Original Research Article

Comparing measured dietary variation within and between tropical hunter-gatherer groups to the Paleo Diet

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ABSTRACT

Background: Although human diets varied considerably before the spread of agriculture, public perceptions of preagricultural diets have been strongly influenced by the Paleo Diet, which prescribes percentage calorie ranges of 19–35% protein, 22–40% carbohydrate, and 28–47% fat, and prohibits foods with added sugar, dairy, grains, most starchy tubers, and legumes. However, the empirical basis for Paleolithic nutrition remains unclear, with some of its assumptions challenged by the archaeological record and theoretical first principles.

Objectives: We assessed the variation in diets among tropical hunter-gatherers, including the effect of collection methods on implied macronutrient percentages.

Methods: We analyzed data on animal food, plant food, and honey consumption by weight and kcal from 15 high-quality published ethnographic studies representing 11 recent tropical hunter-gatherer groups. We used Bayesian analyses to perform inference and included data collection methods and environmental variables as predictors in our models.

Results: Our analyses reveal high levels of variation in animal versus plant foods consumed and in corresponding percentages of protein, fat, and carbohydrates. In addition, studies that weighed food items consumed in and out of camp and across seasons and years reported higher consumption of animal foods, which varied with annual mean temperature.

Conclusions: The ethnographic evidence from tropical foragers refutes the concept of circumscribed macronutrient ranges modeling preagricultural diets.

Keywords: hunter-gatherer, forager, Paleo Diet, Paleolithic, evolution, mismatch

Introduction

There is widespread interest among researchers and the public in the diet humans evolved to eat and whether such a diet is healthy [1]. Following a long tradition of using observations from nonindustrial cultures to make dietary recommendations for industrialized populations [2–4], contemporary interest in so-called "paleo" diets was accelerated by Eaton and Konner's landmark 1985 article on Paleolithic nutrition [5]. Using data from a small sample of contemporary hunter-gatherer diets, they concluded that humans evolved to eat an unprocessed diet that was, by calorie, ~35% protein; ~20% fat, with a low relative abundance of saturated fats; and ~45% carbohydrates derived mostly from nonstarchy fruits and vegetables with high levels of fiber and micronutrients. By integrating an evolutionary framework with epidemiological data from western populations, Eaton and Konner proposed that humans are poorly adapted to modern, processed diets high in simple carbohydrates, saturated fat and salt, and low in fiber and micronutrients such as calcium, leading to an increased prevalence of "diseases of civilization" such as atherosclerosis, type 2 diabetes, and cancers. Subsequent studies [6,7] analyzed an expanded data set of 63 foraging populations in Murdock's Ethnographic Atlas (EA), a compilation of information, often qualitative, on diet and other variables from >1,000 small societies [8,9]. According to these analyses, tropical hunter-gatherers consumed fats that were mostly

polyunsaturated with high ratios of ω-3 to ω-6 fatty acids; ate no sugar except for small quantities of honey; and ate animal foods "whenever and wherever possible," comprising 45%–65% of their energy intake. These studies fostered the popular (trademarked) Paleo Diet, originally formulated by percentages of calories as 19–35% protein, 22–40% carbohydrate, and 28–47% fat, and with most fats being poly-unsaturated from lean meats, fish, and shellfish rich in ω-3 fatty acids. The Paleo Diet also prohibits foods with added sugar, dairy products, grains, most starchy tubers, and legumes [10].

Multiple concerns suggest that the Paleo Diet represents neither the diversity nor composition of human diets before agriculture. First, a recent analysis found that the equations used by Cordain et al. [6] to calculate plant macronutrient consumption by hunter-gatherer populations underestimated the range of variation for protein, carbohydrates, and lipids [11]. Second, archaeological evidence establishes that cereals, starchy tubers, and legumes were consumed in the Paleolithic [12–16]. Third, domestication transformed human diets starting ~600 generations ago by introducing large quantities of grains and dairy, and subsequently natural selection acted on novel mutations and standing genetic variation to partially adapt many farming populations to whole grains and dairy foods. For example, at least 7 populations underwent selection for alleles promoting lactase production after weaning [17], enabling the digestion of lactose into adulthood, and numerous populations bear traces of selection for alleles that improved carbohydrate digestion [18–21], including enhanced salivary amylase production among many populations with starch-rich diets [18]. However, industrial methods began to revolutionize human food supplies again ~2 centuries ago, probably an insufficient time for substantive genomic adaptations to the associated increases in added sugar, refined grains, saturated fats, and seed-derived ("vegetable") oils, reductions in fiber, and alterations to physicochemical properties facilitating ingestion, digestion, and shelf stability. Nevertheless, such changes can reshape the human epigenome and gut microbiome, with digestive and metabolic adaptations occurring over days to months [22–25], contributing some degree of systemic plasticity [26].

A broader theoretical critique of the Paleo Diet is the problem of whether the range of diets consumed by ancestral humans, even if we could identify them, are intrinsically healthy. Natural selection only favors adaptations, including dietary preferences, that increase reproductive success. If there is a net benefit to reproductive success, selection may favor heritable behaviors that diminish long-term health, such as meat and honey consumption, and cravings for salt as well as high-calorie foods rich in fat and sugar [27]. Furthermore, not all aspects of modern diets and food processing technologies are unhealthy. Pasteurization, refrigeration, and novel agricultural foods such as domesticated whole grains, legumes, plain yogurt, and coffee can promote health, highlighting the need to test rather than assume the health consequences of foods, whether ancestral or modern.

A final issue—the focus of this study—is the challenge of defining a "normal" or "natural" human diet. There never was a single Paleolithic diet. Instead, hominin diets evolved in a generally accretional process with new foods and preparation methods added at different stages of human evolution, and with considerable variation due to geography as well as seasonal and annual environmental change. In addition, until the Agricultural Revolution, hunter-gatherers inhabited a much broader range of Old and New World habitats with vastly divergent resources—from tropical to arctic, arid to rainforest, coastal to inland, and sea level to high altitude. Although detailed studies from some surviving hunter-gatherer groups, such as the San, Hadza, Aché, and Inuit, have provided information on

preagricultural diets, they surely sample a tiny fraction of the total variation that used to exist (for example, [28]).

