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The cooperative economy of food: Implications for human life history and physiology

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ABSTRACT

The human diet has undergone substantial modifications since the emergence of modern humans and varies considerably in today's traditional societies. Despite these changes and cross-cultural differences, the human diet can be characterized by several common elements. These include diverse, high quality foods, technological complexity to acquire and process food, and the establishment of home bases for storage, processing and consumption. Together these aspects of the human diet challenge any one individual to independently meet all of his or her daily caloric needs. Humans solve this challenge through food sharing, labor exchange and the division of labor. The cooperative nature of the human diet is associated with many downstream effects on our life history and physiology. This paper overviews the constellation of traits that likely led to a cooperative economy of food, and draws on ethnographic examples to illustrate its effects on human life history and physiology. Two detailed examples using body composition, time allocation and food acquisition data show how cooperation among Savanna Pumé hunter-gatherers affects activity levels, sexual dimorphism in body fat, maturational pace and age at first birth.

1. Introduction

The idea that who we are today is the outcome of a long evolutionary history is well established in the fields of evolutionary medicine and medical anthropology. This approach takes the view that many present-day ailments and disabilities (e.g. obesity, diabetes, osteoporosis, heart disease, impacted wisdom teeth and dental carries) arise because current lifestyles are incompatible with the selective pressures that shaped our bodies and behavior during human evolution [1–7]. This perspective in particular has stressed the mismatch between our current diets and past hunting and gathering diets to which we are metabolically adapted [8]. My aim here is to highlight a somewhat different aspect of our evolutionary legacy by focusing less on the food we eat, than how we get that food. Although human nutritional ecology has undergone substantial changes, notably from dependence on hunting and gathering to domesticated plants and animals, cooperation, sharing and exchange are ubiquitous across subsistence strategies. The fundamentally cooperative nature of the human diet differs markedly from that of our closest primate relatives. To discuss the cooperative economy of food, I first outline traits that distinguish the human diet and propose that the complex of nutrient-rich and diverse foods, resource exploitation across large geographic areas, and dependence on technologically assisted food processing together impose a time constraint for any one person to be self-sufficient. I then discuss how this constraint is resolved through cooperation and pooled energy budgets, and illustrate its implications for human life history and physiology through two detailed examples from my research with hunter-gatherers. Examples are drawn from traditional societies, in particular hunter-gatherers, and comparisons with other primates as a way to appreciate what is unusual about how humans meet their daily caloric needs. Although attention is paid to traditional societies and nonhuman comparisons, many features of the human diet and how we procure food are universal and pertain to our lives today.

This overview builds on participation in the IBRC Symposium “The Pace of Life and Feeding” at Purdue University, which incorporated perspectives on food and feeding from many different disciplines and professions. In keeping with the goals of the conference, this overview is intended to be broadly accessible, focusing on important themes and general patterns in the human diet.

2. Traits that distinguish the human diet

The human diet has undergone considerable modifications since the emergence of *Homo sapiens* approximately 300,000 years ago. For as long as humans can be identified in the archaeological record they have been adopting new foods, and incorporating novel technologies and strategies to procure food. Prior to the Holocene ~11,000 years ago, all humans made their living exclusively by foraging for wild resources.

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With domestication, some hunter-gatherers transitioned to agriculture and pastoralism, which in adaptive time occurred quite recently, some 600 generations ago. Archaeological evidence indicates that while people in many parts of the world shifted their diet to domesticated plants and animals, other hunter-gatherers continued to live a foraging way of life, or pursued mixed economies combining wild resources with small inputs of cultivated plants and animals [9–14]. By the 1960s, hunter-gatherers represented an estimated 1% of the world's population [15]. Today, despite habitat transformation, rapid population growth and globalization, foraging still persists as a viable way of life in remote equatorial to arctic regions [16]. Contemporaneously, subsistence farming is a predominant lifeway in many temperate environments, and small-scale rural farmers and pastoralists account for an estimated 900 million of today's world population [17]. While specific combinations of agricultural foods vary worldwide, reliance on domesticated plants introduced an increased intake of carbohydrates, especially low fiber grains [2]. The novel consumption of highly processed refined carbohydrates, sugar and high saturated fats has occurred very recently, within the last several generations.

Although evolutionary and historic changes in how we make our living have affected dramatic alterations in the basic constituents of the food we eat, several common elements stand out that distinguish the human diet from that of our closest primate relatives (Table 1). First, compared to other great apes, humans consume food that is denser in calories and nutrients [18,19]. While humans and other apes eat a similar suite of foods, those foods are generally consumed in inverse proportions [20]. The majority of the nonhuman ape diet consists of leaves and fruit, with small inputs of insects and game [21–23]. The human diet inversely includes a greater proportion of foods rich in protein and fats, and lower amounts of leaves, fruits and fiber [2,18,24,25].

