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Original Research Article

An assessment of the impact of cross-cultural variation in plant macronutrients on the recommendations of the Paleo Diet

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A B S T R A C T

Background: One of the main recommendations of the Paleo Diet is that individuals replicate the whole-diet macronutrient ranges of hunter-gatherer diets. These are suggested to be 19%–35% protein, 22%–40% carbohydrate, and 28%–58% fat, by energy. However, the plant food contribution to these ranges was estimated exclusively from Australian data, which is a potential problem.

Objectives: We investigated whether estimates of the contribution of protein, carbohydrate, and fat to hunter-gatherer diets are impacted by using plant data from other regions of the world.

Methods: The values that form the basis of the Paleo Diet' s recommended macronutrient ranges were generated with a set of equations. We combined these equations with published plant macronutrient data from a multi-region sample of 5 hunter-gatherer groups to generate new estimated macronutrient percentages and then statistically compared the old and new estimates. Subsequently, we collated plant macronutrient data for a sample of 10 hunter-gatherer groups from several regions and repeated the exercise.

Results: The whole-diet macronutrient percentages we calculated are significantly different from those that underpin the Paleo Diet's recommendations. Additionally, the ranges derived from our whole-diet macronutrient percentages (14%–35% protein, 21%–55% carbohydrate, 12%–58% fat) are markedly wider than those recommended by the Paleo Diet.

Conclusions: The estimated whole-diet macronutrient percentages that form the basis of the Paleo Diet's macronutrient recommendations are not robust. Using plant data from multiple regions leads to significantly different estimates. Additionally, the macronutrient ranges derived from our whole-diet macronutrient percentages overlap with those recommended by the US Department of Agriculture and the WHO. This undercuts one of the main justifications for adopting the Paleo Diet—namely that because it is vastly different from Western diets, it can reduce the probability of experiencing noncommunicable diseases. There may still be reasons for adopting the Paleo Diet rather than a conventional diet, but healthier macronutrient percentages is not one of them.

Keywords: Paleo Diet, wild plant, macronutrient, protein, carbohydrate, fat, hunter-gatherer

Introduction

The Paleo Diet—also known as the Paleolithic Diet, Caveman Diet, or Stone Age Diet—is a dietary regime that encourages people to eat like Paleolithic hunter-gatherers to avoid chronic diseases such as type 2 diabetes, hypertension, and atherosclerosis. Although the roots of the Paleo Diet can be traced to the 1950s [1, 2], the version of the diet that is popular today is based on recommendations outlined in a book by Dr. Loren Cordain called *The Paleo Diet: Lose Weight and Get Healthy by Eating the Foods You Were Designed to Eat*, the first edition of which was released in 2001 [3]. Today, the Paleo Diet is followed by several million people [4], and the industry that has developed in connection with it is estimated to be worth almost US $10 billion [5].

In the present paper, we report a study that focused on a key recommendation of the Paleo Diet, which is to change the macronutrient composition of one's diet so that it mimics that of Paleolithic hunter-gatherers [6]. This recommendation derives from the results of a study by Cordain et al. [7] in which the diets of 229 recent hunter-gatherer groups were analyzed. With the aid of 3 linear equations (see below), these investigators estimated that the macronutrient intake ranges of the groups were 19%–35% protein, 22%–40% carbohydrates, and 28%–58% fat. They argued that these ranges likely characterized Paleolithic hunter-gatherers' diets and suggested that the

Abbreviations used: FAO/INFOODS, Food and Agriculture Organization of the United Nations/International Network of Food Data Systems; WHO, World Health Organization; USDA, US Department of Agriculture.

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"macronutrient characteristics of hunter-gatherer diets may provide insights into potentially therapeutic dietary recommendations for contemporary populations" [7: pg. 691].

The study reported here concentrated on the impact that cross-cultural variation in plant macronutrients has on the Paleo Diet's whole-diet macronutrient recommendations. Although Cordain et al. [7] used several sets of macronutrient values for animal foods, they only employed one set of macronutrient values for plant foods. These were taken from an article by Brand-Miller and Holt [8], and were the mean protein, carbohydrate, and fat values of wild plants traditionally consumed by Indigenous Australians. Thus, built into the study by Cordain et al. [7] is the assumption that the macronutrient composition of wild plants consumed by Australian hunter-gatherers holds for wild plants consumed by all hunter-gatherers. Cordain et al. [7] acknowledged that this was a limitation of their study, but, so far, the effects of their reliance on plant macronutrient data from one region of the world have not been assessed. Changing this state of affairs was the goal of the present study.

