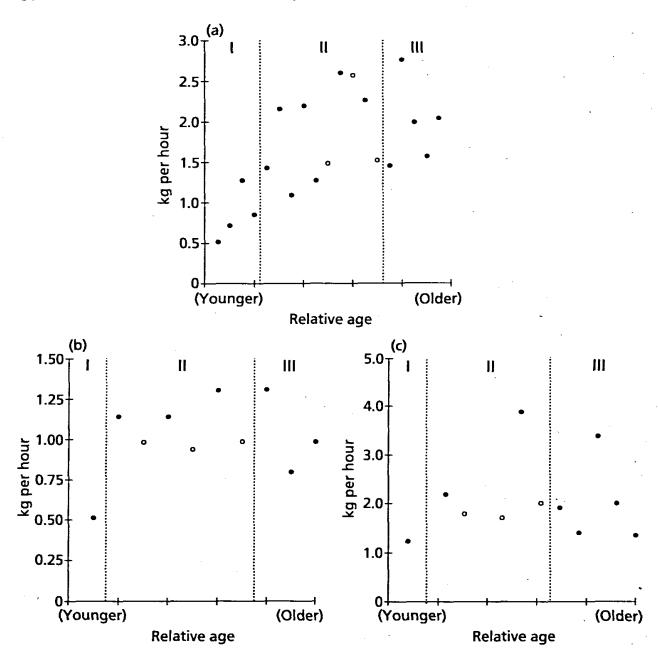


Fig. 3. Return rates by relative age. Relative age, age categories, and nursing status as in Fig. 1. See text for description of methods. (a) Return rates for //ekwa (kg/h in patch), 10 September-1 November 1985. (b) Return rates for kongoro (kg/h in patch) estimated from scans in kongoro patches plus amounts carried home on scan days. (c) Return rates for //ekwa (kg/h in patch), 26 March-19 April 1986.

than do younger women even though they have no young children of their own to feed. The pattern is especially interesting for its marked contrast with Lee's data for the !Kung. He estimated that during the dry season, women spent an average of less than 2 hours a day foraging. He also reports that women between the ages of 20 and 39 worked longer than those 40 to 59, who in turn worked longer than women over 60 (Lee 1979, p. 264, 1985). There are a few reports on older women's work effort among other foragers. The Cuiva of western Venezuela are more like the Hadza in that women over the age of 60 spend more time foraging than do younger women (Hurtado & Hill 1987), at least during the dry season,

when the main resource taken was a tuber. Meehan (1982) reports yet another pattern for the Anbara of Arnhem Land, among whom women between 40 and 50 spent more time collecting shellfish than did women under 40 or over 60. Neither Cuiva nor Anbara women spend as much time foraging as do the Hadza. Guided by evolutionary theory, we draw on concepts and models about adaptive life history strategies in seeking to account for the Hadza patterns. We then briefly consider the differences between these and those reported for other modern hunter-gatherers, particularly the !Kung.

LIFE HISTORY THEORY

The alternative ways in which individuals schedule and adjust their allocation of the limited resources of a lifetime determine their probable contribution to the gene pools of future generations. Growth, maintenance, bearing offspring, and aiding the survival and reproduction of close kin are to a large extent competing expenses. The timing and degree of shifts in investment among them sets probable lifetime reproductive success. The fitness costs and benefits of alternative investment schedules depend on the present and probable future characteristics of the individual itself, of potential competitors, mates, and kin, and on other features of the environment including the food resources available and the costs and benefits of acquiring them.

Reproductive effort can be defined as effort made toward producing offspring, or toward augmenting the reproductive success of kin when that effort spent now feduces the effort which could be spent in the future. Reproductive value can be defined as the probable contribution an individual will yet make to the gene pool. Given those definitions, individuals would maximize their fitness by increasing their reproductive effort as their reproductive value declines (Fisher 1930; Williams 1966; Stearns 1976). As the probability of future reproduction decreases, there is less fitness reason to allocate resources to survival. How these expectations might apply to primates remains to be determined (Altman 1980). Clutton-Brock (1984) points out that it is difficult to tell whether the general prediction is widely met because the correlation of an array of features (e.g. size and experience) with age easing give increasing reproductive success without requiring greater reproductive effort: In the same way, declining reproductive success with age could involve increased reproductive effort if senescence reduced efficiency in offspring production and care.

