Forager Habitat Quality: Quantifying Hunter-Gatherer Habitats, Past and Present

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ABSTRACT

Prior to the advent of agriculture approximately 10,000 years ago, hunting and gathering were the sole means of subsistence for our species. Contemporary populations of part-time foragers, who practicing mixed subsistence strategies that incorporate wild foods, offer powerful models for understanding the behaviors and pressures that shaped the evolution of our species. This dissertation seeks to understand various factors that contribute to the foraging and demographic success of ethnographic (past) and contemporary foragers within different habitat types.

Chapter 2 tests the common conception that contemporary foragers tend to occupy marginal habitats, and that their utility for informing the socioecology of ancient humans may thereby be diminished. It uses a broad ethnographic sample, combined with data on net primary productivity, to make a thorough assessment of the relationship between habitat quality and population density for pre-industrial societies. Results show that habitats occupied by recent foragers have not tended to be marginal.

Wetland and deltaic area have been hypothesized to be productive habitats for human populations. Chapter 3 provides a test of foraging returns in a wet savanna habitat, the Okavango Delta. Women foraged in adjacent wet and dry habitats while observed during focal follows. Post-encounter return rates were paired with detailed analyses of nutritional content and women's energetic expenditure, evaluating the profitability of each habitat. Contrary to expectation, energy returns were generally higher in dry than wet habitats.

Underground storage organs (USOs) are an important component of the plant diet for humans in a wide array of habitat types, and starch is the dominant form of energy stored in USOs. Chapter 4 analyzes the starch content of USOs across several African habitat types relevant to human evolution. The data reveal wide variability in starch content within and among habitats. Rainforest habitats bore surprisingly starchy USO tissues that rivaled those of domesticated species.

Overall, this thesis contributes to our understanding of how foragers would have utilized plant resources across a range of paleoenvironments.

KEY WORDS: HUMAN BEHAVIORAL ECOLOGY, DIET, NUTRITION, HABITAT QUALITY

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YOU NEVER CEASED SUPPORTING
THANK YOU

CHAPTER 1

INTRODUCTION

Hunters and gatherers provide a powerful model for understanding human evolution. Today, however, the only societies that are entirely independent of agricultural foods are unreachable by scientists (such as the Sentinelese of the Andaman Islands). Contemporary populations of part-time foragers, who practice mixed subsistence strategies that incorporate wild foods, still offer important experimental opportunities for understanding the behaviors and pressures that shaped the evolution of our species. Despite changes from the Pleistocene that include significant proportions of agricultural foods in their diet (Marlowe, 2005), these modern human societies offer valuable research opportunities. Anthropologists have studied hunter-gatherer populations across arctic, desert, rainforest, and savanna environments (Bailey and DeVore, 1989; Binford, 1980; Hawkes et al., 1982; Hill et al., 1987; Lee and DeVore, 1976; Marlowe, 2010; O'Connell and Hawkes, 1981; O'Connell et al., 1999; Smith, 1991). Research has strived to understand the causal factors patterning the geographic distribution and population density of foragers. Yet, surprisingly, no consensus has been reached about why some foraging populations lived at higher densities than others, despite common belief that primary productivity and latitude have strong effects (Kelly, 2013). Previous work has demonstrated both positive associations between environmental productivity and population density (Codding and Jones, 2013), and negative effects in environments with very high productivity (i.e. rainforests)(Balmford et al., 2001). In this thesis, I explore different measures to address this question, striving for a better understanding of how human populations access and extract energy from their environments.

The global distribution of human societies, particularly those considered ‘pre-industrial,’ offer insights into broad patterns of human subsistence and survival (Marlowe, 2005; Murdock, 1967; Murdock and White, 1969; Porter and Marlowe, 2007). Hunter-gatherers today, however, frequently live on the edge – economically, politically, and geographically. This perceived marginalization has led some to suggest that hunter-gatherers also occupy habitats that are marginal, relative to other pre-industrial subsistence types. Were this so, it would indicate that hunter-gatherers are less relevant for informing human evolutionary theory. In Chapter 2, my colleagues and I used a sample of 186 pre-industrial societies to test what we dubbed the

Marginal Habitat Hypothesis (MHH)(Cunningham et al., 2019). We extended a test by Porter and Marlowe (2007) by assessing net primary productivity (NPP) for this sample of foragers, horticulturalists, intensive agriculturalists, and pastoralists. In an attempt to link habitat quality to human success, we incorporated population density (PD) as a variable to evaluate environmental productivity as a means of assessing habitat quality. We also used maximum NPP (NPP_{max}), rather than average NPP (NPP_{mean}), to account for the fact that human populations might bias subsistence activities to the most productive parts of their range. NPP_{max} proved to be a reasonable and predictor of population density (PD) for foragers, as they had a higher probability of achieving medium or high population density in more productive habitats.

The global sample used to test for links between environmental productivity (e.g. NPP) and population outcomes (e.g. PD) provided the necessary size and variation necessary to establish general human habitat occupation patterns. Evidence indicates that the majority of the time during which humans (*Homo*) evolved occurred within seasonally dry savanna and woodland habitats of East and South Africa (Bender et al., 2012; Elton, 2008; Foley, 1993; Potts, 1998; Vrba, 1996; White et al., 2009). Given our species' evolutionary origins on the African continent, there are obvious motivations for focusing research on the origins of human foraging to African populations (Marlowe 2005). For this reason, Chapters 3 and 4 focused on aspects of plant foraging within African populations, drawing on established methodologies from behavioral ecology.

