

**PLANTS AND PRESUMPTIONS: AN ASSESSMENT OF
THE IMPACT OF PLANT MACRONUTRIENT
VARIATION AMONG HUNTER-GATHERERS ON THE
RECOMMENDATIONS OF THE PALEO DIET**

by
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Declaration of Committee

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Abstract

The Paleo Diet is a popular but controversial dietary regime that requires adherents to avoid domesticated plants and replicate the macronutrient distribution (i.e., the percentages of carbohydrates, protein, and fat) found in hunter-gatherer diets. In this thesis, I report a study in which I investigated an aspect of the Paleo Diet that has hitherto been overlooked – namely, its reliance on plant macronutrient values from a single country, Australia. First, I replicated the macronutrient consumption ratios reported in the study that underpins the Paleo Diet (Cordain et al. [2000] *American Society for Clinical Nutrition* 71, 682-692). I then examined the impact that an alternate set of plant values that Cordain et al. (2000) presented but did not use had on the macronutrient consumption ratios that Cordain et al.'s (2000) method yields. Next, I generated plant macronutrient values for a worldwide sample of ten recent hunter-gatherer societies, and statistically compared the new values to the ones Cordain et al. (2000) reported. Subsequently, I applied Cordain et al.'s (2000) method to the new plant macronutrient values with a view to generate new macronutrient consumption ratios. Thereafter, I statistically compared the new values to the values obtained by Cordain et al. (2000). The analyses revealed that there were some significant differences between the new plant macronutrient values and those that Cordain et al. (2000) created. The analyses also revealed that, in all cases, applying Cordain et al.'s (2000) method to the new macronutrient values produced macronutrient consumption ratios that differ significantly from those reported by Cordain et al. (2000). Together, the results of the analyses indicate that the Paleo Diet's macronutrient consumption recommendations are dependent on Cordain et al.'s (2000) sample. As such, the recommendations of the Paleo Diet need to be revised or abandoned.

Keywords: Human evolution; evolutionary medicine; human dietary variation; Paleo Diet; macronutrients

Dedication

This thesis is dedicated to my parents, Mary Caravias and William Ruffett.

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Chapter 1.

Introduction

A substantial increase in obesity, diabetes, cardiovascular disease, and other so-called lifestyle diseases in Western societies over the last five decades has prompted a surge of research regarding how individuals can make their diets healthier (e.g., Albenberg and Wu, 2014; Estruch et al., 2013; Lichtenstein et al., 2006; Swinburn et al., 2019; Willett et al., 2019). Changing the contributions of the three macronutrients –protein, carbohydrates, and fat – to people’s diets has been argued to be one way of reducing the probability of experiencing lifestyle diseases (Acheson, 2013; Solon-Biet et al., 2014; Solon-Biet et al., 2015). However, at the moment there is little consensus regarding the percentage of an individual’s diet that each macronutrient should comprise. The US government recommends that 10-30% of dietary calories should come from protein, 45-65% from carbohydrates, and 25-35% from fat (HHS and USDA, 2015), but many other macronutrient targets have been put forward in the last few decades (e.g., Aranceta and Pérez-Rodrigo, 2012; Bier et al., 1999; Brunner et al., 2001; Cordain, 2001, 2010; Prentice, 2005; Seidelmann et al., 2018; Wu, 2016).

One of the most prominent attempts to persuade people to alter their macronutrient intake is known as ‘the Paleo Diet’ (Cordain, 2001, 2010). Proponents of the Paleo Diet, which is sometimes referred to as ‘the Palaeolithic Diet’, ‘the Caveman Diet’, or ‘the Stone Age Diet’, claim that we can improve our health by eating food items that replicate the macronutrient distribution of the diets of humans who lived before the invention of agriculture in the Neolithic period (Cordain, 2001, 2010). They also argue that avoiding domesticated plant foods and dairy products will improve health (Cordain, 2001, 2010). There are two ideas here. One is that Neolithic societies experienced a shift in the relative contribution of carbohydrates, protein, and fat to their diets, and this shift had major negative effects on their health (Cordain, 2001, 2010). The other idea is that there has not been enough time since the Neolithic for the human genome to adapt to an agricultural diet, and this has led to a ‘mismatch’ between our evolved physiology and the highly processed agricultural diets that are the norm in Western societies (Cordain et

al., 2000; Eaton and Konner, 1985; Eaton et al., 1996; Eaton et al., 2001). The proponents of the Paleo Diet claim that this mismatch is responsible for the current pandemic of lifestyle diseases (Cordain et al., 2000; Eaton and Konner, 1985; Eaton et al., 1996; Eaton et al., 2001).

The macronutrient recommendations of the Paleo Diet are based on the results of a study that was published 20 years ago (Cordain et al., 2000). The authors of this study analysed the diets of 229 ethnographically-documented hunter-gatherer groups in an effort to determine the average macronutrient intake across these societies (see Chapter 3 for details of the method used). They found that the diets of the groups in their sample were high in animal-sourced foods and had macronutrient ranges of 19-35% protein, 22-40% carbohydrates, and 28-58% fat. Cordain et al. (2000) argued that these macronutrient ranges likely characterised pre-Neolithic hunter-gatherer diets as well as those of historic hunter-gatherers. They suggested that these ranges should be adopted in Western societies to address the lifestyle disease pandemic.

The following year, Cordain (2001) published a book that promoted the health benefits of a hunter-gatherer-style diet and drew on the results of Cordain et al.'s (2000) study to provide macronutrient recommendations for what such a diet should look like. In addition to the macronutrient recommendations, Cordain (2001) argued against the consumption of dairy, grains, legumes, sugar, and gluten on the grounds that these food items were not consumed in the Palaeolithic. He highlighted evidence for a decline in health after the transition to farming and argued that it was due to the consumption of these food items. Drawing on the aforementioned mismatch, which is commonly referred to as the 'Mismatch Hypothesis', he went on to suggest that dairy, grains, legumes, sugar, and gluten are still causing problems today because there has been insufficient time for humans to adapt to an agricultural diet. Cordain (2001) proposed that by following the diet outlined in his book, people could improve their health, reduce their risk of developing lifestyle-related diseases, and reverse pre-existing obesity, heart disease, and diabetes. Cordain published a revised version of his book in 2010, and this second edition prompted a surge of interest in the Paleo Diet (Figure 1).



Figure 1: A Google Trends Ngram that illustrates the popularity of the term ‘Paleo Diet’ over the last 16 years.

The graph shows how often the term was searched between 2004 and 2020. Here, 100% popularity refers to the point in time that the term was most frequently searched. The other percentages are a function of the term’s maximum popularity. For example, in January 2013 the term ‘Paleo Diet’ was at 100% popularity. Thus, every other point on the graph should be read in relation to January 2013. In January 2018, for example, the term ‘Paleo Diet’ was only 44% as popular on Google as it was in January 2013. This graph clearly shows the upturn in popularity for the term ‘Paleo Diet’ after 2010 when Cordain published his revised Paleo Diet book (see text for details).

Although Figure 1 suggests that interest in the Paleo Diet has declined somewhat in the last few years, it remains very popular. Schwartz and Stapell (2013) have estimated that three million people in the United States alone currently follow the Paleo Diet, and that the diet has millions more adherents elsewhere in the world. The diet’s popularity is also indicated by the fact that it is the focus of numerous recent books (e.g., Vartanian, 2015; Wolf, 2017), blogs (e.g., Rosen, 2020; Walker, 2020), and podcasts (e.g., Tam, 2017; Wolf, 2020). The Paleo Diet’s popularity has resulted in companies creating products to make the diet more accessible. This is illustrated by the existence of companies with brand-names like ‘Caveman’ and ‘Blue Dinosaur’ that sell Paleo Diet products (Figure 2). Additionally, a foundation has made available stickers that companies can use to indicate to consumers that their products are ‘Paleo Diet-friendly’ (Paleo Foundation, 2017; Figure 2). Lastly, there are now Paleo Diet-themed restaurants in a number of big cities, including Portland, Oregon (the ‘Cultured Caveman’ Café) and Vancouver, British Columbia (the ‘Festal Paleo Café’) (Figure 2).

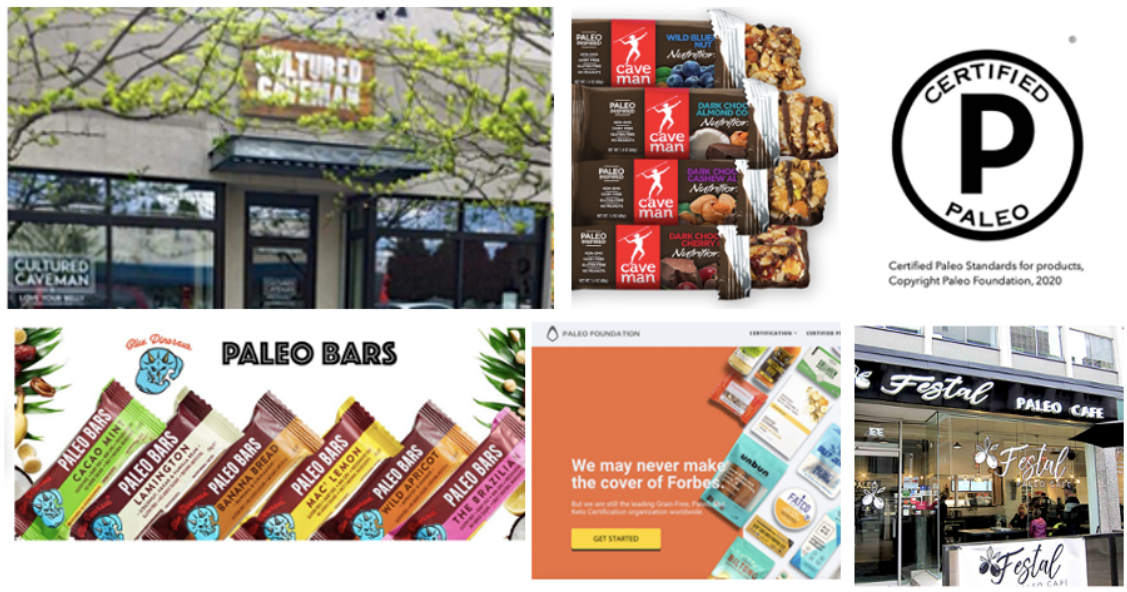


Figure 2: Images showing the Paleo Diet’s popularity in Western society. Top left –entrance of the Cultured Caveman Café in Portland, Oregon (Cultured Caveman, 2020). Top middle -- Caveman brand Paleo Bars (Caveman, 2020). Top right – certified Paleo sticker for Paleo Diet-friendly products (Paleo Foundation, 2020). Bottom left – Blue Dinosaur Paleo protein bars (Blue Dinosaur, 2020). Bottom middle – homepage of the website for The Paleo Foundation at the time this thesis was written (Paleo Foundation, 2020). Bottom right – Festal Paleo Café in Vancouver, BC (Hidden Gems, 2018).

Not surprisingly, given its popularity, the Paleo Diet has been the subject of a number of studies by nutritional scientists. The results of these studies have been mixed. Those that have focused on the diet’s short-term effects have concluded that it can be beneficial for weight loss and some chronic disease management (e.g., Boers et al., 2014; Frassetto et al., 2009; Masharani et al., 2015; Talreja et al., 2014). However, the few studies that have addressed the diet’s longer-term impact suggest it may be harmful over extended periods (Genoni et al., 2019; Jew et al., 2009; Smith et al., 2014). These studies indicate that the reliance on meat and fat and the elimination of dairy, gluten, and legumes increase LDL or ‘bad’ cholesterol, decrease HDL or ‘good’ cholesterol, result in nutrient deficiencies, and decrease gut microbial diversity (Genoni et al., 2019; Jew et al., 2009; Smith et al., 2014). Presently, therefore, it is not clear that the Paleo Diet is beneficial.

The Paleo Diet has also been assessed by a number of evolutionary anthropologists. These researchers have critiqued the diet’s fundamental assumptions as

well as the use of modern ethnographic groups as analogues for humans living in the Palaeolithic (Buckley and Buikstra, 2019; Eaton et al., 2001; Milton, 2000). To date, most evolutionary anthropologists who have reviewed the Paleo Diet have argued against its universality (e.g., Milton, 2000; Speth, 2010; Ungar, 2017). Interestingly, this includes one of the co-authors of the Cordain et al. (2000) paper that gave rise to the diet's macronutrient ranges (Speth, 2010).

The controversy that surrounds the Paleo Diet coupled with the diet's popularity make it an important topic for investigation. In order to understand whether the Paleo Diet actually represents an average hunter-gatherer diet it is necessary to explore the limitations of the founding study by Cordain et al. (2000). One issue that has not been investigated to date is the impact of cross-cultural variation in plant macronutrients on the Paleo Diet's macronutrient recommendations.

As noted earlier, Cordain et al. (2000) collated and analysed data for 229 recent hunter-gatherer groups to estimate average macronutrient values for hunter-gatherer diets. To control for the fact that the body fat of wild animals varies substantially during the year, they used several sets of macronutrient values for animal foods in their calculations. However, they only employed one set of macronutrient values for plant foods. These values were taken from Brand-Miller and Holt (1998) and are based on 829 wild plants that were traditionally consumed by Indigenous Australians.

Cordain et al. (2000) justified relying on Brand-Miller and Holt's (1998) Australian plant values on the grounds that they are similar to the average macronutrient values generated from a sample of five hunter-gatherer societies by Eaton and Konner (1985). However, there are two problems with Cordain et al.'s (2000) course of action. One is that Brand-Miller and Holt's (1998) values are similar to those of Eaton and Konner (1985) rather than identical, and Cordain et al. (2000) did not demonstrate that the differences have no impact on the overall macronutrient values yielded by their model. The other, more profound problem is that more than 80% of the societies in Cordain et al.'s (2000) sample are from North America, and it is not at all clear that it can legitimately be assumed that the macronutrient values of North American plants are similar to those of Australian plants. The similarity between Brand-Miller and Holt's

(1998) Australian values and Eaton and Konner's (1985) values does not help here because none of the five societies in the latter authors' sample is from North America.

This thesis reports a study in which I assessed the impact of Cordain et al.'s (2000) decision to rely on Brand-Miller and Holt's (1998) Australian plant macronutrient values. First, I replicated the Cordain et al. (2000) study to ensure comparability. I then applied Eaton and Konner's (1985) plant values to the Cordain et al. (2000) equations and investigated whether the results were statistically different. Next, I collected data on hunter-gatherer diets from the literature and compiled plant macronutrient tables for a worldwide sample of ten hunter-gatherer groups, including a number from North America. Subsequently, I statistically compared the new plant macronutrient values to the ones utilised by Cordain et al. (2000), i.e., Brand-Miller and Holt's (1998) Australian values. Lastly, I used my data and Cordain et al.'s (2000) method to generate new whole-diet macronutrient values and statistically compared the new whole-diet values with the ones reported by Cordain et al. (2000).

This thesis is structured as follows. In the next chapter, I provide the background information necessary to understand the study. In Chapter 3, I present the materials, methods, and results from replicating the Cordain et al. (2000) study and applying the Eaton and Konner (1985) values to Cordain et al.'s (2000) model. In Chapter 4, I present the materials and methods I employed to derive and compare the contributing plant food macronutrient values from ten hunter-gatherer societies, as well as the results from this analysis. I then present the materials and methods that I used to assess the impact that the values had when applied to the Cordain et al. (2000) model, as well as the results from this analysis. In Chapter 5, I discuss the study's limitations and the implications its results have for the Paleo Diet specifically, and for human nutrition more generally. I also discuss the importance of documenting the diets of traditional human societies. Chapter 5 ends with some recommendations for future research.

Chapter 2.

Background

This chapter provides the background information necessary to understand the analyses presented in Chapters 3 and 4. In section 2.1, I discuss hominin diets over the last 6-8 million years of our lineage's history. In section 2.2, I provide an overview of the findings of modern nutritional science regarding what constitutes a healthy human diet. In section 2.3, I discuss the three macronutrients – carbohydrate, protein, and fat – and their roles in maintaining homeostasis in the body. In section 2.4, I describe the basic tools that are used to interpret and measure the macronutrient composition of foods. In section 2.5, I discuss the standard methods to extract macronutrients from food items. In section 2.6, I outline the principles, background, and origins of the Paleo Diet. And in the final section of this chapter, I discuss the main criticisms of the Paleo Diet.

2.1. The Evolution of Hominin Diets

In this section, I provide a baseline summary of the very large body of research regarding hominin diet and subsistence. It is important to note that there are many aspects regarding hominin diet and subsistence that are still heavily debated or are controversial and are not covered in their entirety in this section. As such, this section provides a general summary of the major changes in hominin diet and subsistence over the last 6-8 million years, however, it does not provide an exhaustive review of all of the literature, theories, or aspects of hominin diets. The review covers the necessary topics and trends that will assist the reader in understanding both the Paleo Diet and the inferences that follow in the discussion and conclusion of this thesis.

Reconstructing the evolution of hominin diets is difficult and complex. This is because direct evidence of what extinct hominins ate is sparse. Due to the rarity of direct evidence of the food items that extinct hominins consumed, researchers have to employ indirect approaches to reconstruct past hominin diets. Currently, they utilise two such approaches. They study the diets of extant non-human primates and contemporary people who are living traditional lives, and they analyse the bones and teeth of extinct hominins

for indications of what they ate (Ungar and Teaford, 2002). The use of these techniques has produced well-accepted evidence that a shift in diet was crucial to the evolution of both early and later *Homo*. What is not well accepted is what the diet shifted to, and how this shift resulted in the physical and ecological traits that characterize modern humans (O’Connell et al., 2002; Ungar, 2017).

When investigating how hominin diets have changed over the last 6-8 million years, the difference between modern human and great ape diets is a useful place to begin. This is because modern human diets differ substantially from those of great apes. All great ape diets are heavily plant-based and generally ‘low-quality’ (Milton, 1999b; Milton, 2003), whereas modern human diets are ‘high-quality’ and include large amounts of animal food (Aiello and Wheeler, 1995; Milton 1999a; WHO, 2018). This difference is thought to be the result of hominin diets broadening over the course of hominin evolution to include more high-quality food (Aiello and Wheeler, 1995; Milton, 1993; Milton, 1999b; Milton, 2003). As a result, researchers think that the diet of the Last Common Ancestor (LCA) between humans and great apes was more similar to that of great apes than to that of modern humans (Lucas et al., 2008; Milton, 1993; Ungar and Teaford, 2002). This means that plant foods probably comprised ~94% of the LCA’s diet, with small animals, eggs, and insects making up the remaining ~6% (Milton, 1993).

Regarding diet, the terms ‘low-quality’ and ‘high-quality’ refer to the nutritional and caloric density of the foods consumed, and the terms ‘flexible’ and ‘specialized’ refer to the types of foods consumed. Here, the term ‘low-quality’ refers to a diet where the foods consumed are low in calories and nutrients, and high in fibre. As a result, large quantities of low-quality foods need to be consumed to satisfy an animal’s calorific and nutrient needs. Examples of low-quality foods are leaves, pith, and bark. In contrast, the term ‘high-quality’ refers to a diet where the foods consumed are high in nutrients and calories, and low in fibre. Smaller quantities of high-quality foods need to be consumed to meet an animal’s calorific and nutrient needs. Examples of high-quality foods are meat, nuts, and Underground Storage Organs (USOs). A ‘flexible’ diet is one where different types of foods and macronutrient combinations can be interchanged with no negative fitness outcomes as long as sufficient calories and nutrients are consumed. Species that have ‘flexible’ diets tend to consume varied diets and often do not adhere to

a specific combination of macronutrients (Cui et al., 2018; Raubenheimer and Simpson, 1997; Raubenheimer and Simpson, 2016; Simpson and Raubenheimer, 2003). Thus, when resources are scarce, species with flexible diets will survive on less preferable foods often referred to as ‘fallback foods’ (Marshall et al., 2009). Conversely, a ‘specialized’ diet, is one where the type of food and macronutrient combination are of primary importance. Species with ‘specialized’ diets will experience fitness consequences when their preferred resource is not available and their intake target macronutrient combination cannot be met (Cui et al., 2018; Poissonnier et al., 2018; Poissonnier et al., 2020).

Many species are thought to have existed between the LCA and modern humans. In order to provide a better understanding of the major dietary changes that have occurred in the hominin lineage since the LCA, I have separated the hominins into six groups. These groups are based on similarities in body size, encephalization, and diet, and correspond roughly to those proposed by Wood and Aiello (1998). Each new group represents a deviation from the previous group in all three respects, although some groups deviate to a larger degree than others. A summary of the hominin groups and their inferred diets is provided in Table 1. This table shows a dietary trend towards a more flexible, general, and high-quality diet as the reader moves from the LCA to the group I call the Later Humans. Each group is discussed in more detail in the text where I include the relevant fossil evidence and more detailed dietary inferences.

Table 1: Hominins and their diets. See text for details.

Hominin group	Inferred diet
LCA	Probably ~94% plant food with small animals, eggs, and insects making up the remaining ~6%.
Australopiths (<i>Australopithecus anamensis</i> , <i>Australopithecus afarensis</i> , <i>Australopithecus africanus</i>)	A gradually more flexible diet than the LCA. Still mostly herbivorous, but with a larger amount of small prey.

Hominin group	Inferred diet
Paranthropines (<i>Paranthropus aethiopicus</i> , <i>Paranthropus boisei</i> , <i>Paranthropus robustus</i>)	A plant-based and extremely flexible diet. The paranthropines were capable of eating soft fruits and animal foods, as well as hard and brittle nuts, seeds, and other tough foods.
Habilines (<i>Homo habilis</i> , <i>Homo rudolfensis</i>)	A very similar diet to the australopiths. Still mostly herbivorous, but likely including more animal food.
Early Humans (<i>Homo erectus</i> , <i>Homo heidelbergensis</i>)	A variable, flexible, more high-quality diet compared to the habilines. Likely containing more soft, high-quality foods than the habilines.
Later Humans (<i>Homo neanderthalensis</i> , <i>Homo sapiens</i>)	A flexible, generalist, and high-quality omnivorous diet.

The australopiths are the first hominin group after the LCA for whom a dietary change is thought to have occurred (Teaford et al., 2002). The species included in this group are *Australopithecus anamensis*, *Australopithecus afarensis*, and *Australopithecus africanus*. The australopiths are estimated to have weighed between 29 and 45 kg, and their average brain size is estimated to have been around 425 cc., which is an increase from an estimated average of 325 cc. for the LCA (McHenry, 1992; McHenry and Coffing, 2000; Pontzer et al., 2012). The australopiths are understood to have had large cheek teeth, strong jaws, and well-developed chewing muscles (Ungar and Sponheimer, 2011). These characteristics are different from the small teeth, jaws, and chewing muscles thought to characterize the LCA (Ungar and Sponheimer, 2011). Additionally, the isotope ratios and dental morphologies of both the LCA and the australopiths are consistent with a gradual increase in dietary flexibility amongst the australopiths (Teaford et al., 2002; Ungar et al., 2006; Ungar, 2017). The australopiths are still thought to have been mostly herbivorous, but the evidence suggests their diet was of marginally higher quality than that of the LCA because they consumed larger amounts of small prey (Sponheimer and Dufour, 2009).

The australopiths overlap in time with the paranthropines, who also exhibit dietary change over time. The species included in this group are *Paranthropus aethiopicus*, *Paranthropus boisei*, and *Paranthropus robustus*. The paranthropines were slightly larger than the australopiths, although they were still small compared to modern *H. sapiens*. The estimated weight for the paranthropines is between 32 and 49 kg, and their estimated average brain size is 525 cc. (Elton et al., 2001; McHenry, 1992). Like the australopiths, the paranthropines are characterized by large and thickly enameled teeth, strong jaws, and well-developed chewing muscles that get bigger as the species exist later in time (Ungar and Sponheimer, 2011). However, the paranthropines had significantly larger jaws and teeth than the australopiths (Wood and Strait, 2004; Ungar and Sponheimer, 2011). Previously, these morphological features were thought to be associated with a specialized dietary adaptation to hard and brittle nuts, seeds, and other tough foods (Wood and Strait, 2004). Now, however, increasing evidence from studies of resource-use, stable isotope analyses, and microwear texture analyses has contradicted the hypothesis that the paranthropines had specialized diets (Wood and Strait, 2004; Ungar and Sponheimer, 2011). As a result of these studies, researchers now think that the paranthropines' specialized anatomy is an adaptation to the foods that they were capable of eating instead of the foods that they habitually consumed. Their specialized anatomy may therefore indicate a more generalized diet, because it allowed less preferable, more difficult-to-process foods to be consumed when the preferred foods were not available (Sponheimer and Dufour, 2009; Sponheimer et al., 2006; Ungar and Sponheimer, 2011; Ungar, 2017).

With the genus *Homo*, the most significant dietary and anatomical changes occur, including significant encephalization. These changes began, although in a minor way, with the habilines. The habilines include the first members of the genus *Homo*: *Homo habilis* and *Homo rudolfensis*. The habilines were of a similar size to the australopiths and paranthropines, although their brains were marginally larger. The habilines are understood to have weighed between 32 and 52 kg, and their brains averaged approximately 650 cc. (McHenry, 1992; Wood, 2014; Wood and Collard, 1999). Their teeth and face sizes were similar to the australopiths (Wood, 2014), although their maxillary central incisors were larger (Teaford et al., 2002; Ungar et al., 2006). This

slight increase in incisor size may indicate that the habilines used their teeth differently from the australopiths and had a more variable diet (Ungar et al., 2006; Ungar, 2017). For a long time, *H. habilis* was thought to be the first hominin to use stone tools (Leakey et al., 1964), and therefore may have consumed more animal food than the australopiths and paranthropines (McHenry and Coffing, 2000; Teaford et al., 2002). If this is the case, the lack of significant differences in dentition may be the result of habilines' use of tools to cut up animal food instead of using their teeth to shear (Teaford et al., 2002). Although there is now evidence for stone tools at 3.3 million years ago (Harmand et al., 2015), which is before *H. habilis* first appears, the habilines are still associated with stone tools and are thought to have habitually used them (Teaford et al., 2002). As such, these inferences suggest that the habilines may have had a more flexible diet than the australopiths because they consumed more animal foods.

With the early humans, there was a substantial increase in brain size and a more obvious dietary change than in the habilines. The term 'early humans' refers to *Homo erectus* and *Homo heidelbergensis* who approached the weight of modern humans with a typical weight between 56 and 66 kg (McHenry and Coffing, 2000; Rightmire, 2003; Wood and Collard, 1999). With this group, the average brain size increased to 1000 cc. and is substantially larger than any of the other hominins before this point (Rightmire, 2003; Wood and Collard, 1999). In the early humans, post-canine tooth size, enamel thickness, and the size and shape of the mandibular corpus shrank to about the level exhibited by modern *H. sapiens* (Teaford et al., 2002; Wood and Collard, 1999; Ungar, 2017; Ungar et al., 2006). These changes suggest that the hominins were eating softer foods than the habilines and paranthropines. Of note, this change in tooth size and shape in the early humans was accompanied by an increased body size, a more simplified digestive anatomy, a more encephalized brain, and an expanded geographical range into more temperate regions (Aiello and Wheeler, 1995; Ungar, 2017). These collective changes suggest a significant dietary transition towards a more flexible, generalized, high-quality diet (Teaford et al., 2002; Ungar, 2017).

Lastly, the trend towards a more variable diet culminates in the later humans. This group comprises *Homo neanderthalensis* and *Homo sapiens*. The later humans are the largest and, by far, the most encephalized of the hominins with a weight range of 53-76

kg and an average brain size of 1400 cc. (Neubauer et al., 2018; Wood and Collard, 1999). They exhibit low levels of mandibular robusticity compared to the earlier hominins with the mandibles of *H. sapiens* being less robust than those of *H. neanderthalensis* (Teaford et al., 2002; Wood and Aiello, 1998). The later humans are also characterized by smaller, more thinly enameled teeth with *H. neanderthalensis* having generally thinner enamel than *H. sapiens* (Smith et al., 2012). Although smaller dentition normally indicates a more specialized diet, because the later humans were actively using tools and fire to process their food, the decrease in teeth and mandible size is thought to be coincident with an increased dietary variety (Fiorenza et al., 2010; Teaford et al., 2002; Ungar, 2017; Wrangham and Conklin-Brittain, 2003). The morphological data in combination with the isotopic and faunal data support a more variable diet for *H. sapiens* and indicate a diet that consisted of small and large prey from the land and sea, as well as an abundance of plant foods (Hoffecker, 2009, Richards et al., 2001). Conversely, the evidence points to the *H. neanderthalensis* diet having been high in animal food and low in plant food with the majority of the diet coming from large terrestrial mammals (Hoffecker, 2009; Richards et al., 2001).

With each hominin group that I have discussed above, I have included the average brain size. It is noteworthy that the changes in diet were frequently accompanied by a marked increase in brain size, that has, in turn, been linked with an equivalent decrease in overall gut size. Aiello and Wheeler (1995) first discussed the relationship between increased brain size and decreased gut size in a paper in which they hypothesized that the metabolic requirements of relatively large brains are offset by a corresponding reduction of the size of the gut in humans. This is now known as the 'Expensive Tissue Hypothesis'. Because brain tissue is metabolically expensive, Aiello and Wheeler (1995) hypothesized that there should be a correlation between relative basal metabolic rate (BMR) and brain size in humans and other encephalized mammals. As the human brain is so large, humans should have a remarkably high resting BMR. However, this is not the case. Aiello and Wheeler (1995) compared several other metabolically expensive organs in the human body and found that the gut is the only one that is noticeably small in relation to body size. Because gut size is correlated with diet, and smaller guts are not compatible with low-quality diets, the relationship between diet and relative brain size is

understood to be a relationship between relative brain size and relative gut size that is dependent on dietary quality (Aiello and Wheeler, 1995; Milton, 1999a). Aiello and Wheeler (1995) suggested that regardless of what selective regime was acting on large brains in humans, it could not be achieved without a shift to a high-quality diet unless there was a rise in the metabolic rate. Because humans do have a high-quality diet and do not have high BMRs, Aiello and Wheeler (1995) proposed that incorporating increasingly greater amounts of high-quality food into the diet facilitated encephalization.

As explained above, the expansion of the hominin brain from 400-500 cc to 1400 cc is associated with a more flexible and higher-quality diet. Although the brain did increase between many of the successive hominin species, there are two periods where the most expansion seems to have occurred (Aiello and Wheeler, 1995). Interestingly, the largest expansions are associated with the most significant dietary changes (Aiello and Wheeler, 1995). The first significant expansion occurred between the habilines and the early humans approximately two million years ago. Between these hominin groups, the brain increased from 650-750 cc to 850-1200 cc. The second period of expansion occurred between the early and later humans when brain size increased from 850-1200 cc. in *H. erectus* and *H. heidelbergensis* to modern levels of around 1400 cc in *H. neanderthalensis* and the earliest *H. sapiens* (Aiello and Wheeler, 1995). In support of the 'Expensive Tissue Hypothesis', the *Homo* diet is marked by versatility and consistent access to high-quality foods (Bibbitt et al., 2011; Sponheimer and Dufour, 2009; Ungar et al., 2006).

To understand how important hominin adaptations, such as the shift to a more variable diet, occurred, Potts (1998a) has proposed the Variability Selection Hypothesis (VSH). In the VSH, Potts (1998a; 1998b; 2002) links the environmental variability of the last five million years and the resource uncertainty that came with that, with adaptive change. The VSH is based on the understanding that species with generalist adaptations do well in a variety of conditions and will outperform species with specialized adaptations who are not able to handle the increased variation that results from environmental change. If there are multiple generations of heightened environmental variability, adaptability will be favoured by selection. Recently, there has been an influx of data that are consistent with a constantly and rapidly changing palaeoenvironment over

the past five million years of hominin evolution (e.g., Potts and Faith, 2015; Ungar, 2017). The oscillations are characterized by alternating cold/dry and warm/wet periods and are correlated with significant changes in hominin evolution including the split with the chimpanzee and bonobo lineage, the appearance of the earliest members of the genus *Homo*, and the spread of *Homo* out of Africa (Potts 1998b; Potts, 2002; Potts and Faith, 2015; Ungar, 2017; Ungar and Sponheimer, 2011). Because hominin diets appear to become more flexible over time, these correlations suggest that dietary flexibility may have been beneficial and selected for in hominins.

It is likely that the fluctuating climate impacted the hominin diet to some degree, possibly resulting in an adaptation to a more generalized diet (Potts, 1998a; Ungar, 2017; Ungar and Sponheimer, 2011). The fluctuating climate would have changed the hominin environment, and, by extension, what was available for hominins to eat (Potts, 1998a, 1998b; Ungar, 2017). This is important because what a species eats is equally dependent on what is available to be eaten and what the species can physically digest (Ungar, 2017). As the climate frequently changed, it would have been increasingly beneficial for hominins to consume varied diets in order to survive in multiple environments (Ungar, 2017). As a result, it is expected that hominin habitats also expanded. Indeed, the earliest members of the genus *Homo* and the later hominins are associated with diverse habitats as well as more flexible diets (Potts, 1998a; Teaford et al., 2002). Furthermore, after the emergence of *H. sapiens*, there is evidence for substantial climate changes during the Pleistocene (Potts and Faith, 2015; Ungar, 2017). These changing conditions would have continued to affect food resources. It is possible, therefore, that a strong selective regime for dietary generalism would have been maintained in *H. sapiens*.

Although *H. sapiens* dietary flexibility is widely understood to be correlated with, and possibly driven by, the shift to a higher quality diet, what these high-quality foods were is not agreed upon. Indeed, it is likely that high-quality food would have been preferable during times when food was scarce since less of it is needed to provide the same amount of energy as low-quality food (Aiello and Wheeler, 1995; Milton, 2003). When this is coupled with the increased energy demands of a large brain, a high-quality diet seems essential. There is debate, however, regarding whether *H. sapiens* high-quality diet was comprised of animal foods (meat, fat, and marrow) or plant-sourced USOs (e.g.,

Conklin-Brittain et al., 2002; Cunnane and Crawford, 2003; Mann, 2018; Milton, 2003; O’Connell et al., 2002). Both animal-sourced foods and plant USOs are nutrient- and calorie-dense and low in fibre. Animal foods provide energy in the form of protein and fat, and USOs provide energy largely in the form of carbohydrates. The debate surrounds whether it was the protein and fat in animal-sourced food that supported encephalization or the carbohydrates in USOs, and most scholars take one of these sides. However, some scholars suggest that both the meat and fat of animals and the high-carbohydrate USOs would have been consumed because both would have supported energetically expensive adaptations like the large brain (Bibbitt et al., 2011; Milton, 2003). These scholars propose that hominins could satisfy their protein needs and their mineral and vitamin requirements by consuming animal foods and could satisfy their energy needs by consuming calorie- and carbohydrate-rich plant foods like fruits, nuts, starchy roots, and honey (Milton, 2003). This combination of animal and plant foods would have resulted in a nutritionally adequate amount of protein, carbohydrates, fats, and micronutrients (Milton, 2003).

Presently, the debate continues, and researchers are not yet clear on which macronutrient was most important in supporting hominin encephalization (Conklin-Brittain et al., 2002; Cunnane and Crawford, 2003; Mann, 2018; Milton, 2003; O’Connell et al., 2002). Regardless, because human societies today consume a wide range of both animal and plant-sourced foods, omnivory, which increases dietary flexibility, must have been an important aspect of human evolution at some point (e.g., Buettner, 2015; Cordain et al., 2000; Willet et al., 2019).

The modern human diet has changed significantly since the first appearance of *H. sapiens* 200-300 kya, and varies considerably in today’s traditional societies (Buettner, 2015; Cordain et al., 2000; Kramer, 2018). One of the biggest dietary changes for many societies occurred at outset of the Neolithic period when there was a largescale lifestyle change from hunting-and-gathering to farming. Although there was not a single Neolithic transition – the subsistence change took place independently and at different times all over the world – the shift from hunting-and-gathering to agriculture and animal husbandry resulted in a significant dietary change, substantial population increase, and considerable technological advancements from which large-scale societies eventually

emerged (Cochran and Harpending, 2009; Cohen and Armelagos, 1984; Larsen, 2006; Larsen et al., 2019). Many societies in different parts of the world adopted agriculture, but many societies did not (e.g., the hunter-gatherers that are the subject of Cordain et al., 2000 and this thesis). The result is that modern humans exhibit a high degree of variation.

The changes in diet associated with the transition to farming correlate with evidence for a decline in health in a number of parts of the world. Poor health is indicated in the archaeological record through a higher frequency of bone pathologies suggestive of increased dental carries and other markers of dental disease, physiological stress marks on bones, and an overall decrease in height (Cohen and Armelagos, 1984; Richards, 2002; Ungar and Teaford, 2002). Some scholars propose that these negative health effects were the result of an increased dependence on cereal grains, decreased dietary breadth, and a reduction of fruit, vegetable, and meat consumption, all of which were previously major dietary components (e.g., Cordain, 1999; Eaton et al., 2002). This argument forms the basis for the Paleo Diet. However, archaeological and ethnographic evidence suggests starchy food was important in pre-agricultural human diets and may have provided key nutrients for hominin encephalization (e.g., Hardy et al., 2015; Reynolds et al., 2019). As a result, it is not possible to make any conclusive statements regarding the reason for the post-agriculture health decline.

2.2. What is a Healthy Diet?

Before discussing what comprises a healthy diet, it is first necessary to define a ‘healthy’ diet. ‘Healthy’ is often used to describe a diet that may do a number of things including maximizing lifespan, minimizing disease, minimizing weight, and maximizing physical function. As this thesis, and the Paleo Diet, utilise an evolutionary framework, a healthy diet is defined as a diet that maximises an individual’s physical function and, by extension, their reproductive fitness.

A focus on better understanding how healthy diets can improve human health and wellbeing has become an important topic as a result of the recent rise in lifestyle diseases. Today, this is even more important because unhealthy diets endanger human health more than unsafe sex, drug, alcohol, and tobacco use combined (Willet et al., 2019). Unfortunately, the majority of Western individuals consume an unhealthy diet and recent

American, British, and European censuses indicate that over half of these populations are either overweight or obese (CDC, 2020; Hales et al., 2015; NHS, 2020; WHO, 2013).

The public understanding of what constitutes a healthy diet is complicated by the relatively new status of nutritional science. While diet and nutrition have been studied for millennia, nutritional science is only a little over 100 years old (Mozaffarian et al., 2018). Because of this, the scientific consensus about what comprises a healthy diet has changed considerably over the last century and remains contested (WHO/FAO, 2003).

Since the 1950s, nutritional guides for the public have changed alongside the data and continue to be updated. For example, the United States Department of Agriculture (USDA) and the US Department of Health and Human Services (HHS) jointly publish a nutritional and dietary information and guidelines report for the general public every five years (HHS and USDA, 2015). However, as evidenced by the growing obesity epidemic, most people are not consuming a healthy diet (WHO, 2018).

Over the past several decades, nutritional research has shifted its focus from investigating the effects that single nutrients have in the body, to considering the complex role that overall nutrition and diet play in non-communicable chronic disease management (Mozaffarian et al., 2018). This is in contrast to earlier nutritional science which focused on the discovery, isolation, and synthesis of essential micronutrients and their role in deficiency diseases (Backstrand, 2002; Dupont and Beecher, 2017; Mozaffarian et al., 2018; Waugh and King, 1932; Willet et al., 2019). The outcomes of early nutritional science reduced the number of nutritional deficiencies in the population, but the findings resulted in a reductionist approach in which single nutrients were thought to directly cause health problems via deficits or excesses (Dupont and Beecher, 2017; Mozaffarian et al., 2018; Scrinis, 2013). This was extended to address the rise in diet-related non-communicable diseases by focusing on total fat, saturated fat, and sugar as the direct causes of heart disease, coronary disease, cancer, and many other conditions (Keys et al., 1986; Kearns et al., 2016; Mozaffarian et al., 2018). In recent years, nutritional science has changed to focus on the nutritional adequacy of the overall diet to mitigate the risk of developing non-communicable diseases. Scientific studies published over the past 20 years suggest that it is overall diet not individual nutrients that negatively impact human health and spur disease (Micha et al., 2017; WHO/FAO, 2003). Nutritional

guidelines do still advise the public to limit excess fat and sugar, but these nutrients are no longer thought to directly cause non-communicable diseases (Health Canada, 2019; HHS and USDA, 2015; Mozaffarian et al., 2018; Willet et al., 2019).