Menopause presents an interesting problem for life-history theory because child bearing terminates in advance of marked senescence (Williams 1957; Gaulin 1980; Mayer 1982). Some have argued that it is not an adaptation, but an artefact of increased longevity in post-industrial societies (see, for example, Weiss 1981). But life expectancy at reproductive age for hunting and gathering and horticultural societies allows most mothers to live past their middle forties (Howell 1979; Lancaster & King 1985). It is likely that long before the industrial revolution most women who lived to reproductive age also went through menopause.

In developing his general theory of senescence, Williams (1957) considered menopause and noted that natural selection could favour termination of offspring production in an organism for whom extended post-natal maternal investment was crucial for offspring survival. As a mother's probable survivorship began to decline, and her pregnancies became increasingly hazardous, she might increase her fitness more through additional investment in children already born, rather than by risking further pregnancies and the possible attendant loss of the dependent children she already had in order to bear another child which she would be unlikely to raise to maturity. She could trade off the probable small fitness gains from that additional pregnancy for the marginal gains from allocating the same investment to offspring (and other kin) already born. Williams emphasized that according to this theory of menopause, life beyond last childbirth is not 'post-reproductive'. Paradoxically, females could be increasing their effective reproductive effort as their reproductive value declined, even though they ceased bearing offspring.

Patterns of increasing probable mortality with age and extended maternal investment are common in primates. Hrdy (1981a) points out that variation in the behaviour of old females, both within and between some species of monkeys, varies in ways consistent with evolutionary theory: old females remaining dominant where a mother's rank can increase the reproductive success of her adult daughters, losing rank where it would not. Nevertheless, menopause, as seen in humans, is rare or non-existent in non-human primates. Sharp drops in fertility, if they occur at all, are associated with marked general senescence (Gould, Flint & Graham 1981; Graham, Kling & Steiner 1979; Dolhinow, McKenna & Vonder Haar Laws 1979). Perhaps the difference non-human mothers can make in the reproductive success of their maturing and adult offspring by abandoning child bearing is rarely great enough to outweigh the possible fitness benefits of continuing pregnancies, even if they are increasingly risky. Beyond nursing, non-human primate females rarely acquire food for their offspring (Silk 1978, 1979). The hominid capacity to feed others regularly in addition to themselves may allow older females to make a much bigger difference in the fertility of their maturing daughters.

We use this background to pose two questions. First, given that they are past child bearing, can the extra foraging of older Hadza women be understood as an optimal expenditure of reproductive effort? Second, can the fitness costs and benefits implied by the behaviour of these women contribute to explaining the evolution of the menopause itself?

THREE HYPOTHESES

The first matter is to consider explanations for the extra foraging of senior Hadza women. In addition to the implications of Williams's theory of senescence, other trade-offs may be different for older than for younger women. Since they are no

longer bearing offspring, older women can have neither the same calls on their time for care of offspring, nor the same relationships with men. We pose three hypotheses, of which only the third draws on life history theory:

- (a) The first hypothesis focuses on the opportunity costs of time spent foraging, i.e. the benefits which could be gained from activities foregone. The older women may give up less by spending time in food acquisition because they have less to gain from non-foraging activities. Since they have ceased bearing children, they might gain less from activities which compete with foraging in female time budgets. They have no young children of their own to tend, and if men provide resources in exchange for mating opportunities from women in child-bearing ages, women beyond those ages may be less likely to gain from time spent with men. Older women might then allocate more time to foraging because for them the cost of opportunities foregone when foraging is lower than it is for younger women.
- (b) The second hypothesis has to do with possible differences in the value of the food acquired to women of different ages. The same amount of food may have higher value for older than for younger women because older women cannot trade sexual favours for resources acquired by men. Perhaps they trade food instead. If older women acquire vegetable foods to reciprocate for resources from men, the value of additional foraged resources would be greater for older women than for young ones who do not need vegetable food (or not so much) to acquire the same resources from men. Foraging longer, other things equal, would pay off for the senior women.
- (c) The third hypothesis deals with the allocation of reproductive effort. Women past child-bearing age are not preparing for pregnancy and lactation. They may therefore get fitness gains by reducing the work load of their younger female kin who can thus allocate more of their own resources to pregnancy and lactation. This is an opportunity cost hypothesis like the first mentioned, but the opportunities at issue are not alternative allocations of time but of other resources. Some foraging activities appear to be very hard work. Digging //ekwa is the salient example. Adolescents might delay their first reproduction and child-bearing women lower their fertility by spending long hours at this energy-expensive task. If so, older women who are not investing in their own pregnancies or lactation might reduce the cost this foraging imposes on the reproduction of their daughters and younger female kin by increasing their own tuber acquisition, distributing the extra to their younger kin and so reducing the amount of digging that their younger kin do. Women of reproductive age with senior helpers would put less effort into tuber digging. Gains in reproductive success could follow from this reduced work. These gains might make the fitness earnings of the older women larger for reducing that work than for alternative allocations of the same investment.