Moreover, recent hunter-gatherer data cannot accurately assess the variation present in Paleolithic diets and are limited by several data quality concerns, many of which have been previously highlighted [29, 30]. First, all modern hunter-gatherer populations that have been studied engaged in some trade with farmers, pastoralists, visiting researchers, and others. For example, the ~350 Hadza who currently follow a predominantly hunter-gatherer lifestyle trade regularly with local Datoga pastoralists and Iraqw farmers, often send their children to school, and obtain food from regular visits by anthropologists and tourists [31,32]. Similarly, the Aché were partially provisioned by local missionaries when their diet was studied [33], and the San have traded for centuries with Herero pastoralists [34–36]. Second, many researchers studying contemporary hunter-gatherers made qualitative observations of foods consumed in camp but did not quantify out of camp consumption or complex food-sharing patterns. Hunter-gatherers consume much food while foraging and share food widely, making it almost impossible to measure accurately what and how much is eaten, and by whom, even when researchers follow individuals as they forage or hunt [37]. In addition, the potential effects of researchers on what is hunted and foraged by the hunter-gatherers they are observing is rarely considered and difficult to quantify. Third, dietary studies of hunter-gatherers are snapshots from specific seasons and years and therefore underrate variability. Fourth, the ethnographic record is biased toward foods most readily recognized as such by researchers. For instance, few studies record insect consumption despite evidence that hunter-gatherers consume more than 1,000 species [38]. Finally, we lack information on the macronutrient and micronutrient composition of most hunter-gatherer foods, methods (if any) for processing these items, and other factors affecting bioavailability (for example, phytochemical load). In sum, most observational studies likely underestimate the diversity and quantity of foods that hunter-gatherers consumed.

The paucity of extant hunter-gatherer groups combined with their interactions with nonforaging populations requires us to evaluate critically the ethnographic record to test hypotheses about the nature of preagricultural human diets and their modern approximations. Here we evaluate published data on hunter-gatherer diets, focusing on the variation to test 2 main hypotheses. First, we hypothesize that the degree of variation among hunter-gatherer diets precludes any simple, accurate characterization of a "normal" ancestral diet in terms of macronutrient composition. Second, we hypothesize that variations in the data collection methods employed by ethnographers account for some differences in inferred diets.

To test these hypotheses, we analyzed available published studies on tropical (nontemperate, non-Arctic) hunter-gatherer diets, including those in the EA that had high-quality, quantified observational data on diet. We focus on tropical hunter-gatherers because their ecological contexts are more relevant to hypotheses about environments of evolutionary adaptiveness in sub-Saharan Africa, where *Homo sapiens* originated. It is also problematic to compare hunter-gatherer diets from tropical habitats with those from cold climates that have less plant biomass to eat and thus rely more heavily on animal foods, require larger home-ranges, and live at much lower population densities [39]. We note that focusing on just tropical hunter-gatherers reduces the variability in hunter-gatherer diets we analyze, contributing to a more stringent test of our hypothesis. For each population, we recorded the reported consumption of plant and animal foods using published nutritional data to estimate the dietary composition not just by weight

but also by calorie. In contrast to prior analyses [5–7], we treated honey as a distinct food category because it is a seasonally important, highly preferred source of calories in many foraging populations, is considered neither plant nor animal, and is often consumed without being brought back to camp and shared [40,41]. In addition, compared with other wild foods, honey is not only carbohydrate-rich but also energy dense. Finally, in addition to assessing the role of annual mean temperature (AMT), which can be expected to influence resource biomass, we investigated whether data quality was biasing dietary proportion estimates by evaluating whether each food item consumed was assessed quantitatively both in and out of camp and across multiple seasons and years.

Methods

Data collection

We collected data only from published studies that directly observed and quantified the diets of modern hunter-gatherer groups in tropical habitats. We defined hunter-gatherers as groups with a nomadic system of collecting, extracting, and hunting wild plants and animals, with no internal practice of agriculture, gardening, or animal husbandry [42]. The studies were accessed through the Anthropology Plus, Anthro Source, and Human Relations Area Files research databases and by searching through the references of published studies (Figure 1). In total, 15 studies [42–56], sampling 11 different hunter-gatherer groups, were analyzed after data were standardized into dietary proportions (see Table 1). Given that almost all hunter-gatherer populations have disappeared over the last few thousand years, leaving just a handful in often marginal environments, the studies used here (and in other studies) cannot be considered a representative sample of tropical hunter-gatherers. Instead, they are the available sample. Note also that including additional studies would serve to increase rather than decrease the variation captured.

To estimate dietary proportions from the foods or food categories reported in each study and to avoid problems inherent in estimating macronutrient value from equations [for example, see [11]], we searched for the nutritional composition of each food item in USDA databases [National Nutrient Database for Standard Reference [57], Foundation Foods [58], and Global Branded Food Products [59]], FAO/INFOODS Food Composition Database for Biodiversity [60], and published literature [61–67]. Where food quantities were reported in a study only by category (for example, "fruits" or "meats") or where no nutritional information on a given food item (or a close analog) could be found, we instead used the average values of foods within the relevant food category. Again, this approach is expected to underestimate variation, contributing to a more stringent test of our hypothesis. To convert dietary compositions by weight into dietary compositions by kcal, we employed traditional Atwater-based multipliers (that is, 4 kcal/g for protein, 4 kcal/g for carbohydrate, and 9 kcal/g for fat) and assigned a caloric value of 2 kcal/g for dietary fiber [68]. Although these conversions do not capture differences in metabolizable energy by macronutrient source [69], they enable us to compare the caloric composition of diets incorporating many sources for which detailed macronutrient information is not available without introducing incremental multiplier-based bias.

To compare dietary proportion outcomes across temperature gradients, we collected historical climate data from WorldClim v. 2.1 [70] at the finest spatial resolution available (30 s). We extracted AMT (°C) from GeoTiff files using the R packages {sp} v. 1.4–5 [71] and {raster} v. 3.4–13 [72]. For each hunter-gatherer group, we averaged AMT values

within a 15-km radius of the longitude and latitude at the centroid of each group's spatial range.

For each study, we assigned a nominal reliability category based on whether the study weighed all food articles consumed in and out of camp, and whether they recorded data from multiple seasons and years. Studies that recorded both variables were scored as 2; studies recording only one of these variables were scored as 1; those recording neither were scored as 0.

Statistical analyses

To summarize variation in dietary proportions across different food and nutrient groups, we visualized data using boxplots and calculated interquartile ranges (the difference between the 75th and 25th percentiles). To illustrate the diversity of food and nutrient proportions across the 11 hunter-gatherer groups sampled, we used stacked bar plots. Because 4 of the 11 hunter-gatherer groups (Aché, Hadza, Hiwi, and San) were sampled more than once, when analyzing data at the group level, we took the average of the observations for each variable within each group to avoid pseudo-replication issues, an approach expected to underestimate variation. Model outcomes were compositional in nature, comprising 3 or more proportions (0 to 1) of dietary categories that summed to unity. Since compositional data carry relative, rather than absolute, information that represent parts of some whole, if one component increases others must necessarily decrease. This constant-sum constraint necessitated that inference be performed using Dirichlet regression models [73], which can account for such complex dependencies in data and avoid the estimation of spurious effects. To generate intuitive quantities of interest, we fitted all models in a Bayesian inferential framework and report 95% highest posterior density intervals (HPDI; the interval within which an unobserved parameter value falls with 95% probability) of effects on the response scale (that is, compositional proportions) as well as posterior probabilities ($\mathbb{P}$) of directional hypotheses (that is, the probability that a hypothesis is supported, given the model and data). All effect size estimates were based on 100,000 postwarmup posterior iterations after 10,000 warmup iterations. For each model, we used weakly informative priors (Student's *t* distribution with 3 degrees of freedom, a mean of zero, and standard deviation of 2.5) for all location effects parameters and confirmed that convergence to a stable posterior distribution had been achieved using 4 Markov chains with an R-hat value criterion of 1.0. All analyses were performed in R v. 4.2.2 [74], using the packages {brms} v. 2.18 [75], {tidybayes} v. 3.0.2 [76], {ggplot2} v. 3.4.0 [77], and {dplyr} v. 1.0.10 [78], with Stan v. 2.27 [79] used as a computational backend for Bayesian inference. Replication code and data are made available in a Zenodo archival repository (https://doi.org/10.5281/zenodo.8121384).