Regarding what constitutes a healthy diet, the current WHO reference diet advocates that individuals consume a sex- and age-appropriate number of calories from a diversity of plant-based foods, lesser amounts of animal-sourced foods, and more unsaturated than saturated fats (Willet et al., 2019). The WHO does not consider the proportion of macronutrients in the diet to be important as long as an individual is consuming a sufficient amount of each (WHO, 2018). Instead of providing macronutrient guidelines, which are dependent on the individual (WHO, 2020), the WHO provides general guidelines that humans globally can refer to (WHO, 2018). The WHO reference diet is high in vegetables, fruits, whole grains, legumes, nuts, and unsaturated oils; contains low or moderate amounts of seafood and poultry; and limits red meat, processed meat, added sugar, refined grains, and starchy vegetables (WHO, 2018; Willet et al., 2019). These recommendations were created in order to address both public and environmental health concerns, as food production can contribute significantly to global climate change (Baroni et al., 2007; Willet et al., 2019). Unfortunately, the typical Western diet lacks fibre and exceeds the upper limits for fat, saturated fat, free sugars, and sodium (WHO, 2018). This is partly due to an over-reliance on processed foods in the West, that, in the quantities consumed, can be harmful to physical and environmental health (Grotto and Zied, 2010; Moubarac et al., 2013).

The WHO reference diet is very similar to the dietary guidelines of most countries as all of these guidelines are modelled off of the same scientific data and the WHO is the global health authority (e.g., Health Canada, 2019; HHS and USDA, 2015; NHS, 2019; Willet et al., 2019). However, the WHO guidelines are different from the Paleo Diet presented by Cordain (2001). This is notable because Cordain's (2001) Paleo Diet is meant to be a reference worldwide human diet. The discrepancy between Cordain's (2001) Paleo Diet and the WHO reference diet will be discussed in section 2.7 where I consider the critiques of the Paleo Diet.

2.3. Macronutrients

All foods that humans consume consist of three macronutrients—protein, carbohydrates, and fat. The body breaks down and utilises these macronutrients for a variety of physical functions including, but not limited to, protein synthesis, energy conversion, and energy storage. Accordingly, sufficient quantities of each macronutrient are important for maintaining health (Goodpaster and Sparks, 2017; Saltin and Gollnik, 1983; Storlien et al., 2004).

I will begin by discussing the function and role of protein in the body. Protein is made up of amino acids, which are the organic compounds that the human body uses to form cells. Amino acids are chemically comprised of an amino group and a carboxylic group (Akram et al., 2011). Amino acids are required to regulate multiple processes in the human body such as gene expression and protein synthesis (Akram et al., 2011; Wu, 2016). There are 20 different types of amino acids (Institute of Medicine, 2005). Nine of them are not synthesized by the human body and are considered essential, while 11 can be synthesized and are considered non-essential (Institute of Medicine, 2005). If an individual does not consume all nine essential amino acids, the body's day-to-day recovery and function are compromised (Institute of Medicine, 2005; Wu, 2016).

Protein is physiologically important. Protein undernutrition results in stunting, anemia, physical weakness, edema, vascular dysfunction, and impaired immunity (Speth, 2010; Wu, 2016). However, more protein is not always better. Negative health effects are also associated with protein overconsumption. These negative effects include digestive, renal, and vascular abnormalities, as well as death in extreme instances (Speth, 1991; Speth, 2010; Wu, 2016). Protein overnutrition is roughly defined as a prolonged protein consumption of greater than 2g/Kg of body weight (BW) in most subjects, and protein undernutrition as an extended protein consumption below 0.75g/Kg BW (Wu, 2016).

Although protein under- and over-nutrition can lead to serious health problems, most people in the West are not at risk of either (Willet et al., 2019). For most individuals, protein quality is more important than protein quantity. This is because not all protein sources are equivalent. For example, most plant-sourced foods do not contain all nine essential amino acids, but animal-sourced foods do (Wu, 2016; Young and

Pellett, 1994). When plant sources are combined, however, it is possible to obtain all the essential amino acids. Adequate consumption of high-quality proteins from animal-derived foods or a combination of plant-source foods is essential for optimal human growth and development (Wu, 2016; Young and Pellett, 1994).

Turning now to carbohydrates, since the 1950s nutritional scientists have identified many types of carbohydrate that vary in chemistry and physical form (FAO, 1998). At the most basic level of organization, carbohydrates are classified as either available or unavailable (Cummings et al., 1997). Available carbohydrates are readily absorbed into the body to provide energy (Cummings et al., 1997). In contrast, unavailable carbohydrates, as their name suggests, are not easily digested by the body but are passed through to the colon where the gut bacteria break them down into absorbable short-chain fatty acids (Cummings et al., 1997).

Carbohydrates are also divided into three major categories based on how many sugar molecules they contain. These categories are sugars, which contain one or two sugar molecules, oligosaccharides, which contain three to ten sugar molecules, and polysaccharides, which contain more than ten sugar molecules (FAO, 1998; Institute of Medicine 2005). Each of these is further divided. Sugars are subdivided into monosaccharides, disaccharides, and sugar alcohols; oligosaccharides are subdivided into malto-oligosaccharides and other oligosaccharides; and polysaccharides are subdivided into starch and non-starch polysaccharides (FAO, 1998; Institute of Medicine, 2005).

The physical structure of the carbohydrate cell wall has been found to affect satiety and both the rate and extent of digestion (Cummings et al., 1997; FAO, 1998; Greenfield and Southgate, 2003). This has led to carbohydrates being considered in terms of their quality. High-quality carbohydrates, also referred to as low-glycemic or complex carbohydrates, are slowly released and utilized by the body whereas low-quality carbohydrates, also referred to as high-glycemic or simple sugars, are rapidly released and absorbed by the body (Cummings et al., 1997). Diets rich in high-quality carbohydrates are understood to protect against non-communicable diseases and may reduce mortality risk. Conversely, diets biased towards low-quality carbohydrates are associated with weight gain and metabolic disease (Reynolds et al., 2019).

Carbohydrates are considered to be an important part of a healthy diet (Ma et al., 2005; WHO, 2018). They are the body's main source of energy and they are responsible for running many of the major organs in the body, including the brain (Institute of Medicine, 2005; Steele, 1981). Although humans can survive on low-carbohydrate diets (e.g., Foster et al., 2003; Westman et al., 2002), brain function and athletic performance are impaired and mortality is thought to increase when this is adhered to long-term (Institute of Medicine, 2005; Michalczyk et al., 2019; Seidelmann et al., 2018; Trichopoulou, 2007).

Most dietary advice is that carbohydrates should be consumed in balance with the other macronutrients (Ma et al., 2005; WHO, 2018). A recent meta-analysis using US data has emphasized the importance of a moderate carbohydrate intake (Seidelmann et al., 2018). The results from this study produced a U-shaped relationship between the percentage of energy from carbohydrates and all-cause mortality, with the lowest risk bracket being 50-55%, and increased mortality with both low (<40%) and high (>70%) carbohydrate diets. Although this potentially indicates the importance of a moderate carbohydrate intake, the study is limited in that carbohydrate quality was not considered.

Dietary fat is the third and final macronutrient that I will discuss. Dietary fat is divided into three categories: triglycerides, phospholipids, and sterols. The vast majority of dietary fats are triglycerides that are stored in body fat cells and are transported through the blood stream (FAO, 2018; Institute of Medicine, 2005). Once triglycerides are consumed through food, they are either used immediately for energy or are stored in body fat and converted into energy between meals. (FAO, 2018; Institute of Medicine, 2005). However, it is not only excess dietary fat that is stored in body fat cells; any excess calories consumed are converted into triglycerides for storage. Triglycerides are made up of three fatty acids that are esterified to a glycerol molecule. Fatty acids are classified according to chain length, the designations of which are 'short chain', 'medium chain', and 'long chain' (FAO, 2018; Institute of Medicine, 2005). These designations correspond to the number of carbon bonds in the chain: 4-6, 8-10, and 12-18 respectively. Triglycerides are also classified according to the presence or absence of double bonds. Unsaturated fats contain them; saturated fats do not (FAO, 2018; Institute of Medicine, 2005). Unsaturated fats are further subdivided into 'monounsaturated fatty acids'

(MUFAs) if they contain one double bond and ‘polyunsaturated fatty acids’ (PUFAs) if they contain multiple double bonds. On the basis of where the double bond starts, a PUFA is called either an omega-3 PUFA or an omega-6 PUFA (FAO, 2018; Institute of Medicine, 2005). Phospholipids and sterols are rarely found in foods, so I will not discuss them here.

Dietary fat is important for overall health and physical function (FAO, 2018). Not only is it an important source of energy, it also facilitates the absorption of fat-soluble dietary components including essential vitamins that cannot otherwise be absorbed (e.g., vitamins A, D, E, and K), and it is the source of essential fatty acids that the body cannot synthesize (Aranceta and Pérez-Rodrigo, 2012; Lichtenstein et al., 1998).

Despite the importance of dietary fat in the diet, it has long been linked with weight gain and metabolic diseases (e.g., Keys et al., 1986). However, recent reports suggest there may be insufficient evidence for these associations (e.g., Melanson et al., 2009; Liu et al., 2017). Although the current evidence suggests that high levels of saturated fats are correlated with lifestyle diseases (e.g., Aranceta and Pérez-Rodrigo, 2012; Riccardi et al., 2004), some researchers suggest that low fat-diets may elicit biological responses that hinder weight loss such as increased hunger, slowed metabolism, and other markers of the starvation response (e.g., Ludwig and Friedman, 2014; Ludwig, 2016). Currently, there are no clear benefits for a low-fat, high-carbohydrate diet in relation to blood lipids, glucose, or blood pressure (Bueno et al., 2013; Yancy et al., 2004). Moreover, although low-fat diets can reduce LDL or ‘bad’ cholesterol, they also reduce HDL or ‘good’ cholesterol, increase triglycerides, and increase the risk of essential fatty acid and fat-soluble vitamin deficiencies (Aranceta and Pérez-Rodrigo, 2012).

The potential negative health effects of low-fat diets are illustrated by the low-fat, high-carbohydrate dietary trend that was popular in the 1980s and 1990s. This fad limited total fat intake to less than 30% of daily energy in an effort to combat the growing obesity epidemic. Today, almost 40 years later, the prevalence of obesity and diabetes has increased significantly, even though the proportion of fat in the US diet has decreased by around 25% (Ludwig, 2016). Although this research cannot definitively blame low-fat diets as the cause of increased obesity prevalence in the American population, some

research on the impact of low-fat diets has shown that subjects on this regime for long periods of time often increase their energy intake resulting in weight gain (Lichtenstein and Van Horn, 1998). Additionally, research over the last 20 years suggests that many foods that were previously restricted because of their high fat content, such as nuts and full-fat dairy, are actually associated with low rates of weight gain (Kratz et al., 2013; Mattes et al., 2008). The majority of the data suggests that dietary fat is best consumed in moderation with the other macronutrients (Willet et al., 2019; WHO, 2018).

2.4. Food composition Databases and nutrient composition tables

Food Composition Databases (FCDs) and nutrient composition tables, also known as nutrient tables, are the basic tools used for quantitative nutrition research (Greenfield and Southgate, 2003). FCDs are databases that contain the macro- and micro-nutrient contributions of foodstuffs (Greenfield and Southgate, 2003). FCDs usually list the composition of foods commonly consumed in a particular country, but FCDs that list the foods commonly eaten by a given culture are sometimes created as well (Greenfield and Southgate, 2003). FCDs have multiple uses. For example, they are used to evaluate diets in order to develop food and nutritional policies for countries. They are also used as a reference in the food industry for nutritional labelling. In addition, they are used to evaluate the results of dietary recall surveys (Greenfield and Southgate, 2003). Nutrient tables, in contrast, are the specific tables that list the approximate calories, macro-, and micronutrients of individual food items (Greenfield and Southgate, 2003).

In order to create FCDs and nutrient tables, the nutritional composition of the food items being included needs to be known. The nutritional composition of a food item is arrived at by extracting the nutrients from the given food item (Greenfield and Southgate, 2003). Because this thesis deals with macronutrients, I will only discuss the methods that are used to extract macronutrients.

There are numerous methods to extract macronutrients from foods, however, not all of the methods will yield the same result (Greenfield and Southgate, 2003). Between the 1950s and early 2000s there was an increase in methodological variability to extract macronutrients (Greenfield and Southgate, 2003). The different methods were not equivalent, but researchers used them interchangeably in nutrient tables and FCDs

(Greenfield and Southgate, 2003). This resulted in inaccuracies in macronutrient extraction, inconsistencies amongst FCDs and amongst nutrient tables, and misrepresentation in the scientific literature (Greenfield and Southgate, 2003). In order to improve this state of affairs, the Food and Agriculture Organization of the United Nations (FAO)/Association of Official Analytical Chemists (AOAC) moved to standardize the methods used in food nutrient analyses and FCDs (Greenfield and Southgate, 1992, 2003). This standardization was imposed to ensure that the most accurate methods were being used to extract macronutrients, and to ensure that dietary analyses were conducted on data that had been extracted in the same way. Today, most researchers adhere to the FAO/AOAC standardized methods when creating FCDs, and dietary comparisons are only considered reliable if the standardized methods were adhered to (Greenfield and Southgate, 2003).

Unfortunately, although the methods for nutrient analyses have been standardized, the standardized methods are not yet universally applied in all nutrient tables (Greenfield and Southgate, 2003). Where and when a food analysis has taken place will influence the methods that were used to extract nutrients. Older nutrient tables or nutrient tables created in laboratories with outdated equipment may use methods that are no longer considered acceptable (Greenfield and Southgate, 2003). This is because methods were only standardized in 2003 and some analytical facilities still have not been updated with the technology to employ the standard methods (Greenfield and Southgate, 2003). Improving FCDs and nutrient tables is a focus of ongoing work. Greenfield and Southgate (2003) discuss how to proceed when it is not possible to use the standardized methods in analyses. They have divided the methods for each macronutrient into optimal methods and acceptable methods so that analyses can be done with older data. These methods are outlined in Table 2 and discussed in section 2.5.

Although the methodology is now both more accurate and consistent, there are complications when calculating food composition due to the variation that is inherent in foods (Greenfield and Southgate, 2003). Foods vary significantly in their composition as a result of genetic and environmental factors. Plant foods tend to vary more in their nutrient composition than animal foods do (De Cortes Sanchez-Mata and Tardio, 2016). Even plant foods from the same region may exhibit different nutrient levels. For example,

a study by Bhandari et al. (2003) showed that four varieties of Nepalese wild yam varied in their macronutrient content based on the environment that the yam was grown in. Similarly, Henry et al. (2019) found that the nutritional quality of plants can be significantly affected by season, habitat, plant type, and plant part. As a result, it is necessary to consider the variability in plant food composition when compiling FCDs. This is done by ensuring a sufficient sample of the plant food being analyzed is collected, and by considering a range when calculating nutrient composition.

Because plant foods are so variable, the sampling method that is employed to construct FCDs is an important determinant of an FCD's overall quality (Greenfield and Southgate, 2003). As such, sampling methods have been standardized to ensure FCD quality (Greenfield and Southgate, 2003). A sufficient sample that accounts for the variation that plant foods exhibit is considered to be between 100-500g of a given plant food (Greenfield and Southgate, 2003). In order to arrive at a reasonable range for the nutrient composition, the macronutrients should be extracted from 10-12 food samples of 100-500g, and an average of these 10-12 samples should be input in the FCD (Greenfield and Southgate, 2003). When this method is followed, any values that lie outside a 'reasonable variability' will be obvious (Greenfield and Southgate, 2003). Reasonable variability depends on the food in question and the variation that is observed for its nutrients (Greenfield and Southgate, 2003). In general, reasonable variability means that any outlier results will not be used in the FCD, and the average for a given food item will be calculated without the outliers (Greenfield and Southgate, 2003). It is important to note that FCDs offer estimates that are the result of an average of the foods sampled. Therefore, they cannot accurately depict the composition of a single food sample (Greenfield and Southgate, 2003).

Wild foods pose particular problems for nutrient assessment because they tend to vary more in composition and maturity than cultivated foods (Greenfield and Southgate, 2003). Additionally, because wild foods are not consumed as frequently as farmed foods in most populations, they may be difficult to identify (Greenfield and Southgate, 2003). Random sampling, which is conducted in such a way that every food item in a population is equally likely to be selected for sampling, is the optimal sampling strategy (Greenfield and Southgate, 2003). However, it is difficult to implement random sampling for wild

foods. Often, ‘convenience sampling’, which refers to taking any samples that one comes across, is the only option (Greenfield and Southgate, 2003). As long as this approach is noted in the database, it is acceptable and represents the standard sampling method for uncultivated foods (Greenfield and Southgate, 2003).

Understanding metabolizable energy is necessary when interpreting FCDs and nutrient tables. Metabolizable energy refers to the energy (in kcal or kJ) that is available to the human body for metabolism and function. The total metabolizable energy of food is most frequently calculated by summing the metabolizable energy of protein, fat, and carbohydrates. In the early 1900s, methods were standardized to calculate the metabolizable energy of macronutrients; these methods are still widely employed today (Atwater and Bryant, 1906; Atwater, 1910). The values currently used for the metabolizable energy of macronutrients (ME_n) are those published by Atwater and Bryant (1906). These values, which are commonly referred to as ‘Atwater factors’, are 4 kcal/g of carbohydrate (c), $ME_c = 4$ kcal/g; 9kcal/g of fat (f), $ME_f = 9$ kcal/g; and 4 kcal/g of protein (p), $ME_p = 4$ kcal/g.

Although the Atwater factors are widely used, they are not perfectly reliable (Baer and Novotny, 2019; Novotny et al., 2012; Zou et al., 2007). Since the early 1900s, the energy content of protein, fat, and carbohydrates of different food items have come to be understood to differ both inherently and due to different rates of digestion, absorption, and metabolism (FAO, 2019b). In some instances, the measured metabolizable energy and the energy calculated by the Atwater factors can differ by as much as 20% (Sánchez-Peña et al., 2017). Although the metabolizable energy from macronutrients does vary, the Atwater factors are still considered reasonably accurate and remain widely used in FCDs and nutrient tables (Southgate and Durnin, 1970).

2.5. Measuring the macronutrient composition of food items

As mentioned above, multiple analytical methods exist to extract each macronutrient from food items. Method standardization has mitigated the problem of inaccurate macronutrient and calorie values (Greenfield and Southgate, 2003). However, the standardized methods are still subject to some error. Currently, the standardized methods are the most accurate methods to extract macronutrients from food (Greenfield and

Southgate, 2003). Because method consistency can mitigate methodological errors, interpretations that are made on the basis of the standardized methods for protein, fat, and carbohydrates can be considered meaningful (Greenfield and Southgate, 2003). In this section I discuss the accepted methods for protein, fat, and carbohydrate extraction. Table 2 provides a summary of the approved standard methods of analysis from Greenfield and Southgate (2003).

Table 2: A summary of the approved standardized methods of analysis (Greenfield and Southgate, 2003).

Macronutrient / Metabolizable Energy	Standard Method
Protein	<p>Optimal: Extracting and summing the amino acids is recommended, although rarely possible.</p> <p>Acceptable: Total N* x 'Jones' factor (sum of amino acids). Note: Nitrogen conversion factor of 6.25 is appropriate where the precise factor is not known).</p> <p>*N should be extracted via the Kjeldahl method ideally although a similar N extraction method like the Dumas method can often be appropriate.</p>
Fat, total (or as triglyceride equivalent)	<p>Optimal: Summing individual triglycerides which are extracted separately, or a mixed solvent extraction.</p> <p>Acceptable: Gravimetric method using a Soxhlet extractor for solid food items that are low in structural fat or another extractor liquid food items or food items high in structural fat.</p>
Carbohydrate, available and/or total	<p>Optimal: Extract the individual carbohydrates present in each food sample and sum the resulting saccharides together.</p> <p>Acceptable: The 'by-difference' method.</p>
Metabolizable energy	<p>Optimal: Calorimeter to directly measure the metabolizable energy.</p> <p>Acceptable: Summing the proximal parts based on the Atwater factors.</p>

Protein is a relatively straightforward nutrient to extract from foods. All protein is made up of nitrogen, and most protein extraction methods determine total protein indirectly by analysing the nitrogen contained in a given food item (animal or plant) (FAO, 2019a). Because protein is not directly extracted, estimates are based on two assumptions. The

first is that dietary carbohydrates and fats do not contain nitrogen, and the second is that nearly all of the nitrogen in the diet is present as amino acids in the proteins (FAO, 2019a). So far, the first assumption holds true, but there is some debate about the second assumption as nitrogen has been found in variable quantities of other compounds such as free amino acids, nucleotides, creatine, and choline (FAO, 2019a.). Despite this, analysing the nitrogen content of food is still the best way to estimate the protein content of foods (Greenfield and Southgate, 2003).

The protein content of foods is determined by extracting the total nitrogen (N) contained in a food item and multiplying the nitrogen by a conversion factor (Greenfield and Southgate, 2003). Protein is understood to contain 16% nitrogen on average (FAO, 2019a). This means that for every 1g of protein, there is approximately 0.16g of nitrogen. In order to convert the extracted nitrogen into protein, a conversion factor of 6.25 was arrived at by dividing 0.16 into 1 (FAO, 2019a). From this, an equation to calculate protein content of a given food was created. The equation is $N \times 6.25$ where N represents the extracted nitrogen in grams (FAO, 2019a). For many years, it was thought that the 16% nitrogen composition of protein was consistent, and 6.25 was used as the standard nitrogen conversion factor (FAO, 2019a). In 1941, however, it was discovered that although on average protein contains 16% nitrogen, the nitrogen content of specific amino acids varies according to the amino acid's molecular weight and the number of nitrogen atoms that it contains (Jones, 1941). Because of this, the nitrogen content of proteins actually varies from 13-19% (Jones, 1941). By dividing 0.13 and 0.19 into 1, this equates to a range of nitrogen conversion factors from 5.26-7.69. When Jones (1941) discovered the varying nitrogen content of protein, he suggested that the conversion factor for nitrogen should be changed to whichever factor is specific to the amino acids in question. The factor is now referred to as the 'Jones factor' and is widely used (FAO, 2019a).

Currently, the FAO-recommended method to calculate the protein content of a food item is to extract the nitrogen, determine what percentage nitrogen the amino acids in question contain, multiply the nitrogen by the appropriate Jones factor, and sum the Jones factors together (Greenfield and Southgate, 2003). Although this is the case, the analysis to extract specific amino acids is costly, and is not frequently used (Greenfield

and Southgate, 2003). When data on amino acids are not available, determining protein based on total nitrogen content by the Kjeldahl method or another similar method multiplied by 6.25 is acceptable (Greenfield and Southgate, 2003).

To run the Kjeldahl nitrogen assay, a food sample must first be heated to between 360 and 410°C with concentrated sulfuric acid (FAO, 2019a). The sulfuric acid decomposes the sample by oxidizing it and the reduced nitrogen is released as ammonium sulfate. Decomposition is complete when the resulting liquid becomes clear and releases fumes (FAO, 2019a). The amount of nitrogen in the sample is then measured via titration (FAO, 2019a). Catalysts can be used in Kjeldahl digestion to accelerate oxidation and more quickly determine the total nitrogen (FAO, 2019a). Mercury, selenium, titanium, and copper are all approved catalysts; however, mercury is no longer widely used due to environmental concerns (Greenfield and Southgate, 2003). The Kjeldahl method is popular because it can be done with the basic equipment that is usually found in a laboratory, unlike other methods of protein extraction which require expensive devices or specialized techniques, the combined total of which can be upwards of \$10,000 US (Greenfield and Southgate, 2003). Today, the Kjeldahl method is still the primary reference method for protein analysis since it is low in cost, reasonably precise, and accurate (Greenfield and Southgate, 2003; Sáez-Plaza, et al., 2013).

Carbohydrates are the most difficult of the three macronutrients to analyze (FAO, 2019a; Greenfield and Southgate, 2003). The AOAC-approved method to calculate available carbohydrates is to extract the individual carbohydrates present in each food sample and sum the resulting saccharides together (Greenfield and Southgate, 2003). Unfortunately, it is difficult and costly to extract individual carbohydrates from food items (FAO, 2019a). Plant materials present additional problems because of the structural carbohydrates that enclose the sugars and starches (Greenfield and Southgate, 2003). As a result, the standard method for carbohydrate extraction is not ubiquitously adhered to (Greenfield and Southgate, 2003).

Because the standard method for carbohydrate extraction is time-consuming and expensive to employ, any analytical procedure for available carbohydrates requires a compromise between the ideal procedure and the practical laboratory procedure (Greenfield and Southgate, 2003; Southgate, 1969). Consequently, most FCDs and

nutrient composition tables still employ an older, now criticized method, called the ‘by-difference’ method, due to limited financial resources (Greenfield and Southgate, 2003). In the by-difference method, the other constituents of a food (protein, fat, water, alcohol, and ash) are determined individually, summed, and then subtracted from the total weight of the food. The resulting number is referred to as ‘total carbohydrate by difference’ (FAO, 2019a; Greenfield and Southgate, 2003). The standard equation for this is:

$$100 - (\text{weight in grams [protein + fat + water + alcohol + ash] in 100g of food})$$

The carbohydrates that are estimated via this equation include fibre. It is well known that most fibre cannot be digested by the human body (Ha et al., 2000). Because of this, ‘available carbohydrates’, which are the carbohydrates that do not include fibre, can also be calculated with the by-difference method (FAO, 2019a; Greenfield and Southgate, 2003). Available carbohydrates refer to the fraction of carbohydrates that can be digested by human enzymes, absorbed, and metabolized (Institute of Medicine, 2005; FAO, 2019a). This is estimated by subtracting the total fibre of a food item from the total carbohydrates (FAO, 2019a). However, even when available carbohydrates are calculated, there is no information regarding the composition of the various saccharides (sugars) that make up the available carbohydrates (FAO, 2019a). Available carbohydrates can be calculated by difference via the following equation:

$$100 - (\text{weight in grams [protein + fat + water + alcohol + ash + dietary fibre] in 100g of food})$$

Before 2003, the by-difference method was ubiquitously used in food nutrient determination because it is reproducible, and produces quick and roughly reliable results (Greenfield and Southgate, 2003; Southgate, 1969). However, it is no longer considered adequate because it is not accurate to view carbohydrates as a single component of foods (Greenfield and Southgate, 2003). Despite this, the by-difference method is still often used due to its low cost and the quick results that it produces (Greenfield and Southgate, 2003). Because of the practical problems involved in implementing the AOAC standard method for carbohydrate extraction, the by-difference method is considered a tolerable alternative (Greenfield and Southgate, 2003).

There are independent methods to extract total fat and individual fatty acids. Total fat is most widely used in FCDs and public health guidelines (Greenfield and Southgate, 2003; Health Canada, 2019; WHO, 2018; Willet et al., 2019), therefore, I will focus on the standardized methods for total fat.

There are two common methods to determine the total fat contribution from food, one is considered optimal and the other is considered acceptable (Greenfield and Southgate, 2003). The former involves separately extracting individual triglycerides gravimetrically (the specifics of which may vary without compromising the results) and then summing the resulting triglycerides (Greenfield and Southgate, 2003). The other method entails extracting the total fat gravimetrically where continuous extraction is performed on dried samples of food (Greenfield and Southgate, 2003; FAO, 2019a). This is often done in a Soxhlet extractor and is sometimes preceded by acid hydrolysis (Greenfield and Southgate, 2003; FAO, 2019a). The second method is significantly less time consuming and less expensive to run than the first and therefore is employed more often (Greenfield and Southgate, 2003).

To utilize a Soxhlet extractor, a sample that has been dried and ground into a powder is placed in an extraction thimble that is then directly immersed in a boiling solvent (Greenfield and Southgate, 2003). The solvent dissolves fats, oils, pigments, and other soluble substances which are collectively termed ‘crude fat’ (Greenfield and Southgate, 2003). After one hour, the sample is removed from the solvent and is flushed with fresh condensed solvent for an additional hour (Greenfield and Southgate, 2003). Lastly, the solvent is evaporated and recovered by condensation. The resulting ‘crude fat’ residue is then dried and weighed (Greenfield and Southgate, 2003). Soxhlet extractors allow for the evaporation and collection of the solvent. This method is standard, but the solvent used will change depending on whether the fat being extracted is solid or liquid (Greenfield and Southgate, 2003).

A variety of solvents are appropriate for fat extraction depending on whether the extraction is a solid-liquid extraction or a liquid-liquid extraction (Greenfield and Southgate, 2003; FAO, 2019a). It is up to the researcher to decide which solvent they use (Greenfield and Southgate, 2003; FAO, 2019a). Although the AOAC provides solvent recommendations, these are not standardized and do not appear to make a difference as

long as the solvent used is appropriate for the state of the food item (i.e., solid or liquid) (Bhandari et al., 2003).

The Soxhlet method is commonly used because Soxhlet extractors are inexpensive and produce reasonably accurate results (Greenfield and Southgate, 2003). However, the Soxhlet method is subject to drawbacks. The main drawback of using the Soxhlet method is that Soxhlet extractors yield incomplete lipid extractions for many foods including baked products, foods containing a considerable amount of structural fat, and liquid samples (Manirakiza et al., 2001). Soxhlet extractors are therefore not recommended for these food items (Greenfield and Southgate, 2003). However, as long as the Soxhlet method is not used to extract fat from the aforementioned food items, it is considered adequate (Greenfield and Southgate, 2003). Although the Soxhlet method does have drawbacks, it is the most common method used for fat extraction, is reasonably reliable, and is understood to be the best method to extract lipids from solid samples (Greenfield and Southgate, 2003; Manirakiza et al., 2001).

2.6. The Paleo Diet

Modern ‘Paleo-dieters’ consume a diet that is low in carbohydrates and high in protein and fat. This contrasts with the current dietary recommendations of the World Health Organization (WHO), which state that “a healthy diet should emphasize a balance of protein, fibre-rich carbohydrates, and unsaturated fats”, with total fats comprising no more than 30% of calories (WHO, 2018:2). The Paleo Diet regime additionally requires adherents to eliminate gluten, dairy, grains, legumes, and refined sugar from their diets on the grounds that these foods would have been absent in the Palaeolithic (Cordain et al., 2000; Cordain, 2010; Eaton and Konner, 1985).

The Paleo Diet is marketed as a reference or standard human diet, and the healthiest diet for modern populations on the basis of the dietary mismatch hypothesis. As explained earlier, this hypothesis states that there has not been enough time since the transition to farming, some 10,000 years ago, for the human genome to have adapted to an agricultural diet (Cordain et al., 2000; Cordain, 2001; Eaton and Konner, 1985).

The dietary mismatch hypothesis is an extension of James Neel’s (1962) ‘thrifty genotype hypothesis’, which proposes that the high rate of diabetes mellitus in

contemporary populations is the result of an evolutionary adaptation to a significantly different environment. Specifically, Neel (1962) proposed that some modern populations have maintained traits that would favour insulin resistance and fat storage when food is scarce. These genes, he argued, have become disadvantageous in the sedentary Western world where food is both highly palatable and over-abundant.

Although Neel (1962) did not directly refer to obesity in his hypothesis, he did propose that the energy storage by means of body fattening during times when food was abundant would have been beneficial when food was scarce because the body would be able to use fat stores for energy. Subsequent studies have suggested that certain differences between early *H. sapiens* dietary patterns and the modern Western diets are associated with ill-health (e.g., Konner and Eaton, 2010; O’Keefe and Cordain, 2010). However, whether this is the result of ‘thrifty’ genes being selected for or genes from which selective regimes have been lifted (nicknamed ‘drifty genes’) is the subject of debate (Speakman, 2007; Speakman, 2008). Regardless of whether the genes were ‘thrifty’ or ‘drifty’, both hypotheses maintain that obesity and diabetes are the result of environmental differences between the past and present.

The idea that a Palaeolithic-type diet might be beneficial for modern populations was first proposed by physician Stanley Boyd Eaton and evolutionary anthropologist and physician Melvin Konner in a 1985 paper titled *Paleolithic Nutrition: A Consideration of its Nature and Current Implications*. Eaton and Konner (1985) hypothesized that because the chronic diseases that are prevalent in contemporary societies affect older, post-reproductive individuals, it is unlikely that these diseases would have had much selective influence during hominin evolution. They further hypothesized that because the diseases have only recently become widespread, the modern epidemic was the result of an environmental shift. It was Eaton and Konner (1985) who initially developed the dietary mismatch hypothesis by proposing that the Neolithic subsistence shift had a negative impact on human health because it did not affect the human genome. They cited negative health outcomes such as shorter stature, dental pathologies, and spinal deformities as a result of the then-new agricultural diet. Eaton and Konner (1985) proposed that chronic non-communicable diseases, such as obesity, cardiovascular disease, and diabetes are

another negative health effect of the Neolithic transition, and are specifically due to a lowered protein intake.

In addition to outlining the idea that eating the way our Palaeolithic ancestors did will improve human health, Eaton and Konner (1985) constructed an example of what a Palaeolithic diet might have been. They examined the diets of 58 regionally diverse ethnographically-documented hunter-gatherer groups who consumed varied amounts of animal and plant foods. They used recent hunter-gatherer diets as the basis of their study since such groups are often used as analogues for *H. sapiens* living in the Palaeolithic. The hunter-gatherer diets included meat, fish, fruit, and vegetables, but did not include cereal grains or dairy foods. Although animal and plant foods were present in varying amounts in each group, Eaton and Konner (1985) used the average ratio of 35% animal foods and 65% plant foods as proposed by Lee and Devore (1969) to calculate the approximate macronutrient contribution in the diets. They concluded that a Palaeolithic diet was composed of 45% carbohydrates, 34% protein, and 21% fat. These results differ from the US dietary guidelines of 45-65% carbohydrates, 10-30% protein, and 25-35% fat (HHS and USDA, 2015). Here I am referring to the US dietary guidelines instead of the WHO guidelines because the former are based on the latter and the latter do not include macronutrient targets.

Although Eaton and Konner (1985) proposed the first Palaeolithic-type diet, the Paleo Diet as it is known today did not take shape until 15 years later, when health and exercise scientist Loren Cordain and his colleagues revisited the idea in a study in 2000. As mentioned earlier, Cordain et al. (2000) calculated the average plant-animal (P-A) percentage contributions in a sample of 229 hunter-gatherer groups and then calculated an average hunter-gatherer diet. Because no singular P-A contribution was representative of all the hunter-gatherer groups in their sample, Cordain et al. (2000) used the average range of P-A contributions to create a mathematical model that enabled them to estimate the average macronutrient distributions of hunter-gatherer diets. The model consisted of three equations, one to calculate the average percentage energy contribution of each macronutrient. In order to consider the P-A variation, they calculated the results of five different P-A contributions. Cordain et al. (2000) then entered animal- and plant-food macronutrient values from the literature into the three equations for each of the P-A

contributions. They considered multiple animal-food macronutrient values in order to account for variations in animal body fat throughout the year, and they relied on the average plant values for Indigenous Australians calculated by Brand-Miller and Holt (1998). Their results are animal-based diet where 55% of the daily energy intake comes from animal food, protein provides 19-35% of the diet, carbohydrates provide 22-40% of the diet, and fat provides 28-58% of the diet. These results represent the updated Paleo Diet, and the macronutrient distribution is even more at odds with the US and WHO dietary recommendations than the one proposed by Eaton and Konner (1985).

The Paleo Diet was introduced to the public through Cordain's 2001 book 'The Paleo Diet: Lose Weight and Get Healthy by Eating the Food You Were Designed to Eat'. In this book, Cordain explains his team's research in an accessible way and outlines a wellness lifestyle around the diet. Cordain revised the book in 2010, and this prompted a further increase in the popularity of the diet.

2.7. Critiques of the Paleo Diet

Since 2001, multiple peer-reviewed studies that expand upon the dietary mismatch hypothesis and test the health effects of the Paleo Diet have been published. So far, clinical trials of the Paleo Diet's effects on weight loss and common health markers have shown that the Paleo Diet regime can result in cardiovascular improvement (e.g., Jönsson, et al., 2009), improved glucose control (e.g., Frassetto et al., 2009; Masharani et al., 2015), better lipid profiles (e.g., Frassetto et al., 2009; Masharani et al., 2015), lower blood pressure (e.g., Frassetto et al., 2009), and weight loss (e.g., Frassetto et al., 2009; Genoni et al., 2016; Österdahl et al., 2008). Although this is encouraging, the sample sizes for all of these studies have been small and the studies have only examined the diet's short-term effects.

Although there are promising data which support the Paleo Diet as a healthy lifestyle choice, there is also some criticism of the diet which makes it a controversial topic in nutritional science. For example, some clinical trials that have reported weight loss in the study participants have also reported negative changes to blood lipid profiles and deficiencies in some essential nutrients as a result of short-term Paleo Diet adherence (e.g., Genoni et al., 2016; Smith et al., 2014). Additionally, the first longer-term study on

the Paleo Diet was published recently and its results conflict with those from the short-term studies (Genoni et al., 2019). Genoni et al. (2019) showed that although the Paleo Diet promotes improved gut health and a decreased risk of cardiovascular disease in the short-term, long-term adherence is associated with different gut microbiota and increased TMAO, a compound that is linked to a greater likelihood of heart disease (Randrianarisoa et al., 2016). Genoni et al. (2019) propose that a variety of fiber components including whole grain sources, which are not considered ‘Paleo’, may be required to maintain gut and cardiovascular health.

Research on the health effects of the Paleo Diet remains in its infancy. As long-term studies are important in order to understand the downstream health effects of a given diet and are essential when considering a particular diet’s application, the results of future long-term studies will shed more light on the topic. Currently, however, most nutritionists advocate a well-balanced diet that includes vegetables, fruit, meat, fish, grains, legumes, and dairy, and limits salt and sugar (e.g., Flight and Clifton, 2006; Thorning et al., 2016; WHO, 2018).

The evolutionary foundations of the Paleo Diet have also been critiqued. Although the dietary mismatch framework makes intuitive sense, it has been argued that the conclusion that there is only one healthy way of eating for *H. sapiens* overlooks several fundamental evolutionary principles (Speth, 2010; Ungar, 2017).

One such principle is that human diets are notable in their diversity, not their similarities (Milton, 2000; Speth, 2010; Ungar, 2017). Humans inhabit nearly every region of the world, and their diets are as varied as their habitats. Some populations subsist almost entirely on plant foods, others almost entirely on animal foods, and others still on almost equal amounts of each (e.g., Kaplan et al., 2000; Kuhnlein et al., 2013; Murdock, 1967). Since humans are able to live long and healthy lives on dramatically different diets, it is difficult to imagine one traditional diet as being better than the rest (Buettner, 2015).

H. sapiens’ generalized diet is suggested to be an integral part of their ability to adapt to different or changing environments (Luca et al., 2010; Teaford and Ungar, 2002; Ungar, 2017). Because of this dietary generalism, some evolutionary anthropologists argue that modern humans evolved to survive and do well on a variety of diets, not a

single diet (Teaford et al., 2002; Ungar, 2017; Ungar and Sponheimer, 2011). Recently, scholars have proposed that the reason *H. sapiens* are able to inhabit a variety of ecological niches is because they are skilled at adapting to local environments (Fan et al., 2016). This has led to the hypothesis that instead of being a generalist species, *H. sapiens* may be a “generalist specialist” (Roberts and Stewart, 2018:542). In either case, it is dietary variability, not constancy, that has been prominent throughout hominin evolution. An obvious corollary of this is that a one-diet-fits-all solution as proposed by proponents of the Paleo Diet is unlikely to solve modern *H. sapiens* nutritional problems.

