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Effects of Evolution, Ecology, and Economy on Human Diet: Insights from Hunter-Gatherers and Other Small-Scale Societies

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Abstract

We review the evolutionary origins of the human diet and the effects of ecology economy on the dietary proportion of plants and animals. Humans eat more meat than other apes, a consequence of hunting and gathering, which arose ~2.5 Mya with the genus *Homo*. Paleolithic diets likely included a balance of plant and animal foods and would have been remarkably variable across time and space. A plant/animal food balance of 50/50% prevails among contemporary warm-climate hunter-gatherers, but these proportions vary widely. Societies in cold climates, and those that depend more on fishing or pastoralism, tend to eat more meat. Warm-climate foragers, and groups that engage in some farming, tend to eat more plants. We present a case study of the wild food diet of the Hadza, a community of hunter-gatherers in northern Tanzania, whose diet is high in fiber, adequate in protein, and remarkably variable over monthly timescales.

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1. INTRODUCTION

The importance of diet and lifestyle for maintaining good health has been recognized for millennia, and probably longer. However, notions of healthy eating have changed considerably over time and continue to shift and churn today. The past several decades of scientific inquiry have produced ample evidence that diet, physical activity, and other lifestyle factors carry profound impacts on the length and quality of our lives. The consensus that diet and lifestyle affect health breaks down, however, in the interpretation of these data and prescriptive strategies for healthy living.

One approach that has been growing in popularity is to look to small-scale populations—hunter-gatherers, horticulturalists, and subsistence farming communities—for insights (16, 24, 64). These populations are remarkably resistant to the maladies (e.g., heart disease, diabetes, cancer, age-related sarcopenia, and frailty) most prevalent among industrialized populations. Further, small-scale societies typically maintain aspects of lifestyle and diet (e.g., high levels of daily physical activity, reliance on minimally processed whole foods, high levels of fiber and micronutrients) that characterized our evolutionary past. The alignment of their current diet and lifestyle with those that shaped our species is thought to protect these populations against so-called diseases of civilization (16, 24, 64).

This evolutionary approach provides a powerful lens on health and nutrition but raises foundational questions. If the diets and lifestyles of our hunter-gatherer past are indeed protective against disease, what were those diets and lifestyles like? What are the salient aspects that we might aim to integrate into our modern, industrialized lives? Rather than a growing consensus, recent work in this area has led to increasingly discordant reconstructions of our past. These disagreements are particularly stark when it comes to past diets: The Paleo movement has become synonymous with a meat-heavy, low-carbohydrate diet (7, 8, 16, 94), while others argue just as strenuously that past diets were largely plant based (53, 54). These arguments, in turn, have come to color prescriptions for our diet today.

In this review, we examine the available dietary evidence for living and archeological populations of hunter-gatherers and other small-scale societies (e.g., horticulturalists, subsistence

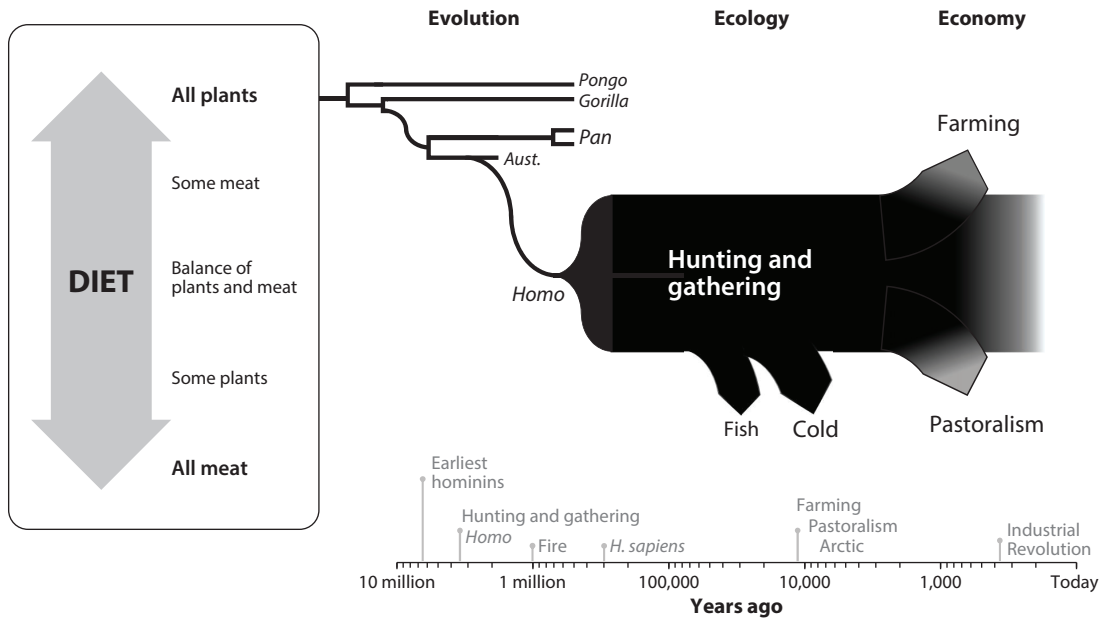


Figure 1

Evolution-ecology-economy model of the human diet. Primate diets fall along a spectrum from all plants (e.g., colobus monkeys) to all animals (e.g., tarsiers). Most apes, including orangutans (*Pongo*) and gorillas (*Gorilla*), are nearly exclusively plant eaters. Humans' closest ape relatives, chimpanzees and bonobos (*Pan*), occasionally hunt monkeys, small herbivores, and other game. Early hominins, such as species in the genus *Australopithecus* (*Aust.*), may have been opportunistic small-game hunters as well. Hunting and gathering, which entails a major change in the mix of plant and animal foods, emerged roughly 2.5 Mya with the origins of the genus *Homo*. Hunter-gatherer populations show a broad range of diets, including everything from heavily plant based to heavily animal based. Local ecology—the foods available—affects diet. Populations with access to fishing or that inhabit cold climates tend to eat more meat. Economy affects diet as well. With subsistence farming, the diet is typically heavily based on a small number of carbohydrate-rich staple crops (e.g., rice, corn, plantains). With pastoralism, the diet becomes more heavily based on meat and other animal products (see **Figure 4**). The timeline at the bottom presents approximate ages for some major evolutionary events and dietary changes in the hominin lineage.

farmers). We use the Hadza community of contemporary hunter-gatherers as a case study in diet for warm-climate foragers, using both published and unpublished data from more than a decade of fieldwork with this population. We develop an evolution-ecology-economy framework (**Figure 1**) for understanding both the trends and the variability in human diet. We discuss how evolutionary history, climate, and local ecology affect hunter-gatherer diets and, in turn, how the adoption of farming and herding changes these diets. Finally, we discuss the proscriptions for modern, industrialized populations that follow from current best evidence of ancestral hunter-gatherer diets.

2. EVOLUTION OF HUNTER-GATHERER DIETS

2.1. Diets of Living Hominoids

Humans are members of the hominoid family of primates, which includes the lesser apes (gibbons and siamangs) as well as the great apes: orangutans (*Pongo* spp.), gorillas (*Gorilla* spp.), chimpanzees (*Pan troglodytes*), and bonobos (*Pan paniscus*) (15). The living apes provide a useful model for reconstructing dietary ecology for early hominins (the human lineage), which diverged from the *Pan* lineage in the late Miocene ca. 7 Mya (15) (**Figure 1**). Long-term field studies of living great apes

reveal a heavily plant-based diet, with fruit and leaves accounting for ~90% of dietary energy intake. Leaves, stems, and other structural parts of plants account for the majority of dietary energy for gorillas, ranging from ~50–60% in Western lowland populations to more than 80% in mountain gorillas (23, 72). For chimpanzees, bonobos, and orangutans, fruits account for ~60–70% of the diet, but leaves remain an important source of energy, providing ~20% of caloric intake (35, 93, 96). For all apes, diets vary seasonally and regionally in response to changes in food (especially fruit) availability (72, 93, 97).