Results

Figures 2 and 3 illustrate the marked variability across the 15 studies examined in dietary proportions of animal, plant, and honey consumption, and associated macronutrient proportions by weight and kcal. Although Cordain et al.'s analysis of EA-based food proportions by weight [7] reported relatively narrow interquartile ranges for hunted animal foods (no fish) of 17% (Q1: 27%, Q3: 44%) and gathered plant foods of 28% (Q1: 19%, Q3: 47%) (for example, their Figure 1), our sample of 15 studies sometimes includes more than twice this variation, with our study finding interquartile ranges by weight of 41% for animal foods (Q1: 23%, Q3: 64%), 35% for plant foods (Q1: 35%, Q3: 70%),

TABLE 1
Dietary proportion data from the 15 studies contributing to our study, shown by kcal (upper half) and by weight (lower half)

Group	Region	Study	Reliability	Collection days	Longitude	Latitude min	Latitude max	Temp mean 15km	Scale (%)	Animal	Plant	Honey	Protein	Lipid	Fiber	Sugar	Other carb
Aché	Eastern Paraguay	Hawkes et al. (1982) [50]	2	66	−55	−22	−28	21.34	kcal	69.64	27.13	3.23	50.44	20.60	5.34	17.49	6.13
Aché	Eastern Paraguay	Kaplan et al. (1985) [52]	2	81	−55	−22	−28	21.34	kcal	60.74	17.56	21.70	41.45	19.51	4.15	28.80	6.09
Anbarra	Northern Territory of Australia	Meehan (1982) [54]	2	109	134.7	−12.2	−12.2	27.08	kcal	44.65	54.92	0.43	42.86	19.94	2.21	24.22	10.76
Batek	Rainforests of peninsular Malaysia	Endicott and Endicott (2008) [49]	1	93	102.5	4.5	5	24.48	kcal	13.77	74.08	12.15	14.37	10.28	2.88	20.08	52.39
Efe	Ituri Forest; Zaire	Bailey and Peacock (1988) [45]	1	33	29	0	3	23.43	kcal	18.11	66.62	15.27	14.49	31.60	2.07	23.94	27.90
Hadza	Tanzania	Berbesque and Marlowe (2009) [47]	0		35.2	−3.8	−3.8	20.75	kcal	33.49	61.49	5.02	33.68	13.22	5.53	24.97	22.61
Hadza	Tanzania	Marlowe (2010) [42]	1		35.2	−3.8	−3.8	20.75	kcal	22.53	59.47	18.00	25.67	15.35	6.64	35.80	16.55
Hiwi	Eastern plains of Colombia; llanos of Orinoquia	Arcand (1976) [44]	0	16	−67	3	10	27.17	kcal	64.08	35.92	0.00	35.98	38.46	2.74	10.22	12.61
Hiwi	Venezuela	Hurtado and Hill (1990) [51]	1	185	−70	0	10	27.13	kcal	73.93	23.67	2.40	34.99	44.54	1.35	8.19	10.92
Jarawas	Andaman Islands in the Bay of Bengal	Barik (2015) [46]	1	19	92.7	10	14	26.41	kcal	51.37	31.91	16.72	33.98	33.79	1.16	22.24	8.84
Kunwinjku	Northern Australia	Altman (1987) [43]	2	296	133.5	−12	−13	26.81	kcal	96.41	3.15	0.44	47.61	47.08	0.27	1.55	3.49
Nukak	Columbian Amazon	Politis (2007) [55]	1	68	−72	0	5	27.17	kcal	7.68	83.37	8.95	15.05	41.09	10.39	15.83	17.65
Onge	Andaman Islands in the Bay of Bengal	Bose (1964) [48]	1	30	92.7	10	14	26.41	kcal	79.56	18.98	1.46	20.44	62.20	0.20	1.89	15.27
San	Botswana; Namibia; Angola	Lee (1979) [53]	1	28	22	−20	−25	22.19	kcal	13.39	86.61	0.00	23.09	65.20	1.72	3.67	6.32
San	Botswana	Wilmsen (1982) [56]	0		22	−20	−25	22.19	kcal	9.36	90.64	0.00	17.13	53.76	2.84	14.12	12.15
Aché	Eastern Paraguay	Hawkes et al. (1982) [50]	2	66	−55	−22	−28	21.34	weight	47.82	51.26	0.92	53.72	9.75	11.37	18.63	6.53
Aché	Eastern Paraguay	Kaplan et al. (1985) [52]	2	81	−55	−22	−28	21.34	weight	53.16	38.84	8.00	44.42	9.29	8.89	30.87	6.52
Anbarra	Northern Territory of Australia	Meehan (1982) [54]	2	109	134.7	−12.2	−12.2	27.08	weight	68.41	31.36	0.23	47.03	9.72	4.86	26.58	11.81
Batek	Rainforests of peninsular Malaysia	Endicott and Endicott (2008) [49]	1	93	102.5	4.5	5	24.48	weight	15.09	78.48	6.43	14.79	4.70	5.93	20.67	53.91
Efe	Ituri Forest; Zaire	Bailey and Peacock (1988) [45]	1	33	29	0	3	23.43	weight	19.42	70.80	9.78	17.14	16.62	4.90	28.33	33.01
Hadza	Tanzania	Berbesque and Marlowe (2009) [47]	0		35.2	−3.8	−3.8	20.75	weight	32.04	66.16	1.80	34.31	5.98	11.26	25.43	23.02