Just as the idea of a single, Palaeolithic reference diet is disputed by evolutionary anthropologists, so is the statement that the human genome has not changed since the Palaeolithic period. Evidence from the archaeological record suggests that human food choices have changed considerably over the last 6-8 million years, including over the last 10,000 years (e.g., Sponheimer and Dufour, 2009; Speth, 2010). The exponential population growth that humans have experienced during this time suggests that the foods humans were eating over the last 10,000 years have been adequate for individuals to survive to reproduction. Additionally, in recent years there has been a considerable increase in genetic work that contradicts the theory that humans have not evolved over the last 10,000 years (e.g., Itan et al., 2009; Perry et al., 2007; Fumagalli et al., 2015). This evidence is consistent with the hypothesis that natural selection not only continued to alter the human genome during the Neolithic period, but may in fact have accelerated (Cochran and Harpending, 2009). What are understood to be important dietary adaptations today are shifts in response to agriculture or similarly recent habitat changes, thus providing evidence for strong selection in the last 10,000 years. Examples of these adaptations are lactase persistence (LP) to digest dairy products, the increase in salivary amylase copy number variations (AMY1 CNV) to digest starch, and the FADS1, FADS2, and FADS3 genes which enable northern Inuit populations to better digest omega-3 fats and high-fat diets (Itan et al., 2009; Perry et al., 2007; Fumagalli et al., 2015).

LP is an autosomal dominant trait that enables the continued production of the lactase enzyme throughout adult life. LP is a derived allele; the ancestral condition is lactase non-persistence (Swallow, 2003). LP is common among people of European ancestry, and is also present in some African, Middle Eastern, and south Asian groups for

whom dairying has been a significant traditional practice (Itan et al., 2009). In these groups, LP is timed with the origins of dairying (Itan et al., 2009). This, in addition with different LP-associated alleles being reported in regionally diverse groups, suggests that LP evolved convergently. Since LP was selected for independently in multiple regions and appeared recently, it must have been subject to strong positive selection (Fan et al., 2016; Itan et al., 2009; Turner and Thompson, 2013).

AMY1 CNV is another gene that has undergone strong selection since the Neolithic. Salivary amylase is the enzyme that is responsible for starch hydrolysis in humans; it exhibits extensive variation in copy numbers across human populations (Perry et al., 2007). Likewise, the starch component of traditional human diets varies with the population. For example, starch is a prominent dietary component of agricultural societies and hunter-gatherers in arid environments but is not a part of the diets of rainforest and circum-arctic hunter-gatherers or many pastoralists (Kuhnlein and Soueida, 1992; Perry et al., 2007; Schoeninger et al., 2001). The variation in both starch consumption and AMY1 CNV made it possible to conduct a study that examined and compared the AMY1 CNV across populations with differing starch consumptions (Perry et al., 2007). Perry et al. (2007) found that the number of AMY1 copies is correlated positively with salivary amylase protein level and that individuals from populations with high-starch diets have, on average, more AMY1 copies than those with traditionally low-starch diets. Based on these results, higher AMY1 copy numbers and protein levels were thought to improve the digestion of starchy foods and to potentially protect against intestinal disease.

AMY1 CNV and LP are not the only dietary adaptation that have occurred in human populations since the start of the Holocene. Another important recent change is Arctic Indigenous peoples' genetic and physiological adaptation to a diet rich in PUFAs (Fumagalli et al., 2015). The Inuit in Greenland have lived in harsh Arctic conditions for thousands of years. As a result of their environment, they have subsisted on a diet that is unusually high in protein and fat, particularly omega-3 PUFAs, and low in carbohydrates (Fan et al., 2016). In 2015, Fumagalli et al. conducted a scan of Inuit genomes to search for signatures of dietary adaptations. They discovered signals at several loci, with the strongest signal located in a cluster of fatty acid desaturases that determine PUFA levels.

The selected alleles are associated with specific metabolic phenotypes and have a significant effect on weight and body shape. They seem to modulate fatty acid composition and may additionally affect growth hormone regulation (Fumagalli et al., 2015).

Intriguingly, the signatures of adaptation in the Inuit are similar to the genetic differences between the brown bear and its descendant the polar bear, the appearance of which involved a shift from a diet that was probably 70% plant-based to one that is almost exclusively animal-based and exceptionally high in fat. Like the Inuit, polar bears are able to digest fat more efficiently than protein (Rinker et al., 2019). Additionally, as with the Inuit, polar bears have a number of genes associated with cardiovascular function and fatty acid metabolism that display signatures of recent positive selection (Rinker et al., 2019).

Each of the diet-related adaptations discussed in this section are currently thought to have evolved in human populations after the Holocene. This gives each of these adaptations a period of only ~10,000 years to be selected for. Since they were selected for in some populations, these examples suggest that dietary changes have a fast and significant impact on a species' evolution. This further presents evidence that at the species-level, human diets continued to broaden over the last 10,000 years.

Two other premises of the Paleo Diet have been challenged. The first is the use of modern hunter-gatherers to recreate the diets of Palaeolithic *H. sapiens* (Milton, 2000; Speth, 2010). Speth (2010) has argued that using ethnographic groups has resulted in the Paleo Diet being arbitrary because the diet “is drawn from the ethnographic present” (Speth, 2010:24). Furthermore, since the ethnographic dietary information from the Cordain et al. (2000) study was never tested against the archaeological record, the Paleo Diet is really “an untested projection of a homogenized view of what is actually a very diverse present” (Speth, 2010:24). Although multiple scholars have made this argument, John Speth's view is particularly important because he is a co-author on the Cordain et al. (2000) paper.

The other contested premise is that hunter-gatherers are not the only modern people who exhibit low instances of metabolic diseases. Many Indigenous people who consume traditional agricultural diets also exhibit low instances of these diseases

(Kuhnlein et al., 2013; Sofi et al., 2013; Buettner, 2015). It has been argued that what these groups have in common is the wide variety of foods that they consume and the low prevalence of processed foods (Milton, 2000). Milton (2000) and Willet et al. (2019) have argued that it is far more likely that the heavily processed, high-calorie, low-fibre diet that is characteristic of modern Western populations is the driving force behind metabolic diseases than improper macronutrient profiles and the consumption of grains, gluten, and dairy.

Together, the criticisms outlined in this section make the Paleo Diet an important and contested topic for investigation.

Chapter 3.

A preliminary assessment of Cordain et al.'s (2000) claims regarding the contributions of the three macronutrients to hunter-gatherer diets

This chapter summarizes Cordain et al.'s (2000) paper as well as my preliminary assessment of Cordain et al.'s (2000) decision to rely on Brand-Miller and Holt's (1998) Australian plant values when estimating the contributions of the three macronutrients to hunter-gatherer diets. In Section 3.1, I provide a detailed description of the methods that Cordain et al. (2000) employed. In section 3.2 I describe how I replicated their study as well as the results that I obtained. In Section 3.3, I describe the methods I used to apply Eaton and Konner's (1985) plant values to Cordain et al.'s (2000) equations. In this section, I also present my results and test whether the macronutrient consumption ratios that result from Eaton and Konner's (1985) plant values differ significantly from the ones that Cordain et al. (2000) calculated with Brand-Miller and Holt's (1998) plant values.

3.1. Cordain et al.'s (2000) Method

Cordain et al. (2000) compiled their data from the *Ethnographic Atlas (EA)* (Murdock, 1967). The *EA* contains data pertaining to 1291 of the world's non-industrial societies. The societies in the *EA* range from hunter-gatherer economies to complex agricultural societies, and the data range from subsistence practices to religious beliefs. The *EA* includes societies from all over the world, but the majority of the societies are from North America and Africa. The data in the *EA* have been verified independently by multiple ethnographers (e.g., White and Brudner-White, 1988).

The *EA* includes data on each society's subsistence economy. It lists five economic practices – gathering, hunting, fishing, animal husbandry, and agriculture – and assigns a value ranging from 0 to 9 to represent a society's percentage dependence on each subsistence method (Table 3). For example, a score of 4 for fishing indicates that the society relied on this economic practice for between 36% and 45% of their subsistence needs. The *EA* does not specify whether the subsistence categories are based on weight or

energy content, but Cordain et al. (2000) examined over 400 of the original references and determined that the estimates reflect weight in most cases.

Table 3: Scoring of percentage economic subsistence dependence in the *Ethnographic Atlas*.

Score	% of subsistence dependence
0	0-5
1	6-15
2	16-25
3	26-35
4	36-45
5	46-55
6	56-65
7	66-75
8	76-85
9	86-100

Cordain et al. (2000) defined hunter-gatherer groups as groups who were 100% dependant on hunting, fishing, and gathering for their subsistence needs. To compile their sample, they selected every group in the *EA* with a score of 0 in both the animal husbandry and agriculture categories.

They next needed to determine the average plant-animal (P-A) subsistence ratio for the hunter-gatherer groups in their sample. They assumed that gathering involved only plant foods and they used the percentage of dependence on gathering as ‘P’. They combined the hunting and fishing percentages of dependence to represent ‘A’. Cordain et al. (2000) then made a histogram to depict how much animal food most of the groups in their sample consume. The histogram for hunted and fished foods is presented in Figure 3 and shows that the majority of societies derived over 60% of their subsistence from animal foodstuffs. Figure 3 also shows that there is substantial variation in the dependence on hunting and fishing amongst the societies. As such, one P-A ratio does not represent all of the groups. Due to the considerable variation in P-A contribution, Cordain et al. (2000) took a range of P-A percent contributions to represent the average range

across the groups. Based on Figure 3, they determined that most societies in their sample consumed between 35-65% animal food.

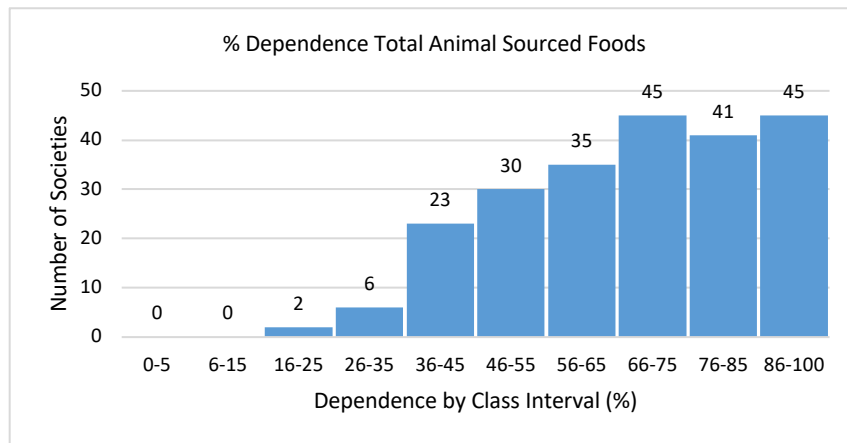


Figure 3: Distribution of animal-sourced food dependence in worldwide hunter-gatherer groups

The next step for Cordain et al. (2000) was to determine the average percentage energy contributions of the three macronutrients to the diets of the societies in their sample. Because the P-A subsistence ratios in the *EA* were made by weight, Cordain et al. (2000) needed to convert them into energy. To do this, they determined the contributing macronutrient information for the plant and animal foods that hunter-gathers consume. Whilst compiling the plant and animal macronutrient information, they determined that the mean energy density of wild plant foods is 6.99 kJ/g and the mean energy density of wild animal foods is 7.24 kJ/g. Because these energy densities are very similar – Cordain et al. (2000) noted that the P-A densities differ by only 3.5% – Cordain et al. (2000) determined that the P-A subsistence ratio based on weight in the *EA* was “virtually identical” to the P-A subsistence ratios based on energy (Cordain et al., 2000:686). Thus, they converted their P-A ratios from a weight percentage to an energy percentage in their calculations (Cordain et al., 2000).

For the plant macronutrient values, they used the wild plant food database compiled by Brand-Miller and Holt (1998). This database lists the nutrient information for 829 plants commonly consumed by Indigenous Australians. Brand-Miller and Holt (1998) estimated that the average macronutrient contribution for the plants in this database to Indigenous Australian diets was 14% protein, 62% carbohydrates, and 24%

fat by energy. This average was similar to the macronutrient values for wild plants in five hunter-gatherer groups that Eaton and Konner (1985) calculated. These values were 13% protein, 68% carbohydrates, and 19% fat by energy.

For the animal macronutrient values, Cordain et al. (2000) used regression equations created by Pitts and Bullard (1968) to determine the amounts of protein and fat energy that animals contribute to hunter-gatherer diets. These values were calculated based on the percentage body fat by weight of the prey animal. It has been shown that hunted and fished animals at the same body fat percentage provide differing amounts of protein and fat to the diet (Pitts and Bullard, 1968). Therefore, Cordain et al. (2000) needed to account for the differing protein and fat contributions that are consumed from land and sea animals at the same body fat percentage before they could use animal macronutrient values in their equations. To do this, Cordain et al. (2000) first established how much of the animal sourced food in hunter-gatherer diets is provided by hunted and fished food. They created histograms of hunted and fished foods to do this (Figure 4). They found that, for most societies, hunted food made up a constant 35% of subsistence (Figure 4). Therefore, for their equations, when considering an animal food percentage of 35%, they assumed that all of those calories came from hunted animals. When considering an animal food percentage above 35%, they assumed that hunted foods made up 35% of the total calories, and that the remaining percentage was fished.

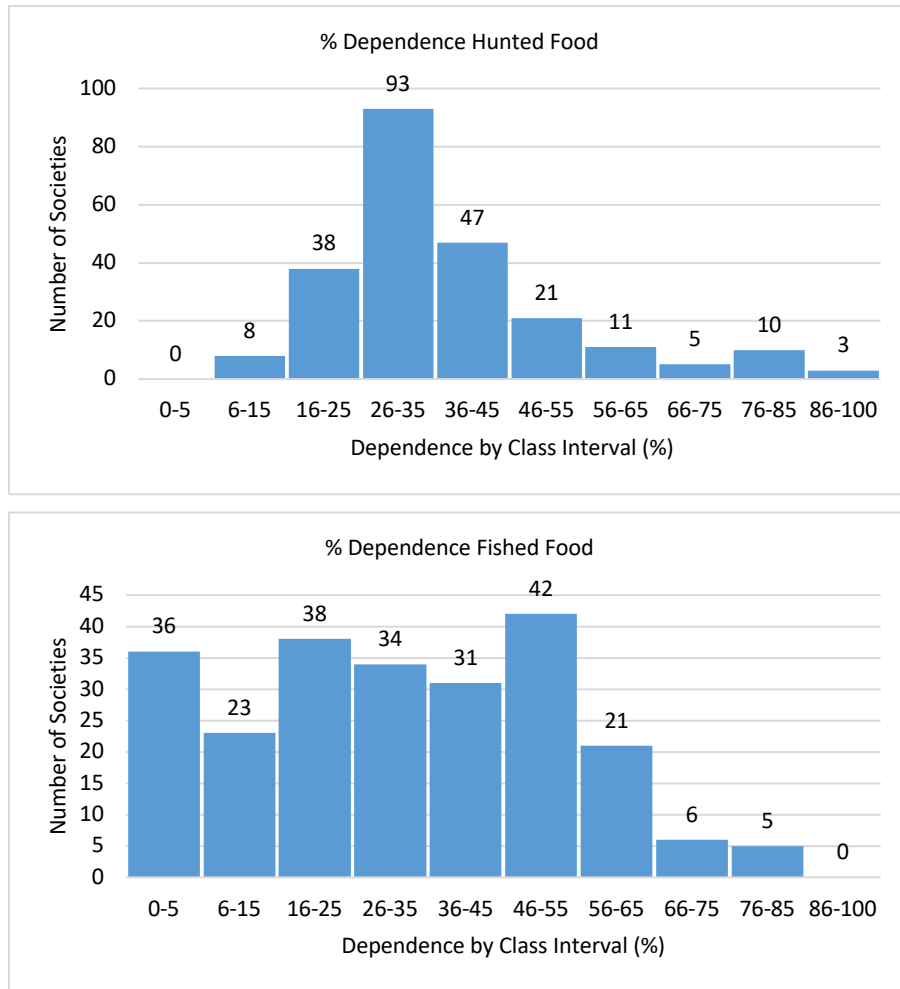


Figure 4: Distribution of hunted (above) and fished (below) food dependence in worldwide hunter-gatherer groups.

Subsequently, Cordain et al. (2000) created a mathematical model with which to calculate the average contributions of the three macronutrients for their sample. Cordain et al. (2000) did not present the model or the equations that they used, but they did provide an example calculation. I used the example calculation to recreate their equations, which are as follows:

$$\text{Protein} = \frac{(M_{pp} * P * T) + (M_{ap} * A * T)}{T}$$

$$\text{Carbohydrates} = \frac{(M_{pc} * P * T) + (M_{ac} * A * T)}{T}$$

$$\text{Fat} = \frac{(M_{pf} * P * T) + (M_{af} * A * T)}{T}$$

The variable T in the three equations represents the mean daily energy requirements for hunter-gatherer males in kilojoules (kJ) and is set at 12,552 kJ based on the results from Cordain et al. (1998).

The variables P and A represent the plant and animal percentage contributions by energy, respectively. Because the P-A subsistence contributions were so variable, Cordain et al. (2000) calculated the macronutrient values that would result from a variety of different P-A contributions. Because they determined that most of the societies in their sample consumed between 35% and 65% animal food (as presented in Figure 3), they calculated the equations at 35%, 45%, 50%, 55%, and 65% animal food.

The variables M_{pp} , M_{pc} , and M_{pf} represent the percentage of protein, carbohydrates, and fat by energy from wild plants. Cordain et al. (2000) used Brand-Miller and Holt's (1998) database for the variables that they used in the equation. Brand-Miller and Holt (1998) estimate that, on average, wild plants contribute 14% protein, 62% carbohydrates, and 24% fat by energy to Indigenous Australian diets.

The variables M_{ap} , M_{ac} , and M_{af} represent the percentage of protein, carbohydrates, and fat by energy derived from hunted and fished animal foodstuff, respectively. Cordain et al., (2000) used the regression equations created by Pitts and Bullard (1968) for both hunted and fished animals to determine the fat and protein contributions for wild hunted and fished animals at 2.5%, 5%, 10%, 15%, and 20% body fat. They then combined the results for hunted and fished food depending on the P-A contribution, as described above, and applied the resulting values into their equation.

There is one important restriction that Cordain et al. (2000) placed on the animal macronutrient values they used in their model. They argued that humans would have selected "animals with $\geq 10\%$ body fat ... to maintain protein intakes below the maximal [rate of urea synthesis]" (Cordain et al. 2000:689). They argued that the dietary protein range that arose from animals with body fat percentages of less than 10% were dangerously high and likely could not have been habitually consumed (Speth, 1991; Speth, 2010). Therefore, although they calculated the dietary macronutrients from animals at 2.5%, 5%, 10%, 15%, and 20% body fat, they later stated that they omitted the results from animals at 2.5% and 5% body fat in their conclusion. The results from Cordain et al.'s (2000) calculations are presented in Table 4.

Cordain et al. (2000) made dietary recommendations based on the range for each macronutrient that their model produced. They suggested that the average hunter-gatherer diet provides 19-35% energy from protein, 22-40% energy from carbohydrates, and 28-58% energy from fat. They suggested that these macronutrient ranges be used as a reference model for the contemporary human diet in order to combat lifestyle diseases.

It is noteworthy that Cordain et al.'s (2000) concluding range of "macronutrient consumption ratios" (MCRs) (Cordain et al., 2000:682) is not consistent with the fat consumption values that they calculated. Although Cordain et al. (2000) stated that animals with less than 10% body fat would not have been habitually consumed, and that the results from animals with these percentage body fats were therefore not applicable for inclusion in their results, they did include the resulting fat consumption values from animals with 5% body fat in their recommendations. They did not do this for protein or carbohydrates, and they did not include the fat consumption values from animals with 2.5% body fat in any of their concluding results. There is no explanation as to why they did this. By using Cordain et al.'s (2000) results and adhering to the method that they noted, the MCRs change to 19-35% energy from protein, 22-40% energy from carbohydrates, and 34-58% energy from fat. The analyses in this thesis are based off of the resulting MCRs from when Cordain et al.'s (2000) method is adhered to. Thus, the range for fat energy that is applicable is 34-58%, not 28-58%. All future references to Cordain et al.'s (2000) recommendations will be for MCRs of 19-35% energy from protein, 22-40% energy from carbohydrates, and 34-58% energy from fat.

The above clearly indicates an unforeseen problem in Cordain et al.'s (2000) study. This being that there is a discrepancy between their concluding results and their methods.

3.2. Replicating Cordain et al. (2000)

I followed Cordain et al.'s (2000) methods in order to replicate their study. To begin, I accessed their sample through the *EA*. Currently, the *EA* is available through the online database *D-PLACE* (Kirby et al., 2016). I used *D-PLACE* to extract the subsistence data for the 229 hunter-gatherer groups and I cross-referenced my sample with that of Cordain et al. (2000), details of which were provided to me by Dr. Cordain via email in 2019.

Following with what Cordain et al. (2000) did, I defined hunter-gatherer groups as groups who were 100% dependant on hunting, fishing, and gathering for their subsistence needs. I then selected every group in the *EA*, via *D-PLACE*, with a score of 0 in both the animal husbandry and agriculture categories. I did not re-analyze the 400 plus original *EA* reference as Cordain et al. (2000) did. I accepted their judgement that the *EA* lists the subsistence dependence as a percentage by weight and made the same assumption.

In order to determine the average P-A subsistence ratio for the hunter-gatherer groups, I, too, assumed that gathering involved only plant foods and I combined the hunting and fishing percentages of dependence to represent animal foods. I replicated Cordain et al.'s (2000) histograms using my data (Figures 3 and 4 are created with my data, and they are equivalent to the ones that Cordain et al. (2000) created). Figure 3 shows that the majority of societies derived over 60% of their subsistence from animal foodstuffs and that there is substantial variation in the dependence on hunting and fishing amongst the societies. As such, one P-A ratio does not represent all of the groups in my sample either. I took the same range of P-A percent contributions that Cordain et al. (2000) did (this being 35-65% animal food) to represent the average range across the groups.

To determine the average percentage energy contributions of the three macronutrients to the diets of the hunter-gatherer societies in the sample, I used Brand-Miller and Holt (1998) and Pitts and Bullard (1968) to determine animal and plant food macronutrient information for hunter-gatherer societies. I made the same assumption that since the energy densities of the plant foods in the Brand-Miller and Holt (1998) database and the animal foods are similar, the P-A ratios can be converted from weight ratios to energy ratios.

I used Pitts and Bullard's (1968) regression equations to determine the macronutrient contributions for hunted and fished foods at 2.5%, 5%, 10%, 15%, and 20% body fat. The equation, my calculations, and the results are presented in the Appendix.

I then replicated the equations that Cordain et al. (2000) used to calculate the average hunter-gatherer diet. I calculated the equations at 35%, 45%, 50%, 55%, and 65% animal food using Brand-Miller and Holt's (1998) Indigenous Australian hunter-

gatherer plant values and the values that I had calculated for animal foods. This resulted in 25 calculations to consider the full range of variation. My results are presented in Table 4 in brackets beside Cordain et al.'s (2000) results. For the most part, my values were the same as Cordain et al.'s (2000). There were, however, a few minor differences of 1% that had to do with rounding discrepancies. I have noted with an asterisk when values are different.

I used my results to replicate Cordain et al.'s (2000) dietary recommendations. Because Cordain et al. (2000) mentioned that animals with less than 10% body fat would not have been habitually consumed, I did not include the results from animals at 5% or 2.5% body fat in my concluding ranges. Thus, my study produced hunter-gatherer MCRs that provide 22-40% energy from carbohydrates 19-35% energy from protein, and 33-57% energy from fat to the diet. These results differ from Cordain et al.'s (2000) adjusted range for dietary fat by 1%. I have noted in Table 4 that this particular value is different due to a rounding discrepancy. To ensure that the results are not considered different, I conducted a paired samples t-test on the fat values. The results from the t-test were not significant with $p = 0.33$. As such, my results can be considered equivalent to Cordain et al.'s (2000) results.

Based on Cordain et al.'s (2000) methods, the MCRs that I calculated are identical to theirs as are my calculations at 2.5%, 5%, 10%, 15%, and 20% body fat. These results demonstrate that the Cordain et al. (2000) results can be replicated.

Table 4: Results from replicating Cordain et al. (2000) with the original plant values. P-A = Plant to animal ratio. * = Indicates a difference that is due to rounding discrepancies

P-A	Protein	Carbohydrate	Fat
35:65			
20% animal fat	21% (21%)	22% (22%)	58% (57*%)
15% animal fat	28% (28%)	22% (22%)	50% (50%)
10% animal fat	35% (35%)	22% (22%)	43% (43%)
5% animal fat	47% (47%)	22% (22%)	32% (31*)
2.5% animal fat	56% (56%)	22% (22%)	23% (22*)

P-A	Protein	Carbohydrate	Fat
45:55			
20% animal fat	20% (21*%)	28% (28%)	52% (52%)
15% animal fat	26% (26%)	28% (28%)	46% (46%)
10% animal fat	32% (32%)	28% (28%)	40% (40%)
5% animal fat	42% (42%)	28% (28%)	30% (30%)
2.5% animal fat	49% (50%)	28% (28%)	23% (23%)
50:50			
20% animal fat	20% (20%)	31% (31%)	49% (49%)
15% animal fat	25% (26*%)	31% (31%)	44% (44%)
10% animal fat	31% (31%)	31% (31%)	38% (39*%)
5% animal fat	39% (39%)	31% (31%)	30% (29%*)
2.5% animal fat	46% (46%)	31% (31%)	23% (23%)
55:45			
20% animal fat	20% (20%)	34% (34%)	47% (46*%)
15% animal fat	24% (24%)	34% (34%)	42% (42%)
10% animal fat	29% (29%)	34% (34%)	37% (37%)
5% animal fat	37% (37%)	34% (34%)	29% (29%)
2.5% animal fat	43% (43%)	34% (34%)	23% (23%)
65:35			
20% animal fat	19% (19%)	40% (40%)	41% (41%)
15% animal fat	22% (22%)	40% (40%)	37% (37%)
10% animal fat	26% (26%)	40% (40%)	34% (33*%)
5% animal fat	32% (32%)	40% (40%)	28% (27*)
2.5% animal fat	37% (37%)	40% (40%)	23% (23%)

3.3. Testing the Model with the Eaton and Konner (1985) Plant Values

One rationale Cordain et al. (2000) offered for applying Indigenous Australian hunter-gatherer plant values to their entire, regionally diverse sample of hunter-gatherers was that their Australian values' were similar to the values reported by Eaton and Konner

(1985). Eaton and Konner (1985) estimated that the plant component of hunter-gatherer diets provides 13% protein, 68% carbohydrates, and 19% fat by energy. These values are based on an average of 44 plant foods consumed by five hunter-gatherer groups: the !Kung, the ≠ Kade San, the Hadza, Australian Aborigines (no group specified), and the Tasaday.

I used Eaton and Konner's (1985) plant macronutrient values in Cordain et al.'s (2000) equations (variables *Mpp*, *Mpc*, and *Mpf*) to calculate the range of macronutrient values that resulted. Because Cordain et al. (2000) stated that the average hunter-gatherer diet would not have included animals with less than 10% body fat on a regular basis, for my comparison I only calculated the equations with these values for animals with 10% body fat or above. Once calculated, I compared the new results with Cordain et al.'s (2000) original results in order to assess the claim that the Indigenous Australian values are equivalent to the Eaton and Konner (1985) values.

The results from using Eaton and Konner's (1985) plant values in the equations are presented in Table 5. Cordain et al.'s (2000) original results are listed in parentheses beside the new results. When I compiled the ranges for each macronutrient based on these values, the average hunter-gatherer diet changed from the 22-40% energy from carbohydrates, 19-35% energy from protein, and 34-58% energy from fat that Cordain et al. (2000) proposed to 24-44% energy from carbohydrates, 18-34% energy from protein, and 30-55% energy from fat (Table 6).

To assess the claim that the Indigenous Australian values are equivalent to Eaton and Konner's (1985) values, I used SPSS to conduct paired samples t-tests on the results presented in Table 5 and Cordain et al.'s (2000) results. The paired samples t-tests test whether the results from the equations are significantly different when alternative plant macronutrient values are used. This, in turn, provides information on whether the Cordain et al. (2000) Paleo Diet macronutrient recommendations are dependent on the plant values. The t-tests returned significant p-values for all three macronutrient ranges. The results for protein, carbohydrate, and fat were significant at $p = 0.019$, 0.000 , and 0.022 respectively. Because the ranges do not appear overly different when listed (Table 6), the results suggest that even small changes to the macronutrients have significant effects on the average hunter-gatherer diet. More importantly for present purposes, these results

indicate that Cordain et al. (2000) were not correct in their assumption that the Indigenous Australian plant values can be used as representative of worldwide hunter-gatherer plant values.

Table 5: Cordain et al. (2000) replicated with Eaton and Konner’s (1985) plant values. The results from Cordain et al. (2000) are presented in brackets for comparative purposes. P-A = Plant to animal ratio

P-A	Protein	Carbohydrate	Fat
35:65			
20% animal fat	21% (21%)	24% (22%)	55% (58%)
15% animal fat	28% (28%)	24% (22%)	48% (50%)
10% animal fat	34% (35%)	24% (22%)	41% (43%)
45:55			
20% animal fat	20% (21%)	31% (28%)	49% (52%)
15% animal fat	25% (26%)	31% (28%)	44% (46%)
10% animal fat	32% (32%)	31% (28%)	38% (40%)
50:50			
20% animal fat	20% (20%)	34% (31%)	47% (49%)
15% animal fat	25% (25%)	34% (31%)	41% (44%)
10% animal fat	30% (31%)	34% (31%)	36% (38%)
55:45			
20% animal fat	19% (20%)	37% (34%)	43% (47%)
15% animal fat	24% (24%)	37% (34%)	39% (42%)
10% animal fat	29% (29%)	37% (34%)	34% (37%)
65:35			
20% animal fat	18% (19%)	44% (40%)	38% (41%)
15% animal fat	22% (22%)	44% (40%)	34% (37%)
10% animal fat	26% (26%)	44% (40%)	30% (34%)

Table 6: A comparison of the Cordain et al. (2000) equation results using the Indigenous Australian plant values and Eaton and Konner's (1985) plant values

Macronutrient	Results with Indigenous Australian Plant Values	Results with Eaton and Konner's (1985) Plant Values
Protein	19-35%	18-34%
Carbohydrate	22-40%	24-44%
Fat	34-58%	30-55%

Chapter 4.

A cross-cultural assessment of Cordain et al.'s (2000) claims regarding the contributions of the three macronutrients to hunter-gatherer diets

In this chapter I report a cross-cultural assessment of Cordain et al.'s (2000) dietary recommendations. I begin by discussing the methods I used to reconstruct the plant component of the diets of ten hunter-gatherer groups including the average plant macronutrient values for each group. Next, I report a set of analyses in which I compared each of the new average plant macronutrient values to the Australian average plant values used by Cordain et al. (2000). Thereafter, I outline a set of analyses in which I used Cordain et al.'s (2000) mathematical model to generate whole-diet macronutrient consumption ratios for the ten societies and I report an analysis in which I compared the whole-diet macronutrient consumption ratios for the ten societies across all of the groups. In the final section, I report a set of analyses in which I compared the whole-diet macronutrient consumption ratios for each of the ten societies to the whole-diet macronutrient consumption ratios reported by Cordain et al. (2000).

4.1. Compiling Food Composition Databases for Ten Hunter-Gatherer Societies

4.1.1. Methods

It was necessary to source FCDs for worldwide hunter-gatherer societies in order to examine whether the plant component of hunter-gatherer diets vary significantly, and, in turn, to test the effects that this variability has on the Paleo Diet recommendations. My intention was to source FCDs for a large sample of worldwide hunter-gatherer societies. Unfortunately, sourcing high-quality FCDs for hunter-gatherers proved difficult. High-quality data on the wild plant food component of hunter-gatherer diets are few and far between, and data on the nutrient composition of such food items are even scarcer (Greenfield and Southgate, 2003). This is partly because there has been little research on

the plant component of hunter-gatherer diets, and partly because nutrient analyses are not often conducted on wild foods (Greenfield and Southgate, 2003; personal communication with Harriet Kuhnlein, November 29th 2019). Based on my research and a number of conversations with experts in the field, I believe the groups analysed in this study represent all the hunter-gatherer groups for whom high-quality data on plant food subsistence are available in the published literature.

I employed a variety of methods to source the FCDs. First, I conducted multiple searches on Google Scholar and Web of Science. Through these searches I compiled a list of papers and hunter-gatherer groups for whom there is some research on the plant-food diet. Second, I contacted several anthropologists who have done extensive work on hunter-gatherer groups in the hope that they could provide me with information regarding the nutritional composition of hunter-gatherer diets and where I might source hunter-gatherer FCDs. The scholars I contacted included Dr. Richard Lee, Dr. Andre Costopoulos, Dr. Tom Headland, Dr. Helga Vierich, and Dr. Nancy Turner.

Through my literature searches and conversations with experts, I came across the work of Dr. Harriet Kuhnlein, who is a professor emeritus at McGill University's School of Human Nutrition. Dr. Kuhnlein has produced FCDs for several traditional societies (e.g., CINE, 2005; Kuhnlein, 1989; Kuhnlein and Soueida, 1992). Her work primarily presents the nutrient information for Indigenous Canadian diets, although the Centre for Indigenous Nutrition and Environment (CINE), which she founded at McGill University, has nutrient information on some worldwide Indigenous diets as well.

CINE includes a database that contains FCDs for many traditional societies. However, the majority of these societies practice agriculture and therefore could not be used in this study. Fortunately, Indigenous Canadians, who were mostly hunter-gatherers before European colonisation, are well represented in the CINE nutrient database. As a result, I used CINE to obtain the FCDs for six traditional hunter-gatherer societies. Five of the six groups that I sourced from CINE – the Baffin Island Inuit, Gwich'in, Nuxalk, Wet'suwet'en, and Sahtú Dene/Métis – are from North America. The other hunter-gatherer group that I sourced from CINE, the Ainu, is from Japan.

The data for the remaining four groups in my sample – the Ache, !Kung, Hadza, and Hiwi – were compiled using high-quality outsourced plant values. 'Outsourced plant

values' refers to values that the authors did not extract themselves, and 'high-quality' means that the nutrients were extracted using the AOAC standard methods for nutrient analysis (Greenfield and Southgate, 2003). In general, the data for these societies is of good quality. However, a few of the plants that these groups habitually consumed did not have nutrient tables in any of my sources. This is likely because they are uncommon plants. Instead of leaving these plants out, I estimated their nutrient values based on the plants' similarity with other foods. This is the standard method when plants are not known, or when values cannot be found (Greenfield and Southgate, 2003). Because my sample is small, I decided that it was preferable to use all of the plants that were listed for each society even if I was required to estimate the values.

To outsource the plant nutrient data, I used the FAO/INFOODS Database (FAO, 2018) and Duke and Atchley's (1986) database. The FAO (2018) database is rigorously checked and frequently updated. It is the database by which all nutrient values today are cross-checked and is widely considered to be reliable, although it does not include nutrient data for many wild plants (Greenfield and Southgate, 2003). Duke and Atchley's (1986) database is the only comprehensive FCD for wild plants that I am aware of. It is also considered to be a good quality database (Laferriere, 1987).

Although Duke and Atchley's (1986) database is useful, it is methodologically different from all of the other sources in this study in that the macronutrient values are listed as percentages, not grams. However, because I was interested in percentage contribution of protein, carbohydrates, and fat, this was a relatively simple problem to overcome. The macronutrient percentages presented in Duke and Atchley (1986) were calculated including the ash (i.e., percentage of protein + carbohydrates + fat + ash = 100%). As such, I calculated the relative percentage of protein, carbohydrates, and fat without the ash considered. I was not able to calculate the relative macronutrient values for any foods that did not have all of the values listed. Any foods for which the values were not complete have been left out of this study. All Kcal numbers were calculated by multiplying the Kcal/Kg weight by 0.1 to get Kcal/100g.

I used Greenfield and Southgate's (2003) screening process, as outlined in Chapter 2, to ensure that the FCDs which I either sourced or compiled were consistent with the standard methods for sampling and extracting macronutrients. I adhered to the

FAO/AOAC optimal or acceptable methods for macronutrient extraction and calorie determination as listed in Table 2 in Chapter 2. By adhering to the acceptable methods when the optimal methods were not possible, I ensured that the FCDs in this study are of the highest possible quality and that discrepancies in the plant values are not due to methodological differences. I have noted whenever a plant value came from a less optimal source. I will discuss which methods were used in the next section.

4.1.2. The Food Composition Databases

I used ethnographic reports to obtain the proportion of each plant food in a given group's diet. This way, the plant macronutrient values that I applied to the Cordain et al. (2000) model are accurate. Because Cordain et al. (2000) were interested in discovering the macronutrient composition of the average hunter-gatherer diet, it was important that the proportion of plants consumed by each group be accurate. If inaccurate values were used in the equations, the whole-diet macronutrient consumption ratios would not represent the average hunter-gatherer diet, and any conclusions made from those results would be erroneous. For most of the groups, a precise breakdown of the proportions of each plant consumed was provided. Where no breakdown was available, I took the mean of all recorded plants. This is the approach employed by Brand-Miller and Holt (1998) and Eaton and Konner (1985), which are the two sources of plant macronutrient values that Cordain et al. (2000) used.

To confirm that my results were comparable, I ensured that the methods used to extract the macronutrients followed the standard methods outlined by Greenfield and Southgate (2003) (see Table 2 in Chapter 2). Consequently, the nutrient tables for the plants included in this study meet the FAO/AOAC standardized requirements for food nutrient analyses.

This study employs indirect methods to compose FCDs for each society. In accordance with the FAO/AOAC standard methods, I took great care appraising and selecting the plant values I included in the FCDs (Greenfield and Southgate, 2003). Original analytical values are preferable when composing FCDs (Greenfield and Southgate, 2003). To ensure that all values used were the original values, I only included

values for which I could refer back to the original source and verify that the methods used were in accordance with the FAO/AOAC current standardized methods.

Table 18 provides a breakdown of the different methods used to determine the calories, protein, fat, and carbohydrates respectively for the wild plants consumed by each society. All sources were based on 100g edible fresh (wet) weight unless otherwise indicated. Exceptions to this were when foods were consumed in a specific form such as dried or frozen. In these cases, the macronutrient contributions were calculated based on the form in which the food was most often consumed. This is common practice (Greenfield and Southgate, 2003). There was one society, the !Kung, for whom the methods were not disclosed, but whose macronutrient values I included anyway. Although in the source that I used the methods were not listed, I was able to find another nutrient analysis by the same author from a similar time in which the standard methods were listed as being followed (Wehmeyer et al., 1966). Based on this, I have assumed that values in the source that I used (Wehmeyer et al., 1969) were established using those same methods.

Despite the limited data that exists on the plant component of hunter-gatherer diets, I was able to arrive at a sample of ten societies. The ten societies are 1) the !Kung of Botswana, 2) the Ache of Paraguay, 3) the Ainu of Japan, 4) the Baffin Island Inuit of the Canadian Nunavut Territory, 5) the Hadza of Tanzania, 6) the Hiwi of Venezuela, 7) the Sahtú Dene/Métis of the Canadian Northwest Territories, 8) the Nuxalk of Bella Coola, British Columbia, Canada, 9) the Wet'suwet'en of northwestern British Columbia, Canada, and 10) the Gwich'in of the Canadian Northwest Territories. As such, the groups in this sample are primarily from Canada. It may strike the reader that the sample is regionally biased as a result of these groups. However, Canada is a large country that includes five major biomes (tundra, boreal forest, deciduous forest, grassland, and mountain forest), each of which houses different plant and animal species. Because the five Canadian societies included in this analysis inhabit diverse biomes, the sample is not biased towards one region.