The study had 2 parts. In the first, we used a plant macronutrient dataset that Cordain et al. [6] highlighted but did not use. The dataset in question was published by Eaton and Konner [9] and comprises macronutrient values for plants traditionally consumed by 5 hunter-gatherer groups from 3 different regions of the world. We combined Eaton and Konner's [9] plant macronutrient values with Cordain et al.'s [7] equations and statistically compared the resulting whole-diet macronutrient values with the ones reported by Cordain et al. [7]. In the second part of the study, we compiled data on the plant component of the diets of a sample of hunter-gatherers that was both larger and more geographically diverse than the samples employed by Brand-Miller and Holt [8] and Eaton and Konner [9]. We then combined the new plant macronutrient dataset with the equations used by Cordain et al. [7] to generate new whole-diet macronutrient values. Lastly, we statistically compared the new whole-diet values with the ones reported by Cordain et al. [7].

Methods

We will start this section by outlining Cordain et al.'s [7] method for estimating whole-diet macronutrient percentages, as it was central to our study. We will then describe the 2 parts of our study. We did not preregister our study, but we have made the data available https://datadryad.org/stash in the Supplementary Material and described the analyses in sufficient detail that they can be replicated easily.

The method of estimating macronutrient percentages by Cordain et al. (2000)

Cordain et al. [7] began by selecting 229 hunter-gatherer groups from the 1291 groups in the *Ethnographic Atlas* [10]. All of the groups they chose were 100% reliant on hunting, fishing, and gathering for their subsistence needs.

Cordain et al. [7] then estimated the percentage contributions of plant and animal foods by weight to the diet of each of the groups in their sample. To do this, they assumed that gathering involved only plant foods and used the percentage dependence on gathering listed in the *Ethnographic Atlas* as the percentage of the diet derived from plants. To obtain the percentage of the diet derived from animals, they summed the percentage dependence on hunting and the percentage dependence on fishing presented in the *Ethnographic Atlas*. Cordain et al. [7] found that, on an average, plants foods contributed 65% to 35% of the diets of the groups in the sample, whereas animal foods contributed 35% to 65%, by weight.

Next, Cordain et al. [7] investigated the relationship between the percentage contributions of plant and animal foods to the diet by weight and the percentage contributions of plant and animal foods to the diet by energy. They did so by reviewing the literature on the energy density of wild plant and animal foods. They found that the mean energy density of wild plant foods is 6.99 kJ/g, and that the mean energy density of wild animal foods is 7.24 kJ/g. They deemed these figures to be "virtually identical" [7: pg. 686] and argued on the basis of this that their figures for the percentage contributions of plant and animal foods to the diet by weight could be treated as the percentage contributions of plant and animal foods to the diet by energy.

Subsequently, Cordain et al. [7] used the following equations to estimate the percentage energy contributions of the 3 macronutrients to the diet of each group in their sample:

$$\text{Protein} = \frac{(Mpp^*P^*T) + (Map^*A^*T)}{T} \quad (1)$$

$$\text{Carbohydrates} = \frac{(Mpc^*P^*T) + (Mac^*A^*T)}{T} \quad (2)$$

$$\text{Fat} = \frac{(Mpf^*P^*T) + (Maf^*A^*T)}{T} \quad (3)$$

Mpp, *Mpc*, and *Mpf* are the percentage contributions of protein, carbohydrates, and fat from plants to the total energy provided by a group's diet. For these variables, Cordain et al. [7] used mean macronutrient values that Brand-Miller and Holt [8] derived from the nutritional analyses of 829 plants that were traditionally consumed by Indigenous Australians. The values in question were 14% protein, 62% carbohydrates, and 24% fat, by energy.

P is the percentage contribution of plant foods to the total energy provided by a group's diet.

T is the mean daily energy requirements for hunter-gatherer males in kilojoules (kJ). Cordain et al. [7] set this at 12,552 kJ based on results obtained in an earlier study [11].

Map, *Mac*, and *Maf* are the percentage contributions of protein, carbohydrates, and fat from animals to the total energy provided by a group's diet. To obtain values for these variables, Cordain et al. [7] used equations developed by Pitts and Bullard [12] to estimate the amount of protein and fat energy that hunted animals and fish provided to the hunter-gatherer groups' diets at 5 different levels of body fat: 2.5%, 5%, 10%, 15%, and 20%. Pitts and Bullard [12] created separate equations for hunted animals and fish because they yield different amounts of protein and fat at the same level of body fat. In their calculations, Cordain et al. [7] assumed that hunted animals always contributed to 35% of the energy provided by diet, and any remaining animal food contribution came from fish.