TABLE 1 (*continued*)

| Group	Region	Study	Reliability	Collection days	Longitude	Latitude min	Latitude max	Temp mean 15km	Scale (%)	Animal	Plant	Honey	Protein	Lipid	Fiber	Sugar	Other carb
Hadza	Tanzania	Marlowe (2010) [42]	1		35.2	−3.8	−3.8	20.75	weight	27.13	64.76	8.11	26.16	6.95	13.53	36.49	16.87
Hiwi	Eastern plains of Colombia; llanos of Orinoquia	Arcand (1976) [44]	0	16	−67	3	10	27.17	weight	58.35	41.65	0.00	44.22	21.00	6.73	12.55	15.50
Hiwi	Venezuela	Hurtado and Hill (1990) [51]	1	185	−70	0	10	27.13	weight	60.99	37.83	1.18	45.68	25.84	3.53	10.69	14.25
Jarawas	Andaman Islands in the Bay of Bengal	Barik (2015) [46]	1	19	92.7	10	14	26.41	weight	67.23	23.83	8.94	41.24	18.23	2.81	26.99	10.73
Kunwinjku	Northern Australia	Altman (1987) [43]	2	296	133.5	−12	−13	26.81	weight	96.74	3.05	0.21	64.23	28.24	0.73	2.09	4.71
Nukak	Columbian Amazon	Politis (2007) [55]	1	68	−72	0	5	27.17	weight	13.62	80.26	6.12	17.19	20.85	23.73	18.08	20.16
Onge	Andaman Islands in the Bay of Bengal	Bose (1964) [48]	1	30	92.7	10	14	26.41	weight	76.00	22.66	1.33	30.08	40.70	0.58	2.78	25.85
San	Botswana; Namibia; Angola	Lee (1979) [53]	1	28	22	−20	−25	22.19	weight	31.08	68.92	0.00	35.26	44.23	5.26	5.61	9.65
San	Botswana	Wilmsen (1982) [56]	0		22	−20	−25	22.19	weight	13.64	86.36	0.00	23.47	32.73	7.79	19.35	16.65
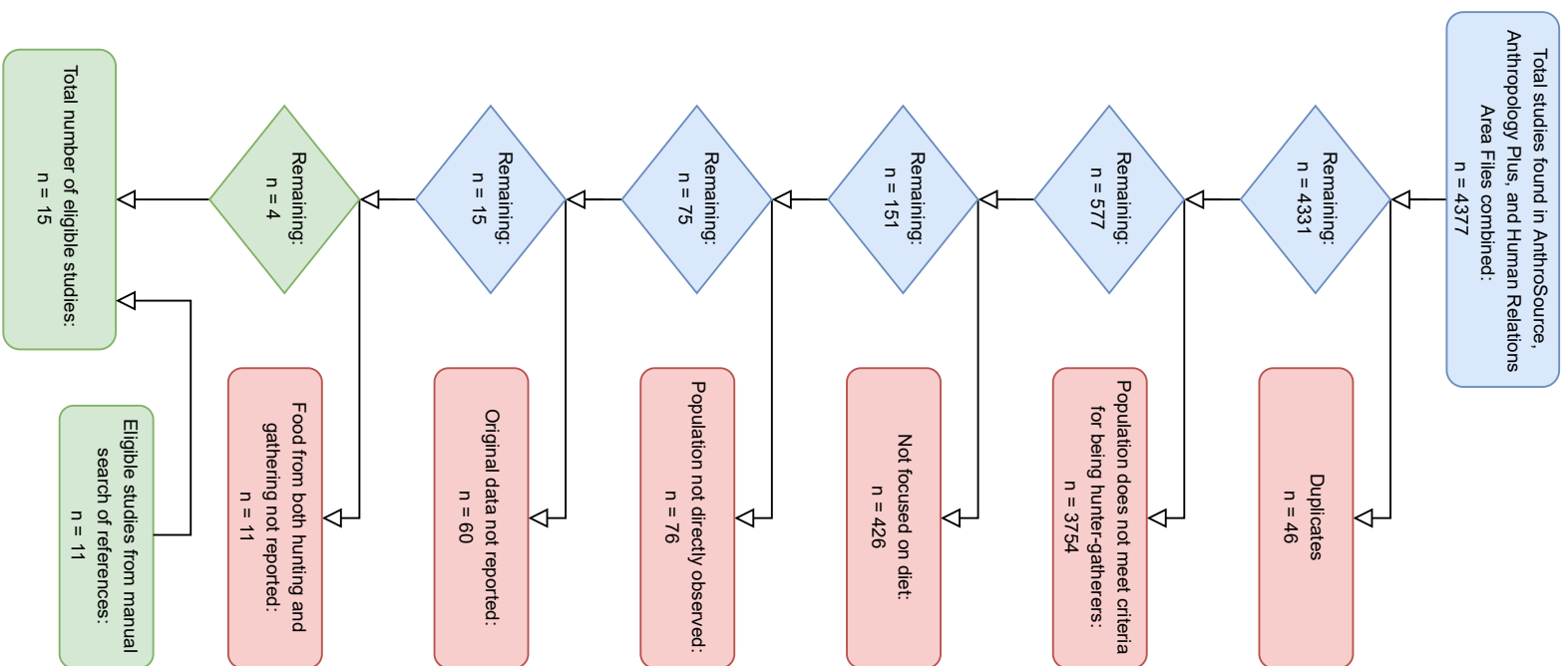
FIGURE 1. Flowchart of article selection and exclusion process.

and 7% for honey (Q1: 0.2%, Q3: 7%). In our analysis, interquartile ranges for kcal were comparably large: 51% for animal foods (Q1: 16%, Q3: 67%), 45% for plant foods (Q1: 25%, Q3: 70%), and 13% for honey (Q1: 0.4%, Q3: 14%).