As a result of the difficulty assembling a sample, there are two groups in this study that include a few non-traditional plant food items. The first is the Ache of Paraguay who consume wild oranges, which are a non-native food. The second group is

the Ainu of Japan. The Ainu are invariably referred to as hunter-gatherers in the published literature (e.g., Hudson, 1999; Ōnishi, 2014; Rokasandic et al., 1988), but they actually include a few cultivars in small quantities in their diet. Although the criterion for inclusion in the Cordain et al, (2000) study was 100% reliance on wild resources, I decided that it was acceptable to use the Ache and Ainu because of their widely agreed upon status as hunter-gatherers, the excellent quality of the data, and the limited good quality data that exists regarding the nutritional information for hunter-gatherer diets.

In the following subsections I document the steps, sources, and reasoning that I used to arrive at the average plant food macronutrient contribution from each society. It is important to note that many reports on hunter-gatherer subsistence classify honey, although an insect food, as a plant food because it is a gathered resource and does not come from a hunted animal (e.g., Murdock and White, 1969; Murray et al., 2001). As a result, and because it is often a major source of carbohydrates for groups that consume it, I included honey in my plant food calculations. Cordain et al. (2000) followed the same course of action.

The FCDs are presented in Tables 7-16. These tables list the total energy contribution per 100g (kcal/100g), as well as the percentage energy for protein, carbohydrates, and fat for each plant food. The sources that I used recorded the macronutrients for each plant food in g/100g. Therefore, I have converted the macronutrients into percentage energy by multiplying each macronutrient by the corresponding Atwater factor and dividing the result by the total energy contributions listed in the tables.

4.1.2.1. The !Kung

The !Kung inhabit the Dobe region of north-west Botswana. Although little is known about their lives before 1950, substantial ethnographies were written by Richard Lee in the 1960s and 1970s (e.g. Lee, 1968, 1970, and 1972). Lee (1968) estimated that the total !Kung population was 466 in the late 1960s. These 466 people lived in 14 small, mobile groups (Lee, 1968). Many !Kung bands lived in the same area because of their small group sizes and the bands would frequently hunt and gather together and share food resources (Lee, 1968; Lee, 1972). Today, almost no !Kung subsist only by hunting and gathering (Yellen, 1990).

By weight, 60-80% of the !Kung's traditional diet came from plant foods (Lee, 1968). Meat was a less predictable resource and consequently animal food made up between 20% and 50% of the !Kung diet by weight, depending on whether hunts were successful (Yellen and Lee, 1976). Approximately 85 edible plants were available to the !Kung at various times during the year, but some were consumed in much greater quantities than others. Twenty-three species made up 90% of the plant diet, and the mongongo nut comprised 50% of the plant food (Lee, 1968; Lee, 1970; Lee, 1973). Because all plants were usually in abundance, the !Kung chose what they considered the best-tasting foods to make up their diet and would only consume from the less palatable 62 species when resources were scarce (Lee, 1968).

Lee's extensive work on the !Kung traditional lifeways throughout the 1960s and 1970s are thought to provide an accurate depiction of the traditional !Kung way of living and subsistence (Hitchcock, 2012). I used Lee's ethnographies to reconstruct the plant-food part of the !Kung diet. I found a list of the plants consumed by the !Kung and their relative dietary importance in Lee (1968) and Chapter 6 of Lee (1970). I used Lee (1973), Wehmeyer et al. (1969), Duke and Atchley (1986), and Owaid et al. (2018) for the nutrient composition information of each plant. For the most part, the macronutrient values were taken from sources that directly analysed the plant in question. However, some of the plants that were listed in Lee (1970) and Lee (1968) did not have nutrient information in the four sources I used for the nutrient tables. As a result, some values were estimated based on their similarity with other foods as is common practice (Greenfield and Southgate, 2003).

Lee (1970) divided the plant species into 'primary', 'major', 'minor', 'supplementary', 'rare', and 'problematic' resources. The 23 plants that were habitually consumed make up the 'primary', 'major', and 'minor' resources. Because I was interested in the foods that were habitually consumed, my sample for the !Kung was taken from the foods in the first three categories. The 'supplementary', 'rare', and 'problematic' plant foods were consumed as fallback foods and were not included in this study. Of the 23 habitually consumed plants included in Lee (1970), the 'chada' plant was not included in any of the aforementioned databases and could not be identified through a library or google search. I left this plant out of the study.

The 22 remaining ‘primary’, ‘major’, and ‘minor’ plants that the !Kung habitually consume are presented in Table 7. The mongongo nut is understood to comprise 50% of the !Kung plant food diet (Lee, 1968). Other than the mongongo nut, the !Kung consumed a variety of fruits, vegetables, tubers, seeds, nuts, and legumes. Most of these plants are high in carbohydrates; however, there are a few important foods, such as the mongongo nut, that are extremely high in fat and low in carbohydrates. As a result, the average macronutrient values that are provided by the !Kung’s plant diet are relatively low in carbohydrates compared to the other groups in this study (see Table 17).

In order to use the plant macronutrient values in the Cordain et al. (2000) equations, I calculated the weighted average of the plants based on how often they were consumed. The calculations for this are presented in the Appendix and the results are presented in Table 17. I applied the values in Table 17 into the Cordain et al. (2000) equations and calculated the average macronutrients for the !Kung whole-food diet.

Table 7: The plant foods commonly consumed by the !Kung and their relative macronutrient percentages. * = Value estimated based on similarity with other foods.

Plant	Kcal/100g	Protein (%)	Carbohydrates (%)	Fat (%)	Total (%)
Mongongo Nut	641	18%	1%	80%	100%
Mongongo Flesh	312	8%	90%	2%	100%
Baobab	454	32%	10%	58%	100%
Vegetable ivory*	423.8	8%	77%	15%	100%
Marula	642.6	19%	1%	80%	100%
Wild orange*	80.2	8%	85%	7%	100%
Sour plum	51	5%	90%	5%	100%
Wild mango	66.62	5%	90%	5%	100%
Tsin Bean	544	23%	17%	60%	100%
Tsin Bean Tuber	46	13%	82%	6%	101%

Plant	Kcal/100g	Protein (%)	Carbohydrates (%)	Fat (%)	Total (%)
Tsama melon	400	8%	82%	10%	100%
Morethlwa	388.25	10%	78%	13%	100%
Mokomphata	388.25	10%	78%	13%	100%
Nakgwa	44.2	8%	87%	5%	100%
Wild orange	80.2	8%	85%	7%	100%
Mogwana	388.25	10%	78%	13%	100%
Mongana	383.8	33%	60%	6%	100%
Bitter melon	400	8%	82%	10%	100%
Heart of Palm	398.6	5%	90%	6%	100%
Maphate	388.25	10%	78%	13%	100%
Truffle*	84.8	21%	66%	13%	100%
Kitwan cucumber*	44.2	8%	87%	5%	100%

4.1.2.2. The Ache

The Ache live in northeastern Paraguay. Prior to the 1980s, they lived as mobile foragers in small bands of 15-28 people (Kaplan and Hill, 1985). Today, the Ache reside in agriculture-based missionary settlements of 100-200 Ache people living in nuclear family units (Gurven et al., 2001; Hill et al., 1984). Even though the Ache now live in agriculture-based permanent missionary settlements, they still regularly embark on hunting expeditions (Gurven et al., 2001; Hill et al., 1984). During these expeditions, they subsist entirely on the wild plants and animals that are obtained (Gurven et al., 2001; Hill et al., 1984). On these trips, the Ache diet consisted of approximately 78% wild game, 12% gathered plant foods, and 9% honey by energy (Hill et al., 1984).

In the years since 1980, the Ache have been well documented by Kim Hill and colleagues (e.g., Hawkes et al., 1982; Hill and Hawkes, 1983; Hill et al, 1984). Although the wild plants that the Ache consume have been documented, the nutrient composition of these wild plants has not been systematically analysed. As a result, I was not able to

find a completely comprehensive source regarding the wild plant component of the Ache diet.

In order to reconstruct the plant component of the Ache diet, I used Hill et al. (1984) in combination with both the FAO/INFOODs (FAO, 2018) and Duke and Atchley’s (1986) databases. Hill et al. (1984) document the plants consumed (including calories and nutrients) during the weeks that the Ache were on hunts. I cross-referenced the nutrient composition of the plants from Hill et al. (1984) with the FAO (2018) and the Duke and Atchley (1986) databases, however, the nutrient compositions did not match. Because the FAO (2018) and the Duke and Atchley (1986) databases are the only comprehensive FCDs for wild plants that I am aware of, and have been classified by reviewers as containing ‘high-quality’ data (Harriet Kuhnlein, personal correspondence; Laferriere, 1987), I used the values presented in these sources when there was a discrepancy.

The 18 plants that the Ache regularly consumed are presented in Table 8. The plants are predominantly high-carbohydrate fruits and honey, but they include some nuts, shoots, and flour, which are low in carbohydrates.

In order to use the plant macronutrient values in the Cordain et al. (2000) equations, I calculated the mean values for each macronutrient. The calculations for this are presented in the Appendix and the results are presented in Table 17. I applied the values in Table 17 into the Cordain et al. (2000) equations and calculated the average macronutrients for the Ache whole-food diet.

Table 8: The plant foods commonly consumed by the Ache and their macronutrient composition. * = species name not listed, but Hill et al. (1984) indicated that the honey from multiple species was consumed.

Plant	Kcal/100g	Protein (%)	Carbohydrates (%)	Fat (%)	Total (%)
Palm Growing Shoot	Unknown	13%	22%	65%	100%
Palm Trunk Fibre	Unknown	13%	22%	65%	100%
Palm Flour	Unknown	13%	22%	65%	100%
Palm Fruit	Unknown	13%	22%	65%	100%

Plant	Kcal/100g	Protein (%)	Carbohydrates (%)	Fat (%)	Total (%)
Fruit (<i>Chrysophyllum gonocarpum</i>)	75	7%	73%	16%	96%
Guanabana (<i>Annona muricata</i>)	68.3	6%	92%	2%	100%
Guanabana (<i>Annona reticulata</i>)	100.3	7%	88%	5%	100%
Guanabana (<i>Annona squamosa</i>)	75.4	9%	90%	1%	100%
Honey (<i>Apis mellifera</i>)	267	0%	100%	0%	100%
Honey (<i>Apis sp.</i>)*	267	0%	100%	0%	100%
Honey (<i>Apis sp.</i>)*	267	0%	100%	0%	100%
Honey (<i>Apis sp.</i>)*	267	0%	100%	0%	100%
Virella	70	6%	63%	26%	94%
Kurilla	41	5%	94%	1%	100%
Palm Nut	442	13%	22%	65%	100%
Fig (<i>Ficus galabrata</i>)	36.5	6%	93%	1%	100%
Fig (<i>Ficus glomerata</i>)	347.6	9%	84%	7%	100%
Wild orange	44.6	5%	91%	4%	100%
Genipap	113	17%	82%	1%	100%
Cassava	132	15%	82%	3%	100%
Sweet Potato	115.6	6%	93%	1%	100%

4.1.2.3. The Ainu

The Ainu live on the Japanese island of Hokkaido. There are few identifying Ainu today and their population is recorded as just over 13,000 (Iwasaki-Goodman et al., 2009; Uzawa, 2019). However, Ainu researchers estimate that the actual Ainu population is somewhere between 100,000 and 300,000 individuals (Uzawa, 2019). The discrepancy between the number of identifying Ainu and the actual population is a result of the

Japanese government's longstanding attempt to assimilate the Ainu into mainstream Japanese culture (Iwasaki-Goodman et al., 2009). Although the Ainu were recognized as Indigenous peoples of Japan in 2008, prior to this the Japanese government did not permit individuals to identify as Ainu and census records did not differentiate between Ainu and Japanese (Iwasaki-Goodman et al., 2009). As a result, there is a knowledge gap regarding how the Ainu live today. Traditionally, the Ainu are thought to have lived in small, mostly sedentary, hunting and gathering groups (Ōnishi et al., 2014). Today, those who identify as Ainu have remained relatively independent from Japanese culture (Uzawa, 2019).

Recently, there has been a movement to reinstate traditional Ainu culture beginning with creating knowledge about the traditional foods (Iwasaki-Goodman et al., 2009). This has caused an increase in research into the nutritional status of the traditional Ainu diet. In order to learn more about the nutritional status of the traditional Ainu diet, a reconstruction of its plant food component was created by Iwasaki-Goodman et al. (2009). Iwasaki-Goodman et al. (2009) provide excellent nutrient composition data for the wild plant foods consumed by the Ainu as well as four traditional cultivated plant foods. All of the plant food values that Iwasaki-Goodman et al. (2009) calculated were extracted using the FAO approved methods and correspond with those approved by Greenfield and Southgate (2003) (Table 18). I used these values in my study.

The plants that the Ainu commonly consume are presented in Table 9. These 17 plants are generally low in fat and high in carbohydrates. The plant foods are varied and include fruits, vegetables, roots, beans, tubers, and grains.

In order to use the plant macronutrient values in the Cordain et al. (2000) equations, I took the mean values for each macronutrient. The calculations for this are presented in the Appendix and the results are presented in Table 17. I applied the values in Table 17 into the Cordain et al. (2000) equations in order to calculate the whole-food diet for the Ainu.

Table 9: The plant foods commonly consumed by the Ainu and their relative macronutrient percentages. * = the plant was traditionally consumed in the listed state. The macronutrient analyses were conducted on the state that the foods were consumed in as per Greenfield and Southgate's (2003) recommendations.

Plant	Protein (%)	Carbohydrates (%)	Fat (%)	Total (%)
Wild Onion, Fresh*	33%	63%	4%	100%
Wild Onion, Dried*	39%	50%	13%	102%
Aha Bean	26%	47%	26%	100%
Anemone, Fresh*	29%	62%	10%	101%
Anemone, Dried*	28%	56%	16%	100%
Angelica, Fresh	8%	86%	6%	100%
Udo Spikenard	15%	82%	4%	101%
Perennial Lily, Root*	6%	93%	2%	100%
Perennial Lily, Powder*	0%	100%	0%	100%
Turep, Fermented*	3%	96%	1%	100%
Ostrich Fern, Dried*	38%	52%	10%	100%
Butterbur, Fresh*	9%	92%	0%	102%
Armur Cork Fruit	12%	67%	21%	100%
Barnyard Millet	11%	80%	9%	100%
Italian Millet	12%	81%	7%	100%
Egg Millet	12%	84%	4%	100%
Potatoes, Frozen*	2%	96%	2%	100%

4.1.2.4. The Baffin Island Inuit

The Baffin Island Inuit are the Inuit peoples who inhabit Baffin Island, which is located in the east of the territory of Nunavut, Canada. The Baffin Island Inuit are the descendants of the Thule people who moved eastwards from Alaska to inhabit the eastern Canadian Arctic around 1000 A.D. (Taylor, 2018). Consequently, the Thule and Baffin Island Inuit have inhabited Baffin Island for 1,500 years (Taylor, 2018). Today, the Baffin Island Inuit population is just under 15,000 and about half of the population lives in Iqaluit – Nunavut’s capital city (Taylor, 2018).

Due to Baffin Island’s harsh Arctic climate, all the traditional foods of the Baffin Island Inuit were hunted or gathered. In the 1990s and early 2000s a significant amount of research was done on the traditional Baffin Island Inuit diet (e.g., Kuhnlein et al., 1991; Kuhnlein and Soueida, 1992; Kuhnlein et al., 1996; and Berti et al., 1999). This work was conducted in order better understand the health benefits of the traditional diet as many Baffin Island Inuit had transitioned to a predominantly ‘market food’ diet of refined grains and flours, sugars, and separated fats. The majority of market foods that are available for the Baffin Island Inuit provide less nutritional value than the traditional foods and was thought to be causing poor health amongst the Baffin Island Inuit population (Kuhnlein et al., 1996). As a part of this research, both the plant and animal components of the traditional Baffin Island Inuit diet were recorded including detailed nutrient tables.

To reconstruct the wild plant diet for the Baffin Island Inuit, I used Kuhnlein et al. (1996), Kuhnlein et al. (1991), Kuhnlein and Soueida (1992), Berti et al. (1999), and the CINE Arctic Nutrient database (CINE, 2005).

The 43 plants that are commonly consumed for the Baffin Island Inuit are presented in Table 10. They include high-carbohydrate berries, sea plants, bark, shoots, roots, and ferns.

In order to use the plant macronutrient values in the Cordain et al. (2000) equations, I took a weighted mean of the Baffin Island Inuit plant values. The calculations for this are presented in the Appendix and the results are presented in Table 17. I applied the values in Table 17 into the Cordain et al. (2000) equations in order to calculate the whole-food diet for the Baffin Island Inuit.

Table 10: The plant foods commonly consumed by the Baffin Island Inuit and their relative macronutrient percentages.

Plant	Kcal/100 g	Protein (%)	Carbohydrates (%)	Fat (%)	Total (%)
Kelp	75	11%	78%	11%	100%
Blackberries	57.17	3%	80%	17%	100%
Blueberries	50.6	6%	84%	11%	100%
Mountain Sorrel	53.7	28%	57%	15%	100%
Blackcap	87.4	5%	80%	14%	100%
Black Hawthorn	73.4	2%	81%	17%	100%
Bog Blueberry	50.6	6%	84%	11%	100%
Bunchberry	69.16	3%	96%	1%	100%
Crowberry	46	2%	83%	16%	100%
Grey blueberry	54.1	8%	84%	8%	100%
Highbush Cranberry	41.6	1%	90%	9%	100%
Kinnikinnick berry	102.3	3%	88%	10%	100%
Mountain bilberry	57.07	4%	95%	0%	100%
Red elderberry	113.2	4%	52%	45%	100%
Red huckleberry	52.73	6%	91%	3%	100%
Salmonberry	52.4	11%	76%	14%	100%
Saskatoon berry	99.2	3%	86%	11%	100%
Soapberry	79.9	9%	83%	8%	100%
Stink current	69.6	5%	80%	16%	100%
Swamp gooseberry	65.5	9%	59%	32%	100%
Thimbleberry	109.6	6%	84%	10%	100%
Watery blueberry	73.8	5%	88%	7%	100%
Wild blue currant	65	4%	87%	8%	100%
Wild black gooseberry	76.7	6%	77%	18%	100%

Plant	Kcal/100 g	Protein (%)	Carbohydrates (%)	Fat (%)	Total (%)
Wild raspberry	72.8	3%	87%	10%	100%
Wild strawberry	60.5	4%	83%	13%	100%
Cloudberry	55	15%	69%	16%	100%
Cranberry	62.4	6%	77%	17%	100%
Green gooseberry	62.4	6%	77%	17%	100%
Purple gooseberry	74.7	5%	91%	4%	100%
Raspberry	76.3	8%	79%	13%	100%
Cow parsnip	19.5	4%	82%	14%	100%
Fireweed	30.4	4%	84%	12%	100%
Lambsquarters	41.4	32%	55%	13%	100%
Salmonberry shoots	27.4	7%	73%	20%	100%
Sheep Sorrel	48.2	9%	80%	11%	100%
Stinging nettle	53	10%	60%	31%	100%
Thimbleberry shoots	28	9%	79%	13%	100%
Licorice fern	141	3%	68%	29%	100%
Lupine	73.2	11%	84%	5%	100%
Riceroots	901.5	1%	98%	0%	100%
Cottonwood bark	113.3	1%	95%	4%	100%
Wild crabapple	90	5%	79%	16%	100%

4.1.2.5. The Hadza

The Hadza live around Lake Eyasi in northern Tanzania. The Hadza population is small, totalling only about 750 people (Hawkes et al., 1997). The Hadza have been well-documented by various ethnographers over the years (e.g., Hawkes et al., 2001; Marlowe, 2010).

The Hadza still subsist as a mostly hunting and gathering society (Marlowe, 2010). This is despite the many attempts by Christian missionaries and governmental programs who encouraged them to adopt an agricultural lifestyle (Hawkes et al., 1997).

To generate the macronutrient values for the plant component of the Hadza diet, I used a dataset that documents the nutritional composition and relative percentage of the most common types of wild plant foods consumed by the Hadza (Murray et al., 2001). Murray et al. (2001) presented the nutritional information on six kinds of honey (making up 15% of the total diet), baobab seed and pulp (making up 14% of the total diet), and six kinds of berries (making up 20% of the total diet). The study presented tubers as contributing 19% of the total diet. Unfortunately, however, it did not provide the nutrient information for the tubers that the Hadza consume. The nutrient information for tubers included in the Hadza diet was taken from Schoeninger et al. (2001).

The plants that the Hadza commonly consume are listed in Table 11. There are 15 types of plant food including honey, nuts, seeds, fruit, and tubers.

In order to use the plant macronutrient values in the Cordain et al. (2000) equations, I calculated the weighted average of honey, baobab, berries, and tubers. The calculations for this are presented in the Appendix and the results are presented in Table 17. I applied the values in Table 17 into the Cordain et al. (2000) equations in order to calculate the whole-food diet for the Hadza.

Table 11: The plant foods commonly consumed by the Hadza and their relative macronutrient percentages. All values in this table were calculated from Murray et al. (2001) except for the tubers which were calculated from Schoeninger et al. (2001). * = The honeys are noted to be from different bee species and plants (Murray et al., 2001).

Plant	Kcal/100g	Protein (%)	Carbohydrates (%)	Fat (%)	Total (%)
Honey - Ba'alako-1*	439	4%	80%	17%	101%
Honey - Ba'alako-2*	429	3%	84%	13%	100%
Honey - N!ateko-1*	422	3%	86%	11%	100%

Plant	Kcal/100g	Protein (%)	Carbohydrates (%)	Fat (%)	Total (%)
Honey - N!ateko-2*	403	3%	94%	3%	100%
Honey - Kanoa-1*	428	3%	84%	13%	100%
Honey - Kanoa-2*	404	2%	95%	3%	100%
Baobab seeds	454	32%	10%	58%	100%
Baobab pulp	203	5%	92%	3%	100%
Kinsinubi	342	15%	80%	5%	100%
Undushibi	324	19%	76%	5%	100%
Masakapi	318	16%	79%	5%	100%
Hlukayebe	337	8%	86%	5%	101%
Kongolubi	330	15%	80%	5%	100%
Pawe	232	6%	86%	8%	100%
Tubers	N/A	6%	67%	27%	100%

The Hiwi

The Hiwi reside in both Venezuela and Colombia. The term Hiwi refers to all people who speak a language called Guahibo and includes both foragers and agriculturalists (Hurtado and Hill, 1990). Here, I will focus on the Hiwi foragers. The Hiwi foragers inhabit poorly drained river basins, clay-rich savannahs, and river headwaters (Hurtado and Hill, 1990).

The size of the Hiwi population is unknown due to social upheaval in Venezuela and neighbouring Colombia. The population in 1980 was estimated to be 800 individuals across Venezuela and Colombia. The Venezuelan Hiwi population was estimated to be 290 individuals in 1988 and the population lived in two large bands, one of 188 individuals and one of 102 individuals.

As of the late 1980s, the Hiwi's wild food resources were dwindling due to competition with local farmers (Hurtado and Hill, 1990). At that time, the Hiwi subsisted mainly on game, fish, and gathered plant foods, although they would occasionally grow

plantain, corn, and squash. Today, the Hiwi still subsist on primarily hunting and gathering, although they live predominantly on government reservations (Hill et al., 2007).

To calculate the macronutrients in the Hiwi plant diet, I used Hurtado and Hill (1990) and Leung and Flores (1961). Hurtado and Hill (1990) estimated some plant values based on their similarity with other foods in Leung and Flores (1961) and the USDA database (USDA, 2019).

The plants that the Hiwi commonly consume are shown in Table 12. There are 16 species in total. These include honey, fruits, tubers, roots, nuts, and seeds. There are many high-carbohydrate plants and a few high-fat plants. One high protein legume is recorded in this table.

In order to use the plant macronutrient values in the Cordain et al. (2000) equations, I took the mean values for each macronutrient. The calculations for this are presented in the Appendix and the results are presented in Table 17. I applied the values in Table 17 into the Cordain et al. (2000) equations in order to calculate the whole-food diet for the Hiwi.

Table 12: The plant foods commonly consumed by the Hiwi and their relative macronutrient percentages * = The macronutrient values were derived via extrapolation from similar sources as indicated by Hurtado and Hill (1990).

Plant	Kcal/100 g	Protein (%)	Carbohydrates (%)	Fat (%)	Total (%)
‘Yatsiro’ Wild Root	130	3%	96%	1%	100%
‘No’o’ Wild Root	107	7%	91%	2%	100%
Ripe Mangos	65.4	3%	94%	3%	100%
Unripe mangos	49.4	3%	93%	4%	100%
Oranges	44.6	6%	90%	4%	100%
Palm Heart*	115	9%	89%	2%	100%
Honey	314.4	1%	99%	0%	100%
Palm Nuts*	442	13%	22%	65%	100%

Plant	Kcal/100 g	Protein (%)	Carbohydrates (%)	Fat (%)	Total (%)
Chiga Legume*	413	48%	24%	27%	100%
‘Hero’ Small Wild Potato*	78	10%	90%	0%	101%
‘Oyo’ Wild root*	77	7%	91%	2%	101%
‘Hewyna’ Wild Root*	79	6%	91%	3%	101%
Guaye fruit*	65.4	3%	94%	3%	100%
Merei Fruit*	49.4	3%	93%	4%	100%
Madrona Fruit*	65.4	3%	94%	3%	100%
Jojjom Fruit*	84.5	12%	85%	3%	100%

4.1.2.6. The Sahtú Dene/Métis

The Dene/Métis, who are also known as the Sahtú Dene, live in the western Canadian Arctic. The towns of Fort Good Hope and Colville Lake in the Northwest Territories are home to the largest Sahtú Dene/Métis populations, and have a combined population of about 800 individuals (Kuhnlein et al., 1994). The Sahtú Dene have lived in the Canadian Arctic for thousands of years. The term Métis refers to Indigenous people who are of combined Indigenous and European, primarily French, background (Gaudry, 2019). The Métis who are of Dene and European background have lived in Fort Good Hope and Colville Lake since the 18th century (Gaudry, et al., 2019; Kuhlein et al., 1994). The Sahtú Dene/Métis traditional diet comprised of hunted animals and gathered wild Arctic plants (Kuhnlein et al., 1994).

In the early 1990s two studies were carried out with a view to preserve the Sahtú Dene/Métis knowledge of their traditional foods and improve nutritional quality of the overall diet (Kuhnlein et al. 1994, 1995). These studies occurred because the Sahtú Dene/Métis were affected by poor nutritional health and it was suspected that this was due to the prevalence of market food in their diet. Kuhnlein et al. (1994, 1995) documented the use and nutrient composition of the traditional Sahtú Dene/Métis foods, and contain information regarding the macronutrient information for each plant habitually

consumed by the Sahtú Dene/Métis. I used Kuhnlein et al. (1994, 1995) to reconstruct the plant component of the Sahtú Dene/Métis diet.

The plant foods that the Sahtú Dene/Métis commonly consume are listed in Table 13. There are seven species in total. They are all berries.

In order to use the plant macronutrient values in the Cordain et al. (2000) equations, I calculated the mean of the plant values for each macronutrient. The calculations for this are presented in the Appendix and the results are presented in Table 17. I applied the values in Table 17 into the Cordain et al. (2000) equations in order to calculate the whole-food diet for the Sahtú Dene/Métis.

Table 13: The plant foods commonly consumed by the Sahtú Dene/Métis and their relative macronutrient percentages.

Plant	Kcal/100g	Protein (%)	Carbohydrates (%)	Fat (%)	Total (%)
Blueberry	64	4%	81%	14%	100%
Blackberry	57	3%	81%	16%	100%
Cloudberry	55	15%	69%	16%	100%
Cranberry	74	4%	82%	15%	101%
Gooseberry, green	62.4	6%	77%	17%	100%
Gooseberry, purple	74.7	5%	91%	4%	100%
Raspberry	76.3	8%	79%	13%	100%

4.1.2.7. The Nuxalk

The Nuxalk inhabit the Bella Coola Valley, located on the central west coast of British Columbia, Canada. The Bella Coola Valley comprises the entire valley around the Bella Coola River and includes the town of Bella Coola. Traditionally the Nuxalk inhabited villages along the Bella Coola river. Today, they live on a reservation that is located near the village of Bella Coola as well as in urban centres (Kuhnlein, 1992). A century ago, the total Nuxalk population of Bella Coola was recorded as being just over three hundred individuals and beginning to increase (McIlwraith, 1922:5). Currently, they number around 1,700 people, with around 900 of these people living in the Bella Coola Valley and the rest living in urban centres (Kennedy and Bouchard, 2020).

The traditional Nuxalk diet comprised fish, marine fat, berries, greens, and root foods. The Nuxalk did not traditionally practice agriculture, although they did tend some wild roots to enhance productivity (Lepofsky et al., 1985).

Throughout the 1980s, Harriet Kuhnlein compiled three reports that included the nutrient composition for the traditional Nuxalk berries, tubers, and wild greens and the relative contributions of each plant to the traditional Nuxalk diet (Kuhnlein, 1984, 1989, 1990). I used these reports to calculate the average macronutrient composition of the traditional Nuxalk plant foods.

The plants that are commonly consumed by the Nuxalk are listed in Table 14. There are 41 plant species in total. These include a large number of high-carbohydrate berry species as well as a variety of sea plants, bark, shoots, roots, and ferns.

In order to use the plant macronutrient values in the Cordain et al. (2000) equations, I calculated the weighted mean for each macronutrient. The calculations for this are presented in the Appendix and the results are presented in Table 17. I applied the values in Table 17 into the Cordain et al. (2000) equations in order to calculate the whole-food diet for the Nuxalk.

Table 14: The plant foods commonly consumed by the Nuxalk and their relative macronutrient percentages.

Plant	Kcal/100g	Protein (%)	Carbohydrates (%)	Fat (%)	Total (%)
Blackcap	87	6%	80%	14%	100%
Bog blueberry	51	5%	83%	11%	99%
Bunchberry	76	3%	87%	9%	100%
Cinquefoil roots	132	9%	89%	4%	103%
Clover rhizomes	74	4%	89%	6%	99%
Cow-parsnip	20	4%	80%	14%	98%
Fireweed shoots	30	4%	85%	12%	101%
Highbush cranberry	42	1%	90%	9%	99%
Kinnikinnik berry	102	3%	88%	10%	100%

Plant	Kcal/100g	Protein (%)	Carbohydrates (%)	Fat (%)	Total (%)
Licorice fern rhizomes	138	3%	70%	30%	102%
Red elderberry, fresh	113	4%	52%	45%	100%
Red huckleberry	56	6%	86%	8%	99%
Riceroor bulbs	98	12%	89%	3%	104%
salmonberry shoots	31	6%	75%	17%	99%
Saskatoon berry	99	3%	86%	11%	100%
seaweed	303	32%	64%	4%	100%
Soapberry, fresh	80	9%	83%	8%	100%
Stink currant	70	5%	79%	15%	99%
Thimbleberry shoots	28	9%	79%	13%	100%
Thimbleberry	110	6%	84%	10%	100%
Watery blueberry	74	5%	88%	7%	100%
Wild blue currant	65	4%	87%	8%	100%
Wild raspberry	73	3%	87%	10%	100%
Cottonwood tree, inner bark	31	3%	81%	15%	98%
Grey blueberry	54	8%	84%	8%	100%
Salmonberry shoots	52	11%	76%	14%	101%
Mountain bilberry	59	4%	89%	8%	101%
Rosehip	82	8%	86%	7%	100%
Stinging nettle	44	16%	72%	12%	100%

Plant	Kcal/100g	Protein (%)	Carbohydrates (%)	Fat (%)	Total (%)
Wild black gooseberry	77	6%	76%	18%	100%
Wild crabapple	90	5%	79%	16%	100%
Wild strawberry	61	4%	82%	13%	99%

4.1.2.8. The Wet'suwet'en

The Wet'suwet'en live around the Bulkley and Fraser River drainage basins in the northern interior of British Columbia, Canada (Gottsfeld, 1995). As of 1993, there were about 1,000 Wet'suwet'en people living in their traditional area (Gottsfeld, 1993).

Traditional Wet'suwet'en subsistence was dominated by fishing, hunting large game, trapping small game, picking berries, collecting shoots and roots, and harvesting pine cambium (Gottsfeld, 1995).

The traditional Wet'suwet'en diet was reconstructed in the 1990s in order to address the rise in poor health that the Wet'suwet'en people were experiencing due to an increased reliance on market food (Gottsfeld, 1995; Kuhnlein, 1989; Kuhnlein, 1990). Gottsfeld (1995), Kuhnlein (1989), and Kuhnlein (1990) contain nutrient information for the plant foods commonly consumed by the Wet'suwet'en. I used these sources to reconstruct the plant food component of the traditional Wet'suwet'en diet.

The plant foods that the Wet'suwet'en traditionally utilised for food are listed in Table 15. There are 30 plant food items in total including berries, ferns, roots, and weeds. With the exception of the red elderberry, all of the plants are high in carbohydrates.

In order to use the plant macronutrient values in the Cordain et al. (2000) equations, I calculated the weighted mean for each macronutrient. The calculations for this are presented in the Appendix and the results are presented in Table 17. I applied the values in Table 17 into the Cordain et al. (2000) equations in order to calculate the whole-food diet for the Wet'suwet'en.

Table 15: The plant foods commonly consumed by the Wet'suwet'en and their relative macronutrient percentages.

Plant	Kcal/100g	Protein (%)	Carbohydrates (%)	Fat (%)	Total (%)
Saskatoon berry	99	3%	86%	11%	100%
Kinnikinnik or bearberry	102	3%	88%	10%	100%
Bunchberry	76	4%	87%	9%	100%
Hawthorn, black	73	2%	81%	17%	100%
Strawberry, wild blueleaf	61	4%	83%	13%	100%
Crabapple	90	5%	79%	16%	100%
Rose, nootka	82	8%	86%	7%	100%
Red raspberry	72	4%	88%	8%	100%
Thimbleberry	110	6%	84%	10%	100%
Saskatoon berry	52	11%	76%	14%	100%
Saskatoon berry	44	9%	91%	2%	102%
Red elderberry	110	11%	50%	39%	100%
Soapberry	80	9%	83%	8%	100%
Alaska blueberry	74	5%	88%	7%	100%
High bush blueberry	44	6%	95%	0%	101%
Black huckleberry	59	4%	88%	8%	100%
Oval Leaf huckleberry	54	8%	84%	8%	100%
Red huckleberry	56	6%	86%	8%	100%

Plant	Kcal/100g	Protein (%)	Carbohydrates (%)	Fat (%)	Total (%)
Vaccinium parvifolium	37	4%	94%	2%	100%
High bush cranberry	42	1%	90%	9%	100%
Spiny wood fern	126	8%	87%	7%	102%
Fireweed	30	4%	84%	12%	100%
Rice root, chocolate lily	98	12%	89%	3%	104%
Cow parsnip (wild rhubarb)	20	4%	82%	14%	100%
Cottonwood, black	31	3%	83%	15%	100%
Western hemlock	118	8%	88%	5%	100%
Pine, lodgepole	48	7%	83%	11%	100%
Pine cambium	48	6%	83%	11%	100%

4.1.2.9. The Tetlit Gwich'in

The Tetlit Gwich'in are an Athabaskan people who reside in the Northwest Territories, Canada (Kuhnlein et al., 2009). They maintained a nomadic hunting and gathering lifestyle until the mid-1800s when the Hudson's Bay Company established trading posts around which the Tetlit Gwich'in formed settlements. Today the Tetlit Gwich'in reside in Tetlit Zeh in the Northwest Territories. The population in that town was recorded as 823 in 2005 (Kuhnlein et al., 2009).

Although the Tetlit Gwich'in are fully settled and consume a primary market-food diet, they still hunt and gather 75-100 species of animals, fish, and plants (Kuhnlein et al., 2009). The traditional Gwich'in diet consisted primarily of animal food, with small amounts of plant foods being harvested during the summer and frozen or jarred for winter use.

The Tetlit Gwich'in plant values were analysed as part of an on-going project to improve the health of Indigenous people worldwide (CINE, 2005). I used the nutrient information from Kuhlein et al. (2009), which resulted from this project, to source the Gwich'in plant values. Kuhnlein et al. (2009) included descriptions plants consumed and the macronutrient composition of each food.

The plant foods that are commonly consumed by the Gwich'in are presented in Table 16. The nine food items are predominantly high-carbohydrate berries.

In order to use the plant macronutrient values in the Cordain et al. (2000) equations, I calculated the mean for each macronutrient. The calculations for this are presented in the Appendix and the results are presented in Table 17. I applied the values in Table 17 into the Cordain et al. (2000) equations in order to calculate the whole-food diet for the Tetlit Gwich'in.

Table 16: The plant foods commonly consumed by the Gwich'in and their relative macronutrient percentages. * = Nutrient information for *Rosa acicularis* was used.

Plant	Kcal (/100g)	Protein (%)	Carbohydrates (%)	Fat (%)	Total (%)
Crowberry/ Blackberry	57	3%	81%	16%	100%
Wild Rhubarb	18.1	13%	82%	5%	100%
Wild Raspberries	76.3	8%	79%	13%	100%
Green gooseberries	62.4	6%	77%	17%	100%
Rose Hips*	82.2	8%	86%	7%	100%
Cloudberries	55	15%	69%	16%	100%
High blueberries	64	4%	81%	14%	100%
Low blueberries	45.9	7%	79%	14%	100%
Low bush cranberries	74	4%	82%	15%	101%

4.1.2.10. The Average Plant Food Macronutrient Values

The macronutrient values presented in Table 17 are the average plant-food macronutrient values for each society. The values are presented as percentages of plant food energy. I applied each of these values in the Cordain et al. (2000) equations in order to calculate the whole-diet macronutrient values for each hunter-gatherer group. The average protein value from plants ranges from 6%-19% for protein, from 60%-84% for carbohydrates, and from 8%-27% for fat. The differences between the values themselves are considered in section 4.2 and the impact that these values have on the Cordain et al. (2000) model are discussed in sections 4.3 and 4.4.

Table 17: The average contributing plant macronutrients from each society.

Society	Protein	Carbohydrates	Fat	Macronutrient Source
Indigenous Australians	14%	62%	24%	Brand-Miller and Holt, 1998
!Kung	13%	60%	27%	Lee, 1973; Wehmeyer et al., 1969; and Duke and Atchley, 1986
Ache	6%	78%	16%	Hill et al., 1984; FAO, 2018; Duke and Atchley, 1986
Ainu	19%	73%	9%	Iwasaki-Goodman et al., 2009
Baffin Island Inuit	7%	80%	13%	Berti et al., (1999); Kuhnlein et al., 1996; Kuhnlein et al., 1991; Kuhnlein and Soueida, 1992; and CINE, 2005
Hadza	11%	72%	18%	from Murray et al., 2001; and Schoeninger et al., 2001
Hiwi	9%	84%	8%	Hurtado and Hill, 1990; Leung and Flores, 1961; and USDA, 2019
Sahtú Dene/Métis	7%	81%	12%	Kuhnlein et al., 1994; and Kuhnlein et al., 1995
Nuxalk	6%	81%	12%	Kuhnlein, 1984; Kuhnlein, 1989; and Kuhnlein, 1990
Wet'suwet'en	6%	84%	10%	Gottsfeld, 1995; Kuhnlein, 1989; and Kuhnlein, 1990
Gwich'in	8%	80%	13%	Kuhnlein et al., 2009

4.1.3. Extracting the Macronutrients

For the purposes of my study, it was necessary to ensure that all of the plant macronutrients were extracted in ways that yield comparable results. In order to do this, I only included macronutrients that were extracted according to the Greenfield and Southgate (2003) optimal or acceptable standard methods (see Table 2 in Chapter 2). Table 18 summarises the methods that were used to extract the plant macronutrients for each society in my sample.