A is the percentage contribution of animal foods to the total energy provided by a group's diet.

Cordain et al. [7] solved the 3 macronutrient equations multiple times for each of the 229 groups in their sample. They did this because the percentage contributions of plant and animal foods to the diets of the groups in their sample were variable, and because the body fat levels of the prey animals were not constant. Each time they solved the equations, they assumed a different percentage contribution of animal foods to the diet and a different prey body fat percentage. Cordain et al. [7] employed 5 different percentage contributions of animal food (35%, 45%, 50%, 55%, and 65%) and 5 prey body fat levels (2.5%, 5%, 10%, 15%, and 20%). Thus, they solved equations

1 to 3 a total of 25 times for each group. The estimates they obtained are reproduced in Table 1.

In the final step of their analysis, Cordain et al. [7] calculated a range for each macronutrient. Cordain et al. [7] did not simply calculate the highest and lowest values because of the existence of research suggesting that there is an upper limit to the percentage of energy that a human can derive from protein over the medium to long term. Cordain et al. [7] argued that the upper limit is 35% of energy and proceeded to use this value to select macronutrient values to include/exclude when calculating the ranges. It is important to note that they did not just drop protein values; they also excluded the carbohydrate and fat values associated with any protein value that exceeded 35%. That is, they disregarded the protein, carbohydrate, and fat values for a given combination of plant to animal ratio and prey body fat that yielded a protein percentage >35%. This process resulted in a protein range of 19%–35% by energy, a carbohydrate range of 22%–40% by energy, and a fat range of 28%–58% by energy.

Methods used in the first part of the study reported here

The goal of the first part of our study was to test Cordain et al.'s [7] assumption that Eaton and Konner's [9] plant data yield whole-diet macronutrient percentages that do not differ significantly from the whole-diet macronutrient percentages that Cordain et al. [7] obtained with Brand-Miller and Holt's [8] plant data. Eaton and Konner [9] estimated that, on an average, plant foods contribute 13% of the protein, 68% of the carbohydrates, and 19% of the fat to the diets of hunter-gatherers. They derived these values from nutritional analyses of 44 plant foods consumed by 5 hunter-gatherer groups—the !Kung and the ≠Kade San of Botswana, the Hadza of Tanzania, the Tasaday of the Philippines, and Australian Aborigines (no group specified).

Table 1
Whole-diet macronutrient percentages reported by Cordain et al. [7].

PAR	PBF	Protein	Carbohydrate	Fat
35:65	20%	21	22	58
	15%	28	22	50
	10%	35	22	43
	5%	47[1]	22[1]	32[1]
	2.5%	56[1]	22[1]	23[1]
45:55	20%	20	28	52
	15%	26	28	46
	10%	32	28	40
	5%	42[1]	28[1]	30[1]
	2.5%	49[1]	28[1]	23[1]
50:50	20%	20	31	49
	15%	25	31	44
	10%	31	31	38
	5%	39[1]	31[1]	30[1]
	2.5%	46[1]	31[1]	23[1]
55:45	20%	19	34	47
	15%	24	34	42
	10%	29	34	37
	5%	37[1]	34[1]	29[1]
	2.5%	43[1]	34[1]	23[1]
65:35	20%	19	40	41
	15%	22	40	37
	10%	26	40	34
	5%	32	40	28
	2.5%	37[1]	40[1]	23[1]

PAR = ratio of plant food to animal food in diet, by calories. PBF = prey body fat percentage.
[1] This value was disregarded by Cordain et al. [7] when calculating their whole-diet macronutrient ranges. For details of their rationale, see the main text.

We proceeded by using equations 1 to 3 and the plant macronutrient values reported by Eaton and Konner [9] to re-calculate the mean percentage contributions of the 3 macronutrients to the total energy provided by the diets of the groups in Cordain et al.'s [7] sample. Following Cordain et al. [7], we calculated the mean percentage contributions at 5 different plant to animal ratios (35:65, 45:55, 50:50, 55:45, and 65:35) and 5 levels of prey body fat (20%, 15%, 10%, 5%, and 2.5%). Subsequently, we used the Wilcoxon signed ranks test to statistically compare the new Eaton and Konner [9] data-based estimates with Cordain et al.'s [7] estimates (see our Table 1). It is important to note that we did not compare the 2 ranges for each macronutrient. Rather, we compared the 2 groups of point estimates for each macronutrient [the 25 point estimates we generated and the 25 point estimates reported by Cordain et al. [7]]. We performed 3 Wilcoxon signed ranks tests, one for protein, one for carbohydrate, and one for fat. These tests were performed in SPSS version 27. We adjusted the significance level for multiple unplanned comparisons using the method described by Benjamini and Hocheberg [13], with the false discovery rate set to 15% [14].