All great ape species are known to consume insects in the wild, but only chimpanzees and bonobos regularly hunt and consume vertebrate prey. No confirmed instances of vertebrate hunting are known for gorillas, and hunting is very rare in orangutans (95). Chimpanzees at several sites are regularly observed hunting, often focusing on monkeys (28, 78, 95) or other primates (67). Bonobos also hunt, and may focus more often on small ungulates (34, 80, 95). Rates of meat consumption in wild chimpanzees vary widely across communities and time, from less than 0.01 to 0.19 kg/day, with males (particularly higher-ranking males) generally obtaining more than females (95).

2.2. Fossil and Archeological Evidence

Throughout the first 4–5 million years of hominin evolution, diet remained heavily plant based. Early hominins were broadly similar in cranial and dental morphology to living great apes, suggesting diets similarly focused on fruit and leaves. *Ardipithecus ramidus*, an ~4.4-million-year-old early hominin species recovered in Ethiopia, had molars that were similar to *Pan* in overall size and enamel thickness (81). However, the incisors of *Ar. ramidus* were somewhat smaller than those of chimpanzees and bonobos, perhaps indicating less reliance on ripe fruit and a somewhat broader, though still plant-based, diet (81).

As with earlier hominins and living apes, the diet of *Australopithecus*, which predominates in the hominin fossil record between 4 and 2 Mya, appears to have been plant based (15). However, the molars of *Australopithecus* are enlarged relative to other hominins, and their enamel much thicker, differences that suggest dietary adaptations to a harder or coarser diet (85, 86). Some have argued that these dental changes reflect the exploitation of roots, tubers, and other underground storage organs (USOs) of plants (43). Species in the genus *Paranthropus* (initially assigned to *Australopithecus*), thought to be an extinct side branch in the hominin lineage, show an extreme degree of dental enlargement, with exceptionally thick enamel, molars four times larger than those of modern humans, and enlarged cranial attachments for the masseter and temporalis muscles (100).

Given their close evolutionary relationship to *Pan* and shared craniodental morphology, it is likely that early hominins and *Australopithecus* also ate insects and occasionally hunted small vertebrates. Beginning ~2.5 Mya, evidence of cut-marked bones associated with late *Australopithecus* and early *Homo* fossils suggests a growing reliance on hunting (and perhaps scavenging). Stone tools become prominent at archeological sites of this time as well [although the earliest stone tools may be considerably older (29)], a development that indicates a behavioral shift away from the heavily plant-focused foraging strategies of earlier hominins and the origins of a hunting and gathering ecology.

Hunting and gathering marks a pivotal change in hominin evolution; it is the defining ecological and dietary strategy of the genus *Homo*. Over the past 2.5 million years of evolution in the genus *Homo*, tool complexity and brain size increase in parallel with increased sophistication in hunting and gathering. Cut marked bones become more common and include larger game. By ~600,000 years ago if not before, Paleolithic *Homo* populations were regularly hunting large ungulates, including horses and elephants (8, 84, 88).

The control of fire and its use for cooking mark another critical dietary change. The earliest evidence for controlled fire is debated, but as early as 1 Mya (10), and certainly by ~450,000 years ago (71), Paleolithic populations were regularly using fire to cook their food. The reliance on cooking had profound changes on hominin diet and physiology (14, 106). Cooking makes many foods easier to digest, including the conversion of resistant starches to soluble forms, which increases the energy gained per gram eaten (14, 106). For example, the metabolizable digestion of potatoes doubles with cooking (14). Human physiology has evolved a dependence on cooked food. There are no credible accounts of human societies, past or present, that do not cook their food (106). Even today, with access to energy-rich, low-fiber domesticates and processed oils and sugars, there is some evidence that raw foodists, who choose to subsist only on uncooked foods, tend to be underweight (body mass index <18.5) and report reduced libido, menstrual irregularities, and fatigue (42).

2.3. Anatomical Adaptations to Diet

The dietary reliance on meat and cooked foods had substantial effects on hominin digestive anatomy and physiology. Dietary energy density (kilocalories per gram) increased considerably, reducing the volume of food eaten each day by ~60% relative to other primates (76). Compared to *Australopithecus*, molar size and enamel thickness are reduced in *Homo* and the crests of the molars in *Homo* are somewhat sharper, changes that reflect a transition to a less mechanically demanding diet with meat and (later) cooked foods (85, 86). Humans today have a shorter large intestine than other apes, most likely reflecting a reduced reliance on fiber fermentation and digestion (1, 52) (**Figure 2**). However, it is important to note that total gastrointestinal tract length and large intestine length in humans fall within the range of other primates, and the ratio of large intestine length to total gastrointestinal length in humans is consistent with a high-energy-density diet (**Figure 2**). Humans also have a low stomach pH of 1.5, typically seen in scavengers (6) (**Figure 2**), consistent with reliance on scavenged or cached carcasses that have developed a substantial pathogen load.

Some have interpreted these morphological changes and the archeological evidence for large-game hunting as evidence that Paleolithic hominins were hypercarnivores, obtaining more than 70% of their daily calories from animals (7, 8). However, the sparse and uneven nature of the archeological record makes discerning the percentage contribution of animal and plant foods in the Paleolithic diet notoriously challenging. Butchered bones and stone hunting tools are more likely to be preserved in the fossil and archeological records than are the remains of plant foods or wooden tools used to harvest them. Several lines of evidence suggest a more even contribution of animal and plant foods to the Paleolithic diet, with considerable variation both geographically and temporally.

First, many reconstructions of Paleolithic diets overlook the contribution of honey. The consumption of honey is widespread among tropical- and temperate-climate hunter-gatherer populations in the ethnographic record (17, 19, 50, 51) and accounts for 10–20% of caloric intake in some populations. Honey exploitation is not readily preserved in the archeological or fossil record, but chimpanzees, bonobos, and orangutans regularly forage for honey (58, 65, 89), and this fact suggests it is a common dietary element for the great apes, including humans and fossil hominins. Hominin exploitation of honey was sufficiently intense to provide a dietary niche for the honeyguide bird (*Indicator indicator*), which is widespread across the African continent and has an evolved symbiotic relationship with human honey hunters (104). Genetic analyses suggest honeyguides evolved approximately 3 Mya (77), in the late Pliocene, contemporaneous with the earliest fossil evidence for the genus *Homo* (91).