These hypotheses are not mutually inconsistent. All three could be supported (or rejected). We can perform no decisive tests here, but report some additional aspects of the pattern of women's work which are relevant to these hypotheses.

7

COMPARISON OF BERRIES AND TUBERS

If senior women forage more because they have fewer other calls on their time, the pattern might be expected to hold across resources. General opportunity costs for time spent foraging can be gauged indirectly by comparing the time devoted to berry and tuber collecting by women of different ages during the March/April period when they take both resources (Fig. 4; Table 1, section D). If child-bearing women must pay the cost of reduced child care or reduced resource extraction from men when they forage, and so they forage less than senior women who would give up less, this might be expected to affect time allocation to all foraging. This would mean that older women spent more time foraging for all resources. Our data indicate that contrary to such an expectation from the first hypothesis, older women do not spend more time in all foraging tasks. Time spent on berry collecting is unrelated to age (difference of means, older women versus others, see Table 1, row D1, P=0.0345). The extra time older women spend foraging during this season is devoted to tubers (difference of means, older women versus others, see Table 1, row D2, P=0.029). If the opportunity costs for tuber-collecting forays are similiar to those for berry collecting trips, then the opportunity costs of foraging time cannot account for the extra tuber digging of the older women.

The extra time devoted to roots rather than berries is also inconsistent with the second hypothesis, that plant foods in general are more valuable for older women. The second hypothesis might also lead us to expect a relationship between extra foraging and hunting success. If older women were acquiring extra tubers to exchange for food with men, their efforts would correlate roughly with periods when men had food to trade. Hunters acquired large quantities of meat in the 1985 dry season, much less in the following wet season. Older women worked longer at tuber digging during both periods. From 13 October to 1 November, the dry season period sampled here (Fig. 4c; Table 1, row D3), hunters in the study camp killed eleven large animals and scavenged considerable portions of another four, earning a total of about 2110 kg of meat, or about 1.83 kg (live weight) per camp resident per day. During the part of the wet season sampled here (Fig. 4a; Table 1, row D1) 26 March to 19 April, hunters in the study camp killed no large game although a giraffe was killed by hunters in a neighbouring camp and some of it was transported to the study camp. This provided a maximum of about 0.2 kg of meat (live weight) per resident-day averaged through the period (although it all came in on one day). Through this season women, all women, did spend less time getting tubers than they had in the dry season. The berries were ripe and some of their foraging time was shifted from tubers to berries. In one sense then variations in time allocated to tuber digging were correlated with the amount of meat available. Yet older women allocated substantially more time to acquiring roots than did other women even when there was little meat to get (Fig. 4a and c; Table 1, rows D1 and 3: difference of means for age categories two and three, P=0.021 and 0.020, respectively). Senior women spent more than twice as much time digging tubers as their juniors whether or not there was meat in camp.