A second general characteristic of the human diet is diversity. Not only are human diets exceptionally varied across societies– we can make a living in virtually all of the world's environments– but within any particular environment, they incorporate many different kinds of resources, including plants, a wide size and habitat range of terrestrial vertebrates, pelagic, tidal and freshwater aquatic resources, birds, insects and insect byproducts. This diversity is reflected in the number of plant and animals species that hunter-gatherers consume. For example, the !Kung (sub Saharan hunter-gatherers) utilize 160 species of plants (105) and animals (55) [26, pp. 159,205]; the Savanna Pumé (South American hunter-gatherers) consume 135 species, including 42 species of fish and 7 insect species [27,28]; the Hadza (sub Saharan hunter-gatherers) eat at least 97 plants and animals species [29, Table 5.2] of the 878 species listed for the region [29, Table 5.2]. Dietary diversity often varies between seasons and with inter- and intra-annual variability in the incorporation of preferred primary and fallback foods.

A third characteristic of the human diet is that we do not directly consume most of the food we eat. Other than some plants, most food requires processing – e.g. cracking, mashing, pounding, grinding, leaching, soaking, pounding, sifting, winnowing, plucking, deboning, butchering, boiling, roasting – and many foods involve multistage processing. The few ethnographic studies that report on processing suggest that while it varies with the particular suite of foods included in a diet, most foods are processed; 70% of Hadza foods are processed (17% of the diet are berries, which are usually eaten unprocessed) [29, Table 5.4], and about 90% of Savanna Pumé foods require processing.

Food processing modifies a variety of resources to be either accessible to human digestion, or more nutritious and has been integrated into human nutritional ecology at least since the Middle Paleolithic [30–32]. Processing has had two key effects on physiology; it softens food reducing its biomechanical impact on teeth [33], and it renders food more digestible [34]. One behavioral consequence of eating softer food is that humans spend far less time chewing each day than do other apes. For example, chimpanzees spend about 38% of daylight hours chewing, while people eating a traditional diet spend about 5%, or 35 min per day [35, Table S1 and S2, human average for 24 traditional societies]. With the very recent consumption of highly processed foods, chewing time drops to ~1% of daily time because much of the fiber we eat is pulverized [2]. The physiological consequences of food processing during human evolution are evidenced in the replacement of the robust dentition with more gracile teeth and thinner enamel [2], diminution of the gastrointestinal tract [18] and brain size expansion [36].

Food processing also can transform foods that are otherwise inedible. Some wild and domestic roots and fruits become bioavailable only after soaking, leaching or fermenting to remove toxins or pith. Examples include bitter manioc, palm starch, baobab, cycad palm nuts and cacao. The temporal utility of other food can be extended by grinding, smoking, drying or salting. These and other storage technologies are critical for hunter-gatherers to solve seasonal shortfalls in resource availability, to overwinter in temperate and high latitudes and to provide food while foragers move through areas of low food availability. For agriculturalists, stored food is critical to get through much of the year.

While food processing liberates chewing time, decreases energy spent in digestion and renders a greater diversity of food available for longer durations, it also takes time. Although few published data specify how much time hunter-gatherers and agriculturalists spend processing food, estimates consistently report between 10 and 20% of daylight hours. As examples Efe (Ituri forest hunter-gatherers) women allocate 17% of daylight hours, and many more nonrecorded evening hours processing roots and palm starch [38, pp. 95–96]. Adult Hadza women allocate 11.2% of daylight hours to food processing [29, Table 4.6]; Hiwi (Venezuelan dry season foragers) women spend 2.3 h per day (~19% of daylight hours) [39, p. 179]. Among Savanna Pumé hunter-gatherers, women over the age of 40 allocate 21.8% (2.6 h) and women ages 13–40 15.3% (1.8 h) of daylight hours to food processing [27, p. 174]. A Yucatec Maya household (subsistence agriculturalists) spends on average 4 h a day in food processing and preparation [40, Table 6.4]. Because much of human food is processed, the added cost of processing appears to be offset by the benefits of expanding the nutritional and temporal availability of food, the geographic range of habitable environments, and the diversity of edible resources.

Table 1
Characteristics of human nutritional ecology.