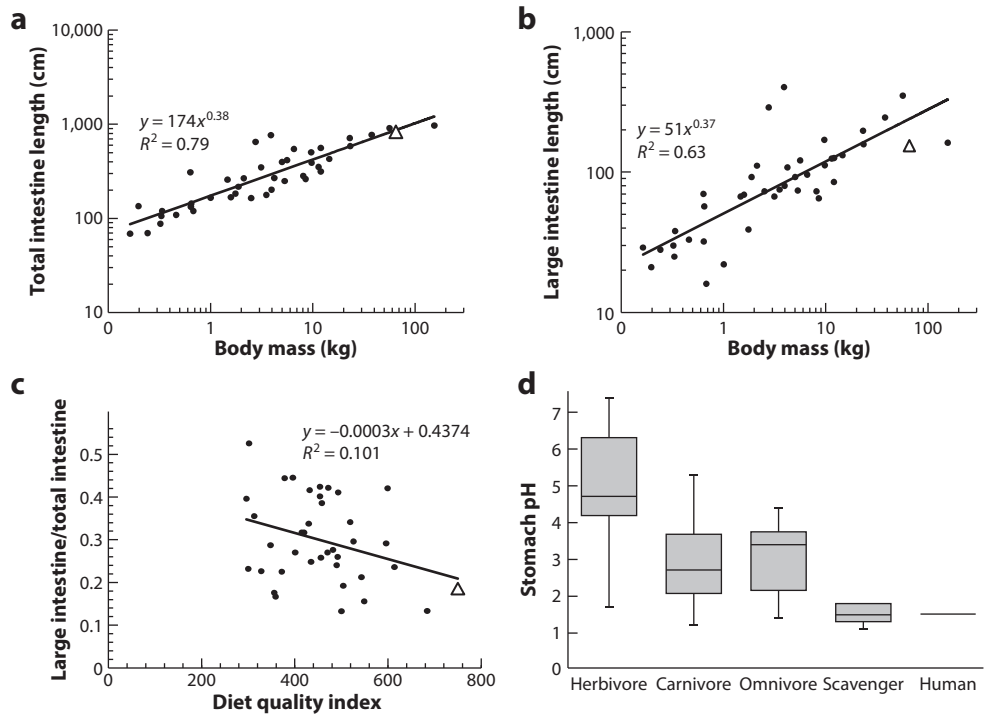


Figure 2

(a) Human (open triangle) total intestinal length fits the regression for all primates (closed circles). (b) The large intestine in humans is somewhat shorter than expected for body size. (c) The proportion of the intestines in humans is consistent with our relatively high-energy, low-fiber diet compared to other primates. (d) Human stomach acid has a low pH (1.5), similar to that observed in bird and mammal species that scavenge meat. Data for panels a–c from McGrosky et al. (52), with human diet quality in panel c modeled at 750. Data in panel d from Beasley et al. (6) with diets condensed to four categories.

Second, recent methodological advances have uncovered the widespread use of plant foods among Paleolithic populations. Melamed and colleagues (53) have reported more than 50 species of dietary plants, including USOs, fruits, vegetables, and nuts, at the 780,000-year-old site of Gesher Benot Ya'aqov, Israel. Henry and colleagues (31, 32, 66), examining microfossils trapped in dental calculus, have reported widespread consumption of plants, including wild grains, in Neanderthal (*Homo neanderthalensis*) and Paleolithic (*Homo sapiens*) populations. Grinding tools for plant processing, including the production of flour, have been recovered at 30,000-year-old sites in Europe (70).

Finally, the ethnographic records of foraging and dietary practices in recent hunter-gatherer groups reveal a diverse mix of plant and animal foods (56, 64). We review and synthesize these ethnographic data below, paying particular attention to recent, detailed analyses of diet, foraging activity, and cardiometabolic health in living small-scale societies.

3. HUNTER-GATHERER ECOLOGY AND DIET

It is a general feature of terrestrial environments in the temperate and tropical zones that plant biomass far outweighs animal biomass by an order of magnitude (3). Further, animals are usually mobile and actively avoid predators, whereas plants are sessile. Consequently, among mammals,

terrestrial carnivores travel approximately four times farther each day to forage compared to similarly sized herbivores (27). Carnivory therefore entails both ecological risk and dietary reward: The hunter incurs large time and energy costs to forage and might still fail but can acquire energy- and protein-rich food if successful. Herbivory, in contrast, requires less foraging and yields a dependable source of comparatively energy-poor foods.

These same dynamics are central to hunting and gathering, the defining foraging strategy of the genus *Homo*. Some members of the community (usually men) hunt animals, while others (usually women) gather plant foods. Food sharing occurs intensively within family units and frequently between them; this food sharing significantly decreases the risks of food shortfalls when hunters fail to make a kill. Gatherers have regular access to animal foods. This complementarity, which provides the nutritional benefits of hunting while mitigating its ecological risks, helped make hunting and gathering incredibly successful throughout the Paleolithic, with hominin species expanding throughout Africa, Eurasia, and eventually the entire planet (15).

Our genus and our species are of African origin, and, over the past 2.5 million years, the large majority of hominins lived in the tropical and milder temperate regions of Africa and Eurasia (15). In warm climates, the biomass of potential plant foods is much higher than that of animal foods. In the Hadza case, tubers are at least 1,000 times more abundant in terms of kilograms per hectare than ungulate mammalian prey (101). The observation that meat contributes substantially to the diets of tropical and temperate foragers (see below) is a strong indicator of a revealed preference for meat. Stated preferences for meat consumption have also been recorded among the Hadza and other hunter-gatherers, consistent with this ecological view (12, 41, 50, 59). Therefore, while foragers make tactical choices that are tied closely to their local environment, they do so guided by a strong preference for animal foods over plant-based sources of calories.

The different ecological demands of hunting and gathering are evident in gender differences in daily activity. Men in hunting and gathering communities walk an average of 14 km per day, ~50% farther than women (48). Our work with the Hadza community, a population of hunter-gatherers in northern Tanzania, shows that men explore three times as much landscape per day as women and nearly always travel alone for the sake of stealth. Women exploit superabundant plant resources, stay closer to home, and forage in large social groups. This basic outline of gendered economic roles, including a male hunting and female gathering specialization, is found in nearly all traditional populations. However, this general trend obscures a great deal of variation among populations in the degree to which each gender specializes and the relative contributions of men's and women's foraging and, hence, the relative proportions of meat and plant foods in the diet (41, 56, 64).

3.1. Meat in Hunter-Gatherer Diets

The balance of hunted and gathered foods varies considerably among hunter-gatherer populations (41, 56, 64). Kelly (40) reported per capita meat consumption for 13 hunter-gatherer populations, ranging from 0.1 kg/day in some periods for rainforest populations (the BaMbuti community of Central Africa and the Nakak community of South America) to 1.8 kg/day for the Ache community, a rainforest population in South America. Assuming an approximate ratio of 1.25 kcal/g for wild animal foods (muscle, organs, fat depots) (**Supplemental Appendix 1**), these rates of consumption translate to roughly 125–2,500 kcal/day. Expressed as a proportion of daily energy requirement for adults (~2,500 kcal/day), meat consumption varies from ~5% to ~90% of daily intake, a remarkable degree of variation among populations.

Even these population averages mask a great deal of temporal variation within communities. Kelly (40, 41) reported wide ranges of meat consumption for four populations, the Efe

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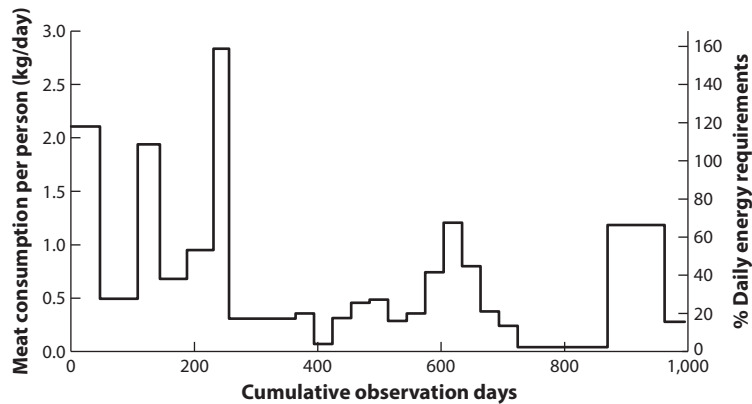


Figure 3

Per capita meat consumption for each of the periods shown in **Table 1**. The monthly values from Marlowe & Berbesque (50) are shown individually.