Cordain et al. [6] did not report fished foods, complicating comparisons with our results, but analysis of the percentage of overall diet
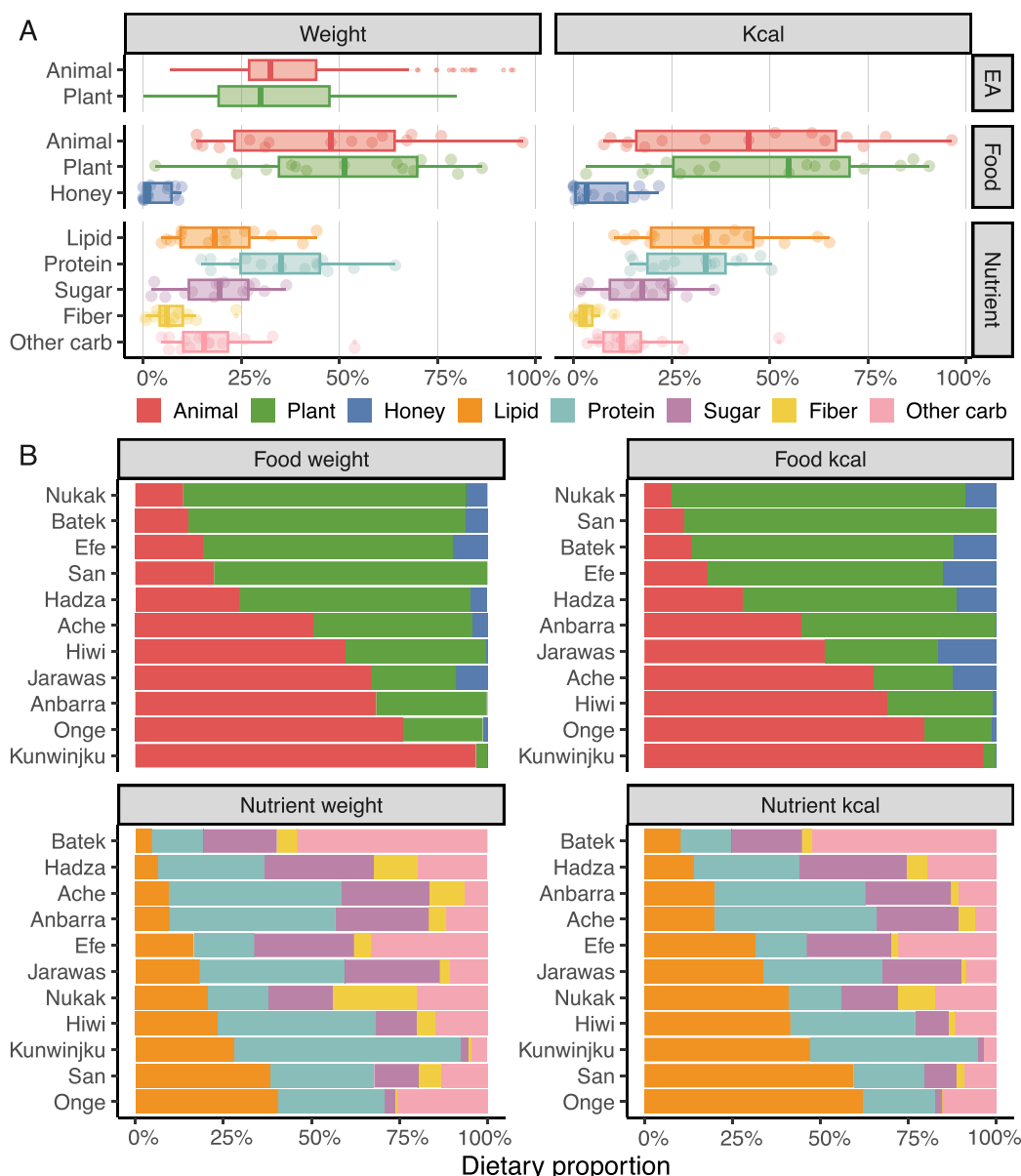
FIGURE 2. Summary of variation in dietary proportions (animal, plant, honey, lipid, protein, sugar, fiber, and other carbohydrate) by weight and kcal, from Table 1. (A) Boxplots showing data from all selected studies ($n = 15$). See Zenodo archival repository for details of how EA data values were calculated. (B) Stacked bar plots showing data from each hunter-gatherer group ($n = 11$), averaging over those with data from multiple studies. EA, Ethnographic Atlas.

by kcal for protein, fat, and carbohydrate among the study populations (Figure 2A, B; Table 1) show that few populations had macronutrient breakdowns consistent with recommended Paleo Diet ranges of 19–35% protein, 22–40% carbohydrate, and 28–47% fat. In general, more studies reported a heavier reliance on plant-based foods than on animal-based foods, and although some populations relied primarily on animal foods (Kunwinjku, Onge, Jarawas, and Hiwi), plant foods dominated the diet in others (Nukak, Batek, Efe, and San). Honey was a small proportion of the diet across all populations (Figures 2–4). Several populations had high proportions of carbohydrates (Batek, Hadza, Efe, and Nukak) and lipids (Onge, San, and Kunwinjku) compared with Paleo Diet ranges, whereas others were much lower in protein (Batek, Efe, and Nukak).

We calculated for each population the proportion of dietary calories from protein, carbohydrate, and fat that was derived from animal,

plant, or honey sources (Supplemental Figure 1, Supplemental Table 1). These data indicate wide variability in how populations sourced their macronutrients. Although animal foods are protein- and lipid-rich, plant foods provided the majority of dietary protein in the San (67%) and Nukak (66%) and the majority of dietary fat calories in the San (94%), Nukak (95%), Efe (67%), Hadza (64%), and Jarawas (50%). Similarly, whereas dietary carbohydrates are often assumed to be derived from plant sources, honey provided a majority of calories from carbohydrate in the Jarawas (57%) and substantive fractions of calories from carbohydrate in the Aché (37%), Nukak (20%), Efe (33%), Hadza (21%), and Batek (19%). Moreover, animal foods contributed the majority of calories from carbohydrate in the Kunwinjku (61%), although we caution that the underlying data for this population may overestimate animal food consumption (see Discussion).
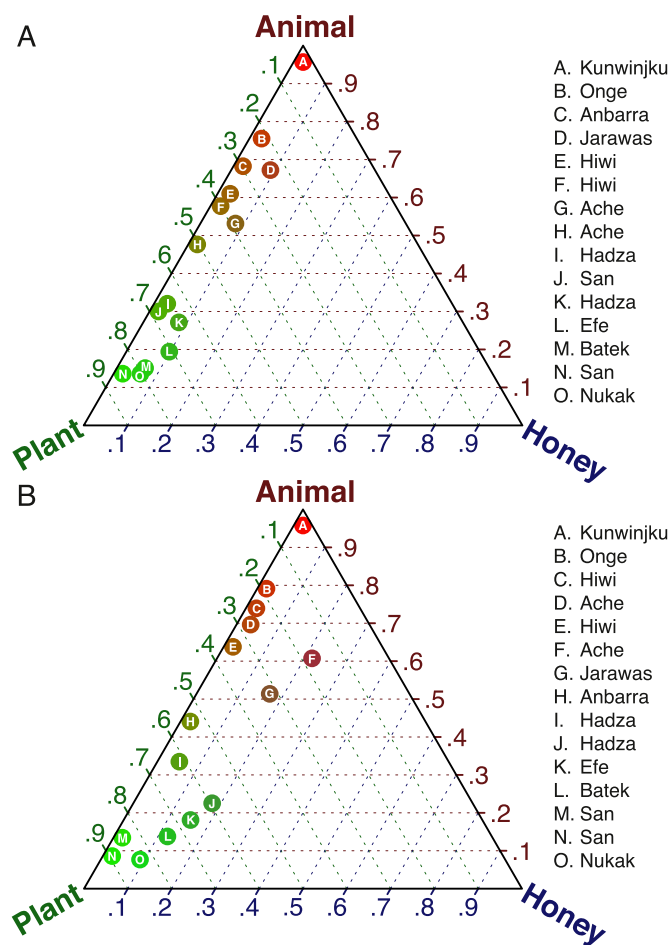
FIGURE 3. Ternary scatterplots of dietary proportions (animal, plant, and honey) from all selected studies (*n* = 15) by (A) weight and (B) kcal.