All of the protein values used in this study were calculated via the Kjeldahl method for nitrogen extraction and the equation $N \times 6.25$. The Kjeldahl method in conjunction with the equation $N \times 6.25$ represent the FAO/INFOODS acceptable method to calculate the protein content of food (Greenfield and Southgate, 2003). As all of the protein values that were used in this study were extracted via the same methods, they can be considered comparable.

All of the sources from which the carbohydrate values were taken used the by-difference method. Although, as I discussed in Chapter 2, the by-difference method is not as accurate as extracting and summing the individual saccharides, it is often used because of its low-cost and reasonable reliability (Greenfield and Southgate, 2003; Southgate, 1969). As such, the by-difference method is the FAO/INFOODS acceptable method and is reasonably accurate for the purposes of this study. The carbohydrate values in this study can therefore be considered comparable.

The values for fat were obtained using the Soxhlet method, however, some of the sources did not list the Soxhlet method by name, but instead listed that the total fat was extracted according to the AOAC method (Table 18). Although this was the case with a number of my sources, I inferred that the Soxhlet method was the method in question as per the Greenfield and Southgate (2003) guidelines. I made this inference because the Soxhlet method is one of the approved methods for fat extraction and is considered the ideal method for solid foods that are low in structural fat, such as wild plant foods (Greenfield and Southgate, 2003). As a result of this inference, all of the fat values were extracted using comparable methods, therefore, the values can be considered comparable.

Table 18: A comparison of the methods used to construct the FCDs for each society.

Society	Energy	Protein	Carbohydrates	Fat
Indigenous Australians	Summing the proximal parts based on the Atwater factors	Kjeldhal method	By-difference method and by Southgate's starch-sugar separation method.	Soxhlet method
!Kung	Summing the proximal parts based on the Atwater factors	Not disclosed, but based on comparison with other nutrient analyses by the same author the Kjeldahal method is inferred	Not disclosed, but based on comparison with other nutrient analyses by the same author the by-difference method is inferred	Not disclosed, but based on comparison with other nutrient analyses by the same author the Shoxhlet method is inferred
Ache	Summing the proximal parts based on the Atwater factors	Kjeldahal method and $N \times 6.25$	By-difference method	Soxhlet method
Ainu	Summing the proximal parts based on the Atwater factors	Kjeldhal method and $N \times 6.25$	By-difference method	According to the AOAC method (Soxhlet)
Baffin Island Inuit	Summing the proximal parts based on the Atwater factors	Kjeldhal method and $N \times 6.25$	By-difference method	According to the AOAC method (Soxhlet)

Society	Energy	Protein	Carbohydrates	Fat
Hadza	Summing the proximal parts based on the Atwater factors	Kjeldhal method and N x 6.25	By-difference method	Determined using a modified AOAC Soxhlet method
Hiwi	Summing the proximal parts based on the Atwater factors	Kjeldhal method and N x 6.25	By-difference method	According to the AOAC method (Soxhlet)
Sahtú Dene/Métis	Summing the proximal parts based on the Atwater factors	Kjeldhal method and N x 6.25	By-difference method	According to the AOAC method (Soxhlet)
Nuxalk	Summing the proximal parts based on the Atwater factors	Kjeldhal method and N x 6.25	By-difference method	According to the AOAC method (Soxhlet)
Wet'suwet'en	Summing the proximal parts based on the Atwater factors	Kjeldhal method and N x 6.25	By-difference method	According to the AOAC method (Soxhlet)
Gwich'in	Summing the proximal parts based on the Atwater factors	Kjeldhal method and N x 6.25	By-difference method	According to the AOAC method (Soxhlet)

4.2. 4.2. Comparing the Plant Values

I next tested whether the plant values themselves exhibited significant differences between societies in order to assess the Cordain et al. (2000) claim that the Indigenous Australian plant values do not differ significantly from the plant values of other hunter-gatherer groups. To do this, I used independent samples t-tests to compare the array of plant values for each society with the array of values for the Australian plants presented by Cordain et al. (2000). In order to ensure that these results were not skewed by the false discovery rate, I adjusted the significance level by using the Benjamini-Hochberg test. I adjusted for a false discovery rate of 0.1 in line with McDonald (2014).

Table 19 shows the results from the comparisons after the significance level had been adjusted via the Benjamini-Hochberg test. Table 20 shows the results from the comparisons before the significance level was adjusted. In both tables, the values that are significant are bolded. Protein exhibited the most differences of the three macronutrients. The protein values for the Sahtú Dene/Métis, Wet'suwet'en, Baffin Island Inuit, Nuxalk, and Gwich'in were significantly different from the Indigenous Australian protein values at $p = 0.026, 0.020, 0.020, 0.020,$ and 0.038 respectively. Interestingly, this is all of the North American societies in the sample. The carbohydrate and fat values exhibited less difference than the protein values. None of the carbohydrate or fat values for any of the societies were significantly different from the Australian values. However, as per the p-values presented in Tables 19 and 20, there is more variation amongst the carbohydrate values than amongst the fat values, the latter of which are identical when adjusted. The adjusted fat values are identical because of the nature of the Benjamini-Hochberg test (Benjamini and Hochberg, 1995). In order to adjust the p-values via the Benjamini-Hochberg test, the p-values are ordered from smallest to largest and are then ranked with the smallest value having a rank of 1, the next smallest value having a rank of 2, and so forth. After this has been completed, the values are adjusted based on the largest original p-value, which will remain unchanged. For example, the Benjamini-Hochberg adjusted p-value for the second largest p-value will be the smaller of two options:

- a) equal to the previous adjusted p-value
- b) $current\ p\text{-value} * \frac{(total\ number\ of\ p\text{-values})}{p\text{-value\ rank}}$

The adjustments will be made in this fashion for all of the p-values. In the case of the fat values for this sample, the previous p-value was the smaller option for all of the values (Benjamini and Hochberg, 1995). Thus, all of the adjusted fat p-values are 0.758 and are not significant.

Table 19: Unadjusted p-values and t-values from t-tests that compare the plant values from the ten hunter-gatherer societies in my sample with the Indigenous Australian plant values. The significant values are bolded.

Society	Protein (p-value, t-value)	Carbohydrate (p-value, t-value)	Fat (p-value, t-value)
Wet'suwet'en	0.00, 3.54	0.04, -2.24	0.155, 1.07
Nuxalk	0.01, 3.19	0.11, -1.69	0.758, 0.63
Baffin Island Inuit	0.01, 3.08	0.17, -1.43	0.302, 0.40
Sahtú Dene/Métis	0.02, 2.27	0.18, -1.36	0.553, 0.31
Gwich'in	0.03, 2.10	0.19, -1.33	0.239, 0.46
Ache	0.10, 1.75	0.20, 0.34	0.696, -0.92
Hiwi	0.23, 1.20	0.35, -1.35	0.496, 1.20
Hadza	0.28, 1.09	0.60, -0.95	0.539, 0.69
Ainu	0.31, -1.04	0.64, -0.54	0.366, 1.49
!Kung	0.95, 0.06	0.72, 0.42	0.653, -0.53

Table 20: Benjamini-Hochberg-adjusted p-values from t-tests that compare the plant values from the ten hunter-gatherer societies in my sample with the Indigenous Australian plant values. The significant values are bolded.

Society	Protein	Carbohydrate	Fat
Wet'suwet'en	0.01	0.34	0.758
Nuxalk	0.01	0.34	0.758
Baffin Island Inuit	0.01	0.34	0.758
Sahtú Dene/Métis	0.05	0.34	0.758
Gwich'in	0.06	0.34	0.758

Society	Protein	Carbohydrate	Fat
Ache	0.09	0.34	0.758
Hiwi	0.21	0.50	0.758
Hadza	0.21	0.71	0.758
Ainu	0.21	0.71	0.758
!Kung	0.57	0.72	0.758

Thus, the results of the t-tests challenge Cordain et al.'s (2000) assumption. The ten additional sets of carbohydrate and fat values were not significantly different from the Australian carbohydrate and fat values used by Cordain et al. (2000). However, a number of the additional sets of protein values were significantly different from the Australian protein value employed by Cordain et al. (2000). Thus, contrary to what Cordain et al. (2000) argued, the plant macronutrient values for Indigenous Australians do not hold for all hunter-gatherers.

4.3. Effects of Different Plant Values on the Cordain et al. (2000) Model Results

The purpose of this study is to examine whether the recommendations that resulted from worldwide hunter-gatherer plant values were significantly different from the Cordain et al. (2000) recommendations. To do this, the average plant macronutrient values for the ten hunter-gatherer societies that I analysed were combined with Cordain et al.'s (2000) model to create alternative hunter-gatherer “macronutrient consumption ratios” (MCRs) (Cordain et al., 2000:682).

In order to arrive at these MCRs, Cordain et al. (2000) based their equations on the relative plant- and animal-food component (i.e., P-A ratio) of the societies in their sample. As I have discussed in previous chapters, no single P-A ratio represented all of the societies in their sample. Therefore, Cordain et al. (2000) calculated the equation at five different P-A subsistence ratios. Additionally, because animals vary in their body fat, Cordain et al. (2000) also calculated the equation at five animal body fat percentages; however, they concluded that only three of these body fat percentages were relevant

regarding average hunter-gatherer diets (see Chapters 3 for a discussion on this). The Indigenous Australian plant values calculated by Brand-Miller et al. (1998) were the only plant values that were used in the equations. The range of macronutrient values that the equations produced represent the macronutrient recommendations for the Paleo Diet. In the 2000 paper, Cordain et al. did not directly refer to these values as the guidelines for the Paleo Diet. This designation has been assigned on the basis of two factors. The first is Cordain et al.'s (2000) suggestions that the "macronutrient characteristics of hunter-gatherer diets may provide insights into potentially therapeutic dietary recommendations for contemporary populations" (Cordain et al., 2000:691), and the second is from Cordain's (2010) Paleo Diet book, where he cites the 2000 study as the source for the macronutrient target ratios that he lists for the Paleo Diet (Cordain, 2010:11).

In order to calculate comparable MCRs for each hunter-gatherer group, I applied the average plant macronutrient values for each society, which I discussed in Chapter 4.1, into the Cordain et al. (2000) equations and calculated the equations at the three relevant animal body-fat levels, which are 20%, 15%, and 10% body fat, and at the five different P-A contributions, which are 65:35, 55:45, 50:50, 45:55, and 35:65. As such, I conducted calculations using the equations 15 times for each macronutrient. The range of values that resulted when each society's plant values were used in the equations represents alternative MCRs. The calculations for all of the societies are presented in the Appendix. The results are presented in Table 21.

To visually compare the MCRs that resulted from each society's plant values against those that resulted from the Indigenous Australian plant values, I created boxplots. To statistically test whether the MCRs changed significantly with each society's plant values, I conducted paired samples t-tests. For these tests, I compared the MCRs that resulted from the equations for each society against the corresponding MCRs from the Indigenous Australian values. For example, for the !Kung I compared the 15 results from each equation with the corresponding 15 results that Cordain et al. (2000) calculated (these are presented and discussed in Table 4 in Chapter 3. 2). Therefore, for each society the t-tests compared the averages of 15 'macronutrient consumption values' for each macronutrient. The values are compared in subsections 4.3.2.-4.3.11.

4.3.1. MANOVA Tests

In order to compare the model results across all societies, I created boxplots that visually present the variation in the protein, carbohydrates, and fat (Figures 5-7). The ranges that are compared in this section represent the MCRs for each society as calculated with the average plant values for each society. These are effectively alternative Paleo Diet macronutrient recommendations and are summarized in Table 21.

Table 21: Macronutrient consumption ratios (MCRs) that result when each hunter-gatherer society’s average plant values are used in the Cordain et al. (2000) equations.

Society	Protein Consumption Ratio	Carbohydrate Consumption Ratio	Fat Consumption Ratio
Indigenous Australian	19-35%	22-40%	34-58%
!Kung	18-34%	20-37%	37-59%
Ache	14-32%	27-51%	28-54%
Ainu	23-37%	26-47%	24-52%
Baffin Island Inuit	14-32%	28-52%	26-53%
Hadza	17-34%	25-47%	30-55%
Hiwi	14-32%	28-53%	26-53%
Sahtú Dene/Métis	14-32%	28-53%	26-53%
Nuxalk	14-32%	28-53%	26-53%
Wet’suwet’en	14-32%	29-55%	24-52%
Gwich’in	15-33%	28-52%	26-53%
Overall Range	14-37%	20-55%	24-59%

Figure 5, which compares the protein consumption ratios for all of the hunter-gatherer societies, exhibits little variation. However, the protein consumption ratios that resulted from the Ainu plant values stand out as being consistently higher than the rest.

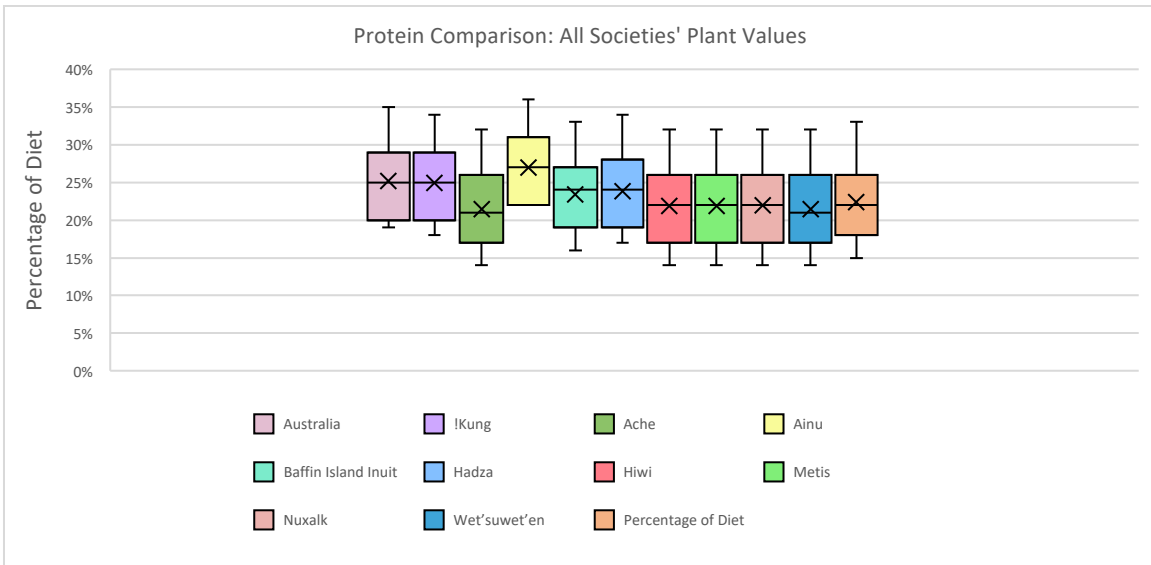


Figure 5: Boxplot comparing all of the protein consumption ratios.

Figure 6 compares the carbohydrate consumption ratios that resulted from each hunter-gatherer group's plant values. The values in Figure 6 appear more variable than those in Figure 5. Of note, the carbohydrate consumption ratios that resulted from the Indigenous Australian plant values and the !Kung plant values are consistently lower than those for the other societies.

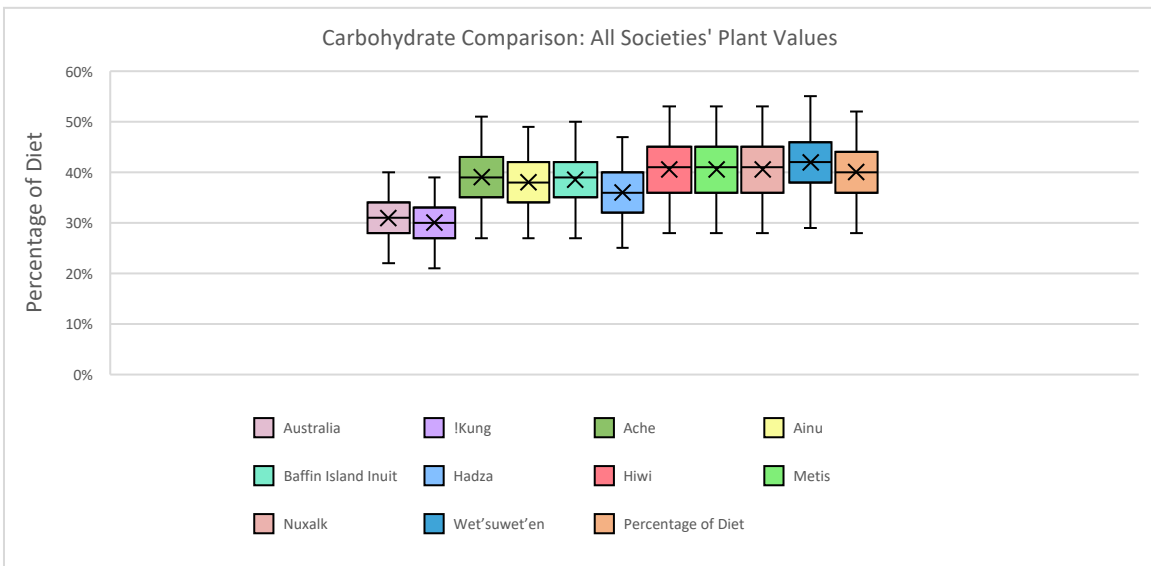


Figure 6: Boxplot comparing all of the carbohydrate consumption ratios.

Figure 7 compares the fat consumption ratios that resulted from each hunter-gatherer group's plant values. Figure 7 demonstrates less variation than Figure 6. It is notable, however, that the !Kung and Indigenous Australian fat consumption ratios are consistently higher than those of the rest of the groups in the sample. The Ainu fat consumption ratios are consistently lower than the other societies, but not by very much.

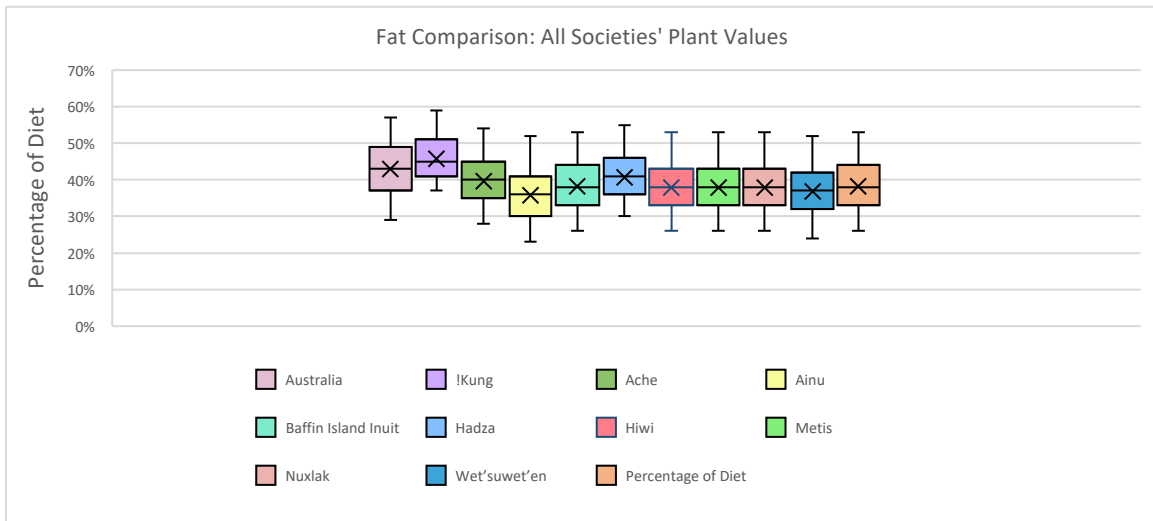


Figure 7: Boxplot comparing all of the fat consumption ratios.

To statistically test whether there are significant differences amongst these samples, I conducted MANOVA tests. In the tests, as in the graphs, each society represents the MCRs that resulted when their average plant values were applied in the Cordain et al. (2000) equations. To structure the tests, I placed the societies as the independent factor and the three macronutrients as the dependant factors in order to test whether the MCRs were significantly dependent on which society they were from.

Although there did not appear to be large differences amongst the hunter-gatherer protein consumption ratios based on the boxplot, the MANOVA results are significant at $p = 0.002$. This suggests that the protein consumption ratios differ significantly as a result of the average plant protein values that were applied to the Cordain et al. (2000) equations.

The carbohydrate consumption ratios exhibit more substantial differences than the protein consumption ratios do. Because there was a lot of variation amongst the carbohydrate consumption ratios in the boxplots, it was not surprising that the MANOVA results were significant at $p = 0.000$. This suggests that the carbohydrate consumption

ratios differ significantly as a result of the average plant carbohydrate values that were applied to the Cordain et al. (2000) equations.

The fat consumption ratios did not appear to differ very much based on the boxplots, however, the MANOVA test was significant at $p = 0.007$. This suggests that there are significant differences in the fat consumption values that resulted from calculating the Cordain et al. (2000) equations with the average plant fat values for each society in this sample.

4.3.2. The !Kung

The !Kung plant macronutrient values that I combined with Cordain et al.'s (2000) equations were 13% protein, 60% carbohydrate, and 27% fat.

Figure 8 shows boxplots that compare the total-diet protein, carbohydrate, and fat consumption ratios for the Indigenous Australians and the !Kung. Figure 8a shows that the protein consumption ratios for the Indigenous Australian and !Kung are nearly identical. The groups' minimum and maximum values only differ by one percent, and their medians are identical. Figure 8b shows that while the Indigenous Australian and !Kung carbohydrate consumption ratios overlap, the Indigenous Australians' are appreciably higher than the !Kung's. Figure 8c shows that the !Kung's fat consumption ratios are slightly higher than the Indigenous Australians'.

All three t-tests were significant when I compared the MCRs for the !Kung with the MCRs for the Indigenous Australians. The p-values for the protein, carbohydrate, and fat comparisons were 0.041, 0.000, and 0.000, respectively. As such, these results indicate that the !Kung plant values yield different MCRs from the Indigenous Australian plant values when applied to the Cordain et al. (2000) equations.

Table 22: Comparison of the Indigenous Australian and !Kung MCRs.

Macronutrient	Indigenous Australians	!Kung
Protein	19-35%	18-34%
Carbohydrate	22-40%	20-37%
Fat	34-58%	37-59%

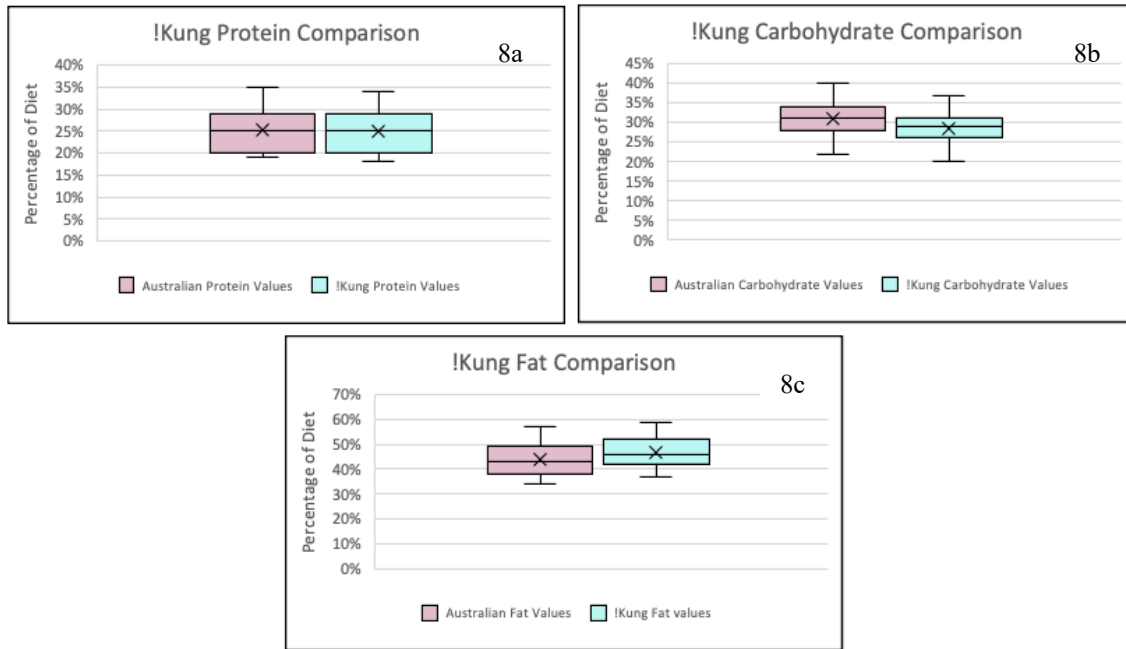


Figure 8: Boxplots comparing the macronutrient consumption ratios created using the Indigenous Australian plant values and those using the !Kung plant values.

Figure 8a compares the protein consumption ratios, Figure 8b compares the carbohydrate consumption ratios, and Figure 8c compares the fat consumption ratios that resulted from applying each group's plant values to the Cordain et al. (2000) equation.

4.3.3. The Ache

The Ache plant macronutrient values that I combined with Cordain et al.'s (2000) equations were 6% protein, 78% carbohydrate, and 16% fat.

Figure 9 shows boxplots comparing the macronutrient consumption ratios created with the Indigenous Australian plant values with those created with the Ache plant values. Figure 9a exhibits differences between the protein consumption ratios for the Indigenous Australians and those for the Ache. The Ache protein consumption ratios are a little lower than those for the Indigenous Australians. Figure 9b shows differences between the carbohydrate consumption ratios for the Indigenous Australians and the Ache. The Ache carbohydrate consumption ratios are appreciably higher than those for the Indigenous Australian carbohydrate values. Finally, Figure 9c shows difference between the fat consumption ratios for the Indigenous Australians and the Ache. The Ache fat consumption ratios are a little lower than those for the Indigenous Australians.

The t-tests were significant when I compared the MCRs for the Ache with those for the Indigenous Australians. The results were $p = 0.000$, $p = 0.000$, and $p = 0.000$ for the protein, carbohydrate, and fat consumption ratios respectively. As such, these results indicate that the Ache plant values yield different MCRs from the Indigenous Australian plant values when applied to the Cordain et al. (2000) equations.

Table 23: Comparison of the Indigenous Australian and Ache MCRs.

Macronutrient	Indigenous Australians	Ache
Protein	19-35%	14-32%
Carbohydrate	22-40%	27-51%
Fat	34-58%	28-54%

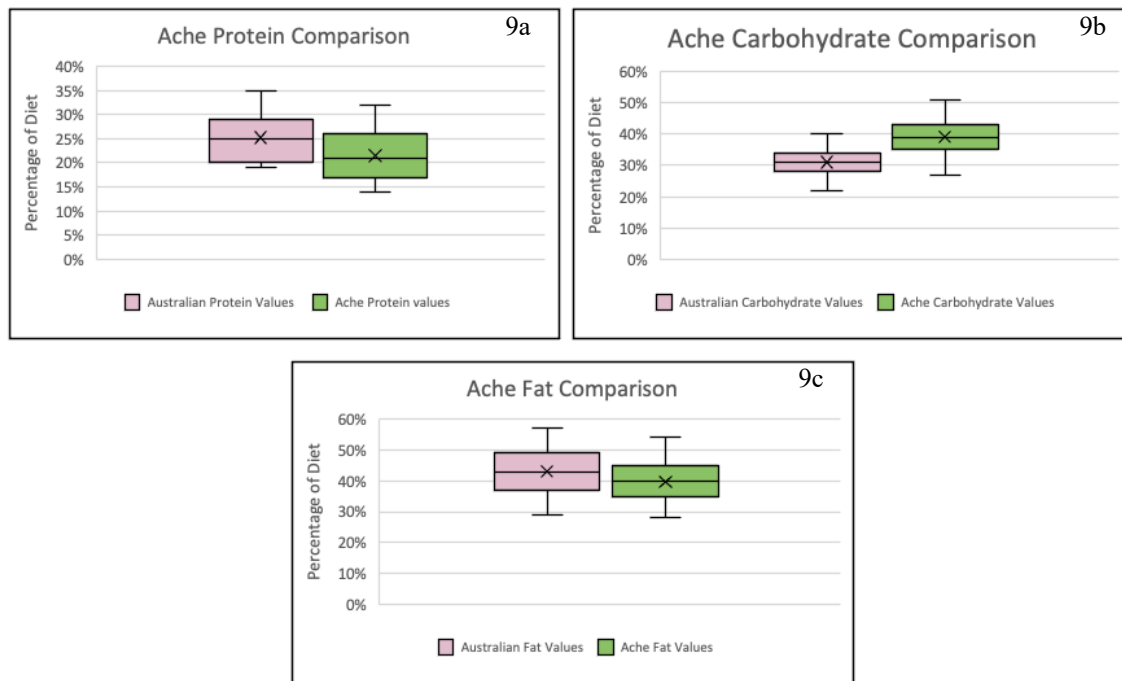


Figure 9: Boxplots comparing the MCRs created using the Indigenous Australian plant values and those using the Ache plant values.

Figure 9a compares the protein consumption ratios, Figure 9b compares the carbohydrate consumption ratios, and figure 9c compares the fat consumption ratios that resulted from applying each group's plant values to the Cordain et al. (2000) equations.

4.3.4. The Ainu

The Ainu plant macronutrient values that I combined with Cordain et al.'s (2000) equations were 19% protein, 73% carbohydrate, and 9% fat.

Figure 10 shows boxplots comparing the macronutrient consumption ratios created with the Indigenous Australian plant values with those created with the Ainu plant values. Figure 10a exhibits differences between the protein consumption ratios for the Indigenous Australians and those for the Ainu. The Ainu protein consumption ratios are a little higher than those for the Indigenous Australians. Next, Figure 10b shows differences between the carbohydrate consumption ratios for the Indigenous Australians and the Ainu. The Ainu carbohydrate consumption ratios are appreciably higher than those for the Indigenous Australians. Finally, Figure 10c shows difference between the fat consumption ratios for the Indigenous Australians and the Ainu. Ainu fat consumption ratios are noticeably lower than those for the Indigenous Australians.

The t-tests were significant when I compared the MCRs for the Ainu with those for the Indigenous Australians. The results were $p = 0.000$, $p = 0.000$, and $p = 0.000$ for the protein, carbohydrate, and fat consumption ratios respectively. As such, these results indicate that the Ainu plant values yield different MCRs from the Indigenous Australian plant values when applied to the Cordain et al. (2000) equations.

Table 24: Comparison of the Indigenous Australian and Ainu MCRs.

Macronutrient	Indigenous Australians	Ainu
Protein	19-35%	23-37%
Carbohydrate	22-40%	26-47%
Fat	34-58%	24-52%

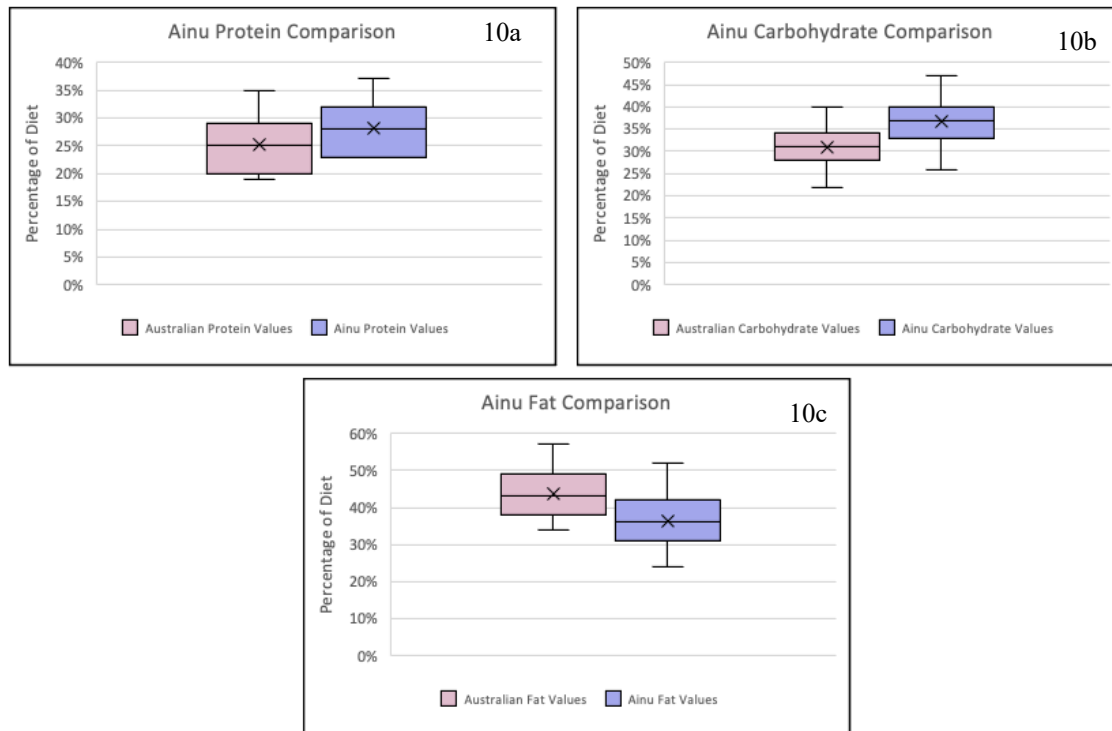


Figure 10: Boxplots comparing the MCRs created using the Indigenous Australian plant values and those using the AINU plant values.

Figure 10a compares the protein consumption ratios, Figure 10b compares the carbohydrate consumption ratios, and Figure 10c compares the fat consumption ratios that resulted from applying each group’s plant values to the Cordain et al. (2000) equations.

4.3.5. The Baffin Island Inuit

The Baffin Island Inuit plant macronutrient values that I combined with Cordain et al.’s (2000) equations were 7% protein, 80% carbohydrate, and 13% fat.

Figure 11 shows boxplots comparing the MCRs created with the Indigenous Australian plant values with those created with the Baffin Island Inuit plant values. Figure 11a exhibits differences between the protein consumption ratios for the Indigenous Australians and those for the Baffin Island Inuit. The Baffin Island Inuit protein consumption ratios are a little lower than those for the Indigenous Australians. Next, the top right box plot shows differences between the carbohydrate consumption ratios for the Indigenous Australians and the Baffin Island Inuit. The Baffin Island Inuit carbohydrate consumption ratios are appreciably higher than those for the Indigenous Australian carbohydrate ratios. Finally, Figure 11c shows difference between the fat

consumption ratios for the Indigenous Australians and the Baffin Island Inuit. The Baffin Island Inuit fat consumption ratios are a little lower than those for the Indigenous Australians.

The t-tests were significant when I compared the MCRs for the Baffin Island Inuit with those for the Indigenous Australians. The results were $p = 0.000$, $p = 0.000$, and $p = 0.000$ for the protein, carbohydrate, and fat consumption ratios respectively. As such, these results indicate that the Baffin Island Inuit plant values yield different MCRs from the Indigenous Australian plant values when applied to the Cordain et al. (2000) equations.

Table 25: Comparison of the Indigenous Australian and Baffin Island Inuit MCRs.

Macronutrient	Indigenous Australians	Baffin Island Inuit
Protein	19-35%	14-32%
Carbohydrate	22-40%	28-52%
Fat	34-58%	26-53%

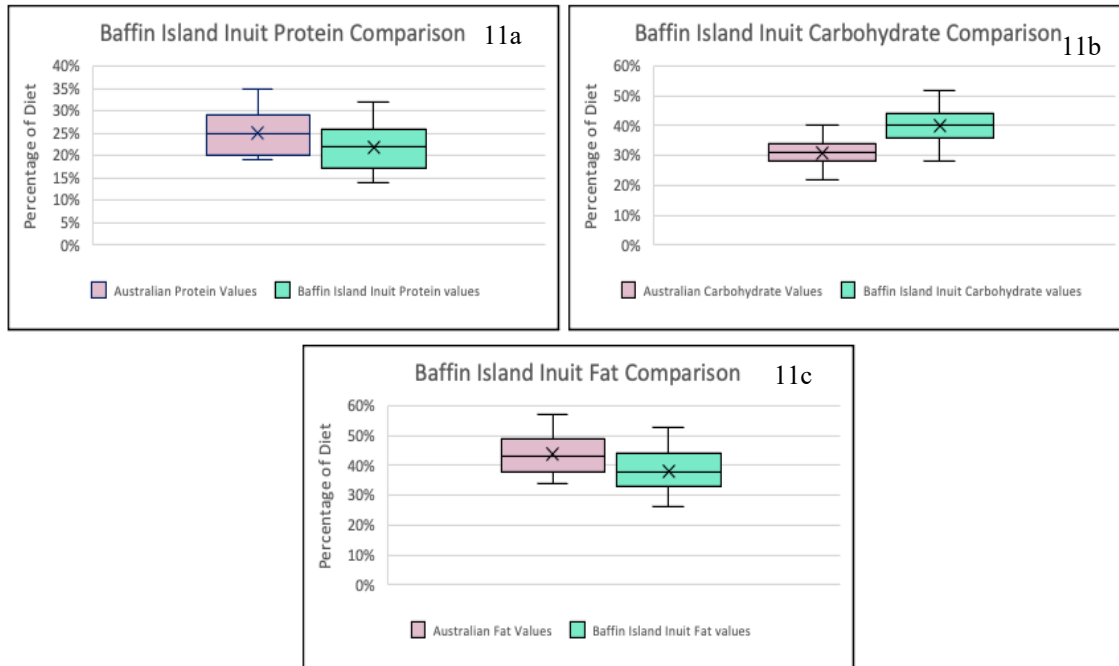


Figure 11: Boxplots comparing the MCRs created using the Indigenous Australian plant values and those using the Baffin Island Inuit plant values.

Figure 11a compares the protein consumption ratios, Figure 11b compares the carbohydrate consumption ratios, and Figure 11c compares the fat consumption ratios that resulted from applying each group's plant values to the Cordain et al. (2000) equations.

4.3.6. The Hadza

The Hadza plant macronutrient values that I combined with Cordain et al.'s (2000) equations were 11% protein, 72% carbohydrate, and 18% fat.

Figure 12 shows boxplots comparing the macronutrient consumption ratios created with the Indigenous Australian plant values with those created with the Hadza plant values. Figure 12a exhibits differences between the protein consumption ratios for the Indigenous Australians and those for the Hadza. The Hadza protein consumption ratios are slightly lower than those for the Indigenous Australians. Next, Figure 12b shows differences between the carbohydrate consumption ratios for the Indigenous Australians and the Hadza. The Hadza carbohydrate consumption ratios are appreciably higher than those for the Indigenous Australian carbohydrate ratios. Finally, Figure 12c shows difference between the fat consumption ratios for the Indigenous Australians and

the Hadza. The Hadza fat consumption ratios are slightly lower than those for the Indigenous Australians.

The t-tests were significant when I compared the MCRs for the Hadza with those for the Indigenous Australians. The results were $p = 0.000$, $p = 0.000$, and $p = 0.000$ for the protein, carbohydrate, and fat consumption ratios respectively. As such, these results indicate that the Hadza plant values yield different MCRs from the Indigenous Australian plant values when applied to the Cordain et al. (2000) equations.

Table 26: Comparison of the Indigenous Australian and Hadza MCRs.