(0.2–0.4 kg/day), Yanomamo (0.2–0.5 kg/day), BaMbuti (0.1–1.1 kg/day), and Nakak (0.1–0.6 kg/day), all rainforest-living communities in Central and West Africa and South America. Hurtado & Hill (37) reported meat consumption as a percentage of total caloric intake varying seasonally between approximately 41% and 72% for the Hiwi community, a population living in a gallery forest and seasonal savannah landscape in Venezuela. This considerable variation reflects sampling variation as well as differences in hunting success across seasons and the effects of different hunting techniques (e.g., nets versus spears).

To examine temporal variation in meat consumption, we compiled hunting and scavenging data for the Hadza hunter-gatherer community, a savannah-living population in northern Tanzania. The Hadza live in camps throughout the Lake Eyasi region and hunt a wide variety of large and small game with bow and arrow (49). Available published data span 25 years, from 1985 to 2010, with mean values for different periods reported in several of the sources (30, 49, 50, 62, 102). Meat acquisition for each period was reported as either the kilograms of meat returned to camp (30, 62, 102) or as a percentage of daily food consumption (49, 50). Returns were converted to per capita consumption using estimated camp size (individuals/camp). Percentage-consumption data were converted to kilograms per day using a value of 1.25 kcal/g for meat and a mean adult energy requirement of 2,240 kcal/day, which is the midpoint of Hadza men’s and women’s daily energy expenditures measured with the doubly labeled water method (64).

As shown in **Table 1** and **Figure 3**, daily meat consumption varied greatly over the 25-year observation period for the Hadza community. Per capita meat consumption ranged from a low of just 0.04 kg/day (~2% of daily energy requirement) for a 146-day period in 2006–2007 to a high of 2.8 kg/day (~159% of daily energy requirement) during a 25-day period in 1989. The long-term weighted average per capita intake over more than 1,000 observation days was 0.67 kg/day, or ~38% of daily energy requirement. These estimates are imperfect; they do not account for variation among individuals nor for meat consumed out of camp [a minor but seasonally important consideration (9)], and the translation to energy values rests on poorly tested assumptions about the ratio of kilocalories per gram and the edible fraction of game. Still, the variability in daily meat consumption among the Hadza (**Figure 3**; **Table 1**) and other communities (40) underscores the dynamic and fluctuating nature of the hunter-gatherer diet. For most purposes, average values are less meaningful than the range of consumption across weeks and months (**Figures 3** and **4**). It

Table 1 Hunting and meat consumption in the Hadza hunter-gatherer community, 1985–2010

Year(s)	Season	Days	Hunters	Camp size ^a	Animals acquired			Per capita consumption		Reference
					Number of large game	Large game per hunter/month ^b	Total kg	kg/day ^c	% Energy requirement ^d	
1985	Late dry	47	10	35.8	30	1.9	3,557	2.11	118%	30
1985–1986	Wet	61	6	23.4	8	0.7	707	0.49	28%	30
1986	Early dry	36	6	23.4	5	0.7	1,640	1.95	109%	30
1986	Late dry	44	10	35.8	13	0.9	1,075	0.68	38%	30
1988	Late dry	43	10	35.8	9	0.6	1,470	0.95	53%	30
1989	Wet	25	6	23.4	6	1.2	1,666	2.85	159%	30
1995–1996	NA	108 ^e	NA	NA	NA	NA	NA	0.31 ^g	19% ^g	49
2001–2006	NA	365 ^f	NA	NA	NA	NA	NA	0.06–0.99 ^h	4–67%	50
2006–2007	Wet	146	6.8	34.7	4	0.1	213	0.04	2%	102
2005, 2006, 2009	Dry	92	14.2	36.8	42	1.0	4,025	1.19	66%	102
2009, 2010	Dry	33	9.7	34.9	3	0.3	321	0.28	16%	62

Abbreviation: NA, not available.

^aFor Wood & Marlowe (102), camp size is the mean number of residents for camps in the wet or dry season analyses. For others, camp size is estimated from the relationship between the number of hunters and camp size from Wood & Marlowe (102) (camp size = $3.1 \times \text{hunters} + 4.8$, $r^2 = 0.61$, $n = 7$ camps).

^bLarge game per hunter/month calculated as (number of large game/hunters)/(days/30).

^cPer capita kilograms per day = total kilograms/(camp size \times days).

^d% energy requirement = $(1,250 \times \text{per capita kilograms per day})/2,240$, which assumes an energy density of 1,250 kcal/kg (**Supplemental Appendix 1**) and a mean daily energy requirement of 2,240 kcal/day (see 64).

^eThese data are from Marlowe (49, table 5.4) and include data from six camps. The days of recorded food returns in each camp are taken from Marlowe's field notes by B.M.W.

^fThese data average consumption for each calendar month (365 days) compiled from data collected in 2001–2006 by Marlowe & Berbesque (50).

^gMeat consumption for men and women combined is reported as a percentage of total caloric consumption and converted to kilograms per day as per capita kilograms per day = % energy requirement $\times 2,240/1,250$, which assumes an energy density of 1,250 kcal/kg (**Supplemental Appendix 1**) and a mean daily energy requirement of 2,240 kcal/day (see 64).

^hPer capita kilograms per day consumption calculated from Marlowe & Berbesque (50, figure 3), who give meat and other food consumption as a percentage of total kilograms of food consumed. We assume that total consumption of all foods must provide 2,240 kcal/day. Energy values are as follows: meat, 1.25 kcal/g (**Supplemental Appendix 1**); tubers, 0.22 kcal/g (**Supplemental Appendix 2**); honey, 3.42 kcal/g (57); baobab, 1.34 kcal/g (99); and berries, 1.00 kcal/g (57) (**Supplemental Appendix 3**).

Supplemental Material ➤

would be a fool's errand to construct dietary guidelines hoping to match both the averages and variation observed in this hunter-gatherer diet.

3.2. Plants in Hunter-Gatherer Diets

In the latter half of the twentieth century, a contingent of anthropologists began to apply microeconomic, evolutionary, and behavioral ecology theory in studies of hunter-gatherers. This produced a shift in theoretical focus and increased rigor in the measurement of time allocation, economic practices, and diet. A watershed moment in this era arose, ironically enough, at the Man the Hunter conference, when Richard Lee and colleagues argued that plant foods constituted the