Where possible, we also estimated the proportion of dietary fat composed of saturated, monounsaturated, and polyunsaturated fatty acids (Supplemental Figure 2A–C). Many nutritional analyses do not quantify lipid subclasses, so these data were often missing for wild foods not contained in USDA databases; to be transparent about the underlying quality of the data, we report the proportion of calories from dietary fat calories that cannot be assigned to lipid subclasses (Supplemental Figure 2A, C). Compared with the high variability of total fat intake across groups, the proportions of each fat type were relatively consistent across populations (Supplemental Figure 2B). The ratio of polyunsaturated to saturated fats in the diet was not consistently associated with the proportion of calories derived from animal foods (Supplemental Figure 2D), reflecting the wide diversity of lipid sources and lipid contents in the animal food substrates consumed.

Figure 4 and Supplemental Figure 3 report results from models testing the hypothesis that data reliability affects estimates of hunter-gatherer diets. Studies with the most reliable data in which food was weighed and researchers accounted for food consumed both in and out of camp (reliability = 2) averaged a much higher ($\mathbb{P} = 0.99$) proportion of animal-based foods (95% HPDI: 47%–78%) than plant-based foods (95% HPDI: 14%–43%) by weight. Correspondingly, studies with the most reliable data (reliability = 2) reported a higher proportion of animal-based foods ($\mathbb{P} \geq 0.99$) and a lower proportion of plant-based foods ($\mathbb{P} \geq 0.99$) than studies with less reliable data (reliability = 0, or reliability = 1). Similar trends were detected when dietary proportions were measured in kcal (Figure 4 and Supplementary Figure 3). These results suggest a bias toward underreporting animal rather than plant foods.

Although we analyzed only hunter-gatherer populations from tropical habitats, AMT varied between ~21°C and ~27°C across the 11 groups sampled. Figure 5 and Supplemental Figure 4 show that honey consumption did not vary with temperature. Contrary to expectation based on greater proportions of animal foods generally reported for
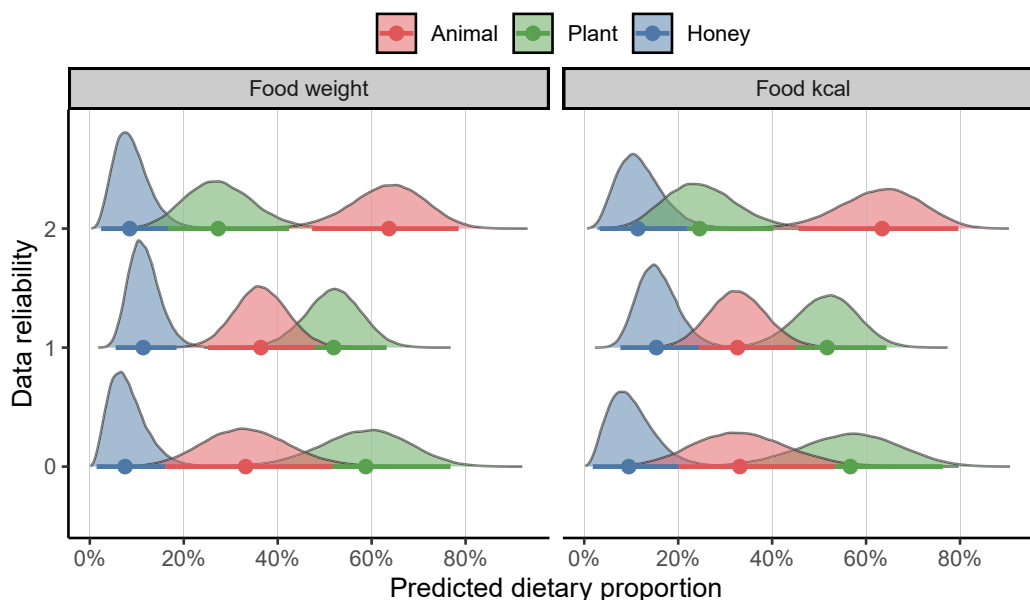

FIGURE 4. Posterior distributions of mean dietary proportions (animal, plant, honey) at each level of data reliability. Points at the base of the distributions are medians, whereas horizontal lines represent 95% HPDIS. The target of inference is the population of studies on tropical hunter-gatherer groups and so we include all selected studies (*n* = 15).
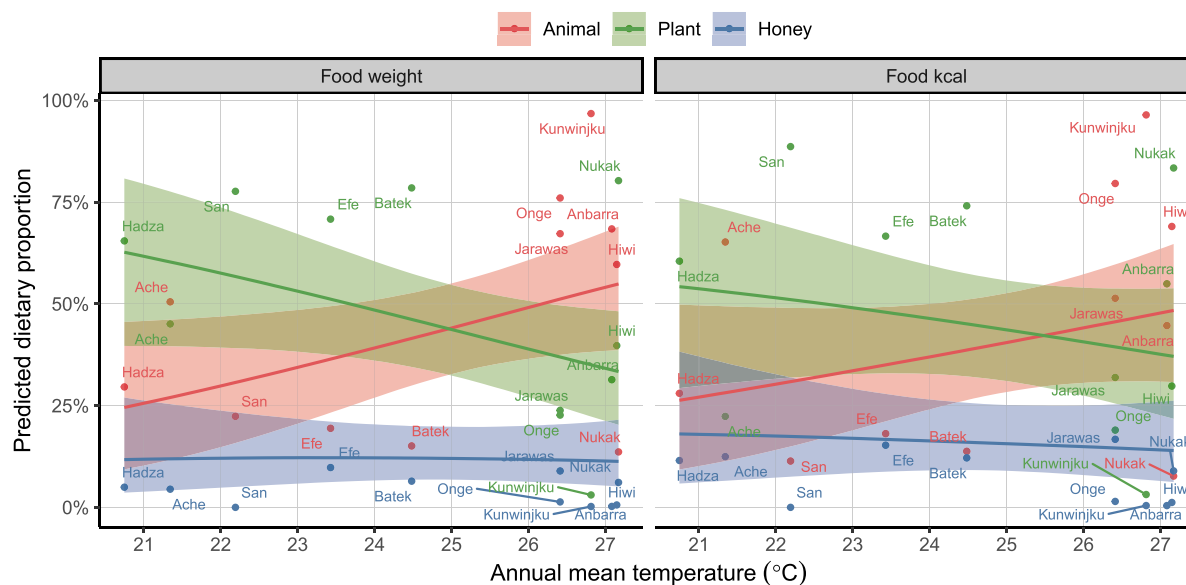
FIGURE 5. Scatterplot of dietary proportion estimates (animal, plant, and honey) at different AMTS (°C). Solid lines represent median values of posterior distributions, whereas polygon ribbons denote 95% HPDIS. Points represent observed data values. The target of inference is the population of tropical hunter-gatherer groups and so we include all unique groups (*n* = 11), averaging over those with data from multiple studies.