Characteristic	Citations
High nutrient density	[2,18,24,64,169]
Species diversity	[26,28,29]
Food processing	
Most food in the diet is processed	[29]
Little time spent chewing	[2,35]
Considerable time spent processing	[27,29,38–40]
Physiological and life history effects	[18,33,34,37]
Establish home bases where processing and consumption often occur	[29,41–47]
Technologically dependent	[26,32,43,44,53,54]
Diet combines foods distributed over large geographic areas	[29,56,58–60]
Cooperation with others to meet caloric needs	
Sexual division of labor	[26,64,71,72,74,76,77,98]
Age division of labor	[40,86,88,90,92,170,171]
Cooperation among nonkin	[62,98–100,104]
Pooled energy budgets	[102,120]

2.1. How we access the food we eat

The consumption of diverse, high-quality foods that are processed has important implications for the strategies humans use to procure food. At its most general, hunter-gatherers are described as central place foragers, meaning that they establish home bases from which men, women and children forage alone or in groups and return with food [29,41–47]. Humans are not unique in this regard; birds, social insects, denning animals and some nesting animals also travel out from and return to a home base. Central place foraging, however, is not a shared great ape strategy and appears to distinguish human behavioral modernity, some ~40,000 years ago, from the foraging patterns of earlier humans [47–50]. Chimpanzees who are diurnal foragers, feed while moving through the environment, and settle and sleep where they end up at the end of the day [51]. While hunter-gatherer camps can be quite transient (e.g. high mobility, as among the Nukak and Hoti, South American foragers), a home base provides a central location for people performing different subsistence tasks to aggregate, exchange, process and consume food, sleep, construct shelter and cache raw materials and tools [47]. In human societies, individuals living in commensal groups or families often disperse to pursue different tasks in different locations during the day, but aggregate later in day. In traditional societies meal times often are not designated in the same way that we might eat together several times a day. Rather, people tend to eat from a common pot when hungry, with different individuals contributing to the food, as well as the water, firewood, and raw materials that constitute the common pot.

Complex technologies are essential to access and process many foods in the human diet and involve spending time both procuring raw materials and manufacturing tools [26,28,32,43,44,52–55]. Of the few data available that distinguish the time cost of technology from other domestic tasks, !Kung adult males and females spend about an hour per day manufacturing and maintaining subsistence tools (men 64 min/daylight hours; women 45 min/daylight hours) [26, p. 277]. While not limited to subsistence technology, among the Savanna Pumé, women spend on average 15.8% (1.9 h) and men 8.0% (1 h) of daylight hours in equipment manufacture (constructing burden baskets, sharpening digging sticks, making bows, arrows, string and fishing gear, constructing shelter and weaving hammocks). Technological innovations have shaped human nutrition by opening up new feeding niches, enhancing bioavailability and integrating an array of energy dense foods into the diet that were otherwise inaccessible. Examples include underground storage organs, pelagic fish, shellfish, large game, arboreal and burrowing animals.

Lastly humans utilize large geographic regions to procure resources. Compared to other great apes, human foragers have greatly expanded day ranges, annual ranges and life-time ranges [56]. Chimpanzees and gorillas travel on average less than 2 km per day [18, p. 7, 61], whereas hunter-gatherer day ranges are 4–5 times larger [57,58]. Although an individual's daily travel distance varies with ecology, season, sex and age, a typical hunter-gatherer travels on average 13 km per day [59]. (Females are estimated to travel 9 km per day and males 15 km [29].) While some field snacking occurs [29], most food is transported back to a central camp to be processed and consumed, increasing foraging distances covered each day [46,60].

2.2. The human diet imposes a unique time constraint

Central-place foraging, home bases, large ranging areas, technological complexity and processing permit humans to successfully rely on high quality, nutrient dense and diverse resources. These attributes together also pose a problem. No one person can do everything needed to feed themselves. Plant and animal foods, both of which are important to the human diet, often have disparate geographic distributions, require different time investments, and have different search and handing requirements. Resources vary in their skill and strength requirements to procure and process such that individuals of different ages and sexes are more proficient or pay different opportunity costs. These complexities introduce a time budget constraint for an individual of any age to be self-sufficient. Simply said, there are insufficient hours in the day for any one person to forage for both plants and animals, process them, haul water, chop firewood and procure and process the raw materials to manufacture the tools necessary to procure and process food, construct clothing and shelter, take care of children and maintain social and information networks.

In sum, the human diet can be characterized by nutrient density, food diversity and processing. These features have important implications for the strategies humans use to procure food including foraging ranges, residential patterns and technological dependence. Although many exceptions exist, this constellation of traits is associated with a dependence on others to meet caloric needs through cooperation, food sharing and a division of labor [48,62–66].