Methods used in the second part of the study reported here

In the second part of the study, we compiled data on the nutrient composition of the plant foods consumed by 10 recent hunter-gatherer groups. These included 5 groups from Canada—the Baffin Island Inuit, the Gwich'in, the Nuxalk, the Wet'suwet'en, and the Sahtú Dene and Métis. The other 5 groups were the Ju/'hosani of Botswana, the Ache of Paraguay, the Hokkaido Ainu of Japan, the Hadza of Tanzania, and the Hiwi of Venezuela. These are, to our knowledge, all of the hunter-gatherer groups for which detailed plant food macronutrient composition data are available. Such data are rare partly because there has been little research on the plant component of hunter-gatherer diets, and partly because nutrient analyses are rarely conducted on wild foods [15]. Further information about our sample is provided in the first section of the Supplemental Material and Supplemental Tables 1–10.

We obtained plant lists and nutrient data for the 5 Canadian groups and the Hokkaido Ainu from an online database developed by the Centre for Indigenous Nutrition and Environment (CINE) at McGill University (https://www.mcgill.ca/cine/resources). Although the CINE database provides dietary data for many Indigenous groups, most of them consumed mostly domesticated species at the time of data collection. The only groups who were entirely dependent on wild food were the Baffin Island Inuit, the Gwich'in, the Nuxalk, the Sahtú Dene and Métis, and the Wet'suwet'en. The Hokkaido Ainu are usually referred to as hunter-gatherers [16, 17], but they actually consumed a few domesticated plants. Although Cordain et al.'s [7] criterion for inclusion was 100% reliance on wild resources, we decided to include the Hokkaido Ainu in our sample because the cultivars they consumed comprised a tiny percentage of their diet and were therefore unlikely to negatively affect our results.

For the Ache, Hadza, and Hiwi we generated plant lists from published ethnographic sources and extracted nutrient data from plant food composition databases. Details of the ethnographic sources we employed are provided in the first section of the Supplementary Material and Supplemental Tables 2, 5, and 6. We used 2 plant food composition databases for the nutrient data: the Food and Agriculture Organization of the United Nations/International Network of Food Data Systems (FAO/INFOODS) database [18] and a database created by Duke and Atchley [19]. The FAO/INFOODS database is rigorously checked and frequently updated. The nutrient values it provides were extracted using the standard protocol, which is outlined by Greenfield and Southgate [15]. It is the database that is normally used to cross-check nutrient values and is widely considered to be reliable [15]. Unfortunately, it has a substantial number of gaps when it comes to wild plants. The database created by Duke and Atchley [19] is the most comprehensive food composition database for wild plants published to date. Its nutrient data were extracted using the standard protocol, and it is considered to be a good quality database [20]. The macronutrient percentages presented by Duke and Atchley [19] were calculated including ash; we re-calculated the percentages without ash.

Some of the plants that were listed in the ethnographies as being habitually consumed by the Hadza, Ache, and Hiwi did not have nutritional data in the FAO/INFOODS database or the Duke and Atchley [19] database, likely because they are uncommon. Instead of leaving these plants out, we estimated their nutrient value based on close relatives. For example, no nutritional data were available for the root of *Calathea allonia*, which is consumed by the Hiwi. Therefore, we used data from *Calathea macrosepala,* which was included in Duke and Atchley's [19] database. Substituting with data for a close relative is a common approach when a plant’s nutritional values are unknown [15].

Honey is often consumed by the Hadza, Hiwi, and Ache. Although technically an insect product, honey is usually treated as a plant food in studies of traditional subsistence [10, 21]. Cordain et al. [7] followed this course of action, and so did we.

The Ache include one non-traditional plant food in their diets—feral oranges. As with the cultivars eaten by the Hokkaido Ainu, the contribution of this non-traditional food to the Ache diet is very small. As such, we judged that its inclusion was unlikely to negatively affect our results.

For the last group in the sample, the Ju/’hosani, we used 2 ethnographies to create the plant list [22, 23]. We obtained nutrient data for the Ju/’hosani’s plant foods from a database compiled by Wehmeyer et al. [24]. These investigators did not disclose the methods they used to extract the plant macronutrient values. However, we found an earlier nutrient analysis by the lead investigator in which the standard protocol was used [25], and we assumed that the values presented by Wehmeyer et al. [24] were generated in the same way.