Macronutrient	Indigenous Australians	Hadza
Protein	19-35%	17-34%
Carbohydrate	22-40%	25-47%
Fat	34-58%	30-55%

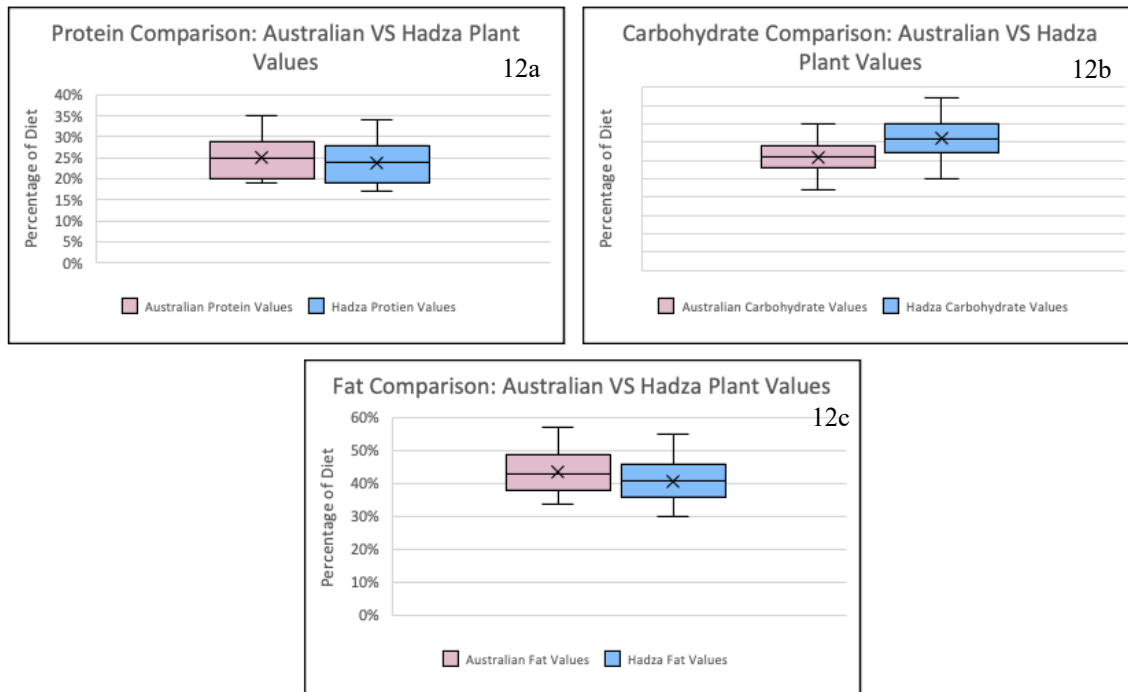


Figure 12: Boxplots comparing the MCRs created using the Indigenous Australian plant values and those using the Hadza plant values.

Figure 12a compares the protein consumption ratios, Figure 12b compares the carbohydrate consumption ratios, and Figure 12c compares the fat consumption ratios that resulted from applying each group's plant values to the Cordain et al. (2000) equations.

4.3.7. The Hiwi

The Hiwi plant macronutrient values that I combined with Cordain et al.'s (2000) equations were 9% protein, 84% carbohydrate, and 8% fat.

Figure 13 shows boxplots comparing the MCRs created with the Indigenous Australian plant values with those created with the Hiwi plant values. Figure 13a exhibits differences between the protein consumption ratios for the Indigenous Australians and the Hiwi. The Hiwi protein consumption ratios are slightly lower than those for the Indigenous Australians. Next, Figure 13b shows differences between the carbohydrate consumption ratios for the Indigenous Australians and the Hiwi. The Hiwi carbohydrate consumption ratios are appreciably higher than those for the Indigenous Australians. Finally, Figure 13c shows difference between the fat consumption ratios for the Indigenous Australians and the Hiwi. The Hiwi fat consumption values are lower than those for the Indigenous Australians.

The t-tests were significant when I compared the MCRs for the Hiwi with those for the Indigenous Australians. The results were $p = 0.000$, $p = 0.000$, and $p = 0.000$ for the protein, carbohydrate, and fat consumption ratios respectively. As such, these results indicate that the Hiwi plant values yield different MCRs from the Indigenous Australian plant values when applied to the Cordain et al. (2000) equations.

Table 27: Comparison of the Indigenous Australian and Hiwi MCRs.

Macronutrient	Indigenous Australians	Hiwi
Protein	19-35%	14-32%
Carbohydrate	22-40%	28-53%
Fat	34-58%	26-53%

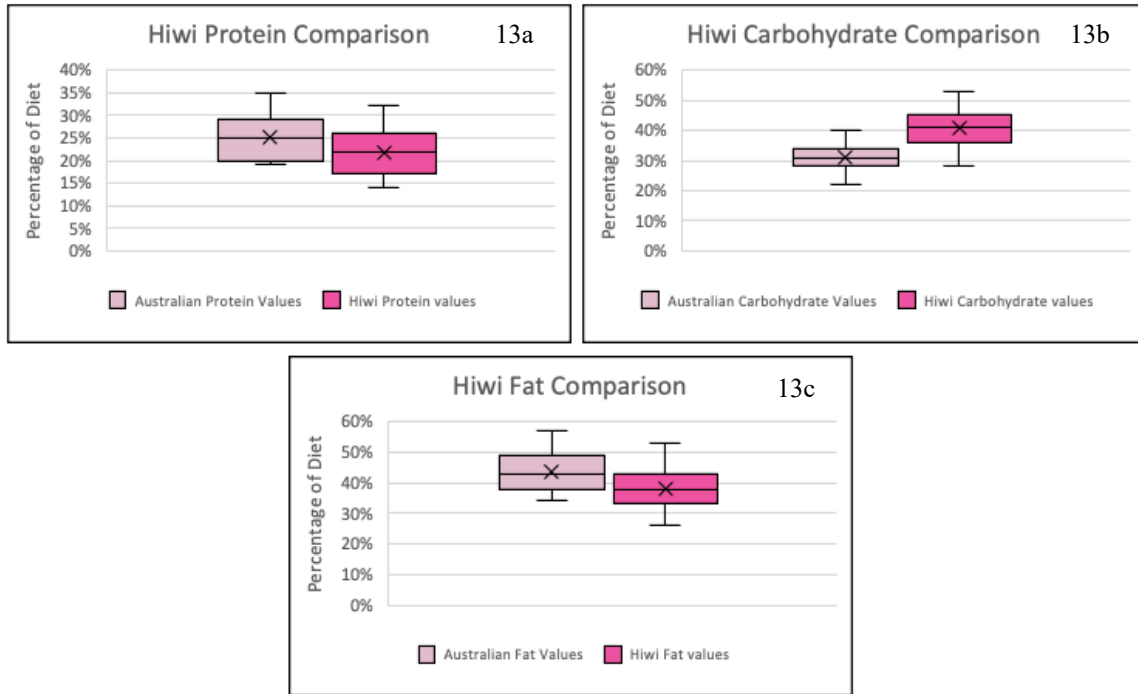


Figure 13: Boxplots comparing the MCRs created using the Indigenous Australian plant values and those using the Hiwi plant values.

Figure 13a compares the protein consumption ratios, Figure 13b compares the carbohydrate consumption ratios, and Figure 13c compares the fat consumption ratios that resulted from applying each group's plant values to the Cordain et al. (2000) equations.

4.3.8. The Sahtú Dene/Métis

The Sahtú Dene/Métis plant macronutrient values that I combined with Cordain et al.'s (2000) equations were 7% protein, 81% carbohydrate, and 12% fat.

Figure 14 shows boxplots comparing the MCRs created with the Indigenous Australian plant values with those created with the Sahtú Dene/Métis plant values. Figure 14a exhibits differences between the protein consumption ratios for the Indigenous Australians and the Sahtú Dene/Métis. The Sahtú Dene/Métis protein consumption ratios are lower than those for the Indigenous Australians. Next, Figure 14b shows differences between the carbohydrate consumption ratios for the Indigenous Australians and the Sahtú Dene/Métis. The Sahtú Dene/Métis carbohydrate consumption ratios are appreciably higher than those for the Indigenous Australians. Finally, Figure 14c shows difference between the fat consumption ratios for the Indigenous Australians and the

Sahtú Dene/Métis. The Sahtú Dene/Métis fat consumption ratios are lower than those for the Indigenous Australians.

The t-tests were significant when I compared the MCRs for the Hiwi with those for the Indigenous Australians. The results were $p = 0.000$, $p = 0.000$, and $p = 0.000$ for the protein, carbohydrate, and fat consumption ratios respectively. As such, these results indicate that the Hiwi plant values yield different MCRs from the Indigenous Australian plant values when applied to the Cordain et al. (2000) equations.

Table 28: Comparison of the Indigenous Australian and Sahtú Dene/Métis MCRs.

Macronutrient	Indigenous Australians	Sahtú Dene/Métis
Protein	19-35%	14-32%
Carbohydrate	22-40%	36-45%
Fat	34-58%	26-53%

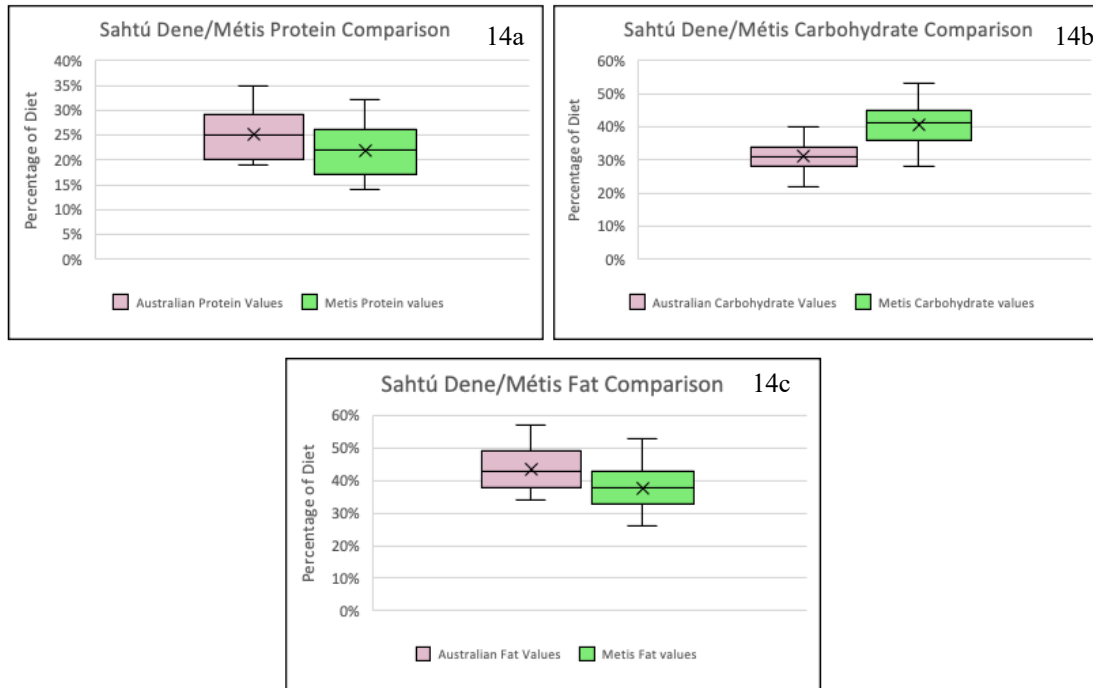


Figure 14: Boxplots comparing the MCRs created using the Indigenous Australian plant values and those using the Sahtú Dene/Métis plant values.

Figure 14a compares the protein consumption ratios, Figure 14b compares the carbohydrate consumption ratios, and Figure 14c compares the fat consumption ratios that resulted from applying each group's plant values to the Cordain et al. (2000) equations.

4.3.9. The Nuxalk

The Nuxalk plant macronutrient values that I combined with Cordain et al.'s (2000) equations were 6% protein, 81% carbohydrate, and 12% fat.

Figure 15 shows boxplots comparing the MCRs created with the Indigenous Australian plant values with those created with the Nuxalk plant values. Figure 15a exhibits differences between the protein consumption ratios for the Indigenous Australians and the Nuxalk. The Nuxalk protein consumption ratios are slightly lower than those for the Indigenous Australians. Next Figure 15b shows differences between the carbohydrate consumption ratios for the Indigenous Australians and the Nuxalk. The Nuxalk carbohydrate consumption ratios are appreciably higher than those for the Indigenous Australians. Finally, Figure 15c shows difference between the fat

consumption ratios for the Indigenous Australians and the Nuxalk. The Nuxalk fat consumption ratios are lower than those for the Indigenous Australians.

The t-tests were significant when I compared the MCRs for the Nuxalk with those for the Indigenous Australians. The results were $p = 0.000$, $p = 0.000$, and $p = 0.000$ for the protein, carbohydrate, and fat consumption ratios respectively. As such, these results indicate that the Nuxalk plant values yield different MCRs from the Indigenous Australian plant values when applied to the Cordain et al. (2000) equations.

Table 29: Comparison of the Indigenous Australian and Nuxalk MCRs.

Macronutrient	Indigenous Australians	Nuxalk
Protein	19-35%	14-32%
Carbohydrate	22-40%	28-53%
Fat	34-58%	26-53%

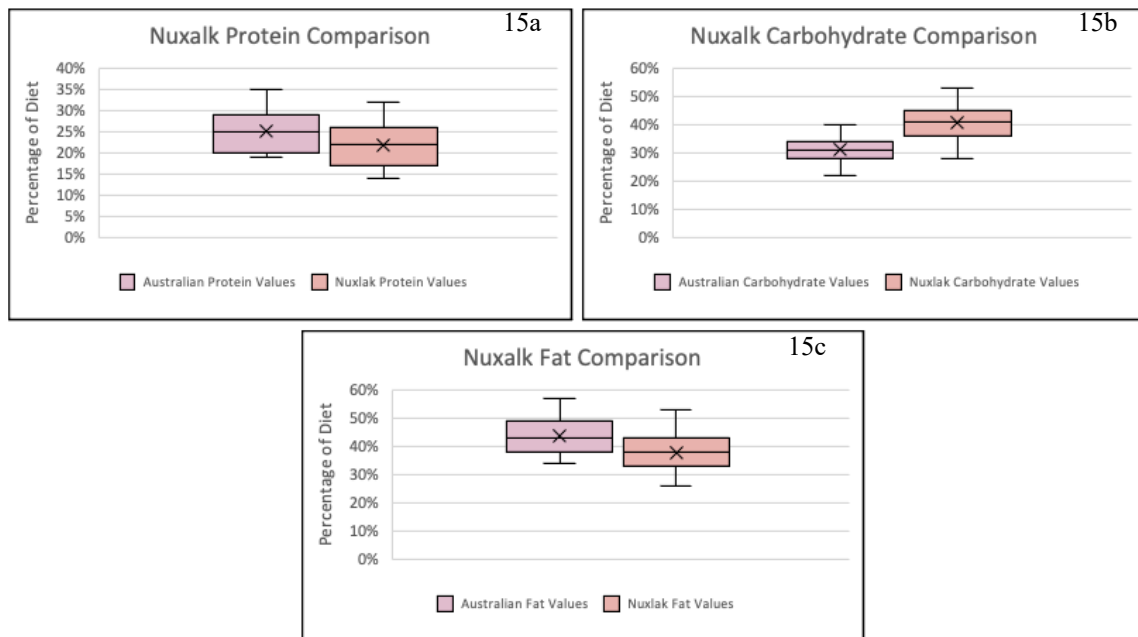


Figure 15: Boxplots comparing the MCRs created using the Indigenous Australian plant values and those using the Nuxalk plant values.

Figure 15a compares the protein consumption ratios, Figure 15b compares the carbohydrate consumption ratios, and Figure 15c compares the fat consumption ratios that resulted from applying each group's plant values to the Cordain et al. (2000) equations.

4.3.10. The Wet'suwet'en

The Wet'suwet'en plant macronutrient values that I combined with Cordain et al.'s (2000) equations were 6% protein, 84% carbohydrate, and 10% fat.

Figure 16 shows boxplots comparing the MCRs created with the Indigenous Australian plant values with those created with the Wet'suwet'en plant values. Figure 16a exhibits differences between the protein consumption ratios for the Indigenous Australians and the Wet'suwet'en. The Wet'suwet'en protein consumption ratios are lower than those for the Indigenous Australians. Next, Figure 16b shows differences between the carbohydrate consumption ratios for the Indigenous Australians and the Wet'suwet'en. The Wet'suwet'en carbohydrate consumption ratios are appreciably higher than those for the Indigenous Australians. Finally, Figure 16c shows difference between the fat consumption ratios for the Indigenous Australians and the Wet'suwet'en. The Wet'suwet'en fat consumption ratios are lower than those for the Indigenous Australians.

The t-tests were significant when I compared the MCRs for the Wet'suwet'en with those for the Indigenous Australians. The results were $p = 0.000$, $p = 0.000$, and $p = 0.000$ for the protein, carbohydrate, and fat consumption ratios respectively. As such, these results indicate that the Wet'suwet'en plant values yield different MCRs from the Indigenous Australian plant values when applied to the Cordain et al. (2000) equations.

Table 30: Comparison of the Indigenous Australian and Wet'suwet'en MCRs.

Macronutrient	Indigenous Australians	Wet'suwet'en
Protein	19-35%	14-32%
Carbohydrate	22-40%	29-55%
Fat	34-58%	24-52%

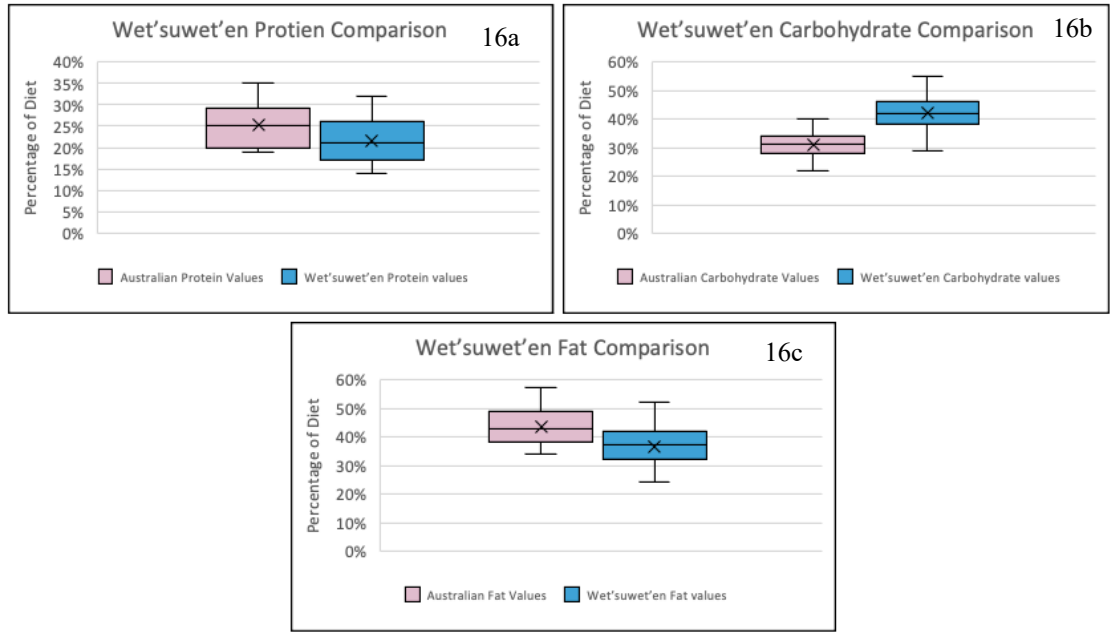


Figure 16: Boxplots comparing the MCRs created using the Indigenous Australian plant values and those using the Wet'suwet'en plant values.

Figure 16a compares the protein consumption ratios, Figure 16b compares the carbohydrate consumption ratios, and Figure 16c compares the fat consumption ratios that resulted from applying each group's plant values to the Cordain et al. (2000) equations.

4.3.11. The Gwich'in

The Gwich'in plant macronutrient values that I combined with Cordain et al.'s (2000) equations were 8% protein, 80% carbohydrate, and 13% fat.

Figure 17 shows boxplots comparing the MCRs created with the Indigenous Australian plant values with those created with the Gwich'in plant values. Figure 17a exhibits differences between the protein consumption ratios for the Indigenous Australians and the Gwich'in. The Gwich'in protein consumption ratios are lower than those for the Indigenous Australians. Next, Figure 17b shows differences between the carbohydrate consumption ratios for the Indigenous Australians and the Gwich'in. The Gwich'in carbohydrate consumption ratios are appreciably higher than those for the Indigenous Australians. Finally, Figure 17c shows difference between the fat consumption ratios for the Indigenous Australians and the Gwich'in. The Gwich'in fat consumption ratios are lower than those for the Indigenous Australians.

The t-tests were significant when I compared the MCRs for the Gwich'in with those for the Indigenous Australians. The results were $p = 0.000$, $p = 0.000$, and $p = 0.000$ for the protein, carbohydrate, and fat consumption ratios respectively. As such, these results indicate that the Gwich'in plant values yield different MCRs from the Indigenous Australian plant values when applied to the Cordain et al. (2000) equations.

Table 31: Comparison of the Indigenous Australian values and Gwich'in MCRs.

Macronutrient	Indigenous Australians	Gwich'in
Protein	19-35%	15-33%
Carbohydrate	22-40%	28-52%
Fat	34-58%	26-53%

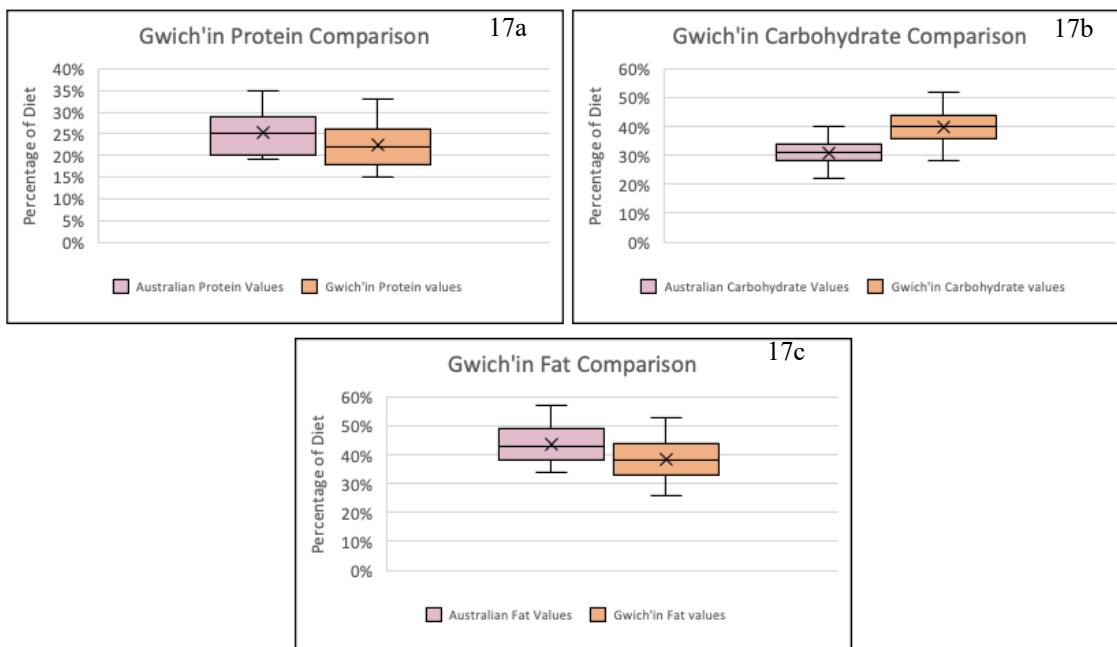


Figure 17: Boxplots comparing the MCRs created using the Indigenous Australian plant values and those using the Gwich'in plant values.

Figure 17a compares the protein consumption ratios, Figure 17b compares the carbohydrate consumption ratios, and Figure 17c compares the fat consumption ratios that resulted from applying each group's plant values to the Cordain et al. (2000) equations.

4.3.12. Summary

A summary of the macronutrient ranges derived from the additional ten society's plant values is presented in Table 20 in section 4.3.1. The Paleo Diet recommendations change with each set of plant values that was applied into the equation. As this section has demonstrated, the average plant values for all ten hunter-gatherer societies whose plant data I reconstructed significantly alter the model results when compared to the Indigenous Australian average plant values. This suggests that Cordain et al. (2000) were incorrect in their assertion that the Indigenous Australian plant values are representative of worldwide hunter-gatherer plant-food diets.

Chapter 5.

Discussion

5.1. Main findings

In Chapter 3 I demonstrated that I was able to successfully replicate the model that Cordain et al. (2000) created in order to estimate macronutrient consumption ratios (MCRs) for the average hunter-gatherer diet. Because I arrived at identical results, I can confirm that Cordain et al.'s (2000) methods can be used to establish MCRs for hunter-gatherers and that the study's inherent make-up is not flawed (Table 4). However, in my replication I discovered that the fat consumption values that Cordain et al. (2000) presented in their conclusion are not consistent with the fat consumption values that they calculated. Although Cordain et al. (2000) stated that animals with less than 10% body fat would not have been habitually consumed, and that the results from animals with these percentage body fats were therefore not applicable for inclusion in their results, they did include the resulting fat consumption values from animals with 5% body fat in their recommendations. They did not do this for protein or carbohydrates, and they did not include the fat consumption values from animals with 2.5% body fat in any of their concluding results. There is no explanation as to why they did this. By using Cordain et al.'s (2000) results and adhering to the method that they noted, the MCRs change to 19-35% energy from protein, 22-40% energy from carbohydrates, and 34-58% energy from fat. This difference presents a discrepancy between Cordain et al.'s (2000) methods and their conclusions for the fat values.

In Chapter 3, I also showed that, contrary to Cordain et al.'s (2000) claim, Eaton and Konner's (1985) plant values produce different MCRs from Brand-Miller and Holt's (1998) plant values when applied to Cordain et al.'s (2000) equations (Tables 6 and 7). Cordain et al.'s (2000) baseline justification for applying only one set of plant macronutrient values to their model was the assumed similarity of the Indigenous Australian plant values with Eaton and Konner's (1985) average plant values for five hunter-gatherer societies. However, when I substituted Eaton and Konner's (1985) plant

values for the Indigenous Australian plant values in the equations all three macronutrient consumption ratios were significantly different with p-values of 0.019, 0.000, and 0.022 for protein, carbohydrates, and fat, respectively. These results suggest that Cordain et al.'s (2000) MCRs might not represent the average diet of the hunter-gatherer groups in their sample. Furthermore, the results suggest that it may be inappropriate to assign one set of plant macronutrient values to a sample of worldwide hunter-gatherers.

In Chapter 4, I derived the plant macronutrient values from a worldwide sample of hunter-gatherer groups. Then, I tested whether the means for the contributing protein, carbohydrate, and fat values for each society's plant foods differ significantly from those of the Indigenous Australian plant foods. The average carbohydrate and fat values were not significantly different for any of the societies, but there were significant differences between the protein values for the North American groups' plants and the protein values from the Indigenous Australian plants that Cordain et al. (2000) employed. Thus, the analyses indicate inter-group differences are sufficiently large that the macronutrient values for one group should not be treated as interchangeable with the macronutrient values for another group.

Also in Chapter 4, I applied each of the derived hunter-gatherer plant values to Cordain et al.'s (2000) equations. My results show that the average plant macronutrient values for my sample of hunter-gatherer groups consistently change the equation results and, by-extension, the Paleo Diet recommendations in a statistically significant way. Every t-test was significant. This indicates that, contrary to what Cordain et al. (2001) claimed, the Indigenous Australian plant values are not interchangeable with the plant values consumed by hunter-gatherers elsewhere in the world. This suggests that wild plant food variation should be considered when calculating MCRs, and that the Paleo Diet's macronutrient recommendations are erroneous.

5.2. Limitations

As with any study, this one is subject to limitations. Here I outline the main ones I have identified and discuss how I attempted to mitigate them.

5.2.1. Sample Size and Data Limitations

One significant limitation of my study is the small size of the sample. Unfortunately, not enough research has been done on wild plant food composition in small-scale societies, especially amongst hunter-gatherer groups. Nutrient information for wild food is poorly documented and there is little information on the specific contributions of plant foods to most hunter-gatherer diets. As a result, it is difficult to find good quality nutritional data for hunter-gatherer groups.

Thankfully, some good quality data does exist. I was able to reconstruct fairly accurate dietary contributions for six of the ten societies largely due to Dr. Harriet Kuhnlein's research on Indigenous diets (e.g., CINE, 2005; Kuhnlein, 1989; Kuhnlein and Soueida, 1992). Until the early 2000s, Kuhnlein's data, was restricted to North American Indigenous groups. However, over the past 15 years Kuhnlein has directed a program called CINE (2005) that has resulted in an increased amount of nutrient data for traditional groups elsewhere in the world. Thus, the data for six of my ten societies were taken from a combination of Kuhnlein's published work and work published by scholars who are affiliated with CINE.

The data for the remaining four groups in my sample—the Ache, the !Kung, the Hadza, and the Hiwi—were compiled using outsourced plant values (i.e., plant values that the authors did not extract themselves). The outsourced data is of good quality; however, nutrient tables did not exist for some of the traditional plants. Instead of leaving the plants out, I estimated the nutrient values for these plants based on their similarity with other foods. This is the standard method when plants are not known or values cannot be found (Greenfield and Southgate, 2003). Since my sample is small, it is preferable to use all of the plants that were listed for each source, even if that did require me to estimate the values.

One reason for the serious lack of available data is because it is very expensive to run macronutrient analyses. For example, the price of running macronutrient analyses according to AGAT Laboratories is \$140 for one sample if only the main macronutrients—fat, protein, moisture, ash, carbohydrates, and calories—are required. If one is interested in the full nutrition label, which for Canada includes humidity, fat, acid hydrolysis, protein, sugar, ash, carbohydrates, calories, fatty acid profile (poly,

monounsaturated, trans, omega) dietary fibers, cholesterol, calcium, iron, and sodium, the cost is \$750 *per* sample (Nadai, Sylvie, personal correspondence, December 16th, 2019). Unfortunately, these prices add up quickly when multiple samples are run, and it is essential to run multiple samples for accurate nutrient analyses (Greenfield and Southgate, 2003). As a result, research projects that involve nutrient analyses require substantial funding. Unfortunately, nutrient analyses on traditional diets are rarely successful in securing sufficient financial backing (Harriet Kuhnlein, personal correspondence, January 2020).

An important effect of the limited data was that I was not able to expand my sample beyond ten societies. Since smaller samples are subject to greater variation, my results may appear more variable than they should, and it is possible that there are false positives within my sample. I addressed this limitation by adjusting the significance levels of my tests with the Benjamini-Hochberg procedure. By doing this, I decreased the number of false positives that my results yielded and increased the statistical power of my results. My results are therefore fairly robust, although conducting further tests with data from other hunter-gatherer societies would improve this state of affairs.

5.2.2. Food Nutrient Limitations

This study is based on food nutrient analyses. Food nutrient analyses are critical but are considered a weak link in studies of dietary status because they are subject to a high degree of error (Kuhnlein and Turner, 1991). Food nutrient analyses are necessary to create calculated dietary intakes for a given population. However, the quality of calculated dietary intakes is limited by the FCDs from which they are taken (Kuhnlein and Turner, 1991). For example, if an FCD were created with unreliable methods, the calculated dietary intakes that are calculated based on the FCD will not be reliable as they will have been created with inaccurate data. On the whole, it is difficult to ensure the accuracy of nutrient tables and FCDs, especially when one does not create the tables themselves (Kuhnlein and Turner, 1991). Because the nutrient tables employed in this study consisted of data that were extracted according to the AOAC standard methods for nutrient extraction (Greenfield and Southgate, 2003; Table 18), I was able to guarantee that the plant food dietary intakes that I calculated for each society were of high-quality.

Additionally, I clarified the quality of these sources via correspondence with Dr. Harriet Kuhnlein (personal correspondence, January 2020).

A limitation of nutrient tables and FCDs is that it is difficult to characterise a specific diet through the sole use of nutrient tables. Although the nutrition tables used in this study and the FCDs that I created are as accurate as possible, they cannot be used to make specific nutritional claims for any of the groups. For this study I was interested in broad trends across overall diets and was not interested in making specific nutritional claims. Therefore, because I ensured consistency in the methods used to compose each composition table, and the FCDs are as accurate as possible, my results examine the differences and overall variation between the different groups' plant food intake. I do not make any comments regarding the nutritional adequacy of each group's diet based on the FCDs.

A common limitation in using pre-prepared FCDs is that the data are often compiled from diverse sources that employ different methods of analysis (Southgate, 1974). This can result in inaccurate and incomparable data. The use of standard methods for nutrient analysis in forming FCDs over the past 30 years has helped to minimize inconsistencies that arise when and method diversity are present in FCDs (Greenfield and Southgate, 1992; Greenfield and Southgate, 2003). As long as FCDs and nutrient tables follow the Greenfield and Southgate (2003) standard methods, they can be considered sufficiently accurate and comparable. For this study, I was able to check all of the sources that were employed in compiling the FCDs. Although the sources are diverse, the methods are consistent, and the data can therefore be considered of good quality.

I have already discussed the Atwater factors' inherent inaccuracy (see Chapter 2.2). Since commercial food labels continue to, for the most part, use Atwater factors to calculate the total metabolizable energy, this inaccuracy has likely resulted in a host of incorrect nutrient tables. All of the nutrient tables used in my study are subject to this limitation as all were based on summing the proximate parts of food based on the Atwater factors. However, since I did not use the specific gram values, but rather used the Atwater factors to estimate the percentage value that each macronutrient contributes to the diet and kept this method consistent across all groups, the Atwater factors' inaccuracy

is not a limitation of my study. Although the errors do exist in the data, they do not impact my findings.

Lastly, sampling is an important potential source of error in food nutrient analyses and is one that I was not able to control for. Although I only included studies in my sample that adhered to the sampling strategies outlined in Greenfield and Southgate (2003) (discussed in section 4.1), since I did not oversee the sampling itself, I cannot be sure of the exact procedures that were employed. Sampling can be subject to food identification errors, incorrect sampling protocol, contamination during transport, incorrect mixing or homogenization, and incorrect storage (Greenfield and Southgate, 2003). Most of these limitations can be overcome by proper laboratory techniques and supervision, but these can be expensive. It is therefore possible that there are sampling errors distributed among the plant values for the groups in my sample. Because I am dealing with the means of a large number of plant food macronutrients, a few errors will not affect the results to any significant degree.

5.3. Implications of Findings

My results show that the plant component of hunter-gatherer diets is variable both in the plants themselves and in the results once applied to Cordain et al.'s (2000) equations. Therefore, even if a Palaeolithic-style diet were the optimal diet for modern humans and modern hunter-gatherer diets could be used as direct analogues for Palaeolithic human diets, the results from Cordain et al.'s (2000) study do not represent that diet. The significant differences that occur when the contributing plant values are changed implies that human diets vary extensively and are not interchangeable.

I used MANOVA tests (Figures 5-7) to compare the results across societies and discern whether there were significant differences across the MCRs for the societies in my sample and the Indigenous Australian MCRs. That there were significant differences within these results, suggests that these hunter-gatherers are not selecting plant foods that will keep the across group MCRs in a tight range for each macronutrient.

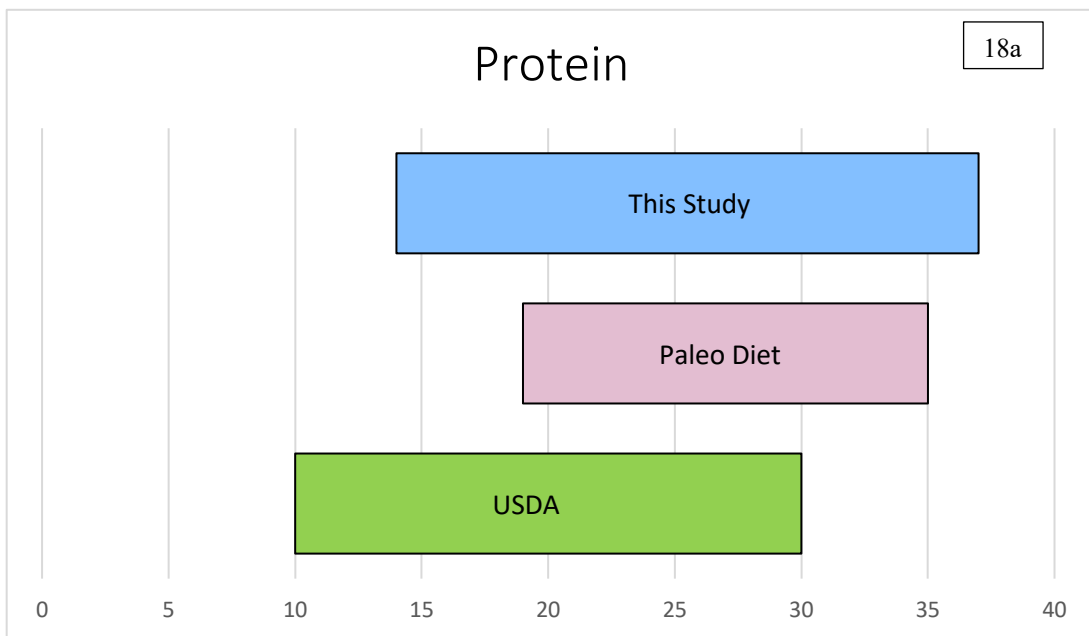
Table 21 exhibits the range of MCRs that resulted when each societies' plant values were applied to Cordain et al.'s (2000) equations. The MCRs for each society can be considered alternative Paleo Diet recommendations because the results from the

Indigenous Australian values formed the basis for the current Paleo Diet (Cordain, 2010). Each set of MCRs is different in some respect from the Paleo Diet recommendations. Some of the MCRs are substantially higher or lower than those produced by Cordain et al. (2000). For example, the Baffin Island Inuit macronutrient consumption ratios differ by 3% protein, 10% carbohydrates, and 2% fat from the Indigenous Australian recommendations whereas the !Kung recommendations differ by 1% protein, 2% carbohydrates, and 1% fat when compared to the Indigenous Australian ratios calculated by Cordain et al. (2000). These differences correlate to the environment that each group inhabits. For example, the groups that inhabit environments most similar to Australia (e.g., the !Kung) exhibit the smallest dietary differences, whereas those that live in environments that are more different from Australia (e.g., the Baffin Island Inuit) exhibit the greatest differences. Although there is variation in the MCRs, all of the t-test results from comparing each society's MCRs against those of the Indigenous Australians are significantly different. That the MCRs that appear less significantly different are, for the most part, equally different statistically, may point to a sensitivity in the testing method.

Because Cordain et al. (2000) were interested in establishing the average hunter-gatherer diet, I combined all of the hunter-gatherer MCRs to examine what MCRs resulted for the full range of hunter-gatherers in my sample. I included the Indigenous Australian MCRs in this compilation. Combining all of the MCRs changed the average hunter-gatherer diet from 19-35% protein, 22-40% carbohydrate, and 34-58% fat as presented in Cordain et al. (2000), to 14-37% protein, 21-55% carbohydrate, and 23-59% fat (see Figure 18 for a visual comparison). This is a 7% change in the protein range, a 16% change in the carbohydrate range, and an 12% change in the fat range. That the carbohydrate variation increased by 16% is particularly notable and shows that hunter-gatherers vary considerably in their carbohydrate consumption.

The new MCRs have important implications for the Paleo Diet. The Paleo Diet is often touted as a high-protein, low-carbohydrate, and high-fat diet (Cordain, 2010). However, when all of the societies' plant values are considered, the protein variation extends down into a moderate range as per the USDA/WHO recommendations of 10-30%, and the carbohydrate variation extends up into a moderate range as per the USDA/WHO recommendations of 45-65% (HHS and USDA, 2015; WHO, 2018).