3. The cooperative economy of food and pooled energy budgets

Across human societies, men and women, adults and children do different food procurement and processing tasks, target different resources and share food. While role specialization is not unique to humans, the combination of cooperation across age, sex and tasks is unmatched in other animals. In some biparental bird and insect species, male and female parents specialize in specific offspring care tasks (raptors are a good example of sex-based specialization [67,68]). In some animals, males and females may eat different foods. The greater meat consumption by male chimpanzees [69], and the greater consumption of nuts [70] and insects [51] by females are instances of differential resource focus. What is unusual about the human pattern is that males and females, adults and children do different subsistence tasks, and then share in the redistribution, preparation and consumption of food. While this of course does not happen with all foods at all times, cooperation across age and sex is foundational to the human diet (see Table 1) [71–74].

Among hunter-gatherers, men tend to produce high-protein animal foods [64,75,76]. For example, in eight of nine groups of hunter-gatherers, men minimally produce 70% of dietary protein [77]. Females tend to pursue resources that are more predictable to find and collect such as roots, tubers, cereals, grains, nuts, berries, fruit, insects and shellfish [26,29,78,79]. There are exceptions to this general pattern [80], but what is usually highlighted about the sexual division of labor is that women commit to resources that are more reliable to feed children, and to tasks that do not energetically compromise reproductive function and are compatible with primary infant care and cannot be substituted by others [26,81–84]. In subsistence economies this may include collecting, harvesting and processing food, manufacturing clothing and shelter, among other domestic activities. One analogy in industrialized and postindustrial societies is that males tend to spend more time away from home as wage earners than women [85].

An age division of labor also characterizes human subsistence [86]. Although children depend on adults for difficult-to-acquire food, they produce other resources that contribute directly to their own energy budgets and are often shared with others [40,87–92]. Common children's activities include foraging for fruit and berries, digging small tubers, hunting for small game, fishing, collecting shellfish, harvesting grain and fetching water and firewood. Hadza children spend 5–6 h a day foraging for food, primarily berries, roots, baobab fruit and small animals. By the age of five, they supply about 50% of their own calories during some seasons [93, p. 367]. In a measure of the labor needed to support a household, Maya children produce 50% of what they consume by age six, much of which benefits other household members [40,94]. Although largely unreported, children are also important food processors. !Kung children, for example, spend little time foraging [87,95]; however, over the age of 8, they crack and remove the meat from most of the mongongo nuts that they eat, an important constituent of the diet [26].

As examples of the cooperative economy of food within families, a Savanna Pumé boy living on the llanos of Venezuela has an average return (amount of food produced per foraging trip) of 4.5 k of wild fruit (~3200 kcal), and 0.5 k of fish (~700 kcal). This is what he returns to camp after whatever field snacking that he might do and is a sufficient calorie return to feed himself and at least some of his family. He also is dependent on shares of processed plant food and hunted game from others [96]. Mikea girls of southwestern Madagascar dig for small roots but are unable to transport large quantities back to camp, a task that their mothers and grandmothers do [92]. Among Western Desert Australian foragers, children collect grubs and fruit and successfully capture small reptiles and rodents. They may share these with their siblings, and also depend on adults for processed carbohydrates and larger game [97]. Married Hadza males and females focus on different foods, but have similar daily calorie returns (~3000 kcal), which are shared within and across families [29, Table 5.5]. These examples make the point that human food interdependence is lifelong and occurs across all ages and sexes and involves a broad range of tasks.

Nonfamily members also exchange food resources and subsistence labor, and at a broader scale, social networks that form across groups function to exchange food and other resources [72,75,98–105]. The explanation that has received considerable attention for why nonkin and more distantly related individuals cooperate is that because resources are heterogeneously distributed, often over large geographic areas and in disparate locations, local needs are optimally met through pooling resources. Cooperation and exchange are hypothesized to be an effective means to reduce risk and smooth day-to-day and individual variance in food supply [64,72,75,105].

3.1. Traditional and pooled energy models

The effect that the cooperative economy of food acquisition and sharing has on life history and physiology can be illustrated by contrasting two energy allocation models. Following Gadgil and Bossert's [106] seminal model, an individual expends a given unit of energy on either maintenance or production. Maintenance includes somatic processes such as pulmonary, cardiac, digestive and immune functions. Energy balance in excess of maintenance is available for production, which can be allocated to growth in an immature individual or to reproduction in a sexually mature individual [107,108]. The traditional allocation model assumes that the energy available to survive, grow or reproduce is constrained by the calories that an individual itself can harvest from the environment. This characterizes energy allocation for most animals since most are self-provisioning and do not rely on food from others (a notable exception are cooperative breeding birds and mammals). However, the energy available to a growing or reproducing human is not constrained by what he or she alone produces. As an example of the effect that cooperation has on an individual's energy availability, in human societies food is typically cooked at one hearth and then shared out to many individuals. The energy that a woman spends chopping and collecting firewood is 500 fewer calories that her pregnant older daughter or younger growing son would have to expend if there was no cooperation.