temperate than tropical populations [for example, ref. [39]], there was a positive association between AMT and animal contribution to diet by weight ($\mathbb{P} = 0.98$) or kcal ($\mathbb{P} = 0.91$) and a negative association between AMT and plant contribution to diet by weight ($\mathbb{P} = 0.97$) or kcal ($\mathbb{P} = 0.85$; Figure 5 and Supplemental Figure 4). Consequently, there was a tradeoff in the relative dietary proportions of animal- and plant-based foods across the temperature gradient sampled within the tropics by weight ($\mathbb{P} = 0.98$) or kcal ($\mathbb{P} = 0.89$). At the lower end of the gradient, groups procured higher proportions by weight of plant-based foods (95% HPDI: 40%–81%) than animal-based foods (95% HPDI: 9%–46%), whereas at the higher end of the gradient, this relationship was reversed (95% HPDI: plants = 20%–48%, animals = 39%–69%). Analogous tradeoffs were detected when proportions were indexed by kcal (Figure 5 and Supplemental Figure 4).

Discussion

Our analysis of data from 15 studies of 11 tropical hunter-gatherer groups reveals that hunter-gatherer diets vary greatly, supporting the first hypothesis, and refuting the concept of a single ancestral diet with circumscribed macronutrient ranges. Although the tropical groups we studied represent a miniscule fraction of the hunter-gatherer populations that have existed, their dietary variation is impressive. Some groups subsist primarily on plants, others mostly on animal foods. Although rainforest groups like the Nukak and Batek generally acquire only a small percentage of calories from animals and have high-carbohydrate/low-lipid/low-protein diets, others living in more open habitats such as the San and Onge consume highly varied percentages of animal foods and nutrients including lipids, protein, and carbohydrates. Groups also vary in how they acquire their macronutrients, with some populations (for example, San and Nukak) deriving the majority of their protein and fat from plant foods rather than animal foods, and some (for example, Jarawas and, by one account, Aché) deriving the majority of their carbohydrates from honey rather than plant foods. Between these extremes there is much additional diversity, and within

single groups, there is often considerable variation by year or season. For instance, for 2 of the 4 groups (San and Aché) with data from 2 reports, there was greater than a 10% difference in the proportions of plant food exploitation by weight across reports (Figure 3). Accordingly, the percentages by weight and calories of carbohydrates, including simple sugars and fiber, as well as lipids and protein can also vary considerably. Because our analysis excluded hunter-gatherers from temperate and Arctic environments, the degree of variation must be far greater than that quantified here. These results challenge the concept of a "typical" preagricultural diet in terms of macronutrient ranges or ratios of animal versus plant foods.

The results also support the second hypothesis that differences in collection methods introduce biases in estimating food type proportions in hunter-gatherer diets. Even in ideal circumstances, there is substantial uncertainty in measures of foragers' dietary intake. Hunter-gatherer diets vary over multiple timescales, including annually and seasonally. Furthermore, food sharing is widespread and complex, and we lack precise data on the nutrient composition of most wild foods, which varies for plants (for example, ripeness) and animals (for example, fat content) over seasons, yet researchers often collect data during just one season. These uncertainties are compounded by the failure or inability of researchers to accurately measure foods hunter-gatherers consume while foraging, or unconscious bias toward reporting recognizable foods or items of greatest research interest. Hunter-gatherers may similarly highlight prestige foods or foods that fulfill what they believe are the researchers' expectations. Given these caveats, data analyzed here show that studies which weighed food items consumed in and out of camp and across multiple seasons and years reported ~30% higher animal food and ~30% lower plant food consumption, on average, by weight and calories than studies that did not collect these data (Figure 4). The bases for this bias are unclear but could conceivably result from high consumption of animal food outside of camp, systematic underestimation of plant food consumption out of camp, concealment of small animal foods within camp, overestimation of the edible fraction of animal foods consumed outside of camp, greater seasonal variation of available animal than

plant foods, or structural bias among the limited subset of studies reporting food intake both inside and outside of camp (for example, researchers joining foraging parties may travel more often with hunters than gatherers).

Both the snapshot nature of ethnographic studies of diet and potential biases toward reporting of prestige foods may help to explain why some reported dietary signatures seem inconsistent with long-term human physiological needs. For instance, protein was reported to contribute 48% of dietary calories in the Kunwinjku, an average of 46% in the Aché, and 43% in the Anbarra, levels that would likely exceed the physiological capacity of the liver for urea synthesis and induce hyperammonemia and hyperaminoacidemia—a metabolic condition known as "rabbit starvation"—if maintained over time [7]. Because these populations are not known to possess adaptations for more efficient urea elimination, we can infer that the underlying ethnographic data likely overestimated intake of protein-rich foods in these cases or else failed to record consumption of other foods.

These sources of error and uncertainty highlight how estimates of dietary variation may often be underestimates. Beyond undermeasuring food diversity for individual hunter-gatherer groups, few foraging populations across different environments have had their diets systematically and carefully studied, limiting our understanding of variation in preagricultural diets. Within our restricted sample of 11 tropical foraging groups, we found a positive association between AMT and consumption of animal versus plant foods. Although somewhat surprising, given that animal-dominated diets are most readily found in regions with low AMT, among tropical hunter-gatherers this association could potentially be due to the relative ease of hunting animals in more open (typically, hotter and drier) tropical habitats. Further research is necessary to characterize variations caused by this and other environmental factors that influence food availability for hunter-gatherers, including rainfall, seasonality, altitude, and geography (for example, proximity to lakes, rivers, and seas). Cultural behaviors also contribute to variation [80], as do interactions with competing hunter-gatherer groups, neighboring farmers and pastoralists, researchers, tourists, missionaries, government agencies, and trade organizations who influence land-use patterns. Finally, individual differences represent a critical source of variation that we did not address. In all hunter-gatherer populations, women and men tend to forage for different foods, leading to differences in consumption that may be accentuated by age and reproductive status [33,42,81,82].

The least variable food is honey, which many studies do not capture or assess as a separate category despite its widespread status as a preferred food [40,83]. Why honey consumption was often not included in prior studies is unknown but may involve challenges placing honey into traditional categories. Honey is produced by animals from plants, is an animal-derived food that is nearly pure carbohydrate, a high-carbohydrate food that is primarily obtained by men, and a food neither foraged nor hunted but found and secured by quieting bees with smoke or plant volatiles [40,41,83,84]. Honey consumption was not reported in one of the populations included (San), in terms of weight was <2% of the diet in 4 others (Kunwinjku, Anbarra, Hiwi, and Onge), and comprised between 4.5% and 9.8% of the diet in the remaining 6 populations. By kcal, honey provides >9% of calories in 6 of the 11 populations sampled (Nukak, Jarawas, Efe, Aché, Batek, and Hadza), reinforcing previous studies that show that it is sometimes an important resource, especially when meat is scarce [83]. The widespread distribution in sub-Saharan Africa of honeyguide birds that mutualistically help human foragers find honey suggests that honey consumption has ancient roots, perhaps coincident with the human control of fire [41,83,85] or predating it [84].