Some of the ethnographic reports we consulted indicated the relative importance of different plant species and/or different types of plant (e.g., tubers, berries, etc.) in a group’s diet. In these cases, we were able to calculate weighted means for the macronutrient percentages. When no information about the relative importance of different plant species and/or different types of plant was available, we followed the lead of Brand-Miller and Holt [8] and calculated unweighted means for the macronutrients, from all the plant species in the diet. In theory, the weighted mean approach is more accurate than the unweighted approach. Thus, our plant macronutrient percentages were either as accurate or more accurate than the ones Cordain et al. [7] used to generate their whole-diet macronutrient percentages.

Once we had compiled our dataset, we combined the mean plant macronutrient values for the 10 groups with equations 1 to 3 to create whole-diet macronutrient percentages. As in the preceding analysis, we calculated each macronutrient percentage at 5 different plant to animal ratios (35:65, 45:55, 50:50, 55:45, and 65:35) and 5 different levels of prey body fat (20%, 15%, 10%, 5%, and 2.5%). Thus, we calculated the macronutrient percentages 25 times for each hunter-gatherer group.

Next, we conducted a series of Wilcoxon signed ranks tests. In these tests, we compared the whole-diet macronutrient percentages we calculated with the whole-diet macronutrient percentages that Cordain et al. [7] reported (once again, see Table 1 for their estimates). As in the first part of the study, we did not compare the ranges, we compared the point estimates. We performed a total of 30 Wilcoxon signed ranks tests—10 for protein, 10 for carbohydrate, and 10 for fat. In each test, we compared the 25 estimates for a macronutrient for one of our groups with the 25 estimates for the same macronutrient reported by Cordain et al. [7]. As before, these tests were performed in SPSS version 27, and we adjusted the significance level for multiple unplanned comparisons using the method described by Benjamini and Hocheberg [13]. The false discovery rate was set to 15% [14].

Results

Table 2 compares the whole-diet macronutrient percentages we obtained with the plant macronutrient values by Eaton and Konner [9] and the whole-diet macronutrient percentages reported by Cordain et al. [7]. Just over a third of the protein percentages were different and so were all of the carbohydrate and fat percentages. Consistent with this, the 3 Wilcoxon signed rank tests returned significant *P*-values after correction for multiple unplanned comparisons (Table 3). Thus, contrary to what Cordain et al. [7] assumed, Eaton and Konner's [9] plant data yield whole-diet macronutrient percentages that are significantly different from those reported by Cordain et al. [7].

Tables 4–6 summarize the results obtained in the second part of the study. Table 4 shows the mean amount of protein, carbohydrate, and fat that plants contribute to the diet of each group in the sample we compiled. The amount of carbohydrate that plants contributed varied by 24%, with the lowest amount being 60% in the diet of the Ju/’hosani and the highest being 84% in the diets of the Hiwi and Wet’suwet’en. The amount of fat that plants contributed varied by 19%, from 8% in the Hiwi and Hokkaido Ainu diets to 27% in the Ju/’hosani diet. The protein contributed by plants varied least. There was just a 11% difference between the lowest contribution, which was 6% in the diets of the Ache and Wet’suwet’en, and the highest contribution, which was 17% in the diet of the Hokkaido Ainu.

Table 5 presents the ranges for the whole-diet macronutrients that were obtained when we combined our plant macronutrient values with Cordain et al.'s [7] equations (see Supplemental Tables 11–13 for the full set of whole-diet macronutrient values generated for each group). This time, when no protein cap was used, the fat values were the most variable (12%–58%), the carbohydrate values were the least variable (21%–55%), and the protein values were intermediate (14%–57%). When the 35% protein cap favored by Cordain et al. [7] was employed, the fat values were the most variable (12%–58%), the protein values were the least variable (14%–35%), and the carbohydrate values were intermediate (21%–55%).

The results of the Wilcoxon signed ranks tests performed in the second part of the study are summarized in Table 6. All of the tests were significant after correction for multiple unplanned comparisons, which indicates that the differences between the plant macronutrient values we generated for the 10 groups in our sample and the plant macronutrient values used by Cordain et al. [7] are large enough to have a significant impact on the whole-diet macronutrient values. This is inconsistent with Cordain et al.’s [7] assumption that their whole-diet macronutrient percentages are representative of hunter-gatherers in general.

Table 2
Whole-diet macronutrient percentages reported by Cordain et al. [7] compared with whole-diet macronutrient percentages obtained when plant values by Eaton and Konner [9] were employed in Cordain et al. [7] equations.