To give a life history example of the effects of food cooperation, if mothers did not receive food from others, they would have to increase their calorie production by 14% to 28% to fund gestation and lactation, respectively (this assumes that pregnancy across gestation costs an average of an extra 282 kcal/day, lactation costs an average of 567 extra kcal/day and a typical nonpregnant woman consumes 2000 kcal/day; other sources vary slightly around these calorie estimates [109–112]). However, pregnant and lactating mothers often decrease, not increase, their time spent foraging for food, in agricultural work or other domestic activities [82,113–116]. To illustrate the implications of food cooperation on maternal energy budgets, Lancaster et al. [77] found that to support lactation baboon mothers, who receive no help from others, increased the time they spend foraging each day from 65% to 85% of daylight hours. Conversely, Ache mothers (South American foragers) forage less when lactating, decreasing their food returns by about a third, from 3300 to 2100 kcal/day. They physiologically manage this reduction in calories because others share with them, substituting for their lost labor.

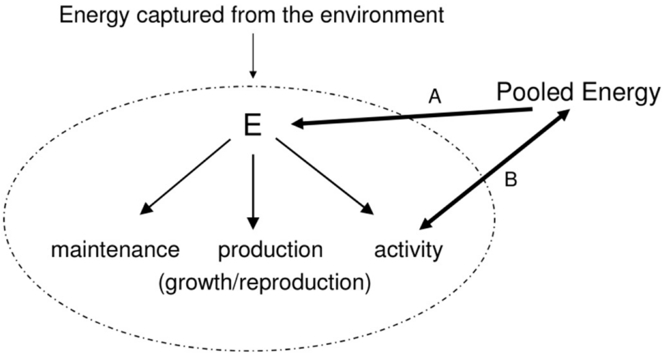

Fig. 1. The pooled energy model is a modification of the traditional two-way tradeoff model between maintenance and production [106]. In the pooled energy model [102] a given calorie can be allocated to maintenance, production or activity, and an individual's energy budget can be modified through direct calorie transfers (A) or adjustments in physical activity (B). Activity is specified as a third alternative energy allocation to account for the energy savings and deficits that occur as a result of cooperation.

In allocation models derived from Gadgil and Bossert's original formulation, energy allocated to activity is assumed to be a function of BMR and body size, and subsumed as a part of maintenance. However, because we share food and labor, energy expended to produce food is not necessarily a function of body size (e.g. as in the above examples, lactating and pregnant women may underproduce, while others overproduce) [102]. Consequently in a modification of the traditional allocation model, a third tradeoff with physical activity is added to account for the effects of cooperation (the energy savings or expenditures) on an individual's energy budget [102] (Fig. 1). If maintenance, production and activity are competing expenditures, any downward adjustment in physical activity level should increase the energy available for either maintenance or production (for example to fight an infection, mature more quickly or to fund lactation).

Food cooperation and adjustments to energy balance are associated with a number of derived human life history features including short birth intervals, young age at weaning, rapid reproductive pace, juvenile dependence and high juvenile survivorship [64,77,117–120]. For example when labor saving technology was introduced in a remote Maya village in the 1970's, maturing girls spent less time in energetically demanding work, a savings on the order of 325 kcal/day, which is associated with earlier maturation and age at first birth [111,121,122]. The next section presents two examples of the effects that food cooperation and activity budgets have on sexual dimorphism in body fat and the pace of maturation.

3.2. Physiological and life history implications for the cooperative economy of the human diet

The first example draws on anthropometric data from a group of hunter-gatherers to illustrate how the cooperative economy of food can affect body fat composition. The Savanna Pumé are semi-nomadic foragers who live on the savannas (llanos) of west-central Venezuela [28,53,79,123,124]. They move camp five to six times a year in response to rainfall and changes in the water table and subsistence base. The Venezuelan llanos are a hyperseasonal savanna, and the year is divided into a 6-month dry season and a pronounced 6-month wet season, during which 85% of the rainfall occurs. How the Savanna Pumé make their living tracks these seasonal rainfall differences, which affect distinct variation in the availability of plants and animals [46]. During the dry season, subsistence is focused almost exclusively on fish and tree fruit. During the wet season when the savannas flood and fish are difficult to locate, the resource base shifts to small terrestrial game (lizards and other burrowing animals) and roots [79]. In this relatively depauperate and highly seasonal faunal environment, meat constitutes