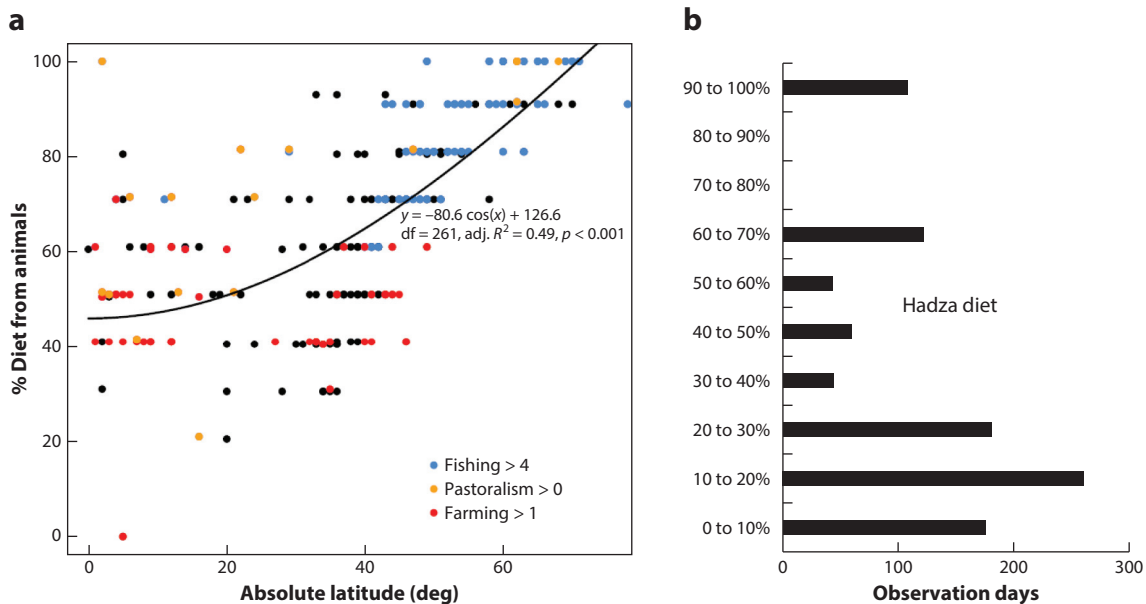


Figure 4

Variability in the contribution of animal foods to the hunter-gatherer diet (*a*) among populations and (*b*) over time within the Hadza population. Points in panel *a* represent $n = 263$ populations in Murdock's (56) *Ethnographic Atlas*, shaded by dependence scores for fishing, pastoralism, and farming. In a general linear model, the percentage of the diet from animals varied as $y = 92.4 \pm 4.4 - 49.2 \pm 5.1 \cos(\text{latitude}) + 4.0 \pm 0.4 \text{ fishing score} + 4.1 \pm 1.5 \text{ pastoralism score} - 2.8 \pm 0.6 \text{ farming score}$. All factors were significant ($p < 0.01$). Model adjusted $R^2 = 0.66$, standard error = 11.4, degrees of freedom (df) = 258, and $p < 0.0001$. The equation in the figure gives the relationship to latitude only. Bars in panel *b* depict the cumulative number of observation days in each 10% increment of caloric contribution of meat to the Hadza diet (data in **Table 1**).

majority of the diet of Ju/'hoansi (!Kung) foragers (46). In the subsequent decades, a major re-thinking of hunter-gatherer subsistence has transpired, and models that ignore the key role of plant foods in human evolution are no longer tenable.

Plant foods are essential to the survival of all warm-climate forager populations. Unfortunately, the sample of populations with detailed dietary data for plant foods is quite limited. This sample includes studies of the Ju/'hoansi of the northern Kalahari desert, the /Gui and //Gana of the central Kalahari, and the Hadza of northern Tanzania. The central Kalahari foragers are estimated to acquire ~80% of their diet from plant foods and the northern Kalahari groups 60–70% (45, 60, 75, 82, 83). The Hadza live in a more productive environment than either of the Kalahari groups, and at times they have been observed acquiring much more meat (**Table 1**). But during other observation periods, especially during the wet season, the Hadza diet is heavily plant based. Early ethnographic accounts of Australian Aboriginal populations similarly suggest that the majority of the diet came from plants (98).

As with meat, the contribution of plant foods to the diets of hunter-gatherers is variable across populations (**Figure 4**) and over time. For example, in the Hadza population, the contribution of tubers ranged from an estimated 1% to 18%, berries from 3% to 72%, and baobab from 5% to 20% of daily energy intake across months in the analysis by Marlowe & Berbesque (50) (**Figure 5**; **Table 2**). Cumulatively, the contribution of plant foods ranged from 20% to 80% of estimated caloric intake (50) (**Figure 5**).

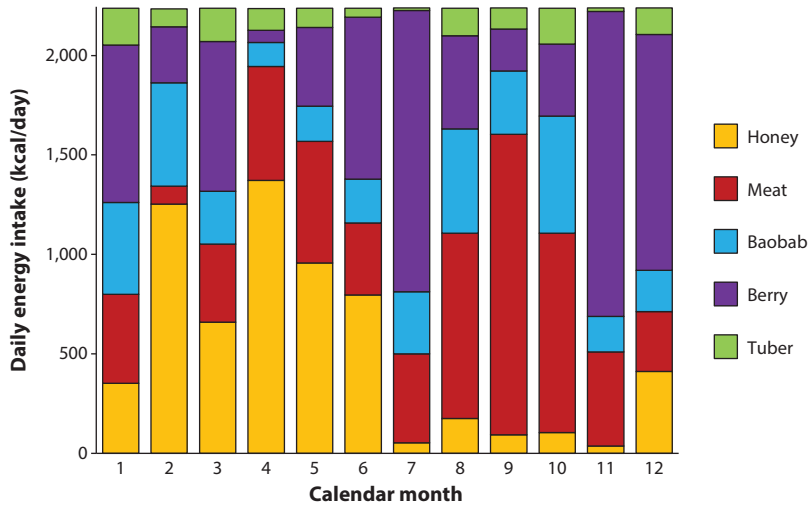


Figure 5

Estimated daily energy contribution of different food types to the Hadza diet by calendar month. Measurements of kilograms per day for each food from Marlowe & Berbesque (50) (see **Table 2**) were converted to energy per day assuming energy intake sums to 2,240 kcal/day and using the energy values for each food type as shown in **Table 1**.

Table 2 Estimated mean daily per capita intake across calendar months for Hadza adults

Month	Food type (g/day) ^a					Nutrient (g/day) ^b			
	Honey	Meat	Baobab	Berry	Tuber	Fiber	Protein	Fat	Carbohydrate
1	103	358	345	788	830	101	124	49	326
2	367	72	390	280	405	74	64	43	400
3	193	314	198	750	750	78	105	41	363
4	402	458	90	60	492	24	103	49	347
5	281	488	134	393	432	45	119	50	330
6	233	289	166	811	200	66	98	39	375
7	16	357	233	1,409	57	102	129	41	340
8	51	745	392	466	620	88	183	72	216
9	27	1,209	237	210	475	52	243	89	118
10	31	801	440	361	813	93	194	77	194
11	11	378	133	1,528	80	94	129	36	350
12	120	241	155	1,181	596	90	101	32	387

^aPer capita grams per day consumption for adults estimated from Marlowe & Berbesque (50, figure 3), who give monthly averages for food types as a percentage of total kilograms of food consumed. We assume that total consumption of all foods must provide 2,240 kcal/day. Energy values for foods were taken from the literature: meat, 1.25 kcal/g (16); tubers, 0.22 kcal/g (**Supplemental Appendix 2**); honey, 3.41 kcal/g (57); baobab, 1.34 kcal/g (99); and berries, 1.00 kcal/g (57) (**Supplemental Appendix 3**).

^bNutrient intake calculated from wet-weight values (grams per 100 g of wet weight) for each food type. Fiber: honey, 0; meat, 0; baobab, 13.7 (57); berry, 4.9 (57); and tuber, 1.87 (**Supplemental Appendix 2**; assuming 10% of quid is ingested). Protein: honey, 2.4 (57); meat, 17.6 (**Supplemental Appendix 1**); baobab, 7.7 (99); berry, 3.3 (57) (**Supplemental Appendix 3**); and tuber, 0.4 (**Supplemental Appendix 2**). Fat: honey, 3.8 (57); meat, 6.0 (**Supplemental Appendix 1**); baobab, 5.9 (99); berry, 0.3 (57); and tuber, 0.1 (**Supplemental Appendix 2**). Carbohydrate: honey, 74.4 (57); meat, 0.1 (**Supplemental Appendix 1**); baobab, 12.3 (99); berry, 21.1 (57) (**Supplemental Appendix 3**); and tuber, 4.9 (**Supplemental Appendix 2**).