PAR	PBF	Protein		Carbohydrate		Fat	
		Cordain et al. [7]	Eaton and Konner [7]	Cordain et al. [7]	Eaton and Konner [9]	Cordain et al. [7]	Eaton and Konner [9]
35:65	20%	21	21	22	24	58	55
	15%	28	28	22	24	50	48
	10%	35	34	22	24	43	42
	5%	47	46	22	24	32	30
	2.5%	56	55	22	24	23	21
45:55	20%	20	20	28	31	52	49
	15%	26	26	28	31	46	44
	10%	32	32	28	31	40	38
	5%	42	41	28	31	30	28
	2.5%	49	49	28	31	23	20
50:50	20%	20	20	31	34	49	47
	15%	25	25	31	34	44	41
	10%	31	30	31	34	38	36
	5%	39	39	31	34	30	27
	2.5%	46	46	31	34	23	20
55:45	20%	19	19	34	37	47	43
	15%	24	24	34	37	42	39
	10%	29	29	34	37	37	34
	5%	37	37	34	37	29	26
	2.5%	43	43	34	37	23	20
65:35	20%	19	18	40	44	41	38
	15%	22	22	40	44	37	34
	10%	26	26	40	44	34	30
	5%	32	32	40	44	28	24
	2.5%	37	36	40	44	23	20

PAR, ratio of plant food to animal food in diet, by calories; PBF, prey body fat percentage.

Table 3
Results of Wilcoxon signed ranks tests in which the whole-diet macronutrient values reported by Cordain et al. [7] were compared with whole-diet macronutrient percentages generated from plant data by Eaton and Konner [9] in the first part of the study reported here.

Comparison	Protein	Carbohydrate	Fat
Cordain et al. vs. Eaton and Konner	$Z = -2.646$ $P = 0.008$*	$Z = -4.496$ $P = <0.001$*	$Z = -4.465$ $P = <0.001$*

**P*-value significant after correction for multiple unplanned comparisons with Benjamini and Hocheberg's [13] method, with the false discovery rate set at 15% (14).

Table 4
Mean percentage contributions of plant protein, carbohydrate, and fat to the diets of the hunter-gatherer groups in the sample compiled for the present study.

Group	Protein	Carbohydrate	Fat
Ache	6	80	14
Baffin Island Inuit	10	77	13
Gwich'in	8	80	13
Hadza	11	72	18
Hiwi	9	84	8
Hokkaido Ainu	17	76	8
Ju/'hosani	13	60	27
Nuxalk	7	81	12
Sahtú Dene and Métis	7	81	12
Wet'suwet'en	6	84	10

Discussion

The present study focused on the wild plant and whole-diet macronutrient percentages at the heart of the Paleo Diet. The whole-diet macronutrient ranges recommended by the Paleo Diet were originally calculated by Cordain et al. [7] with the aid of a set of wild plant macronutrient values for Indigenous Australians reported by Brand-Miller and Holt [8]. Cordain et al. [7] assumed that Brand-Miller and Holt's [8] wild plant macronutrient values are representative of all hunter-gatherers, but this assumption had not been tested before our study.

We began by recalculating whole-diet macronutrient percentages in the manner outlined by Cordain et al. [7] after replacing Brand-Miller and Holt's [8] data with Eaton and Konner's [9] macronutrient values for wild plants consumed by a sample of hunter-gatherer groups from Africa, Australia, and the Philippines. We used wild plant macronutrient values reported by Eaton and Konner [9] because Cordain et al. [7] suggested that they yielded similar whole-diet macronutrient percentages to those obtained in the study by Brand-Miller and Holt [8]. Subsequently, we repeated the exercise with wild plant macronutrient values we collated for a globally distributed sample of hunter-gatherer groups.

The results of the first analysis were clear-cut. We found that, contrary to what was assumed by Cordain et al. [7], Eaton and Konner's [9] data yielded significantly different whole-diet macronutrient ranges from the ones calculated with Brand-Miller and Holt's [8] data. The results of the second analysis were in line with those of the first. In every case, the differences between our wild plant macronutrient values and those reported by Brand-Miller and Holt [8] were large enough to have a significant impact on the whole-diet macronutrient estimates.

Table 5
Ranges of whole-diet macronutrient percentages obtained when the plant data compiled for this study were combined with Cordain et al.'s [7] equations for estimating macronutrient percentages, with and without use of the protein limit suggested by Cordain et al.'s [7].