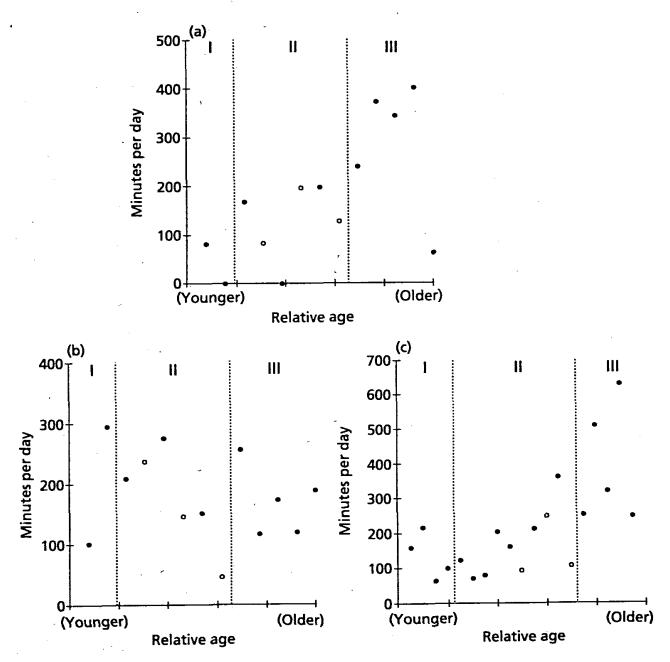


Fig. 4. Time spent on berries and tubers by relative age. Relative age, age categories, and nursing status as in Fig. 1. See text for description of methods. (a) Time spent on tuber-digging forays (min/day), 26 March—19 April 1986. (b) Time spent on berry-picking forays (min/day), 26 March—19 April 1986. (c) Time spent on tuber-digging forays (min/day), 13 October—1 November 1985.

The relationship between meat availability and extra tuber foraging by senior women merits further comment. It could be that longer-term relations of reciprocity play a role, so that women who did not provide tubers during periods of little meat risked penalties later. On the other hand, camp composition is flexible, so that co-residents at one time might later be living in different camps (Woodburn 1968b also reports this pattern). Even for those who remain co-resident throughout the year, actions over recent days or hours may be at least as important in reciprocal relationships as actions months past. More problematic is the fact that

very small amounts of meat may be of very high value when there is little available.

A satisfactory account of the age difference in time allocated to berries and tubers would include a more general explanation of the pattern of alternating between these resources during periods when berries are ripe. This in turn demands an evaluation of return rates in nutritional terms. Such analysis is not yet complete. Here we can only note that switching between tubers and berries remains to be explained. Women do spend substantial amounts of time acquiring both. When both are available, they are usually taken on separate foraging trips, often in daily rotation.

We turn to the third hypothesis focused on reproductive effort. The apparent differences in the energetic expenditure associated with these two resource types are suggestive. For kongoro collecting, the main effort involves the walk to and from the patches and the load carried home. During the period covered by data reported above, the walk averaged 76 (± 37) minutes each way. The cost of such walks in the sun cannot be negligible, but children over the age of 8 not only make these walks, but also collect enough to feed themselves. Even young girls always collect enough to carry some home. Releasing young women from some of this work may have little effect on their fertility, and so add little to the fitness of their mothers, grandmothers, and aunts. In contrast, tuber digging appears to be very hard work, and so may impose a fertility cost. In Blurton Jones, Hawkes & O'Connell (this volume) we argue that the low reproductive cost of older Hadza children implies that ecological constraints on child production fall mostly on pregnancy and lactation. Help with a young woman's energy budget may thus be especially productive of increased numbers of descendants.

Tests of this suggestion are simple in principle, but not in practice. We would expect differences in time spent digging tubers to make more difference in reproductive success than differences in time collecting berries. We would expect women with senior helpers to spend less time digging tubers, and to have higher reproductive success. The first of these predictions might be assessed through test of correlations between different amounts of foraging time spent in these activities and ovulatory regularity (Ellison, Peacock & Lager 1986). Satisfactory tests of the second are impeded by the small study population and the general problem of correlated features in individuals (Clutton-Brock 1984; Horn & Rubenstein 1984). For example, women who work harder may have higher reproductive success because women in very good condition do both, even though those same women may be lowering their potential fertility by their hard work. Still, we hope to perform such tests.