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While the contribution of plants to daily energy intake in hunter-gatherers can converge, in some cases, on the high degree of dependence seen in chimpanzees and other nonhuman primates, there are notable differences in the types of plant foods eaten. Humans eat far fewer leaves and stems (39, 43, 50). For example, leafy greens play a very minor role in the diet of the Hadza and are apparently not a major food for Kalahari foragers. In the wet season sample of Wood & Marlowe (102) listed in **Table 1**, just 0.8% of the total weight of foods brought to camp were leafy greens, and in the dry season, only 0.4%. Females acquired 98.8% of these greens. Lee (45) reported that the Ju/'hoansi consume six species of leafy greens but did not consider any of them a major component of the diet. These data are consistent with observations in South American and Australian foragers. Hurtado & Hill (37) did not list any leafy vegetables among the diet of the Hiwi population in Venezuela. Hill and colleagues (33) reported food acquisition for the Ache population in Paraguay, a rainforest-living community that was settled in a Catholic mission at the time of study but regularly engaged in multiday forest treks to hunt and gather wild foods. On those treks, Hill and colleagues (33) recorded more than 90 different foods eaten, including more than 30 types of plant food; none were leafy vegetables. White (98), in a thorough review of dietary data for Australian hunter-gatherers, noted the variability in plant and animal contributions to the diet within and between populations and reported that leaves and stems account for only 32 of 994 known plant foods across 10 Aboriginal populations.

Hunter-gatherer diets are also notable for the proportion of processed plant foods, such as nuts and seeds, which provide considerable fat and protein in addition to carbohydrates. Australian Aborigine populations consume a wide variety of seeds that they grind into flour to bake and consume (98). In east and south Africa, three important tree species, baobab (*Adonsonia digitata*), marula (*Sclerocarya birrea*), and mongongo (*Schinziophyton rautanenii*), produce an edible fruit rich in carbohydrates that also contains an interior nut or seeds rich in fat and protein. Each of these plant species is eagerly targeted by human foragers. Foragers in the Kalahari eat all three of these species, and the mongongo is a particularly important food in northern Kalahari groups (45). Baobab are very abundant in the Hadza region, and this fruit makes up a large fraction of the Hadza diet (**Figure 5; Table 2**). The Hadza state a preference for eating baobab relative to tubers (50), which are superabundant but provide little protein or fat (74). Marula is not widely distributed across Hadza land, but it is eagerly consumed when encountered. Other nonhuman primates also eat these tree fruits, but they swallow whole the interior nuts or seeds and later defecate them undigested. Marula nuts and baobab seeds accumulate in large piles at olive baboon sleeping sites in the Hadza region. The Hadza collect huge amounts of these and process them in a second harvest, pounding the hard shells to break them open and extracting the valuable nutmeat. By processing the baobab fruit and accessing the nutmeat, the Hadza acquire three times the calories that they would if they had simply eaten the fruit. Rather than acquiring just the ~0.1 g of fat that exists in the pulp of one baobab fruit, the Hadza acquire ~5 g of fat per fruit by processing the seeds. The caloric gain from processing these foods underscores the nutritional advantages imparted by humans' cognitive and technological adaptations.

Plant USOs (roots, corms, and tubers) are a key part of the diet in hunter-gatherer populations in tropical and temperate climates and are central to their ability to survive during hard times by providing a critical buffer against caloric shortfalls of other, more preferred foods. For the hunter-gatherers who inhabited the very arid central Kalahari, tubers were also a critical source of water (45). Indeed, at ~70–90% moisture content (**Supplemental Appendix 2**), tubers can provide a considerable amount of water for any populations that consume them. Critically, there are few nonhuman competitors for these underground, protected resources. Measures of preference and food acquisition indicate that the Hadza harvest and consume tubers as a fallback food, relied upon more heavily when preferred foods are not available (50), analogous to the consumption of

leaves and stems during fruit-poor periods by nonhuman apes (97). Exploiting USOs rather than leaves as fallback foods markedly increases the energy content of the human diet. Tubers gathered by the Hadza (50), once they are peeled, yield approximately 77 kcal per 100 g of fresh weight (**Supplemental Appendix 2**), or roughly three times more energy than leaves.

Other plant species appear to be targeted in proportion to their energy density. Berries, especially those of the genus *Grewia*, are a seasonally important food to both the Hadza and Kalahari foragers. Because berries do not require any special technologies to harvest, and can be easily collected by children, these foods are likely to have been a major component of hominin diets for millions of years. Many of the berries consumed by the Hadza are rather dry when ripe and are notable for their high fiber content, quite unlike the typical Western notion of a berry.

3.3. Macronutrient Complement of Hunter-Gatherer Diets

Fluctuation in the contribution of plants, animals, honey, and other foods to the diet leads to variation in macronutrient intake. Determining macronutrient proportions is challenging due to lack of detailed measures of food intake and nutrient content. The nutrient content of wild foods has been examined in some previous studies (11, 13, 18, 57, 73, 74, 92), but these have rarely been combined with field measures of food intake. Conversely, ethnographic accounts of food acquisition or intake (33, 37–40, 50, 102, 103) are not often paired with nutritional analyses of those same foods (often, related domesticates or other species are used). We compiled data on the nutrient content of Hadza foods [meat (**Supplemental Appendix 1**), tubers (**Supplemental Appendix 2**), berries and honey (**Supplemental Appendix 3**), and baobab (99)] and combined them with field measures of food acquisition (50) to assess macronutrient intake for Hadza adults.

Estimated protein intake for Hadza adults, based on monthly dietary data from Marlowe & Berbesque (50), ranged from 64 to 243 g/day, or roughly 11–43% of total energy intake (**Table 2**); fat intake ranged from 32 to 89 g/day (13–36% of energy); carbohydrate intake ranged from 118 to 400 g/day (21–71% of energy); and fiber intake ranged from 24 to 102 g/day. Notably, recommended protein intake for Hadza men [~ 50 kg body mass (62)] would be 40 g/day (38), meaning that protein intake was more than adequate even when meat contributed less than 5% of the diet. Median estimated macronutrient contributions to total energy intake were 21% protein, 18% fat, and 61% carbohydrates for the period in their study, but the proportion of protein and fat would increase during periods of greater meat consumption (**Figure 3**; **Table 1**). Thus, long-term average macronutrient contributions are consistent with established dietary guidelines in industrialized populations (38), but the high degree of variability belies any notion of consistent daily nutrient intake. The wide range of variation evident across populations (**Figure 4**) and over time (37, 40, 41, 98) indicates that such dietary variation is the norm for hunter-gatherers.

Temporal changes in diet do not appear to have affected the remarkable cardiometabolic health maintained by the Hadza community. The earliest studies of blood pressure and serum profiles among the Hadza, half a century ago, indicated low cholesterol levels and a near absence of hypertension, even among the elderly (4). Our recent measurements are entirely consistent with those early findings (64, 68, 69). The mix of foods in the Hadza diet, together with their high volume of daily physical activity (68), appears to provide a nutritional framework that supports excellent cardiometabolic health.

4. CULTURE AND CLIMATE: THE DIETARY EFFECTS OF SUBSISTENCE ECONOMY

4.1. Relative Contribution of Animals and Plants

Many factors, including the nature of the local ecosystem, differences in cultural practices, and seasonal or yearly changes in food availability, affect the makeup of the hunter-gatherer diet. Foragers

make tactical choices about foraging that are tied closely to the opportunities afforded by their local environment, guided by a strong preference for meat. Perhaps the single biggest factor is climate. In regions that are colder or have lower primary plant productivity (a function of temperature and rainfall), populations consume a lower proportion of plant foods and a correspondingly greater proportion of meat (including fish) (40, 41, 48, 64).