Table 2

Savanna Pumé adult body composition during dry (plenty) and wet (lean) seasons (means and standard deviation).[a]

		Males	Females
Dry season	Weight (kg)	59.0 ± 4.4	49.8 ± 6.0
	% body fat[b]	7.2% ± 2.6	22.7% ± 4.4
	Lean body mass[c]	54.7 ± 3.8	38.4 ± 4.4
	Fat mass[d]	4.3 ± 1.7	11.6 ± 3.6
Wet season	Weight (kg)	55.7 ± 3.3	44.8 ± 4.9
	% body fat	4.4% ± 1.8	15.0% ± 5.5
	Lean body mass	53.3 ± 3.2	38.1 ± 4.4
	Fat mass	2.5 ± 1.0	6.8 ± 2.8

[a] Measurements taken during two dry seasons for 39 males (ages 18–63) and 34 females (ages 18–54), and two wet seasons for 30 males (ages 18–62) and 31 females (ages 20–54).

[b] Body density calculated from suprailiac and triceps skinfolds using methods described in Durnin & Womersley 1974 [172]. The Siri eq. [173] is then used to calculate % body fat (%BF) from body density where %BF = (495/body density) − 450].

[c] Lean body mass = Weight-Fat mass.

[d] Fat mass = %BF ∗ Weight.

a relatively small portion of the diet (~4% of the annual diet by weight, and 5% by kcal). Annual estimates are based on dietary data collected through focal follows and weighing plant and animals foods that were returned to camp over a 1-year period, $n = 1057$ foraging trips for men, women and children. Weights were converted into edible calories, dressed carcass weight in the case of meat, using published standard values for species used by the Pumé, or closely related species [125,126]; see [46,127] for description of field methods.

Seasonality in food availability is common in many traditional societies [9,26,124,128–130]. For the Savanna Pumé fat and protein are in relatively short supply during the wet season. Anthropometric measurements (height, weight, triceps and suprailiac skinfolds) were collected from adults ($n = 101$ adults ages 18–63) once during two dry and two wet seasons, and are used to calculate percent body fat, fat mass and lean body mass (Table 2). Women lose on average 4.95 kg or 9.9% of their body weight, and men 5.6% during the wet season [132]. For females, this seasonal swing in weight is comparable to changes among Tamang (Nepali agro-pastoralists) [133], Lese (Ituri forest horticulturalists) [134] and Gambian women (west African agriculturalists) [135]. Seasonal differences in male and female body fat composition also are striking (Fig. 2). From the dry (season of plenty) to the wet (lean season) season, adult female body fat declines from 22.7% (± 4.4) to 15.0% (± 5.5), and male body fat from 7.2% (± 2.6) to 4.4% (± 1.8).

Why females have both higher absolute levels of body fat during the season of plenty (females have 3.2 times the body fat of males) and why they do not drop as low as males during lean times is in part explained by evolved physiological mechanisms. For instance, women have a metabolic advantage in being more efficient than males in converting dietary fatty acids and carbohydrates into stored body fat [136–139]. Although the sex difference in postprandial fat storage has only been studied in reference to western diets, if it is a universal trait it helps to explain the sexual dimorphism in Savanna Pumé body fat. The dry season weight increase for both males and female is associated with the marked increase in the consumption of fish, which are in peak condition, and fruit. However, the change in the specific kinds of food consumed to those that women can take greater metabolic advantage of likely accounts for some of the sexual dimorphism in body fat. (Seasonal changes in weight are largely due to a change in fat mass, with little change in lean body mass, which we expect to be conserved except under dire circumstances.) The Savanna Pumé have survived in this environment for as long as a recorded history exists [79], at least several hundred years, suggesting that they are adapted to seasonal vicissitudes in resource availability [132]. Besides physiological mechanisms that allow women to make the most of fat and carbohydrate calories, seasonal sex differences in activity loads are also substantial [46,123], which further mediate dimorphism in body composition.

Savanna Pumé women would lose even more body fat during the lean season if men and women did not cooperate. The division of labor is most pronounced during the wet season when 100% of roots are collected by women, and all meat is the product of male labor (Fig. 3). The significance of this division of labor to body composition is that roots and game have different energetic costs due to differences in search and travel times. Roots are located in known patches, and their condition monitored throughout the year. Women walk directly to these patches, fill their baskets and return to camp with a predictable quantity. In contrast, the location of game is unpredictable, and men spend considerable time searching the environment [123, pp. 137,139]. These differences in search costs are reflected in distances traveled. When women forage for roots they average a roundtrip distance out from and back to camp of 3.9 km (± 2.9; $n = 50$ root collection trips).