Data on body weights are potentially relevant. If older women are reducing the energy costs of their junior kin, this might show up as differential weight changes between the two categories of women. Over a given period of time, senior women spending more energy digging tubers might lose more weight (or gain less) than younger women, with differences between senior women and others varying in magnitude depending on the relative amounts of root digging. Our data on weights during the two periods under discussion are insufficient to provide a critical test; but data from the 1986 dry season are quite striking. During this season, the study camp contained six older women, eight child-bearing women, and five girls with marked breast development who had not yet had a pregnancy. Percentage of time spent foraging by women of different age categories is shown in Table 2. As in earlier seasons, older women devoted more time to this activity than did child-bearing women and girls (difference in means for category 3 versus categories 1 and 2 combined, P=0.00001). Excluding one woman who bore a child, women lost an average 0.276 (± 1.84) kg during this period. The difference in weight lost by child-bearing women and unmarried girls is not significant. However, the older women lost significantly more than either child-bearing women or girls (P=0.029 and 0.0385, respectively).

DISCUSSION

The data show that all Hadza women spend a substantial amount of time foraging. This observation should help correct a tendency to see the small amount of foraging time reported in Lee's classic work diaries for the Dobe !Kung as typical of hunter-gatherers (see also Hawkes & O'Connell 1981; Hawkes et al. 1985; Hill et al. 1985; Hurtado et al. 1985; Hawkes 1986). The data on return rates show that among the Hadza, women's foraging efficiency increases from adolescence to a peak in middle adulthood, displays minor declines associated with the presence of nursing infants, and falls off only slightly after menopause. Hadza women generally work long hours foraging, grandmothers the longest. Higher foraging effort among older women is generally associated with tuber collecting. While we cannot decisively reject the possibility that differences in age-related opportunity costs of foraging or in age-related exchange values for tubers encourage extra work among older women, the contrast between time allocated to berries and roots and the persistence of extra work for older women in lean meat seasons are inconsistent with the simplest version of either hypothesis.

The available data are most consistent with the proposition that senior women reduce the energy costs of foraging to their younger female kin by acquiring extra tubers for them. Although the pertinent data have not yet been analysed, it is our impression that the sharing of vegetable food is directed differentially toward close kin. The high tuber income of the senior women and the patterns of weight change among age ranks imply that much of what older women acquire is transferred to younger women. That older women lose more weight than younger ones could indicate that older women are not only investing reproductive effort, but that they are, paradoxically as 'post-reproductives', increasing their relative reproductive effort as their reproductive value declines. It is important to note that we have not analysed data on meat distributions, and the greater weight loss of the older women could also result from a lack of access to meat; but we think this is unlikely.

Unmarried girls Child-bearing women Older women Mean S.D. n Weight change; September—November 1986 Veight change; September—November 1986 Veight change; September—November 1986 Veright change; September—November 1986	description of methods						9	in the case of the		2
Mean S.D. n Mean S.D. n Mean S.D. f 0.714 0.084 5 0.725 0.106 8 0.970 0.048 -0.63 1.96 5 -0.142 1.795 7 -0.958 0.539		Uni	narried girls		Child-l	bearing wome	5	PIO	er women	
f 0·714 0·084 5 0·725 0·106 8 0·970 0·0480·63 1·96 50·142 1·795 70·958 0·539		Mean	S.D.	z	Mean	S.D.	ĸ	Mean	S.D.	u
-0.63 1.96 5 -0.142 1.795 7 -0.958 0.539	Fraction of 33 observation days spent out of camp foraging; September-November 1986	0.714	0.084	8	0.725	901.0	œ	0.970	0.048	9
	Weight change; September-November 1986	-0.63	96-1	S	-0.142	267-1	7	-0.958	0.539	9

If older Hadza women dig more tubers as a means of increasing their reproductive effort, why do senior women in some other foraging societies spend less time getting food? The answer may involve differences in the fitness-related costs and benefits of foraging. In the !Kung case, for example, two aspects of local ecology may be pertinent. First, the relatively harsh pressures imposed by seasonally high temperatures and lack of water in the Kalahari may make senior women's foraging return rates low, and their survivorship costs high (Blurton Jones & Sibly 1978). Draper (1975) describes a degree of exhaustion on return from a gathering trip for a woman with a 'grown daughter' unlike anything we observed among the Hadza. Second, for reasons yet unclear, babysitting seems to involve much more active supervision among the !Kung than it does among the Hadza. The amount of babysitting available plays a large role in the foraging income a !Kung woman can earn (Blurton Jones 1986, 1987; Blurton Jones, Hawkes & O'Connell, this volume), and so seniors may get the greatest increment in inclusive fitness by increased babysitting.