As also shown by Ruffett and Collard [11], the interquartile ranges calculated by weight or kcal for dietary protein, carbohydrate, and lipid consumed by the 11 hunter-gatherer groups we analyzed document considerably greater variation than the Paleo Diet, whose prescriptions are based on an analysis of the EA hunter-gatherer data [7]. Furthermore, the data used in our study likely underestimate the dietary diversity of these populations. Despite these limitations, only 2 of our 11 groups (Jarawas and Hiwi) fit within or very close to the kcal ranges of protein (19–35%), carbohydrate (22–40%), and lipids (28–47%) prescribed by the Paleo Diet [7,10]. Thus, although the Paleo Diet approximates the average macronutrient content across the tropical hunter-gatherer populations sampled here, our results highlight the important points that 1) hunter-gatherers evolved to eat a wide range of diets and 2) few forager diets resemble the Paleo Diet in terms of macronutrient composition. Of the 15 articles representing the 11 groups sampled, 67% (n = 10 articles) described a diet with at least one macronutrient within the Paleo Diet's prescribed range; 13% (n = 2) described a diet with 2 macronutrients within this range, and just 7% (n = 1) described a diet with all 3 macronutrients in the prescribed range (Table 1). Altogether, the Paleo Diet does not capture the dietary diversity in terms of macronutrients for most specific populations and may differ substantially from the macronutrient proportions consumed by many preagricultural populations.

Oversimplistic characterization of ancestral diets by resource or macronutrient type is a critical limitation of studies, including ours, that rely on ethnographic and ethnohistoric data to infer food consumption among hunter-gatherers. Most detailed dietary data come from a few recent foraging populations, especially the few hundred intensively studied Hadza, the focus of much recent academic attention because they are among the last hunter-gatherer groups in Africa and are relatively easy to access [31]. Although it would be helpful to have more complete and accurate data on the foods the Hadza seek and consume, they are a population in transition and just one population in one habitat. Thus, they are not proxies for all hunter-gatherers. This limitation poses a dilemma because there are almost no other hunter-gatherer populations left to study using modern methods. Our reliance on published ethnographic and ethnohistoric studies compel the use of heuristic methods, such as those employed here, to assess ways in which the available data may be inaccurate, incomplete, and biased.

Beyond understanding preagricultural human diets, the diversity of hunter-gatherer diets has relevance to multiple other areas. Research on dietary variation among foraging populations is overshadowed by the Paleo Diet's popularity, which promotes a simplified view of these diets. Another concern is the naturalistic fallacy that hunter-gatherer diets—even if their composition and diversity could be accurately quantified—are necessarily healthier than agricultural diets. There are many problems with this concept. First, natural selection has continued and sometimes accelerated postagriculture, helping adapt farming populations to domesticated foods such as dairy products and cereals [17,18]. Second, many hunter-gatherer diets, such as those reliant on fermentation or caching [86,87], may pose health risks that would be amplified in unacculturated populations. In addition, the environmental context of diets, including levels of physical activity, is also relevant. For example, despite eating a high-carbohydrate diet, Tsimane farmers in the Amazon, who also fish and hunt, have almost no evidence for coronary heart disease or metabolic syndrome [88,89].

Another problem with oversimplified dietary depictions and prescriptions based on hunter-gatherer diets is that they can promote the perception that diets beneficial for one human population will benefit all human populations. However, a diet may have differential metabolic consequences across individuals or populations because of genomic

and metagenomic differences. The energetic advantages of improved lactose and starch digestion likely drove the evolution of lactase persistence and salivary amylase copy number variation in agricultural populations [17,18] and reciprocal changes in gut microbiome function [90]. Similarly, nonindustrialized gut microbiomes exhibit consistent differences in composition and function versus industrialized gut microbiomes [91,92], including an enhanced capacity for complex carbohydrate fermentation into short-chain fatty acids that can influence host metabolic health [93,94]. Viewing average hunter-gatherer diets as optimal also fails to consider that natural selection typically acts most strongly during periods of scarcity when lower quality, nonpreferred "fallback" foods are used [95,96]. Consequently, the foods that hunter-gatherers most frequently consume may not be the foods that humans are most strongly adapted to eat.

Finally, and critically, natural selection favors heritable features that promote reproductive success. Humans evolved to crave and consume foods that benefit reproduction not long-term health, which is selected for only to the extent that it promotes reproductive success [97]. Natural selection will favor behaviors, including food preferences, that increase morbidity and mortality if these behaviors enhance fertility during the reproductive period [98]. Therefore, highly valued "natural" foods consumed by hunter-gatherers such as fatty meat or honey do not necessarily promote health. Conversely, modern foods like whole grains and dairy were rarely consumed by hunter-gatherers but are not necessarily unhealthy.

The challenges of characterizing hunter-gatherer diets and their variation do not negate the value of studying contemporary hunter-gatherer diets for evaluating modern diets. For instance, studies of hunter-gatherer diets reinforce evidence regarding what humans are poorly adapted to eat. Substantial variation among hunter-gatherer diets indicates that humans are adapted to and adapt to many different foods, but also emphasizes that no hunter-gatherer or nonindustrial farming population routinely consumes ultraprocessed foods with fiber removed and sugars, salt, saturated and/or trans fats, preservatives, colorants, and emulsifiers added. Although debate persists over the health effects of different processing methods, there is consensus that ultraprocessed foods contribute to rising incidences of noncommunicable diseases because humans are not adapted to consume these foods in large quantities. Other aspects of hunter-gatherer diets considered in the context of the exposome including viruses, bacteria, and eukaryotic parasites and commensals may also inform the pathogenesis of autoimmune and other modern disorders. Defining the range of hunter-gatherer diets and their contrasts to modern diets can provide a richer understanding of what humans are adapted to eat and help identify hypotheses of mismatch that can then be tested rigorously with epidemiological and experimental data.

Author contributions

The authors' responsibilities were as follows – DEL, RNC, OD, CMP: planned the project; SW, LDS, CMP: analyzed the data; DEL, RNC, OD: initially drafted the manuscript; and all authors: revised the manuscript.

Conflict of interest

The authors report no conflicts of interest.

Funding

Data availability

Data described in the manuscript, code book, and analytic code will be made publicly and freely available without restriction at https://doi.org/10.5281/zenodo.8121384.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ajcnut.2023.06.013.

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