Cultural practices also affect the diet. Populations with technologies to exploit locally abundant resources, such as fish or other aquatic game, can exhibit a greater dependence on those resources. Similarly, populations that augment their hunting and gathering with pastoralism (herding livestock) may show an increase in animal consumption, while those that engage in horticulture or subsistence farming may show a greater proportion of plant foods in the diet.

To examine the effects of climate and culture, we analyzed the dietary records of 263 small-scale societies from Murdock's (56) *Ethnographic Atlas*. The *Ethnographic Atlas* scores each group's dietary dependence on a variety of subsistence activities; a score of 0 indicates 0–5% dependence, 1 indicates 6–15% dependence, 2 indicates 16–25% dependence, and so on. Of the 263 populations in our analysis, most ($n = 181$) were exclusively hunter-gatherers, with scores of 0 for both farming and pastoralism. Seventy-four populations engaged in some farming, with scores of 1 ($n = 16$), 2 ($n = 16$), 3 ($n = 10$), or 4 ($n = 32$). Seventeen populations engaged in some pastoralism, with scores of 1 ($n = 13$), 3 ($n = 2$), or 4 ($n = 2$). Nine populations engaged in some degree of pastoralism and farming. We calculated the percentage of the diet for each population derived from animals (based on the group's hunting, fishing, and pastoralism scores) and the percentage of the diet derived from plants (based on the gathering and farming scores). The percentages of animal and plant foods for each group summed to 100%.

We then analyzed the percentage of animal foods in the diet using a general linear model with the cosine of latitude, fishing score, farming score, and pastoralism score as predictor variables. Note that if diet was entirely dependent upon climate, then the cosine of latitude (which accounts for the incidence of sunlight, and is our proximate measure of climate) would predict the percentage of meat in the diet but cultural factors would not. Groups that farmed more would gather less; groups that engaged in pastoralism would fish and hunt less. Instead, we found that all three cultural indices as well as climate (indexed as cosine of latitude) were significant predictors of diet composition. Populations engaged in farming consumed less meat, while populations that engaged in pastoralism or were more dependent on fishing ate more meat (**Figure 4**).

The impacts of culture and climate underscore the need for precision when discussing the diets of contemporary small-scale societies as models of the past. Some researchers have used the diets of contemporary pastoralists (e.g., the Maasai population of East Africa) or indigenous arctic communities as exemplars for Paleolithic diets, suggesting that the ancestral human diet was high in fat and other animal foods and low in carbohydrates and plant foods (94). In fact, both arctic living and pastoralism are relatively recent phenomena, less than ~10,000 years old (2, 26, 90), and are not representative of Paleolithic hunter-gatherer cultures. Other researchers [including us (64)] have included contemporary small-scale societies engaged in some degree of horticulture or farming in discussions of hunter-gatherer diets and health. Our analyses here indicate that even a limited dependence on farming can inflate the percentage of plant foods in the diet of small-scale societies.

4.2. Effects of Domestication on Foods

Farming and pastoralism affect more than just the dependence on different food types. These cultural practices also change the nutritional composition of domesticated plants and animals. Farmed plant foods have been artificially selected to increase energy content, decrease fiber

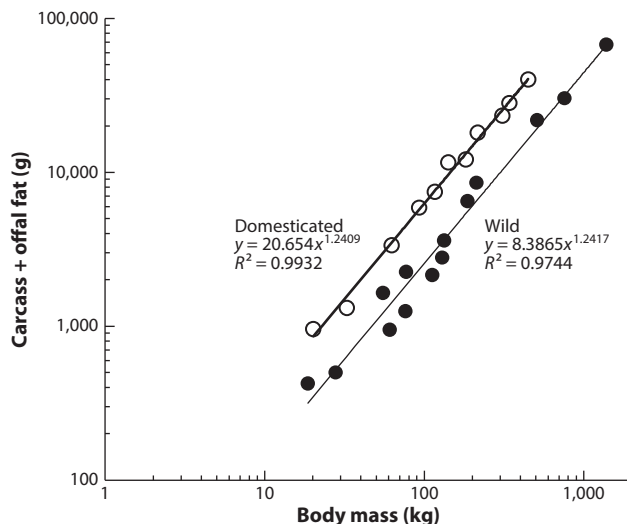


Figure 6

Combined carcass and offal fat for farm-raised pigs (44) and cattle (21) (*open symbols*) compared to values for $n = 14$ wild game species (13). For pigs and cattle, each symbol represents the mean body mass (total body weight or live weight) and fat mass (carcass fat plus internal fat) for one age class. For wild species, each symbol represents the mean body values for one species.

content, or both (11). Domesticated rice has roughly the same energy content (~ 350 kcal per 100 g raw) as wild rice but only one-tenth the fiber content (107), and domesticated varieties produce more grains per plant (47). Modern maize produces more, and much larger, kernels than the ancestral teosinte (22), and corn flour made from domesticated varieties has somewhat higher fat and carbohydrate content (5). Domesticated USOs (yams, potatoes, cassava, and taro) contain roughly 50% more energy and one-tenth the fiber of wild species eaten by the Hadza community (74). In at least some cases, domestication has also reduced the nutritional content of staple foods. Wild rice holds more protein, riboflavin, vitamin E, and thiamin than does domestic white rice, for example (107). Brand-Miller & Holt (11) analyzed nutritional values for more than 800 wild plant foods eaten by Australian Aboriginal hunter-gatherer populations, including fruit, USOs, and nuts, and found the wild foods consistently much higher in fiber, protein, and micronutrients than their domesticated counterparts.

Similar effects are apparent in domesticated animals. Measurements of carcass and offal fat (depots that are visible and separable from other structures during butchery) in wild prey animals (13) and domesticated pigs (44) and cattle (21) raised using modern methods show that these fat stores are $\sim 50\%$ smaller, on average, in wild game (**Figure 6**). Moreover, the fat content of lean muscle in wild game mammals is $\sim 50\%$ of that of farm-raised beef, lamb, and pork (20). These differences have a considerable effect on the energy content of an entire animal. Assuming that all major organs, muscle, bone marrow, and fat depots (carcass and offal) of an animal are consumed, the greater muscle fat content and larger fat depots of a domesticated 100-kg mammal result in nearly twice as much fat consumed and a substantially greater energy content of the edible fraction (1.79 kcal/g) than is estimated for a 100-kg wild game mammal (1.34 kcal/g) (**Supplemental Appendix 1**). The fatty acid profiles of farm-raised animals also differ from wild game, with domesticates having a ratio of saturated to polyunsaturated fats of ~ 2 or greater, while this ratio was generally ~ 1 or less for wild species (20). The extent to which these differences reflect

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genetic changes wrought by artificial selection versus the fat-promoting nature of modern farming practices remains unclear. Fine & Davidson (25) reported fatty acid profiles in laboratory-raised pigs that are similar to those of wild warthog and different from farm-raised pigs, suggesting that farming practices can play an important role in the composition of animal foods.

Whatever the relative contributions of genetic changes and modern farming practices to the nutritional content of domesticated foods, the substantial differences between farmed and wild foods must be considered when interpreting the diets of contemporary hunter-gatherers and other small-scale societies. Plant-based or meat-based diets (including Paleo diets) popular in industrialized populations today are unlikely to converge nutritionally on the diets of ancestral hunter-gatherers, because the foods available in grocery stores and farmers markets are qualitatively different from wild foods. Similarly, the foods and diets of pastoralists, horticulturalists, and other small-scale societies may differ substantially in their nutritional profile from the diets of populations that hunt and gather exclusively.