Although it is interesting that the fat variation expanded the least, it is not surprising since the variation was initially the largest. Furthermore, the fat recommendations moved to overlap completely with the 25-35% recommendations for fat from the USDA/WHO (see Figure 18). That the extended ranges overlap with modern nutritional recommendations makes the discordance considerably smaller (HHS and USDA, 2015). This is critical, as it conflicts with one of the foundational arguments of the Paleo Diet—namely, that the difference in the relative macronutrient combinations that hunter-gatherers and contemporary Westerners consume is the reason for the lifestyle disease epidemic. If the macronutrient consumption values of hunter-gatherer diets overlap with those in modern diets, the Paleo Diet recommendations are obsolete.



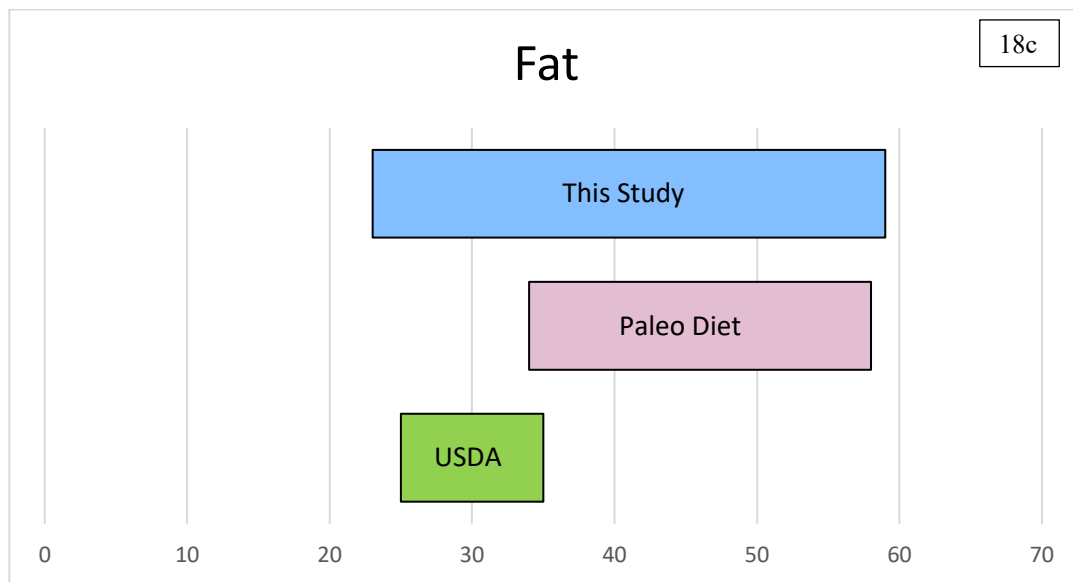
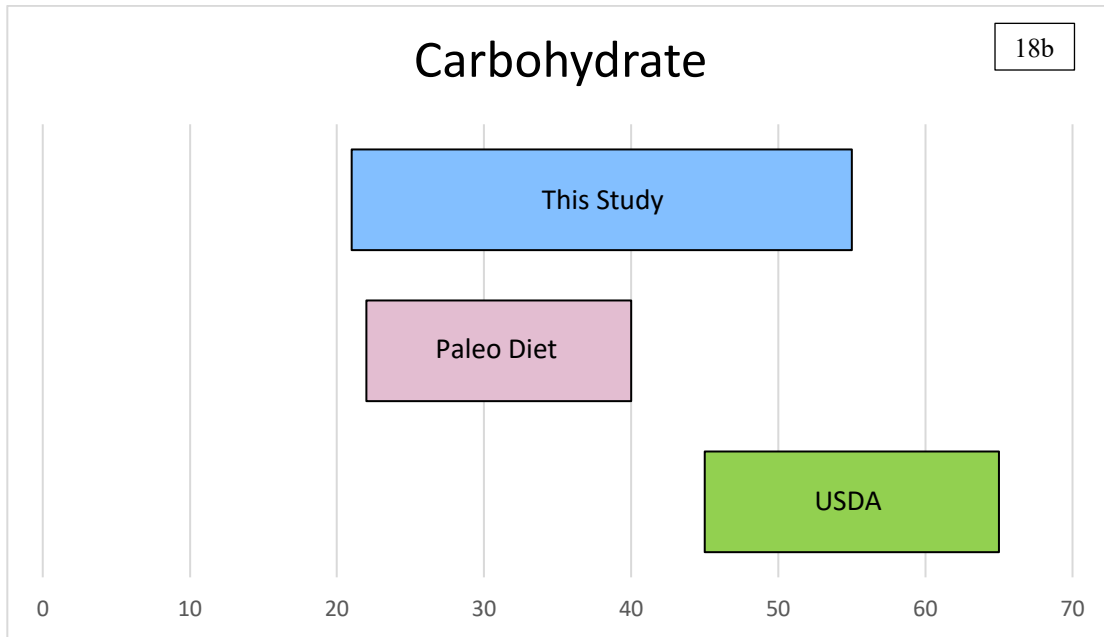


Figure 18: A comparison of the Paleo Diet’s macronutrient recommendations with those of the USDA and the total range calculated from this study.

Figure 18a compares the protein ranges, Figure 18b compares the carbohydrate ranges, and Figure 18c compares the fat ranges

The combination of these results shows that the MCRs created in Cordain et al. (2000), which are proposed to represent the average hunter-gatherer MCRs and form the foundation for the Paleo Diet, were established through at least one erroneous assumption. Thus, these findings provide evidence to refute the idea that a diet of 19-35%

protein, 22-40% carbohydrate, and 34-58% fat is a reference diet for humans.

Furthermore, the wide variety of MCRs that are created when different societies' plant values are used in the Cordain et al. (2000) equations indicates that hunter-gatherer diets are variable. This variability stands in contrast to the idea of a reference standard diet for humans. When interpreted in association with the literature, as I do in the proceeding sections, the findings suggest that the Paleo Diet's main premise, that the pre-Neolithic diet is the reference standard diet for *H. sapiens*, is without foundation and should be abandoned.

5.3.1. Plant Protein Considerations

The plant protein consumption values for the societies in my sample was 14-37%. This is a range of 23% and a difference of 7% from the Indigenous Australian protein consumption values. I was particularly interested in the variation in protein consumption ratios because scholars generally agree that there are upper and lower limits for human protein consumption (Cordain et al., 2000; Speth, 2010; Wu, 2016). A 9% difference between the lowest and highest protein consumption ratios does not sound particularly large. However, the MANOVA test results for the protein ratios were significant.

These results seem at odds with the present literature that suggests free-feeding humans naturally adhere to protein limits (e.g., Cui et al., 2018; Simpson et al., 2003). Some scholars hypothesize that because humans experience relatively immediate negative effects when too much or too little protein is consumed, they autoregulate protein consumption despite being a generalist species (Cui et al., 2018). One 2003 study showed that protein intake in free-feeding humans was mostly constant at the expense of carbohydrate and fat (Simpson et al., 2003). Simpson et al. (2003) found that when normally free-feeding humans are placed on a high or low protein diet for two days, they will under- or over-eat protein containing foods when they return to free feeding over the following days to maintain an average protein intake of between 12-15% of total energy. Simpson et al. (2003) hypothesized that 12-15% of total energy is the "intake target" ratio (Simpson et al., 2003:124) for sedentary ad libitum feeding humans. This intake target, however, is probably a rough estimate, as Simpson and Raubenheimer (1999) had

previously concluded that an animal's nutrient intake target is not static. They hypothesize that nutrient targets may vary with a variety of factors (Simpson et al., 2003).

Simpson and Raubenheimer have undertaken a considerable amount of research on macronutrient regulation (e.g., Simpson and Raubenheimer, 1993; Raubenheimer and Simpson, 1993; Simpson and Raubenheimer, 1999). In the 1990s, they created a model that quantitatively evaluates ad libitum macronutrient consumption (first introduced in Raubenheimer and Simpson, 1993; later reviewed in Raubenheimer and Simpson, 1999). In the years since they have applied this model to many insect and mammal species, and more recently to humans (e.g., Gosby et al., 2011; Gosby et al., 2014; Simpson et al., 2003; Simpson and Raubenheimer, 2005). Although the model and its implication are still under analysis, there are data that indicate that humans do have a capacity to regulate protein (Simpson et al., 2003). Interestingly, humans are not the only primates who seem to exhibit protein regulation; it has also been observed in spider monkeys, which suggests that there may be an evolutionary explanation (Felton et al., 2009).

Although the results from my study may appear inconsistent with the literature, they do not necessarily disagree with the existence of putative upper and lower limits for human protein consumption. The suggested upper and lower protein limits for humans cover a wide range and vary depending on an individual's body size, amount of physical activity, and muscle mass (Speth, 1991, Speth, 2010; Wu, 2016). For example, the putative protein limits for a sedentary 70 kg individual are 53g/day, or roughly 10% of total energy, to 236g/day, or about 50% of total energy (Speth, 1991, Speth, 2010; Wu, 2016). These limits result in a range of 183g of protein for a 70 Kg individual. As this range is so considerable, it is not surprising that differences between human protein consumption ratios may be statistically significant, as was found with the hunter-gatherers in my study.

In order to support the hypothesis that humans autoregulate protein consumption, the protein values in my study should exhibit less variation than the carbohydrate and fat values. Indeed, this was the case. When I combined the MCRs, the hunter-gatherers vary the least for protein where there is a 23% difference between the lowest and the highest values, compared to carbohydrates and fat where each MCR differs by 34% between the lowest and highest values. Because the literature suggests that only excessively low or

excessively high protein diets are dangerous, a considerable range of protein intakes can be considered sufficient for human health (Speth, 2010; Wu, 2016).

The differences among the plant protein values may additionally be partially consistent with a target protein intake in free-feeding humans. The results from the t-tests in which I compared each societies' average plant values with the Indigenous Australian average plant values were only significant for the North American societies' plant protein values. Because the more northerly societies consume a higher proportion of animal food, which contributes more protein to the diet than plant food does, by consuming plants that have less protein than those consumed by more southerly societies, who consume a lesser amount of animal food and by extension less protein, the average overall protein intake of northern and southern groups may be similar. The results from this study only show differences between the northerly and southerly societies plant protein values. Therefore, these data only support the hypothesis that there is an upper limit to protein consumption, instead of there being an intake target with lower and upper bounds. As such, these results may imply that the more northerly groups are choosing higher carbohydrate plant foods in order to keep their protein intake below the maximum limit.

5.3.2. Carbohydrate Considerations

The carbohydrate consumption ratio for all of the societies is 21-55%. This is a range of 34% and a difference of 16% from the Indigenous Australian carbohydrate consumption ratio. As these results present a wide range of carbohydrate consumption ratios and a noticeable difference when compared with the Indigenous Australian carbohydrate consumption ratios, it is not surprising that the t-tests and MANOVA test showed significant differences. The high degree of variation amongst the carbohydrate consumption ratios suggests that humans do not adhere to upper and lower limits for carbohydrate consumption, or a carbohydrate intake target. The literature is consistent with this. Unlike protein, there is no quality support in the literature for the existence of upper and lower limits for carbohydrate consumption in humans. Seidelmann et al.'s (2018) study does suggest that mortality increases with long-term low (< 40%) or high (> 70%) carbohydrate intake in humans, however, absolute carbohydrate intake is not necessarily the reason for these results. Low fruit and vegetable intake by those on the

low-carbohydrate diet, high refined-carbohydrate diet, and the general inaccuracy of dietary recall methods all affect the study's results (Beaton et al., 1979; Beaton et al., 1983; Jonnalagadda et al., 2000). Before any conclusions on carbohydrate maximum and minimum intake levels are reached, more research is needed to understand the impacts of good quality high- and low- carbohydrate diets on human health.

Of note, these results should indicate that the average plant carbohydrate values from each group vary significantly. Conversely, my analysis on the plants themselves showed that most of the plants do not vary significantly in their carbohydrate values when compared to the Indigenous Australian carbohydrate values. Because the plants themselves do not vary significantly in their average carbohydrate content, it is odd that the carbohydrate consumption ratios do. This may be because the independent samples t-test was not sensitive enough to pick up the variation that the paired t-tests and MANOVA tests did.

5.3.3. Fat Considerations

The fat consumption ratio for all of the societies is 23-59%. This is a range of 36% and a difference of 12% from the Indigenous Australian fat consumption ratio. These results exhibit a high degree of variation amongst the carbohydrate fat ratios and suggest that humans do not adhere to upper and lower limits for fat consumption, or a fat intake target. As with carbohydrates, the literature regarding upper and lower limits for fat consumption is not conclusive, although negative health effects may be associated with very low- or very high-fat diets (Aranceta and Perez-Rodriguez, 2012; Jéquier, 1999; Koebnik et al., 1999; Wrangham and Conklin-Brittain, 2003). For example, there is evidence that when fat intake is below 20% of energy for an extended period of time, HDL (good) cholesterol is reduced, triglycerides are increased, and the uptake of essential fatty acids and fat-soluble vitamins are insufficient (Aranceta and Perez-Rodriguez, 2012; Jéquier, 1999; Koebnik et al., 1999; Wrangham and Conklin-Brittain, 2003). Similarly, when fat intake is very high for an extended period of time, individuals are at a greater risk of developing cardiovascular or other non-communicable diseases (Greenwood and Winocur, 2005; Hu and Willet, 2002; Keys et al., 1986). Although certainly sub-optimal, the proposed negative effects of chronically low- or high-fat diets

are not as immediate as those that result from low- or high-protein consumption and have not been shown to result in upper or lower limits for fat consumption in the same way.

As with the carbohydrates, my analysis on the plants themselves showed that most of the plants do not vary significantly in their fat values when compared to the Indigenous Australian fat values. Because the plants themselves do not vary significantly in their average fat content, it is odd that the fat consumption ratios do. Again, this may be because the independent samples t-test was not sensitive enough to pick up the variation that the paired t-tests and MANOVA tests did.

5.3.4. Regarding Macronutrient ‘Balance’

Based on these results, it is possible that hunter-gatherers intentionally or otherwise select plant foods that keep their macronutrient intake generally ‘balanced’. A notable trend among the societies is that the more northerly groups for whom animal-source foods make up the bulk of the energy intake, derive more carbohydrates and less protein and fat from plants. For example, the Sahtú Dene/Métis plants contribute an average of 7% protein, 81% carbohydrates, and 12% fat to the diet. This is less protein and fat energy and more carbohydrate energy than the across-society plant average of 10% protein, 75% carbohydrates, and 15% fat. Because a total protein intake of more than 50% of energy is suggested to be problematic and northern mammals already provide a substantial amount of fat to northern hunter-gatherer diets, the more northerly groups may be choosing higher carbohydrate plants to ‘balance’ their diets.

Conversely, for societies that live in more equatorial regions for whom plant foods make up the majority of energy intake, plants tend to provide more protein and fat and fewer carbohydrates. For example, the !Kung plants contribute an average of 13% protein, 60% carbohydrates, and 27% fat to the diet. This is more protein and fat energy and less carbohydrate energy than the across-society average. Although the !Kung do consume as much animal food as they can, the mammals in Africa are exceptionally lean compared to animals that live in other parts of the world (Speth, 2010). It is therefore conceivable that the !Kung are subconsciously choosing plants with higher fat ratios in order to ‘balance’ their otherwise low-fat diet.

This phenomenon was not consistent across equatorial groups because some societies, such as the Ache, prioritize animal food but do not consume exceptionally high-fat plants. This may be because the animals that they are consuming contain more fat and the Ache do not need to prioritize high-fat plant foods. It is therefore possible that because some equatorial groups generally consume a higher percentage of plant foods in their diets, these groups may not need to keep the carbohydrates from plants as high in order to keep their overall protein intake from exceeding 50% of their energy. The combination of these tendencies may imply hunter-gatherers are selecting plant foods that keep macronutrient intake generally balanced, specifically where protein is concerned. However, because, nutrient balance in humans is not known and my sample is small, it is not possible to make any conclusions based on these observations. In order to more adequately interpret these tendencies, a larger sample of hunter-gatherer groups as well as the actual MCRs for each group would need to be created, as opposed to the MCRs based on the Cordain et al. (2000) equation. This way, one could analyze how the contributing plants impact the actual diets. Without a more thorough investigation, these observations are consistent with Simpson et al.'s (2003) hypothesis that protein intake is regulated in free feeding humans. However, they do not necessarily support an intake target ratio.

5.4. What Should Modern Humans Eat?

Although studying human evolution can help establish what hominins ate in the past, it cannot provide information regarding what humans should eat today. Instead, studying the diets of past hominins can show trends that explain what humans are able to eat. As discussed in Chapter 2, the evolutionary trend for humans is towards a flexible diet that includes carbohydrates, protein, and fat in varying amounts (Ungar, 2017).

H. sapiens are dietary generalists. Therefore, we should, in theory, show a flexible response for macronutrient regulation where macronutrients are interchangeable, i.e., a deficit in one can be offset by a surplus in another (Cui et al., 2018; Raubenheimer and Simpson, 1997; Raubenheimer and Simpson, 2016; Simpson and Raubenheimer, 2003). This would mean that when environmental conditions do not permit the intake target ratio of macronutrients (if, indeed, that exists), humans can over-feed on some macronutrients and underfeed on others with no negative health effects. For *H. sapiens* this appears true

for carbohydrates and fats but may not be true for protein (e.g., Simpson et al., 2003; Speth, 1991; Speth, 2010; Wu, 2016). Because there is no consistent research regarding upper and lower limits for carbohydrates and fat, some scholars speculate that non-protein energy is not regulated in humans (Cui et al., 2018; Simpson et al., 2003). From this, it is hypothesised that although humans may be generalists in the type of foods they consume, they may be semi-specialists regarding relative macronutrient consumption, at least for protein (Cui et al., 2018; Simpson et al., 2003).

This study's results do not support a specific range of any macronutrient for humans, but they may support Raubenheimer and Simpsons' (2003) hypothesis that ad-libitum feeding humans consume within a range of protein. The protein consumption values calculated in this study vary by 24 % amongst all of hunter-gatherer societies, whereas the carbohydrate and fat consumption values each vary by 34% (Table 17). These results do not necessarily indicate that the hunter-gatherers are regulating their protein intakes, but they are consistent with Raubenheimer and Simpsons' (2003) hypothesis that protein energy is more tightly regulated than carbohydrate and fat energy.

The same extrapolation cannot be made for carbohydrates and fat based on these results. At present there is some data that suggests both 'low-carb, high-fat' and 'high-carb, low-fat' diets can be beneficial in the short term, but there is no consensus regarding the long-term effects of these diets (Brouns, 2018; Wood et al., 2016). The limited available data suggest that carbohydrates and fat may not have the same hard limits as protein does. Future research will help to determine if they have upper and/or lower limits.

For overall health, therefore, it is difficult to determine what macronutrient 'balance' is. Although there is great interest in understanding what a reference human diet might look like, the results from this study do not support the idea that such a diet exists for humans or that such a diet should be based on what recent hunter-gatherers eat. This study rather supports the hypothesis that human diets and macronutrient consumption ratios vary by region, latitude, culture, and environment. Macronutrients may very well be important, as the literature suggests, but the healthy range that humans can consume is extremely wide. As such, it is likely that consuming sufficient calories is more important than specific macronutrient contributions for general health so long as no

single macronutrient is consistently under- or over-consumed (Willet et al., 2019; WHO, 2018). Thus, it is unlikely that a reference human diet exists.

5.5. Future Directions

There are several avenues that require further research in order to more confidently assess the results of this study. Firstly, more work on traditional hunter-gatherer diets is needed. Specifically, nutrient analyses of hunter-gatherer plant foods should be conducted so that this study can be redone with a larger sample and the conclusions can be more robust.

Additionally, more research regarding macronutrient regulation in humans should be conducted. In order to discuss upper and lower macronutrient limits with any certainty, there is a need for a more conclusive body of literature regarding protein intake targets in humans, as well as better data on carbohydrate and fat consumption. The literature regarding hard upper and lower limits for the latter two macronutrients is not at all clear from my research. If macronutrient limits are to be suggested in dietary guidelines, such as the Paleo Diet, a more conclusive understanding regarding whether long-term adherence to ‘imbalanced’ diets causes health risks for most humans is needed.

Lastly, additional work regarding the long-term effects of the Paleo Diet in modern populations is necessary. So-called ‘fad’ diets like the Paleo Diet are not likely to disappear as a result of studies like this one that rarely make it into the attention of the public at large. As a result, many people will continue to follow the Paleo Diet and other such diets, even if they promote ill health, for weight loss and what is assumed to be optimal health. As such, it is crucial that more research regarding the Paleo Diet be done so as to ensure that the people who do follow it are not endangering their long-term health via nutrient deficiencies and the like. All such work will strengthen the area of human nutrition.

Chapter 6.

Conclusions

The Paleo Diet's popularity today and the nutritional debate surrounding its use make it an important topic for investigation. Specifically, it is necessary to ensure that the macronutrient and food recommendations of the Paleo Diet were based on sound science. The Paleo Diet is presumed to represent an average hunter-gatherer diet and is based on Cordain et al.'s (2000) study where the average macronutrient consumption ratios of worldwide hunter-gatherers were calculated. However, there was one important limitation in the founding study by Cordain et al. (2000) that warranted investigation. This was the impact that cross-cultural variation in plant macronutrients has on the Paleo Diet's macronutrient recommendations.

In calculating the average hunter-gatherer macronutrient composition, Cordain et al. (2000) only employed one set of macronutrient values for plant foods. These values were taken from Brand-Miller and Holt (1998) and are based on 829 wild plants that were traditionally consumed by Indigenous Australians. Cordain et al. (2000) justified relying on Brand-Miller and Holt's (1998) Australian plant values on the grounds that they are similar to the average macronutrient values generated from a sample of five hunter-gatherer societies by Eaton and Konner (1985).

However, Cordain et al.'s (2000) approach is subject to two problems. One is that Brand-Miller and Holt's (1998) values are similar to those of Eaton and Konner (1985) rather than identical, and Cordain et al. (2000) did not demonstrate that the differences have no impact on macronutrient consumption ratios (MCRs) yielded by their model. The other problem is that more than 80% of the societies in Cordain et al.'s (2000) sample are from North America, and it cannot be assumed that the macronutrient values of North American plants are similar to those of Australian plants. Furthermore, that Brand-Miller and Holt's (1998) Australian values and Eaton and Konner's (1985) values appear similar is irrelevant in this situation because none of the five societies in Eaton and Konner's (1985) sample is from North America.

Therefore, it was necessary to assess whether the plant foods consumed by worldwide hunter-gatherers differ inherently, and whether these differences impact the outcome of the Paleo Diet. By examining these differences, I was able to discuss whether the Paleo Diet, as created from Cordain et al.'s (2000) equations, actually represents an average hunter-gatherer diet.

In this thesis I reported a study in which I assessed the impact of Cordain et al.'s (2000) decision to rely on Brand-Miller and Holt's (1998) Australian plant macronutrient values. To do this, I first replicated the Cordain et al. (2000) study to ensure comparability. I then applied Eaton and Konner's (1985) plant values to the Cordain et al. (2000) equations and investigated whether the resulting MCRs were statistically different from the ones that Cordain et al. (2000) calculated. Next, I collected data on hunter-gatherer diets from the literature and compiled plant food composition databases with the macronutrient information for a worldwide sample of ten hunter-gatherer groups. A number of groups from North America were included in this sample. Subsequently, I statistically compared the new plant macronutrient values to Brand-Miller and Holt's (1998) Australian values that Cordain et al. (2000) used in their study. Lastly, I used my data and Cordain et al.'s (2000) method to generate new MCRs for each society and statistically compared the new MCRs with the ones reported by Cordain et al. (2000).

The results from this study show that the plant macronutrient values from different hunter-gatherer groups vary significantly. They also show that when regionally diverse hunter-gatherer plant values are applied to Cordain et al.'s (2000) equations, the resulting MCRs are significantly different from the MCRs that Cordain et al. (2000) created with Brand-Miller and Holt's (1998) values for Indigenous Australians.

These results suggest that the Cordain et al. (2000) study does not accurately represent the average MCRs of the hunter-gatherer groups in their sample. As such, these results also suggest that the proposed macronutrient intake targets for the Paleo Diet of 19-35% protein, 22-40% carbohydrates, and 34-58% fat are erroneous. Furthermore, the variability that exists amongst hunter-gatherer plant values suggests that there is no single set of MCRs that represent hunter-gatherer diets. As such, these results contrast the idea of a reference standard diet for humans that is central to the Paleo Diet.

The idea of a reference diet for *H. sapiens* is attractive because it would provide a one-size-fits-all approach to cure the obesity and non-communicable disease pandemic. However, when the results from this study are interpreted in association with the existing literature, this idea seems too good to be true. Because worldwide *H. sapiens* vary in their diets and habitats, it is impossible to pinpoint a single reference diet for the species. For example, there is no known ‘optimal’ macronutrient intake ratio for humans, and it seems unlikely that one will be discovered.

One reason it is difficult to pinpoint a reference diet for *H. sapiens* is that humans are dietary generalists in the types of food they consume and are, at most, semi-specialists regarding macronutrient distribution (Cui et al., 2018; Simpson et al., 2003; Ungar, 2017). Although humans appear to consume within a range of each macronutrient, these ranges are broad. Furthermore, it is not clear that there are detrimental effects when humans go beyond these ranges. That the differences between the MCRs in this study were significant, suggest that there is no single reference diet for hunter-gatherers. As hominins seem to have adapted towards a varied, omnivorous diet over the last 6-8 million years, a single reference diet for *H. sapiens* seems unlikely. Similarly, the nutritional science literature is consistent with a varied and nutritionally adequate diet supporting modern human health, regardless of whether or not the macronutrient composition of one’s diet mimics that of Palaeolithic humans. As such, the findings from this study and the supporting literature suggest that not only are the Paleo Diet’s MCRs not correct, but the Paleo Diet’s main premise, that the pre-Neolithic diet is the reference standard diet for *H. sapiens*, is without foundation and should be abandoned.

Overall, it is my hope that this study has shed light on the erroneous conclusions of the Paleo Diet and can reduce the craze that surrounds the diet. Not only was the foundational study for the Paleo Diet based on at least one false assumption, but the evolutionary claims are inaccurate. Instead of eating the way Palaeolithic humans did, individuals should follow a diet that provides the appropriate number of calories for their particular body, is relatively balanced in energy contributing macronutrients, consists of a variety of mostly whole foods, and limits processed foods (as per Health Canada, 2019; WHO, 2018; Willet et al., 2019). Although this is less glamorous, it should keep more people healthy.

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Appendix

Sample

Extracted from D-Place, cross-referenced with the data from Cordain et al., (2000)

D-PLACE						
society_id	society_name	Gathering Code	Hunting Code	Fishing Code	Animal Husbandry Code	Agriculture Code
Aa1	!Kung	8	2	0	0	0
Aa8	/Xam	5	4	1	0	0
Nc10	Achumawi	3	4	3	0	0
Nd46	Agaiduka	3	3	4	0	0
Sj5	Aimore	5	4	1	0	0
Sg5	Alacaluf	1	2	7	0	0
Na9	Aleut	1	3	6	0	0
Nb10	Alkatcho	1	4	5	0	0
Nb28	Alsea	1	2	7	0	0
Eh1	Andamanese	4	2	4	0	0
Id13	Anindilyagwa	3	1	6	0	0
Nd49	Antarianunts	5	3	2	0	0
Ne9	Arapaho	2	8	0	0	0
Ne11	Assiniboine	2	7	1	0	0
Nd23	Atsakudokwa	5	3	2	0	0
Nc4	Atsugewi	4	3	3	0	0
Na7	Attawapiskat Cree	1	3	6	0	0
Sj3	Aweikoma	4	6	0	0	0
Na13	Baffin Island Inuit	0	2	8	0	0

Nd63	Bannock	3	5	2	0	0
Nd33	Beatty	8	2	0	0	0
Na29	Beaver	3	5	2	0	0
Nd12	Bitterroot Salish	3	4	3	0	0
Ne12	Blackfoot	2	8	0	0	0
Nd45	Bohogue	3	5	2	0	0
Si1	Bororo	4	5	1	0	0
Ne14	Bungi	2	6	2	0	0
Nc31	Cahuilla (Desert)	6	4	0	0	0
Na21	Caribou Inuit	1	5	4	0	0
Nc5	Central Sierra Miwok	6	3	1	0	0
Sh6	Chamacoco	6	4	0	0	0
Ne5	Cheyenne	2	8	0	0	0
Ni5	Chichimeca	5	4	1	0	0
Nd8	Chilcotin	2	3	5	0	0
Nb33	Chimariko	4	3	3	0	0
Nh1	Chiricahua	6	4	0	0	0
Na10	Chugach	0	2	8	0	0
Nc28	Chumash	4	1	5	0	0
Ne21	Coahuilteco	4	5	1	0	0
Nc15	Coast Yuki	4	2	4	0	0
Nd14	Coeur d'Alene	3	4	3	0	0
Ne3	Comanche	1	9	0	0	0
Nb14	Comox	2	3	5	0	0
Nb21	Coos	1	3	6	0	0
Na3	Copper Inuit	0	4	6	0	0
Nb26	Cowichan	2	3	5	0	0
Ne4	Crow	2	8	0	0	0
Nc32	Cupeno	6	4	0	0	0
Na16	Deline	1	4	5	0	0

Na19	Dakelh	2	4	4	0	0
Na8	Deg Xit'an	1	4	5	0	0
Na26	Dena'ina	1	4	5	0	0
Na30	Dene	0	6	4	0	0
Na17	DeneTha	1	5	4	0	0
Id4	Diyari	7	3	0	0	0
Aa2	Dorobo	4	6	0	0	0
Na31	Eastern Cree	2	5	3	0	0
Nd30	Eastern Mono	5	4	1	0	0
Na39	Eastern Ojibwa	3	3	4	0	0
Nc18	Eastern Pomo	4	3	3	0	0
Nd42	Elko Shoshoni	5	2	3	0	0
Nb5	Eyak	2	3	5	0	0
Id11	Gidjingali	5	3	2	0	0
Nd48	Gosiute	5	4	1	0	0
Ne1	Gros Ventre	2	8	0	0	0
Aa9	Hadza	6	4	0	0	0
Nb1	Haida	2	2	6	0	0
Nb8	Haisla	2	3	5	0	0
Nb23	Heiltsuk	2	3	5	0	0
Nd65	Hualapai	6	4	0	0	0
Nc16	Huchnom	4	3	3	0	0
Nd5	Hukundika	5	3	2	0	0
Nb35	Hupa	4	1	5	0	0
Na22	Iglulik Inuit	0	5	5	0	0
Na14	Inughuit (Northern Greenland)	1	4	5	0	0
ec13	Itelmen	3	2	5	0	0
Ne13	Kainai	2	8	0	0	0

Na25	Kalaallit (West Greenland)	1	2	7	0	0
Nd13	Kalispel	3	4	3	0	0
Ne16	Karankawa	3	3	4	0	0
Id5	Kariyarra	3	5	2	0	0
Nb34	Karuk	4	1	5	0	0
Na4	Kaska	1	4	5	0	0
Na38	Katikitegon	3	3	4	0	0
Nc27	Kawaiisu	5	3	2	0	0
Nd24	Kidutokado	4	4	2	0	0
Nc34	Kiliwa	4	3	3	0	0
Ne17	Kiowa	1	9	0	0	0
Ne2	Kiowa Apache	2	8	0	0	0
Nb12	Klahoose	2	3	5	0	0
Nb16	Klallam	1	3	6	0	0
Nc8	Klamath	3	2	5	0	0
Nd17	Klikitat	3	3	4	0	0
Nc6	Kumeyaay	5	4	1	0	0
Na20	Kutchin	1	4	5	0	0
Nd7	Kutenai	3	3	4	0	0
Nd27	Kuyuidokado	5	2	3	0	0
Nb3	Kwakwaka'wakw	3	2	5	0	0
Na23	Labrador Inuit	0	4	6	0	0
Nc21	Lake Miwok	4	3	3	0	0
Nb37	Lassik	3	3	4	0	0
Nd34	Lida Shoshoni	6	4	0	0	0
Nd9	Lillooet	2	3	5	0	0
Nh24	Lipan Apache	6	4	0	0	0
Nb19	Lower Chinook	2	2	6	0	0
Nc33	Luiseno	6	2	2	0	0

Nb15	Lummi	3	2	5	0	0
Nc12	Maidu	5	3	2	0	0
Nb24	Makah	2	2	6	0	0
ec15	Mansi	2	3	5	0	0
Nb38	Mattole-Bear River	3	4	3	0	0
Aa5	Mbuti	3	7	0	0	0
Na41	Mi'kmaq	1	5	4	0	0
Na45	Mistissini Cree	1	6	3	0	0
Nd60	Moache	4	5	1	0	0
Nd59	Moanunts	3	5	2	0	0
Nd51	Moapa	6	4	0	0	0
Nc9	Modoc	5	3	2	0	0
Ej6	Moken	1	1	8	0	0
Na32	Montagnais	2	6	2	0	0
Id7	Murriny Patha	7	2	1	0	0
Na1	Nabesna	2	6	2	0	0
Aa7	Naron	7	3	0	0	0
Na5	Naskapi	1	7	2	0	0
ec17	Negidal	2	3	5	0	0
Na43	Netsilik	0	4	6	0	0
Nd20	Nez Perce	3	3	4	0	0
ec12	Nganasan	0	8	2	0	0
Id9	Ngiyambaa	3	3	4	0	0
Na35	Nipigon	2	5	3	0	0
Nc13	Nisenan	5	3	2	0	0
Ec1	Nivkh	2	3	5	0	0
Nd10	Nlaka'pamux	2	3	5	0	0
Nc1	Nomlaki	6	3	1	0	0
Id1	Northern Aranda	6	4	0	0	0

Nc3	Northern Foothill Yokuts	4	3	3	0	0
Nc17	Northern Pomo	5	3	2	0	0
Na33	Northern Saukteaux	2	4	4	0	0
Na12	Nunamiut	1	7	2	0	0
Na6	Nunivak	1	3	6	0	0
Nb11	Nuu chah nulth	2	2	6	0	0
Nb9	Nuxalk	2	2	6	0	0
Sg3	Ona	1	6	3	0	0
ec20	Oroch	2	3	5	0	0
ec19	Orok	2	3	5	0	0
Nd57	Pahvant	3	5	2	0	0
Nd50	Panguitch	6	3	1	0	0
Sb5	Paraujano	3	1	6	0	0
Nc22	Patwin	5	3	2	0	0
Na34	Pekangekum	2	4	4	0	0
Ne18	Piegan	2	8	0	0	0
Ne19	Plains Cree	2	6	2	0	0
Nb17	Puyallup	3	2	5	0	0
Nb18	Quileute	1	3	6	0	0
Nb25	Quinault	2	3	5	0	0
Nd37	Railroad Valley Shoshoni	7	3	0	0	0
Na37	Rainy River Ojibwe	3	4	3	0	0
Nc26	Salinan	5	3	2	0	0
Nd4	Sanpoil	3	2	5	0	0
Ne7	Sarcee	2	8	0	0	0
Nd25	Sawakudokwa	5	3	2	0	0
Na28	Sekani	1	5	4	0	0
Ej3	Semang	4	3	3	0	0

Ni4	Seri	2	2	6	0	0
Nc30	Serrano	6	4	0	0	0
Nb32	Shasta	4	3	3	0	0
Sd6	Shiriana	3	4	3	0	0
Nd11	Shuswap	3	3	4	0	0
Nd15	Sinkaitk	3	3	4	0	0
Nb39	Sinkyone	4	3	3	0	0
Nb29	Siuslaw	1	3	6	0	0
Na11	Sivokakmeit	0	2	8	0	0
Nd53	Southern Paiute (Kaibab)	7	3	0	0	0
Nc19	Southern Pomo	4	3	3	0	0
Nd2	Southern Ute	3	6	1	0	0
Nc24	Southern Valley Yokuts	5	2	3	0	0
Nb13	Squamish	2	3	5	0	0
Nb27	Stolo	3	3	4	0	0
Nc2	Tubalulabal	5	3	2	0	0
Nd32	Tumpisa Shoshone (Saline and Panamint)	6	4	0	0	0
Nd21	Tagotoka	4	3	3	0	0
Na27	Tahltan	1	5	4	0	0
Nb30	Takelma	4	3	3	0	0
Na44	Taqagmiut	0	6	4	0	0
Na2	Tareumiut	0	3	7	0	0
Na24	Tasiilaq	0	2	8	0	0
Id8	Tasmanians (northwestern)	4	4	2	0	0
Nd61	Taviwatsiu	3	5	2	0	0
Sg4	Tehuelche	2	7	1	0	0
Nd1	Tenino	3	2	5	0	0

Ne8	Teton	1	9	0	0	0
Nb20	Tillamook	2	3	5	0	0
Id3	Tiwi	5	3	2	0	0
Na15	Tlicho	2	3	5	0	0
Nb22	Tlingit	1	3	6	0	0
Nd28	Toedokado	6	3	1	0	0
Nb6	Tolowa	4	2	4	0	0
Nc29	Tongva	4	2	4	0	0
Nb7	Tsimshian	2	2	6	0	0
Nd40	Tubaduka	6	3	1	0	0
Nd47	Tukudika	3	4	3	0	0
Nd29	Tunava (Deep Springs and Fish Lake)	6	3	1	0	0
Nb31	Tututni	3	2	5	0	0
Nb2	Twana	1	3	6	0	0
ec21	Udihe	2	4	4	0	0
Nd58	Uintah Ute	3	4	3	0	0
ec18	Ulch	2	3	5	0	0
Nd19	Umatilla	3	3	4	0	0
Nd62	Uncompahgre Ute	4	5	1	0	0
ec14	Ungazikmit	1	2	7	0	0
Eh4	Vedda	4	3	3	0	0
Nd22	Wadadokado	5	3	2	0	0
Nd41	Wadaduka	6	3	1	0	0
Nd26	Wadatkuht	6	3	1	0	0
Id10	Walbiri	6	4	0	0	0
Nc20	Wappo	5	3	2	0	0
Nd6	Washo	4	3	3	0	0
Nd16	Wenatchi	3	3	4	0	0

Nc23	Western Mono	5	3	2	0	0
Nd43	White Knife Shoshoni	5	4	1	0	0
Id6	Wikmunkan	4	4	2	0	0
Nd64	Wind River Eastern Shoshone	3	5	2	0	0
Nc14	Wintu	3	3	4	0	0
Nd18	Wishram	3	2	5	0	0
Nd36	Wiyambituka	7	3	0	0	0
Nb36	Wiyot	4	1	5	0	0
Nc25	Wukchumni	4	3	3	0	0
Nd44	Yahanduka	3	2	5	0	0
Sg1	Yahgan	1	2	7	0	0
Nc11	Yana	5	2	3	0	0
Nd66	Yavapai	6	4	0	0	0
Id12	Yir Yoront	5	3	2	0	0
Id2	Yolngu, Dhuwal	5	3	2	0	0
Ec6	Yukaghir	1	5	4	0	0
Nc7	Yuki	4	3	3	0	0
Nb4	Yurok	4	1	5	0	0

Calculations

1. Calculating macronutrient contributions for hunted and fished foods at 10%, 15%, and 20% bodyfat using the linear regression curve equations presented in the Cordain et al. (2000) study.