Group	Without protein limit			With protein limit		
	Protein	*Carbohydrate*	*Fat*	*Protein*	*Carbohydrate*	*Fat*
Ache	14–53	28–52	16–54	14–35	28–52	16–54
Baffin Island Inuit	16–54	27–50	16–53	16–35	27–50	16–53
Gwich'in	15–54	28–52	16–53	15–34	28–52	16–53
Hadza	17–55	25–47	19–55	17–35	25–47	19–55
Hiwi	16–54	29–55	12–52	16–34	29–55	12–52
Hokkaido Ainu	21–57	27–49	12–52	21–34	27–49	17–52
Ju/'hosani	18–55	21–39	23–58	18–34	21–39	29–58
Nuxalk	14–53	28–53	15–53	14–33	28–53	15–53
Sahtú Dene and Métis	14–53	28–53	15–53	14–33	28–53	15–53
Wet'suwet'en	14–53	29–55	14–52	14–35	29–55	14–52
All groups	14–57	21–55	12–58	14–35	21–55	12–58

Table 6
Results of Wilcoxon signed ranks tests in which the whole-diet macronutrient values reported by Cordain et al. [7] were compared with whole-diet macronutrient percentages generated for the second part of this study.

Comparison	Protein	Carbohydrate	Fat
Cordain et al. vs. Ache	Z = −4.432 *P* = <0.001*	Z = −4.392 *P* = <0.001*	Z = −4.400 *P* = <0.001*
Cordain et al. vs. Baffin Island Inuit	Z = −4.551 *P* = <0.001*	Z = −4.418 *P* = <0.001*	Z = −4.403 *P* = <0.001*
Cordain et al. vs. Gwich'in	Z = −4.457 *P* = <0.001*	Z = −4.392 *P* = <0.001*	Z = −4.403 *P* = <0.001*
Cordain et al. vs. Hadza	Z = −4.562 *P* = <0.001*	Z = −4.392 *P* = <0.001*	Z = −4.463 *P* = <0.001*
Cordain et al. vs. Hiwi	Z = −4.526 *P* = <0.001*	Z = −4.392 *P* = <0.001*	Z = −4.386 *P* = <0.001*
Cordain et al. vs. Hokkaido Ainu	Z = −4.532 *P* = <0.001*	Z = −4.392 *P* = <0.001*	Z = −4.386 *P* = <0.001*
Cordain et al. vs. Ju/'hosani	Z = -2.646 *P* = 0.008*	Z = -5.000 *P* = <0.001*	Z = −4.420 *P* = <0.001*
Cordain et al. vs. Nuxalk	Z = −4.478 *P* = <0.001*	Z = −4.392 *P* = <0.001*	Z = −4.399 *P* = <0.001*
Cordain et al. vs. Sahtú Dene and Métis	Z = −4.478 *P* = <0.001*	Z = −4.392 *P* = <0.001*	Z = −4.399 *P* = <0.001*
Cordain et al. vs. Wet'suwet'en	Z = −4.432 *P* = <0.001*	Z = −4.392 *P* = <0.001*	Z = −4.390 *P* = <0.001*

* = p-value significant after correction for multiple unplanned comparisons with Benjamini and Hocheberg's [13] method, with the false discovery rate set to 15% [14].

Thus, our study showed that Cordain et al.'s [7] assumption that the wild plant macronutrient data reported by Brand-Miller and Holt [8] are representative for hunter-gatherers is incorrect. Significantly different whole-diet macronutrient ranges are obtained when wild plant macronutrient data for other groups of hunter-gatherers are used.

The obvious potential limitation of the study is the small size of the sample of hunter-gatherer groups used by Eaton and Konner [9] and the sample we assembled. To reiterate, Eaton and Konner [9] obtained data for 5 groups and we collated data for 10. The reason the samples are so small is that nutritional data for wild plant food items are very limited [15]. However, large samples would not have changed the key findings of our study. Including data for additional hunter-gatherer groups would not have decreased the new plant macronutrient ranges. Either it would have not altered the plant macronutrient ranges or it would have increased them. In the former case, the results of the study would have been the same, obviously. In the latter case, the assumption by Cordain et al. [7] that the wild plant macronutrient data by Brand-Miller and Holt [8] are representative for hunter-gatherers would have been refuted even more strongly, and the difference between the whole-diet macronutrient ranges reported by Cordain et al. [7] and our whole-diet macronutrient ranges would have been even larger. Thus, the small size of the samples we employed is not in fact a cause for concern vis-à-vis the key findings of our study.