Fig. 2. Savanna Pumé women during the (a) dry season and (b) wet seasons. Both women are in their early 40s and similar in stature. Photo credits Russell D. Greaves.

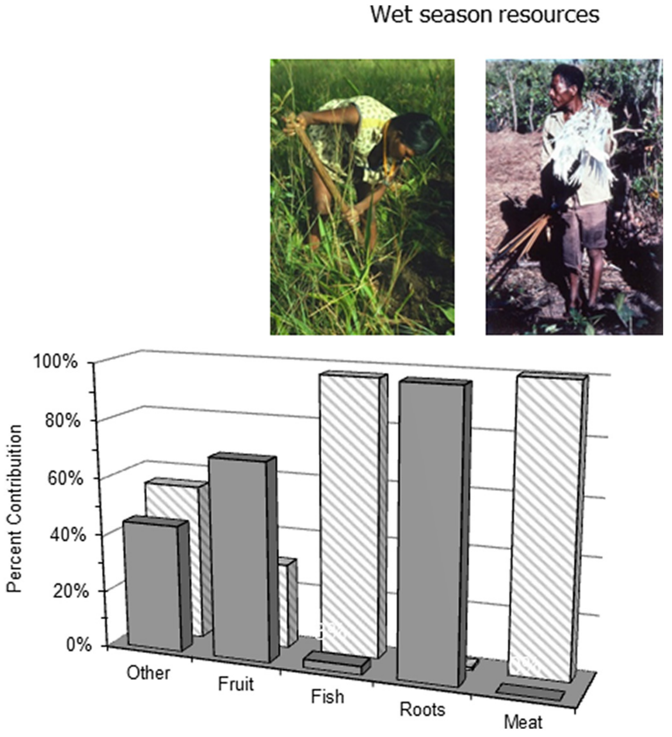

Fig. 3. Division of labor for the annual Savanna Pumé subsistence base showing proportional male (stripe bars) and female (gray bars) contributions to principle food categories by weight. Roots and meat are main wet season (lean season) resources. Proportions derived from focal follows and food returned to camp over a 3-year period (n = 1963 foraging trips). Photo credit Russell D. Greaves.

The average roundtrip distance on a hunting trip is 11.6 km (± 8.3; *n* = 44 hunting trips). Using an estimated expenditure of 50 kcal/1 km of brisk walking [140], women can save on the order of 385 kcal on days that they forage, a sufficient energy savings to meet most of the daily caloric demands of lactation or pregnancy.

Cooperation buffers women's energy expenditure particularly during their prime reproductive years. In addition to traveling less than men, young women spend less time overall in subsistence work [96, Fig. 4) and have lower foraging returns [141, Fig. 5) than do older women of similar body size. Based on scan sampling observations (*n* = 6616), and foraging return rates (*n* = 200 root collection trips), women ages 15–24 work less and produce about half that of women ages 25–50. (Women ages 15–24 have a return rate of 1 kg/hr compared to women ages 25–34 who have a return of 2.0 kg/hr for small roots and 1.5 kg/hr compared to 3.0 kg/hr for large roots). Younger women, who are more likely to be pregnant or lactating, can afford to underproduce during the critical lean season because older women share their returns with them. This age division of labor is not unexpected and is documented for many other foragers [82,142,143].

The second example draws on data from the same group of hunter-gatherers to illustrate the effects that cooperation has on female activity levels and its implications for maturational pace. Besides distinct seasonal undernutrition, Savanna Pumé girls grow up in an environment with high immunological stress, chronic intestinal parasite loads, endemic malaria, and no access to healthcare or immunization [144]. While we cannot know the direct caloric cost, the expectation would be that under these epidemiological conditions, a greater proportion of girls' energy budget is allocated to immune function and less energy should be available for growth [145–147] (see Fig. 1). Yet despite growing up in this environment, Savanna Pumé girls mature quickly and begin childbearing in their midteens [141].

Dry season anthropometric data collected in three Savanna Pumé camps (n = 50 females ages 4–20) show that girls achieve a greater proportion of their adult stature during middle childhood (ages 3–10) compared to normative growth expectations [140, Figure 2] (Table 3). By the end of juvenility, at age 10, population-specific growth curves show that Savanna Pumé girls have achieved 88% of mean adult stature, and 57% of mean adult weight [148, p. 305]. Compared to other foragers and horticulturalists [149], these girls are at the upper range of variation of height, and in the mid-range for weight. While adult women lose considerable body weight during the wet season, adolescent girls do not experience an equivalent decline [124]. They reach menarche on average at age 12.9 and 90% have their first born child between the ages of 15–19 [150]. A fast maturational pace and life history are broadly predicted across animals when mortality rates are high or variable, or life expectancy is low [149,151–153]. For the Savanna Pumé, who live in a high mortality environment, teen motherhood has been shown to be the best strategy to both minimize infant mortality and maximizes the length of women's reproductive careers [148]. This, however, does not explain where the extra calories come from to support fast growth and maturation. In this case the extra calories are in part made available through food sharing, but also through low activity levels [96].