Legend:

x = animal's body fat percentage (10%, 15%, 20%)

Equation to determine hunted animals' fat %:

$$y = 3.21 + (7.92 \times x) - (0.403 \times x^2) + (0.0090 \times x^3)$$

Calculation at 20% bodyfat:

$$y = 3.21 + (7.92 \times 20) - (0.403 \times 20^2) + (0.0090 \times 20^3)$$

$$y = 3.21 + 158.4 - 161.2 + 72$$

$$y = \mathbf{72\%}$$

Calculation at 15% bodyfat:

$$y = 3.21 + (7.92 \times 15) - (0.403 \times 15^2) + (0.0090 \times 15^3)$$

$$y = 3.21 + 118.8 - 90.675 + 30.375$$

$$y = \mathbf{62\%}$$

Calculation at 10% bodyfat:

$$y = 3.21 + (7.92 \times 10) - (0.403 \times 10^2) + (0.0090 \times 10^3)$$

$$y = 3.21 + 79.2 - 40.3 + 9$$

$$y = \mathbf{51\%}$$

Calculation at 5% bodyfat:

$$y = 3.21 + (7.92 \times 5) - (0.403 \times 5^2) + (0.0090 \times 5^3)$$

$$y = 3.21 + 39.6 - 10.075 + 1.125$$

$$y = \mathbf{34\%}$$

Calculation at 2.5% bodyfat:

$$y = 3.21 + (7.92 \times 2.5) - (0.403 \times 2.5^2) + (0.0090 \times 2.5^3)$$

$$y = 3.21 + 19.8 - 2.519 + 0.141$$

$$y = \mathbf{21\%}$$

Equation to determine hunted animals' protein %:

$$y = 96.79 - (7.92 \times x) + (0.403 \times x^2) - (0.0090 \times x^3)$$

Calculation at 20% bodyfat:

$$y = 96.79 - (7.92 \times 20) + (0.403 \times 20^2) - (0.0090 \times 20^3)$$

$$y = 96.79 - 158.4 + 161.2 - 72$$

$$y = \mathbf{28\%}$$

Calculation at 15% bodyfat:

$$y = 96.79 - (7.92 \times 15) + (0.403 \times 15^2) - (0.0090 \times 15^3)$$

$$y = 96.79 - 118.8 + 90.675 - 30.375$$

$$y = \mathbf{38\%}$$

Calculation at 10% bodyfat:

$$y = 96.79 - (7.92 \times 10) + (0.403 \times 10^2) - (0.0090 \times 10^3)$$

$$y = 96.79 - 79.2 + 40.3 - 9$$

$$y = \mathbf{49\%}$$

Calculation at 5% bodyfat:

$$y = 96.79 - (7.92 \times 5) + (0.403 \times 5^2) - (0.0090 \times 5^3)$$

$$y = 96.79 - 39.6 + 10.075 - 1.125$$

$$y = 66\%$$

Calculation at 2.5% bodyfat:

$$y = 96.79 - (7.92 \times 2.5) + (0.403 \times 2.5^2) - (0.0090 \times 2.5^3)$$

$$y = 96.79 - 19.8 + 2.519 - 0.141$$

$$y = 79\%$$

Equation to determine fished animals' fat %:

$$y = 2.21 + (9.29 \times x) - (0.508 \times x^2) + (0.0117 \times x^3)$$

Calculation at 20% bodyfat:

$$y = 2.21 + (9.29 \times 20) - (0.508 \times 20^2) + (0.0117 \times 20^3)$$

$$y = 2.21 + 185.8 - 203.2 + 93.6$$

$$y = 78\%$$

Calculation at 15% bodyfat:

$$y = 2.21 + (9.29 \times 15) - (0.508 \times 15^2) + (0.0117 \times 15^3)$$

$$y = 2.21 + 139.35 - 114.3 + 39.4875$$

$$y = 67\%$$

Calculation at 10% bodyfat:

$$y = 2.21 + (9.29 \times 10) - (0.508 \times 10^2) + (0.0117 \times 10^3)$$

$$y = 2.21 + 92.9 - 50.8 + 11.7$$

$$y = \mathbf{56\%}$$

Calculation at 5% bodyfat:

$$y = 2.21 + (9.29 \times 5) - (0.508 \times 5^2) + (0.0117 \times 5^3)$$

$$y = 2.21 + 46.45 - 12.7 + 1.463$$

$$y = \mathbf{37\%}$$

Calculation at 2.5% bodyfat:

$$y = 2.21 + (9.29 \times 2.5) - (0.508 \times 2.5^2) + (0.0117 \times 2.5^3)$$

$$y = 2.21 + 23.225 - 3.175 + 15.625$$

$$y = \mathbf{22\%}$$

Equation to determine fished animals' protein %:

$$y = 97.67 - (9.45 \times x) + (0.535 \times x^2) - (0.0127 \times x^3)$$

Calculation at 20% bodyfat:

$$y = 97.67 - (9.45 \times 20) + (0.535 \times 20^2) - (0.0127 \times 20^3)$$

$$y = 97.67 - 189 + 214 - 101.6$$

$$y = \mathbf{21\%}$$

Calculation at 15% bodyfat:

$$y = 97.67 - (9.45 \times 15) + (0.535 \times 15^2) - (0.0127 \times 15^3)$$

$$y = 97.67 - 141.75 + 120.375 - 42.8625$$

$$y = \mathbf{33\%}$$

Calculation at 10% bodyfat:

$$y = 97.67 - (9.45 \times 10) + (0.535 \times 10^2) - (0.0127 \times 10^3)$$

$$y = 97.67 - 94.5 + 53.5 - 12.7$$

$$y = \mathbf{44\%}$$

Calculation at 5% bodyfat:

$$y = 97.67 - (9.45 \times 5) + (0.535 \times 5^2) - (0.0127 \times 5^3)$$

$$y = 97.67 - 47.25 + 13.375 - 1.5875$$

$$y = \mathbf{62\%}$$

Calculation at 2.5% bodyfat:

$$y = 97.67 - (9.45 \times 2.5) + (0.535 \times 2.5^2) - (0.0127 \times 2.5^3)$$

$$y = 97.67 - 23.625 + 3.344 - 0.198$$

$$y = \mathbf{77\%}$$

Summary of the Results:

Table A1: Contributing fat and protein values for fished and hunted animal sourced foods at body fat percentages of 20%, 15%, 10%, 5%, and 2.5%

	Fished		Hunted	
Body Fat	Fat %	Protein %	Fat %	Protein %
20%	78%	21%	72%	28%
15%	67%	33%	62%	38%
10%	56%	44%	51%	49%
5%	37%	62%	34%	66%
2.5%	22%	77%	21%	79%

2. Sample calculation to determine the animal macronutrient values that will be contributing for each subsistence percentage.

Cordain et al. calculated the macronutrient values that would arise from P-A percentages of 35:65, 45:55, 50:50, 55:45, and 65:35. In order to replicate their study, I needed to determine the animal macronutrient values contributed from animals with 10%, 15%, and 20% at each of those P-A contributions

Ex. For animals with 10% body fat and an animal-food subsistence contribution of 65%

Legend

A = animal-food subsistence contribution

T = 12552 kJ (total kJ consumed by the average hunter-gather male (Cordain et al., 2000))

t = Total kJ from animal food

H = Total kJ from hunted food

F = Total kJ from fished food

f = Percentage contribution of fished food

h = Percentage contribution of hunted food

- a) Determine how many kJ come from animal-food at this subsistence contribution

$$t = (T \times A)$$

$$t = (12552 \times 0.65)$$

$$t = 8158.8 \text{ kJ}$$

Therefore, for a P-A subsistence contribution of 35:65, animal-food is contributing 8158.8 kJ

- b) Determine how many of the kJ determined in step 1 come from hunted animals and how many come from fished animals

Hunted

$$H = (T \times 0.35)$$

Fished

$$F = (t - H)$$

Therefore, for a P-A subsistence contribution of 35:65, 4393.2 kJ will come from hunted foods and 3765.6 kJ will come from fished foods

- c) Determine what percentage of kJ hunted and fished foods contribute

$$h = \frac{H}{t}$$

$$f = \frac{F}{t}$$

$$h = \frac{4393.2}{8158.8}$$

$$f = \frac{3765.6}{8158.8}$$

$$h = 54\%$$

$$f = 46\%$$

Therefore, for a P-A subsistence contribution of 35:65, 54% of the animal food energy will come from hunted foods and 46% of the animal food energy will come from fished foods

- d) Calculate the contributing macronutrient values for animals at 10% body fat when animal food makes up 65% of the diet.

Legend:

f = percentage contribution of fished food

h = percentage contribution of hunted food

ff = percentage of contributing fat from fished food sources

fp = percentage of contributing protein from fished food sources

hf = percentage of contributing fat from hunted food sources

hp = percentage of contributing protein from hunted food sources

In this sample calculation I am determining the contributing macronutrient values from hunted and fished foods at 10% body fat. The values for ff , fp , hf , and hp were calculated in the first set of calculations

$$\begin{aligned} \text{Total Carbohydrate} &= 0 \\ \text{Total Fat} &= (f \times ff) + (h \times hf) \\ \text{Total Protein} &= (f \times fp) + (h \times hp) \end{aligned}$$

$$\begin{aligned} \text{Total Carbohydrate} &= 0 \\ \text{Total Fat} &= (0.46 \times 0.56) + (0.54 \times 0.51) \\ \text{Total Protein} &= (0.46 \times 0.44) + (0.54 \times 0.49) \end{aligned}$$

$$\begin{aligned} \text{Total Carbohydrate} &= 0 \\ \text{Total Fat} &= (0.26) + (0.28) \\ \text{Total Protein} &= (0.20) + (0.26) \end{aligned}$$

$$\begin{aligned} \text{Total Carbohydrate} &= \mathbf{0\%} \\ \text{Total Fat} &= \mathbf{54\%} \\ \text{Total Protein} &= \mathbf{46\%} \end{aligned}$$

Therefore, the macronutrient values from animals at 10% body fat when animal food makes up 65% of the diet will be 0% Carbohydrates, 54% Fat, and 46% Protein

- e) Repeat for each body fat percentage at each percentage contribution of animal foods. The results are in Table A2

Animal Values per subsistence percentage

Table A2: The macronutrient contributions from combined hunted and fished animal food at a variety of body fat percentages and P-A ratios.

Subsistence Ratio (A)	Protein	Carbohydrate	Fat
65% Animal foods			
20% animal fat	25%	0%	75%
15% animal fat	36%	0%	64%
10% animal fat	46%	0%	54%
55% Animal foods			
20% animal fat	26%	0%	74%
15% animal fat	36%	0%	64%
10% animal fat	47%	0%	53%
50% Animal foods			
20% animal fat	26%	0%	74%
15% animal fat	37%	0%	63%
10% animal fat	47%	0%	53%
45% Animal foods			
20% animal fat	27%	0%	73%
15% animal fat	37%	0%	63%
10% animal fat	48%	0%	52%
35% Animal foods			
20% animal fat	28%	0%	72%
15% animal fat	38%	0%	62%
10% animal fat	49%	0%	51%

Hunted and Fished Contributions

Table A3: Hunted and fished contribution calculations

Animal Food Subsistence Contribution	Total kJ	Total animal kJ	Total Hunted kJ	Total Fished kJ	% Fished	% Hunted
0.65	12552	8158.8	4393.2	3765.6	0.46	0.54
0.55	12552	6903.6	4393.2	2510.4	0.36	0.64
0.5	12552	6276	4393.2	1882.8	0.30	0.70
0.45	12552	5648.4	4393.2	1255.2	0.22	0.78
0.35	12552	4393.2	4393.2	0	-	1.00

Contributing Animal Macronutrient Values

Table A4: The contributing macronutrient values for hunted and fished animals at each body fat percentage

Body Fat %	% Hunted Fat Contribution	% Hunted Protein Contribution	% Fished Fat Contribution	% Fished Protein Contribution
10	51	49	56	44
15	62	38	67	33
20	72	28	78	21

Total Fat

Table A5: Percentage contribution of total animal food for each of fished and hunted animals at each P-A level

Animal Food Subsistence Contribution	%Fished	% Hunted
0.65	0.46	0.54
0.55	0.36	0.64
0.5	0.30	0.70
0.45	0.22	0.78
0.35	-	1.00

Contributing Fat and Protein

Table A6: Calculations for total protein and fat contributed by hunted and fished animals at each subsistence contribution

Animal Food Subsistence Contribution	% Fished	% Hunted	Animal Body fat %	% Fished Fat	% Fished Protein	% Hunted Fat	% Hunted Protein
0.65	0.46	0.54	0.1	0.56	0.44	0.51	0.49
0.65	0.46	0.54	0.15	0.67	0.33	0.62	0.38
0.65	0.46	0.54	0.2	0.78	0.21	0.72	0.28
0.55	0.36	0.64	0.1	0.56	0.44	0.51	0.49
0.55	0.36	0.64	0.15	0.67	0.33	0.62	0.38
0.55	0.36	0.64	0.2	0.78	0.21	0.72	0.28
0.5	0.3	0.7	0.1	0.56	0.44	0.51	0.49
0.5	0.3	0.7	0.15	0.67	0.33	0.62	0.38
0.5	0.3	0.7	0.2	0.78	0.21	0.72	0.28
0.45	0.22	0.78	0.1	0.56	0.44	0.51	0.49
0.45	0.22	0.78	0.15	0.67	0.33	0.62	0.38
0.45	0.22	0.78	0.2	0.78	0.21	0.72	0.28
0.35	0	1	0.1	0.56	0.44	0.51	0.49
0.35	0	1	0.15	0.67	0.33	0.62	0.38
0.35	0	1	0.2	0.78	0.21	0.72	0.28

The total fat and total protein are presented in table 4 of the thesis

Table A7: Results for total fat and protein contributed by animals at 10%, 15%, and 20% body fat at each P-A contribution

Animal Food Subsistence Contribution	Total Fat	Total Protein
0.65, 10% BF	0.53	0.47
0.65, 15% BF	0.64	0.36
0.65, 20% BF	0.75	0.25
0.55, 10% BF	0.53	0.47
0.55, 15% BF	0.64	0.37
0.55, 20% BF	0.75	0.25

Animal Food Subsistence Contribution	Total Fat	Total Protein
0.5, 10% BF	0.53	0.47
0.5, 15% BF	0.63	0.37
0.5, 20% BF	0.74	0.26
0.45, 10% BF	0.52	0.48
0.45, 15% BF	0.63	0.37
0.45, 20% BF	0.74	0.26
0.35, 10% BF	0.51	0.49
0.35, 15% BF	0.62	0.38
0.35, 20% BF	0.72	0.28

3. Example calculation for the range of macronutrients

Below is the legend and equation that I used in order to calculate the macronutrient values. I have solved one equation here, the rest follow in a Microsoft Word-modified Excel table.

Legend

M_{pc} = carbohydrate percentage from plant database

M_{ac} = carbohydrate percentage from animal database

M_{pf} = fat percentage from plant database

M_{af} = fat percentage from animal database

M_{pp} = protein percentage from plant database

M_{ap} = protein percentage from animal database

P = plant percentage of diet

A = animal percentage of diet

T = total daily energy consumption (in kJ) in the average hunter-gatherer male diet

$$\text{Carbohydrate} = \frac{(M_{pc} * P * T) + (M_{ac} * A * T)}{T}$$

$$\text{Fat} = \frac{(M_{pf} * P * T) + (M_{af} * A * T)}{T}$$

$$\text{Protein} = \frac{(M_{pp} * P * T) + (M_{ap} * A * T)}{T}$$

Example equation. Solving for 20% animal fat at a P-A contribution of 35:65

Plant Values: 62% Carbohydrate, 24% Fat, 14% Protein

Animal Values: 0% Carbohydrate, 54% Fat, 46% Protein

(Taken from Table A1)

$$M_{pc} = 0.62$$

$$M_{ac} = 0$$

$$M_{pf} = 0.24$$

$$M_{af} = 0.54$$

$$M_{pp} = 0.14$$

$$M_{ap} = 0.46$$

$$P = 0.35$$

$$A = 0.65$$

$$T = 12552 \text{ kJ}$$

$$\text{Carb} = \frac{(0.62 \cdot 0.35 \cdot 12552) + (0 \cdot 0.65 \cdot 12552)}{12552}$$
$$\text{Fat} = \frac{(0.24 \cdot 0.35 \cdot 12552) + (0.54 \cdot 0.65 \cdot 12552)}{12552}$$
$$\text{Protein} = \frac{(0.14 \cdot 0.35 \cdot 12552) + (0.46 \cdot 0.65 \cdot 12552)}{12552}$$

$$\text{Carbohydrate} = 22\%$$

$$\text{Fat} = 43\%$$

$$\text{Protein} = 35\%$$

Repeat for each body fat percentage at each percentage contribution of animal foods. **The remaining calculations follow in Tables A8 to A19 in a modified Excel format.**

Table A8: Calculations with Indigenous Australians' plant values. The Indigenous Australians Plant Values are 62% Carbohydrate, 24% Fat, 14% Protein

P	A	Ma c	Maf (20%)	Map (20%)	Maf (15%)	Map (15%)	Maf (A10%)	Map (10%)	Mp c	M pf	Mp p
0.35	0.65	0	0.75	0.25	0.64	0.36	0.54	0.46	0.62	0.24	0.14
0.45	0.55	0	0.74	0.26	0.64	0.36	0.53	0.47	0.62	0.24	0.14
0.5	0.5	0	0.74	0.26	0.63	0.37	0.53	0.47	0.62	0.24	0.14
0.55	0.45	0	0.73	0.27	0.63	0.37	0.52	0.48	0.62	0.24	0.14
0.65	0.35	0	0.72	0.28	0.62	0.38	0.51	0.49	0.62	0.24	0.14

Protein - 20%	Carb - 20%	Fat - 20%	Protein - 15%	Carb - 15%	Fat - 15%	Protein - 10%	Carb - 10%	Fat - 10%
21%	22%	57%	28%	22%	50%	35%	22%	44%
21%	28%	52%	26%	28%	46%	32%	28%	40%
20%	31%	49%	26%	31%	44%	31%	31%	39%
20%	34%	46%	24%	34%	42%	29%	34%	37%
19%	40%	41%	22%	40%	37%	26%	40%	33%

Table A9: Calculations with Eaton and Konner's (1985) plant values. Eaton and Konner's (1985) plant values are the average for the !Kung, the ≠ Kade San, the Hadza, the 'Australian Aborigines', and the Tasaday. This equals 68% Carbohydrate, 19% Fat, 13% Protein

P	A	Ma c	Maf (20%)	Map (20%)	Maf (15%)	Map (15%)	Maf (A10%)	Map (10%)	Mp c	M pf	Mp p
0.35	0.65	0	0.75	0.25	0.64	0.36	0.54	0.46	0.68	0.19	0.13
0.45	0.55	0	0.74	0.26	0.64	0.36	0.53	0.47	0.68	0.19	0.13
0.5	0.5	0	0.74	0.26	0.63	0.37	0.53	0.47	0.68	0.19	0.13
0.55	0.45	0	0.73	0.27	0.63	0.37	0.52	0.48	0.68	0.19	0.13
0.65	0.35	0	0.72	0.28	0.62	0.38	0.51	0.49	0.68	0.19	0.13

Protein - 20%	Carb - 20%	Fat - 20%	Protein - 15%	Carb - 15%	Fat - 15%	Protein - 10%	Carb - 10%	Fat - 10%
21%	24%	55%	28%	24%	48%	34%	24%	42%
20%	31%	49%	26%	31%	44%	32%	31%	38%
20%	34%	47%	25%	34%	41%	30%	34%	36%
19%	37%	43%	24%	37%	39%	29%	37%	34%
18%	44%	38%	22%	44%	34%	26%	44%	30%

Table A10: Calculations with !Kung plant values. The !Kung average plant values are 60% Carbohydrate, 28% Fat, 13% Protein

P	A	Mac	Maf (20%)	Map (20%)	Maf (15%)	Map (15%)	Maf (A10%)	Map (10%)	Mpc (Mean)	Mpf (Mean)	Mpp (Mean)
0.35	0.65	0	0.75	0.25	0.64	0.36	0.54	0.46	0.6	0.28	0.13
0.45	0.55	0	0.74	0.26	0.64	0.36	0.53	0.47	0.6	0.28	0.13
0.5	0.5	0	0.74	0.26	0.63	0.37	0.53	0.47	0.6	0.28	0.13
0.55	0.45	0	0.73	0.27	0.63	0.37	0.52	0.48	0.6	0.28	0.13
0.65	0.35	0	0.72	0.28	0.62	0.38	0.51	0.49	0.6	0.28	0.13

Protein - 20%	Carb - 20%	Fat - 20%	Protein - 15%	Carb - 15%	Fat - 15%	Protein - 10%	Carb - 10%	Fat - 10%
21%	21%	59%	28%	21%	51%	34%	21%	45%
20%	27%	53%	26%	27%	48%	32%	27%	42%
20%	30%	51%	25%	30%	46%	30%	30%	41%
19%	33%	48%	24%	33%	44%	29%	33%	39%
18%	39%	43%	22%	39%	40%	26%	39%	36%

Table A11: Calculations with Ache plant values. The Ache average plant values are 80% Carbohydrate, 14% Fat, 6% Protein

P	A	Mac	Maf (20%)	Map (20%)	Maf (15%)	Map (15%)	Maf (A10%)	Map (10%)	Mpc (Mean)	Mpf (Mean)	Mpp (Mean)
0.35	0.65	0	0.75	0.25	0.64	0.36	0.54	0.46	0.8	0.14	0.06
0.45	0.55	0	0.74	0.26	0.64	0.36	0.53	0.47	0.8	0.14	0.06
0.5	0.5	0	0.74	0.26	0.63	0.37	0.53	0.47	0.8	0.14	0.06
0.55	0.45	0	0.73	0.27	0.63	0.37	0.52	0.48	0.8	0.14	0.06
0.65	0.35	0	0.72	0.28	0.62	0.38	0.51	0.49	0.8	0.14	0.06

Protein - 20%	Carb - 20%	Fat - 20%	Protein - 15%	Carb - 15%	Fat - 15%	Protein - 10%	Carb - 10%	Fat - 10%
18%	28%	54%	26%	28%	47%	32%	28%	40%
17%	36%	47%	23%	36%	42%	29%	36%	35%
16%	40%	44%	22%	40%	39%	27%	40%	34%
15%	44%	41%	20%	44%	36%	25%	44%	31%
14%	52%	34%	17%	52%	31%	21%	52%	27%

Table A12: Calculations with Ainu plant values. The Ainu average plant values are 73% Carbohydrate, 19% Fat, 9% Protein

P	A	Mac	Maf (20%)	Map (20%)	Maf (15%)	Map (15%)	Maf (A10%)	Map (10%)	Mpc (Mean)	Mpf (Mean)	Mpp (Mean)
0.35	0.65	0	0.75	0.25	0.64	0.36	0.54	0.46	0.76	0.08	0.17
0.45	0.55	0	0.74	0.26	0.64	0.36	0.53	0.47	0.76	0.08	0.17
0.5	0.5	0	0.74	0.26	0.63	0.37	0.53	0.47	0.76	0.08	0.17
0.55	0.45	0	0.73	0.27	0.63	0.37	0.52	0.48	0.76	0.08	0.17
0.65	0.35	0	0.72	0.28	0.62	0.38	0.51	0.49	0.76	0.08	0.17

Protein - 20%	Carb - 20%	Fat - 20%	Protein - 15%	Carb - 15%	Fat - 15%	Protein - 10%	Carb - 10%	Fat - 10%
22%	27%	52%	29%	27%	44%	36%	27%	38%
22%	34%	44%	27%	34%	39%	34%	34%	33%
22%	38%	41%	27%	38%	36%	32%	38%	31%
22%	42%	37%	26%	42%	33%	31%	42%	28%
21%	49%	30%	24%	49%	27%	28%	49%	23%

Table A13: Calculations with Baffin Island Inuit plant values. The Baffin Island Inuit average plant values are 77% Carbohydrate, 13% Fat, 10% Protein

P	A	Mac	Maf (20%)	Map (20%)	Maf (15%)	Map (15%)	Maf (A10%)	Map (10%)	Mpc (Mean)	Mpf (Mean)	Mpp (Mean)
0.35	0.65	0	0.75	0.25	0.64	0.36	0.54	0.46	0.77	0.13	0.1
0.45	0.55	0	0.74	0.26	0.64	0.36	0.53	0.47	0.77	0.13	0.1
0.5	0.5	0	0.74	0.26	0.63	0.37	0.53	0.47	0.77	0.13	0.1
0.55	0.45	0	0.73	0.27	0.63	0.37	0.52	0.48	0.77	0.13	0.1
0.65	0.35	0	0.72	0.28	0.62	0.38	0.51	0.49	0.77	0.13	0.1

Protein - 20%	Carb - 20%	Fat - 20%	Protein - 15%	Carb - 15%	Fat - 15%	Protein - 10%	Carb - 10%	Fat - 10%
20%	27%	53%	27%	27%	46%	33%	27%	40%
19%	35%	47%	24%	35%	41%	30%	35%	35%
18%	39%	44%	24%	39%	38%	29%	39%	33%
18%	42%	40%	22%	42%	36%	27%	42%	31%
16%	50%	34%	20%	50%	30%	24%	50%	26%

Table A14: Calculations with Hadza plant values. The Hadza average plant values are 72% Carbohydrate, 18% Fat, 11% Protein

P	A	Mac	Maf (20%)	Map (20%)	Maf (15%)	Map (15%)	Maf (A10%)	Map (10%)	Mpc (Mean)	Mpf (Mean)	Mpp (Mean)
0.35	0.65	0	0.75	0.25	0.64	0.36	0.54	0.46	0.72	0.18	0.11
0.45	0.55	0	0.74	0.26	0.64	0.36	0.53	0.47	0.72	0.18	0.11
0.5	0.5	0	0.74	0.26	0.63	0.37	0.53	0.47	0.72	0.18	0.11
0.55	0.45	0	0.73	0.27	0.63	0.37	0.52	0.48	0.72	0.18	0.11
0.65	0.35	0	0.72	0.28	0.62	0.38	0.51	0.49	0.72	0.18	0.11

Protein - 20%	Carb - 20%	Fat - 20%	Protein - 15%	Carb - 15%	Fat - 15%	Protein - 10%	Carb - 10%	Fat - 10%
20%	25%	55%	27%	25%	48%	34%	25%	41%
19%	32%	49%	25%	32%	43%	31%	32%	37%
19%	36%	46%	24%	36%	41%	29%	36%	36%
18%	40%	43%	23%	40%	38%	28%	40%	33%
17%	47%	37%	20%	47%	33%	24%	47%	30%

Table A15: Calculations with Hiwi plant values. The Hiwi average plant values are 84% Carbohydrate, 8% Fat, 9% Protein

P	A	Mac	Maf (20%)	Map (20%)	Maf (15%)	Map (15%)	Maf (A10%)	Map (10%)	Mpc (Mean)	Mpf (Mean)	Mpp (Mean)
0.35	0.65	0	0.75	0.25	0.64	0.36	0.54	0.46	0.84	0.08	0.09
0.45	0.55	0	0.74	0.26	0.64	0.36	0.53	0.47	0.84	0.08	0.09
0.5	0.5	0	0.74	0.26	0.63	0.37	0.53	0.47	0.84	0.08	0.09
0.55	0.45	0	0.73	0.27	0.63	0.37	0.52	0.48	0.84	0.08	0.09
0.65	0.35	0	0.72	0.28	0.62	0.38	0.51	0.49	0.84	0.08	0.09

Protein - 20%	Carb - 20%	Fat - 20%	Protein - 15%	Carb - 15%	Fat - 15%	Protein - 10%	Carb - 10%	Fat - 10%
19%	29%	52%	27%	29%	44%	33%	29%	38%
18%	38%	44%	24%	38%	39%	30%	38%	33%
18%	42%	41%	23%	42%	36%	28%	42%	31%
17%	46%	37%	22%	46%	33%	27%	46%	28%
16%	55%	30%	19%	55%	27%	23%	55%	23%

Table A16: Calculations with Sahtú Dene/Métis plant values. The Sahtú Dene/Métis average plant values are 81% Carbohydrate, 12% Fat, 7% Protein

P	A	Mac	Maf (20%)	Map (20%)	Maf (15%)	Map (15%)	Maf (A10%)	Map (10%)	Mpc (Mean)	Mpf (Mean)	Mpp (Mean)
0.35	0.65	0	0.75	0.25	0.64	0.36	0.54	0.46	0.81	0.12	0.07
0.45	0.55	0	0.74	0.26	0.64	0.36	0.53	0.47	0.81	0.12	0.07
0.5	0.5	0	0.74	0.26	0.63	0.37	0.53	0.47	0.81	0.12	0.07
0.55	0.45	0	0.73	0.27	0.63	0.37	0.52	0.48	0.81	0.12	0.07
0.65	0.35	0	0.72	0.28	0.62	0.38	0.51	0.49	0.81	0.12	0.07

Protein - 20%	Carb - 20%	Fat - 20%	Protein - 15%	Carb - 15%	Fat - 15%	Protein - 10%	Carb - 10%	Fat - 10%
19%	28%	53%	26%	28%	46%	32%	28%	39%
17%	36%	46%	23%	36%	41%	29%	36%	35%
17%	41%	43%	22%	41%	38%	27%	41%	33%
16%	45%	39%	21%	45%	35%	25%	45%	30%
14%	53%	33%	18%	53%	30%	22%	53%	26%

Table A17: Calculations with Nuxalk plant values. The Nuxalk average plant values are 81% Carbohydrate, 12% Fat, 7% Protein

P	A	Mac	Maf (20%)	Map (20%)	Maf (15%)	Map (15%)	Maf (A10%)	Map (10%)	Mpc (Mean)	Mpf (Mean)	Mpp (Mean)
0.35	0.65	0	0.75	0.25	0.64	0.36	0.54	0.46	0.81	0.12	0.07
0.45	0.55	0	0.74	0.26	0.64	0.36	0.53	0.47	0.81	0.12	0.07
0.5	0.5	0	0.74	0.26	0.63	0.37	0.53	0.47	0.81	0.12	0.07
0.55	0.45	0	0.73	0.27	0.63	0.37	0.52	0.48	0.81	0.12	0.07
0.65	0.35	0	0.72	0.28	0.62	0.38	0.51	0.49	0.81	0.12	0.07

Protein - 20%	Carb - 20%	Fat - 20%	Protein - 15%	Carb - 15%	Fat - 15%	Protein - 10%	Carb - 10%	Fat - 10%
19%	28%	53%	26%	28%	46%	32%	28%	39%
17%	36%	46%	23%	36%	41%	29%	36%	35%
17%	41%	43%	22%	41%	38%	27%	41%	33%
16%	45%	39%	21%	45%	35%	25%	45%	30%
14%	53%	33%	18%	53%	30%	22%	53%	26%

Table A18: Calculations with Wet'suwet'en plant values. The Wet'suwet'en average plant values: 84% Carbohydrate, 10% Fat, 6% Protein

P	A	Mac	Maf (20%)	Map (20%)	Maf (15%)	Map (15%)	Maf (A10%)	Map (10%)	Mpc (Mean)	Mpf (Mean)	Mpp (Mean)
0.35	0.65	0	0.75	0.25	0.64	0.36	0.54	0.46	0.84	0.1	0.06
0.45	0.55	0	0.74	0.26	0.64	0.36	0.53	0.47	0.84	0.1	0.06
0.5	0.5	0	0.74	0.26	0.63	0.37	0.53	0.47	0.84	0.1	0.06
0.55	0.45	0	0.73	0.27	0.63	0.37	0.52	0.48	0.84	0.1	0.06
0.65	0.35	0	0.72	0.28	0.62	0.38	0.51	0.49	0.84	0.1	0.06

Protein - 20%	Carb - 20%	Fat - 20%	Protein - 15%	Carb - 15%	Fat - 15%	Protein - 10%	Carb - 10%	Fat - 10%
18%	29%	52%	26%	29%	45%	32%	29%	39%
17%	38%	45%	23%	38%	40%	29%	38%	34%
16%	42%	42%	22%	42%	37%	27%	42%	32%
15%	46%	38%	20%	46%	34%	25%	46%	29%
14%	55%	32%	17%	55%	28%	21%	55%	24%

Table A19: Calculations with Gwich'in plant values. The Gwich'in average plant values are 80% Carbohydrate, 13% Fat, 8% Protein

P	A	Mac	Maf (20%)	Map (20%)	Maf (15%)	Map (15%)	Maf (A10%)	Map (10%)	Mpc (Mean)	Mpf (Mean)	Mpp (Mean)
0.35	0.65	0	0.75	0.25	0.64	0.36	0.54	0.46	0.8	0.13	0.08
0.45	0.55	0	0.74	0.26	0.64	0.36	0.53	0.47	0.8	0.13	0.08
0.5	0.5	0	0.74	0.26	0.63	0.37	0.53	0.47	0.8	0.13	0.08
0.55	0.45	0	0.73	0.27	0.63	0.37	0.52	0.48	0.8	0.13	0.08
0.65	0.35	0	0.72	0.28	0.62	0.38	0.51	0.49	0.8	0.13	0.08

Protein - 20%	Carb - 20%	Fat - 20%	Protein - 15%	Carb - 15%	Fat - 15%	Protein - 10%	Carb - 10%	Fat - 10%
19%	28%	53%	26%	28%	46%	33%	28%	40%
18%	36%	47%	23%	36%	41%	29%	36%	35%
17%	40%	44%	23%	40%	38%	28%	40%	33%
17%	44%	40%	21%	44%	36%	26%	44%	31%
15%	52%	34%	19%	52%	30%	22%	52%	26%

4. T-test Results

The results from all of the t-tests not presented in the text follow.

Paired Samples Statistics

		Mean	N	Std. Deviation	Std. Error Mean
Pair 1	Australian Protein Values	25.2000%	15	4.98856%	1.28804%
	Eaton and Konner (1985) Protein Values	24.8667%	15	5.15290%	1.33047%
Pair 2	Australian Carbohydrate Values	31.0000%	15	6.21059%	1.60357%
	Eaton and Konner (1985) Carbohydrate Values	34.0000%	15	6.83478%	1.76473%
Pair 3	Australian Fat Values	43.0000%	15	7.36788%	1.90238%
	Eaton and Konner (1985) Fat Values	41.1333%	15	6.73866%	1.73991%

Paired Samples Correlations

		N	Correlation	Sig.
Pair 1	Australian Protein Values and Eaton and Konner (1985) Protein Values	15	.996	.000
Pair 2	Australian Carbohydrate Values and Eaton and Konner (1985) Carbohydrate Values	15	1.000	.000
Pair 3	Australian Fat Values and Eaton and Konner (1985) Fat Values	15	.925	.000

Paired Samples Test

		Paired Differences					t	df	Sig. (2-tailed)
		Mean	Std. Deviation	Std. Error Mean	95% Confidence Interval of the Difference				
					Lower	Upper			
Pair 1	Australian Protein Values - Eaton and Konner (1985) Protein Values	0.33333 %	0.48795%	0.12599%	0.06312%	0.60355%	2.646	14	.019
Pair 2	Australian Carbohydrate Values - Eaton and Konner (1985) Carbohydrate Values	3.00000 %	0.65465%	0.16903%	3.36254%	2.63746%	17.748	14	.000
Pair 3	Australian Fat Values - Eaton and Konner (1985) Fat Values	1.86667 %	2.79966%	0.72287%	0.31627%	3.41707%	2.582	14	.022

Table A20: Paired Samples T-test results

Society	T-test results
!Kung	Protein: Sig. 2-tailed = .041 Carbohydrates: Sig. 2-tailed = .000 Fat: Sig. 2-tailed = .000
Ache	Protein: Sig. 2-tailed = .000 Carbohydrates: Sig. 2-tailed = .000 Fat: Sig. 2-tailed = .000
Ainu	Protein: Sig. 2-tailed = .000 Carbohydrates: Sig. 2-tailed = .000 Fat: Sig. 2-tailed = .000
Baffin Island Inuit	Protein: Sig. 2-tailed = .000 Carbohydrates: Sig. 2-tailed = .000 Fat: Sig. 2-tailed = .000
Hadza	Protein: Sig. 2-tailed = .000 Carbohydrates: Sig. 2-tailed = .000 Fat: Sig. 2-tailed = .000
Hiwi	Protein: Sig. 2-tailed = .000 Carbohydrates: Sig. 2-tailed = .000 Fat: Sig. 2-tailed = .000

Society	T-test results
Sahtú Dene/Métis	Protein: Sig. 2-tailed = .000 Carbohydrates: Sig. 2-tailed = .000 Fat: Sig. 2-tailed = .000
Nuxalk	Protein: Sig. 2-tailed = .000 Carbohydrates: Sig. 2-tailed = .000 Fat: Sig. 2-tailed = .000
Wet'suwet'en	Protein: Sig. 2-tailed = .000 Carbohydrates: Sig. 2-tailed = .000 Fat: Sig. 2-tailed = .000
Gwich'in	Protein: Sig. 2-tailed = .000 Carbohydrates: Sig. 2-tailed = .000 Fat: Sig. 2-tailed = .000

5. MANOVA Results

The MANOVA Results Follow

Protein:

Variab le	Observatio ns	Obs. with missing data	Obs. without missing data	Minimu m	Maximu m	Mea n	Std. deviation
Protein	165	0	165	0.140	0.370	0.240	0.054

Variable	Categories	Frequencies	%
Society	!Kung	15	9.091
	Ache	15	9.091
	Ainu	15	9.091
	Australia	15	9.091
	Baffin Island Inuit	15	9.091
	Gwich'in	15	9.091
	Hadza	15	9.091
	Hiwi	15	9.091
	Metis	15	9.091
	Nuxalk	15	9.091
	Wet'suwet'en	15	9.091

Wilks' test (Rao's approximation):

	Society
Lambda	0.837
F (Observed values)	2.990
DF1	10
DF2	154
F (Critical value)	1.893
p-value	0.002

H0: The variable or the interaction of the corresponding column has no significant effect on the dependent variables.
Ha: The variable or the interaction of the corresponding column has a significant effect on the dependent variables.
Society: As the computed p-value is lower than the significance level $\alpha=0.05$, one should reject the null hypothesis H0, and accept the alternative hypothesis Ha.
The risk to reject the null hypothesis H0 while it is true is lower than 0.18%.

Carbohydrate:

Variable	Observations	Obs. with missing data	Obs. without missing data	Minimum	Maximum	Mean	Std. deviation
Carbohydrate	165	0	165	0.210	0.550	0.375	0.085

Variable	Categories	Frequencies	%
Society	!Kung	15	9.091
	Ache	15	9.091
	Ainu	15	9.091
	Australia	15	9.091
	Baffin Island Inuit	15	9.091
	Gwich'in	15	9.091
	Hadza	15	9.091
	Hiwi	15	9.091
	Metis	15	9.091
	Nuxalk	15	9.091
	Wet'suwet'en	15	9.091

Wilks' test (Rao's approximation):

	Society
Lambda	0.799
F (Observed values)	3.868
DF1	10
DF2	154
F (Critical value)	1.893
p-value	0.000

H0: The variable or the interaction of the corresponding column has no significant effect on the dependent variables.
Ha: The variable or the interaction of the corresponding column has a significant effect on the dependent variables.
Society: As the computed p-value is lower than the significance level $\alpha=0.05$, one should reject the null hypothesis H0, and accept the alternative hypothesis Ha.
The risk to reject the null hypothesis H0 while it is true is lower than 0.01%.

Fat:

Variable	Observations	Obs. with missing data	Obs. without missing data	Minimum	Maximum	Mean	Std. deviation
Fat	165	0	165	0.240	0.590	0.394	0.074

Variable	Categories	Frequencies	%
Society	!Kung	15	9.091
	Ache	15	9.091
	Ainu	15	9.091
	Australia	15	9.091
	Baffin Island Inuit	15	9.091
	Gwich'in	15	9.091
	Hadza	15	9.091
	Hiwi	15	9.091
	Metis	15	9.091
	Nuxalk	15	9.091
	Wet'suwet'en	15	9.091

Wilks' test (Rao's approximation):

	Society
Lambda	0.857
F (Observed values)	2.567
DF1	10
DF2	154
F (Critical value)	1.893
p-value	0.007

H0: The variable or the interaction of the corresponding column has no significant effect on the dependent variables.
Ha: The variable or the interaction of the corresponding column has a significant effect on the dependent variables.
Society: As the computed p-value is lower than the significance level $\alpha=0.05$, one should reject the null hypothesis H0, and accept the alternative hypothesis Ha.
The risk to reject the null hypothesis H0 while it is true is lower than 0.67%.