The primary implication of the present study for the Paleo Diet is that its recommended target ranges for whole-diet protein, carbohydrate, and fat need to be revised. To reiterate, the whole-diet macronutrient ranges reported by Cordain et al. [7] were 19%–56% for protein, 22%–40% for carbohydrate, and 28%–58% for fat. Cordain et al. [7] argued that 35% is the maximum percentage of energy that humans can derive from protein and suggested that the protein range should therefore be capped at 35%. This upper protein limit was incorporated into the Paleo Diet, and so its recommended target ranges for whole-diet protein, carbohydrate, and fat are 19%–35%, 22%–40%, and 28%–58%, respectively.

None of the whole-diet macronutrient ranges generated in the second part of the present study (Table 5) is identical to the ranges reported by Cordain et al. [7]. Some of the ranges we calculated have lower low points than those reported by Cordain et al. [7]. For example, our range for protein for the Ache is 14%–35%, whereas our range for fat for the Hiwi is 12%–52%. Other ranges among those we computed have higher high points than those reported by Cordain et al. [7]. This is the case for all but one of the carbohydrate ranges. Thus, our results suggest that the Paleo Diet's macronutrient target ranges need considerable adjustment. Applying the protein limit suggested by Cordain et al. [7], the new whole-diet protein range is 14%–35%; the new whole-diet carbohydrate range is 21%–55%; and the new whole-diet fat range is 12%–58%. All 3 of these ranges are wider than those reported by Cordain et al. [7].

Recently, Pontzer and Wood [26] reported the results of an analysis of the Hadza diet in which they combined data on the macronutrient content of foods with field measures of food acquisition. They found considerable variation in the contribution of protein, carbohydrate, and fat to the Hadza diet over the course of a year. Protein ranged from 11% of total calories to 43%; carbohydrate ranged from 21% of total calories to 71%; and fat ranged from 13% of total calories to 36%. The median values for protein, carbohydrate, and fat were 21%, 61%, and 18% respectively. These results are noteworthy in the present context for 2 reasons. First, the lower limits of the ranges reported by Pontzer and Wood [26] are less than their Paleo Diet equivalents (protein: 11% vs. 19%; carbohydrate: 21% vs. 22%; fat: 13% vs. 28%), and the upper limit of the carbohydrate range reported by Pontzer and Wood [26] is higher than its Paleo Diet equivalent (71% vs. 40%). Thus, the results reported by Pontzer and Wood [26] support the idea that the Paleo Diet's current recommended macronutrient ranges are too narrow. The second reason why Pontzer and Wood's [26] results are noteworthy in the present context is that their ranges differ from the ones we obtained for the Hadza (11%–43% vs. 17%–35% protein, 21%–71% vs. 25%–47% carbohydrate, 13-36% vs. 19%–55% fat). This suggests that even the new recommended macronutrient ranges for the Paleo Diet we outlined in the preceding paragraph should be treated with caution. Although they are almost certainly more reliable than the Paleo Diet's original recommended macronutrient ranges, it should always be kept in mind that these are estimates derived from a particular set of data and equations and therefore may not represent the true values.

The Paleo Diet is often presented as a high-protein, low-carbohydrate, high-fat alternative to conventional recommended diets such as those put forward by the US Department of Agriculture (USDA) and World Health Organization (WHO) [3]. However, our whole-diet macronutrient ranges for hunter-gatherers overlap with the whole-diet macronutrient ranges recommended by the USDA and WHO, which are 10%–30% of calories from protein, 45%–65% from carbohydrate, and 25%–35% from fat [27, 28]. This means that the revised whole-diet macronutrient ranges for the Paleo Diet suggested by our study (14%–35% protein, 21%–55% carbohydrate, and fat 12%–58%) overlap with those of conventional recommended diets. This in turn casts doubt on one of the main justifications for adopting the Paleo Diet—namely that because it is vastly different from the conventional modern Western diet, it can reduce the probability of experiencing diseases associated with the typical modern Western lifestyle. Even if adhering to the revised whole-diet macronutrient ranges were to reduce the probability of experiencing lifestyle diseases, the fact that the ranges overlap with the whole-diet macronutrient ranges recommended by the USDA and WHO means that conventional recommended diets can also reduce the probability of experiencing lifestyle diseases. There may still be reasons for adopting the Paleo Diet rather than conventional recommended diets, but healthy whole-diet macronutrient percentages is not one of them.

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Author contribution

AR and MC designed the project. AR collected the data under MC's supervision. AR and MC ran the analyses, interpreted the results, and wrote the manuscript. Both AR and MC read and approved the final version of the manuscript.

Conflict of interest

The authors report no conflicts of interest.

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Data Availability

Data described in the manuscript are provided in the Supplementary Material.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ajcnut.2022.12.003.

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