Table 3
Height, weight, BMI and skinfolds for Savanna Pumé females ages 4–20 (n = 50) at age 10, at mean age of menarche and at mean age of first birth relative to the adult mean. Dry season measurements [148].

	At age 10	At menarche[a]	At first birth[a]	Adult mean[b]
Height				
Mean (cm)	133.1 ± 3.7	141.0 ± 4.2	147.5 ± 2.3	151.5
% adult mean	88%	93%	97%	
Weight				
Mean (kg)	29.2 ± 0.8	36.7 ± 3.9	43.5 ± 2.1	51.5
% adult mean	57%	70%	84%	
BMI				
Mean	16.5 ± 1.3	18.6 ± 1.8	19.9 ± 0.8	22.4
% adult mean	74%	84%	89%	
Triceps Skinfold				
Mean	7.2 ± 1.9	13.0 ± 3.7	12.9 ± 3.6	12.2
% adult mean	59%	106%	106%	

[a] Estimates taken at the average age of first menses, age 12.9, and average age at first birth, age 15.5 [150].

[b] Adult mean given for females ages 21–40 (n = 25), and is within the range of normal for other native South Americans [173, p. 156].

Return rate analyses showed that girls underproduce proportional to their body size while women ages 30–50 overproduce [96, Fig. 4]. For example, a 10-year old girl is 88% of adult body size (see Table 3), but she spends only 31% of the mean adult time in subsistence tasks [96, Fig. 2]. Compared to girls, women produce 1.6–6 times the amount of food in weight per unit time (200 root foraging trips and 149 wild fruit foraging trips), depending on the resource and their age group [141]. Not only is food shared to girls to meet their caloric requirements, but because they work less to meet their caloric needs than would be required without cooperation, they expend less energy in physical activity, which liberates more energy for growth [96]. Based on behavioral observations (*n* = 2933 scan observations), Savanna Pumé girls ages 3–10 have substantially lower physical activity levels than do other girls in cross-cultural comparison. Matched for age, Savanna Pumé girls have an average physical activity level (PAL) of 1.56 (± 0.149), while Maya girls have a PAL of 1.95 (± 0.115). The lower activity level saves Savanna Pumé girls approximately 162 kcal/day, a savings sufficient to meet the added daily caloric demands of juvenile growth [154], and helps explain where the extra energy comes from to support rapid growth in a food and immune challenged environment. If Savanna Pumé girls did not receive food from these older females, they would have to increase their work effort and their caloric expenditure on physical activity. This is consistent with other studies showing that reduced energy expenditure has positive effects on maturation pace [121,155,156] and growth [157,158].

In sum, physical activity is an important mediating factor in total energy availability [102,111,122,159], which is a key constraint on female life history in all but the most well fed populations [134,160,161]. Both Savanna Pumé examples illustrate that without cooperation females would have to increase their work effort to meet metabolic requirements. Because foraging effort and food are shared, the energy that females would otherwise expend in foraging activities is conserved to reallocate to fat deposition, rapid maturation and early reproduction.

4. Conclusion

Much of our success as a species derives from our ability to access a diverse, high quality diet. While meat often is the focus of discussions about human dietary uniqueness [48,49,162–164], tubers and other calorically dense foods also feature in evolutionary arguments about dietary shifts, expansion into novel environments, food sharing and the division of labor [165–168]. No doubt high-quality food has been a critical driving force in human evolution. However, how we access that food is also key in setting the human diet apart. Across societies and since deep in the ancestral past, the human diet depends on complex and technologically assisted food access and processing. Food, raw materials, fuel, water and other resources are often located long distances apart and transported back to central locations. This is the case for hunter-gatherers, but also for agricIturalists and pastoralists, and in today's global food economy. This constellation of traits presents a time budget problem for any one individual to independently meet his or her daily caloric needs. Humans solve this challenge through food sharing, labor exchange and a division of labor. Dependence on cooperation to meet caloric needs is a well-studied and derived human trait. The importance of cooperation to human physiology and life history is emphasized here in association with mediating expenditure on physical activity as a mechanism through which energy available for growth and reproduction is modulated. This may help to explain human derived sexual dimorphism in body composition, and flexibility in maturational pace in response to environmental variation.

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