THE EVOLUTION OF MENOPAUSE

The argument developed above has interesting implications for the explanation of interspecific differences in female reproductive effort and their evolution. Females of some non-human primate species may cease sexual cycling before death (Graham, Kling & Steiner 1979), but such phenomena are rarely observed (Lancaster & King 1985). By contrast, human females who survive long enough to bear a child not only stop bearing early enough to see their last child reach sexual maturity, but can live on to see that child's children have children. The degree of senescence at menopause and the rate of senescence after it are remarkably low for women by non-human standards (Williams 1957; Lancaster & King 1985). As reviewed above, life history theory predicts that reproductive effort will increase as the probability of future reproduction declines (Fisher 1930). In the case of senior females, their lower probable survivorship lowers the probable fitness benefit of another pregnancy (Williams 1957). The magnitude of the fitness gains they might get from investing more in children already born, instead of bearing more, depends on the contribution they can make to the reproductive success of their younger close kin.

The data and interpretation presented in this paper suggest that the suite of resources exploited, and the age-specific costs and benefits of acquiring them may have a marked effect on age-specific reproductive effort. A major difference between humans and other primates is the difference in their extractive efficiency (Gaulin & Konner 1977). Early hominids may have been able to tap resources which were much higher quality than those exploited by their ancestors, allowing one individual to acquire enough to feed others as well as herself. Extraction of a high quality resource which is also energy expensive to acquire would provide an opportunity for females to make larger contributions to the reproductive success of their daughters, nieces, and granddaughters by foraging for them. Mechanisms

such as critical fat (Frisch 1984) or direct work effort effects on fertility (Bentley 1985; Ellison, Peacock & Lager 1986) could be implicated. If older females could be productive enough, those who ceased child bearing and invested in their younger female kin may have earned greater fitness than those who did not.

By this line of argument, early termination of child bearing would be adaptive only where age-specific mortality and the importance of extended maternal investment reduced probable fitness gains from additional pregnancies, and where resource acquisition patterns could produce large enough marginal gains from assistance to younger kin. If females who stopped bearing infants earlier had higher fitness, it would enhance the fitness of their descendants to curtail the associated physiological preparation for pregnancy at an earlier age, thereby reducing personal maintenance costs, which in turn would allow them to allocate more resources to more effective 'reproductive effort'.

Perhaps menopause and a wider coincidence of interest among adult females are part of a common human, or even hominid pattern. This is not to suggest that women do not compete with each other. Conflicts of interest are expected between females because their fitness interests are rarely identical. It may be that ethnographers have failed to note the kinds of reproductive competition now being reported for non-human primates (Hrdy 1981b; Nicholson 1986) simply because they have not looked for them. On the other hand, one implication of the argument presented here is that greater cooperation means more in fitness terms for women than it does for other female primates.

Among modern hunter-gatherers, specific features of subsistence strategies and local ecology may determine the choice between childcare for grandchildren, resource acquisition for younger kin, or other alternatives including departure or death when an ageing senior might compete with younger kin for valuable resources. The costs and benefits of tuber exploitation in environments like that of the Hadza may provide an opportunity for seniors to raise the reproductive success of younger kin more by digging tubers than they could through other activities. By taking greater work costs themselves and so reducing these costs for their younger kin, allowing the latter to increase the number of offspring they bear, seniors may earn higher returns on their 'reproductive effort'.

Even if our argument about the relationship between Hadza women's foraging activities, reproductive effort, and features of their resource base is wrong, this inquiry should serve to make a very general point: many of the observations commonly made about the causes and consequences of divisions of labour and food sharing between the sexes (Lovejoy 1981; Lancaster & Lancaster 1983) should apply equally within the sexes, for example among individuals of different ages. Among other things, this suggests that divisions of labour and food sharing among adults could evolve under certain ecological circumstances as a result of adaptive adjustments in female life history strategies. We may come to see menopause as a consequence of foraging patterns among our female ancestors.

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