Given the use of hunter-gatherer diets in discussions of obesity and cardiometabolic health in industrialized populations (16, 24, 64), it is noteworthy that domesticated animal and plant foods are lower in fiber and protein, nutrients that promote satiety and curb consumption (36), on a per gram or per calorie basis than wild foods (see above). Regulation of caloric consumption takes on particular importance in light of metabolic evidence from hunter-gatherers; this evidence suggests that unhealthy weight gain and obesity among industrialized populations are primarily driven by recent changes in energy intake, not expenditure. Despite their high levels of physical activity, the Hadza and other small-scale societies maintain total daily energy expenditures similar to more sedentary, industrialized populations (62–64, 87). It may be the nutritional profiles of wild plants and animals and their effects on hunger and satiety, rather than the particular proportions of these foods in the diet, that so effectively protect hunter-gatherer populations against obesity.

5. UNRESOLVED ISSUES AND FUTURE DIRECTIONS

One longstanding point of debate in discussions of the ethnographic evidence from contemporary hunter-gatherers is the extent to which these populations are representative of ancestral groups (8). Critics rightly point out that hunter-gatherer populations living today and in the recent past often occupy marginal environments, having been displaced from more productive habitats by farmers, pastoralists, and (recently) industrialized populations. Extinction of megafauna and the extirpation or diminishment of other species have undoubtedly reduced the number and size of game. Given these recent changes, it is certainly possible that the contribution of animal foods to the diet of contemporary hunter-gatherers is considerably lower than in the Paleolithic.

It is probably impossible to determine conclusively what effect these changes in landscape and species diversity might have on the diets of contemporary foragers. A reduction in large game could certainly decrease the amount of meat eaten. However, hunter-gatherer populations have been responding to local shortages in large game since the Paleolithic, regularly exploiting small game when large game was less abundant (55, 79). Further, even during periods when large game was generally plentiful, it seems likely that populations would have experienced periods in which hunters were unlucky or game was scarce. And even when hunter-gatherer groups are able to meet their caloric needs with game, the available ethnographic data indicate that they still gather and eat plant foods as well.

The complex dynamics between game abundance and meat intake are evident in the Hadza community. In the days immediately following the taking of large game, women continue to forage for plant foods. While the largest game species, Cape buffalo (*Syncerus caffer*), has not been regularly seen in the eastern Hadza region since the 1980s and encroachment from neighboring

pastoralist groups has consistently grown for the past several decades, there is little evidence that the proportion of meat in the diet has changed substantially. There is an apparent marginal decline in meat consumption and large-game acquisition over the 25-year period from 1985 to 2010, but the variability among observation periods makes this difficult to assess, and meat consumption and the number of large game acquired per hunter per month reported for some periods in the early 2000s by Wood & Marlowe (102) and Marlowe & Berbesque (50) fit well with reported values in the late 1980s (30) (**Figure 3; Table 1**). Further, Woodburn (105), from his foundational work with the Hadza community in the early 1960s, estimated that plant foods accounted for ~80% of the Hadza diet by weight, which is similar to that reported half a century later by Marlowe & Berbesque (50) (mean: 68%, range: 43–84%). Thus, while large game have likely become less abundant in the Hadza region in recent decades, it is not clear whether these changes have substantially impacted daily meat consumption. These secular changes in diet do not appear to have affected health or body composition, which appear to be the same today as they were in early reports (4, 68). Perhaps long-term data from other foraging populations, or improved temporal resolution in archeological sites to reveal short-term variance in diet, will help to resolve whether recent changes in climate, landscape, and species abundance have greatly reduced meat consumption in contemporary foragers. More granular data on the relationships between diet and ecology will also be crucial for understanding, and possibly mitigating, the effects of climate change, which is expected to stress food production and reduce food security in small-scale, subsistence economies in the coming decades (61).

Additional measurements of the nutritional content of wild foods would also improve our understanding of ancestral hunter-gatherer diets. There have been several studies examining the macro- and micronutrient profiles of wild plant foods (11, 18, 57, 73, 74, 92), but the full complement of wild plants eaten by foraging groups is vast and remains grossly understudied. More work is needed on the nutritional composition of wild game species as well. Much of the available data come from African species (13, 20, 25), with less known about other regions. For both plant and animal foods, more ethnographic observation is needed on preparation techniques that may affect nutritional yields.

Another limitation is the imprecise nature of dietary intake data in small-scale societies. Food intake is a fundamentally difficult behavior to observe and measure even under controlled conditions, let alone in the field. Advances in noninvasive sensors or other technologies could augment traditional modes of data collection, leading to larger and more accurate samples of food consumption data across diverse economic contexts.

Finally, new techniques are needed for examining nutrition in archeological samples. Recent advances, such as the analysis of microfossils in dental calculus (31, 32), make us hopeful that future work will continue to improve the resolution of hominin diets in the Paleolithic. As challenging as it is to interpret, the archeological and fossil records remain the only direct evidence of the diet, culture, and biology of ancestral populations. The available evidence suggests a broad mix of animal and plant foods, but future studies may allow us to pinpoint the contributions of different foods and their variation over time.

6. SUMMARY: HUNTER-GATHERER DIETS AND EVOLUTIONARY PERSPECTIVE ON HEALTH

Those of us in industrialized populations, struggling with the epidemic of obesity and cardiometabolic disease, have long looked to ancestral populations to inform our diets. Much of this work has sought to establish relatively narrow proscriptions for the proportions of meat, plants, and other foods (7, 8, 16, 24, 94). Our review of the archeological and ethnographic data here

challenges any notion of a singular, narrowly defined ancestral diet. Contemporary hunter-gatherers consume a diverse array of diets (**Figure 4**). The contributions of meat and plants are generally balanced at around ~40–60% of each in warm-climate foragers, but these ratios vary widely across populations and over time. Consumption of particular foods, such as fish, mammals, roots, fruits, nuts, and leafy greens, varies as well. Even foods often vilified in Paleo diet recommendations, such as grains and starch-rich USOs, are commonly found in the diets of Paleolithic hominins and contemporary hunter-gatherers. The only unifying features among hunter-gatherer diets are breadth and variability.

Despite this impressive dietary diversity, small-scale societies appear to be universally protected against obesity, cardiometabolic disease, and other noncommunicable diseases common in the industrialized world. Hunter-gatherers maintain healthy body weight throughout their lives and have incredibly low rates of hypertension or other evidence of metabolic disease even at older ages (16, 24, 64). Subsistence farmers and pastoralist communities, despite their increased dependence on plants or animal foods, respectively (**Figure 4**), are similarly healthy. Clearly, humans can avoid heart disease, diabetes, and other so-called diseases of civilization by following a broad range of diets, particularly when paired with the volume of daily physical activity typical of hunter-gatherer and other small-scale societies.

Advancing our understanding and use of hunter-gatherer diets in public health and nutrition will require that we move beyond the recommendations of certain food types and focus more on the nutritional profiles of the foods themselves. Domestication has changed the nature of the foods we eat, not just the proportions. Wild foods are higher in protein, fiber, and micronutrients than their domesticated counterparts (11, 13, 20, 74, 107). Emphasizing these elements in industrialized diets could have important benefits in regulating consumption, reducing unhealthy weight gain, and meeting micronutrient requirements.

The origins of hunting and gathering in the early Pleistocene and its development over the subsequent millennia have fundamentally shaped our biology and behavior (**Figure 1**). Hunting and gathering is the defining ecological strategy of the genus *Homo*, providing the ecological flexibility that enabled Paleolithic hominins to expand across the globe. That same adaptability will be essential as we tackle the nutritional challenges facing our species today.

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