The field of human behavioral ecology has built upon the strong foundation and traditions of ethnographic research in anthropology, adding empirical methods, and producing scores of foraging studies and advancing theory over the previous half century (Krebs and Davies, 1987; Smith et al., 1983; Stephens and Krebs, 1986). Returns on the basis of energy and nutrients returned per unit time have shaped much of what we know about human foraging (Hawkes et al., 1982; O'Connell and Hawkes, 1981). Additionally, a focus on camp returns and time budgets have helped to describe foraging behavior and hunter-gatherer diets from an even broader array of populations, particularly those persisting in contemporary African environments (Lee, 1979; Marlowe, 2010; Murray et al., 2001; Vincent, 1985). An extension of this foundational research into hunter-gatherer diets has been on the sexual division of foraging tasks, and on the constraints, goals, and nutritional complementarity of male and female foragers (Berbesque and Marlowe, 2009; Bird et al., 2001; Bliege Bird et al., 2002; Bliege Bird et al., 2009; Hawkes and Bird, 2002; Hurtado et al., 1985; Hurtado et al., 1992; Marlowe, 1997, 2004, 2007; Wood, 2006). As a result of previous research conducted among African populations, and to some extent hunter-gatherer populations more generally, it has been asserted that women tend to collect (or, target) items that reduce variance in their daily returns. Women predominantly gather plant resources, and these make up greater than 50% of the diet for many populations (by weight or by calories) (Marlowe 2010; Lee 1979; but see Kaplan et al. (2000) for a different conclusion).

Chapters 3 and 4 seek to understand how foragers, particularly women, access and use the products of primary productivity modeled globally in Chapter 2. Plant and animal foods are useless to human consumers if they lack the ability to access such resources. Contemporary foragers offer a valuable means of directly assessing how available resources are. Measures of return rates, yields, and the nutritional composition of wild-derived foods all provide direct evidence of habitat quality as experienced by human populations. Calories derived from carbohydrates are particularly important to many human societies. As a result of the sexual division of labor, women are often responsible for collecting carbohydrate-rich staple foods. Women’s foraging is thus a crucial piece of understanding human socioecology. In Chapter 3, I contrast the returns and energetic costs from women’s foraging expeditions in xeric savanna (Dry) woodlands of the Kalahari with those from wet savanna (Wet) floodplain habitats of the Okavango Delta, Botswana. The mosaic environment of the Okavango presents a needed contrast to the monolithic concept of the savanna generally discussed in human evolution (Bender et al., 2012; Domínguez-Rodrigo et al., 2014).

In Chapter 4, five savanna (S) habitats are compared with five non-savanna rainforest (RF) habitats. This comparison focused on a single aspect of nutritional value, non-resistant starch content, from a single class of foods important to female foragers – underground storage organs (USOs). Starch is the primary source of dietary carbohydrates for much of the modern world (Robyt, 2008), and is presumably one of the main reasons why certain foods (such as USOs) are targeted by foragers. I documented starch concentrations for 32 species of USO, and found that the starch content differed among habitats. Rainforest USOs had significantly higher starch content than savanna USOs. These results suggested that there may be more to explaining the incorporation of USOs in the diets of savanna foragers than merely starch content.

Collectively, this work aims to answer key questions of human behavioral ecology and biological anthropology from understudied aspects of human foraging large and small. Large-scale patterns exist for human populations past and present, such as the global patterns that govern plant productivity. Individuals are influenced at smaller scales, as they work to extract the plant energy needed to survive and reproduce within their habitat. This dissertation presents new findings from both perspectives, large and small. I have provided evidence of novel links among global productivity, subsistence patterns, and population density. At a smaller spatial scale, I offer new data and insights into the energetic outcomes of female foragers – specifically those in savanna and rainforest habitats of Sub-Saharan Africa. These findings provide evidence of ways in which dry savannas are both productive for human foraging populations (as assessed by post-encounter return rates), and inferior to some adjacent alternative habitats (based on starch content and search time). I hope this works encourages future research into more comprehensive and thorough between habitat comparisons, particularly in the areas of wet savanna habitats and starch availability.

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CHAPTER 2

DO MODERN HUNTER-GATHERERS LIVE IN MARGINAL HABITATS?

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"Do modern hunter-gatherers live in marginal habitats?"

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Abstract

Anthropologists often assert that modern hunter-gatherer societies have been relegated to marginal habitats compared to their agricultural neighbors, with the implication that modern social organization and behavior provide little insight into Paleolithic hunter-gatherers. We refer to this idea as the marginal habitat hypothesis (MHH). Despite widespread use of the term ‘marginal,’ there is little consensus as to what comprises a low quality habitat for humans. Here we reassess the MHH by comparing the net primary productivity (NPP) of habitats occupied by, and the population density (PD) of, a sample of 186 pre-industrial societies (foragers, horticulturalists, intensive agriculturalists, and pastoralists). We found that the nature of the NPP-PD relationship varied by subsistence type, and that foragers did not occupy significantly lower net primary productivity habitats compared to other subsistence types. These results do not support the MHH. We conclude by discussing the limitations of using modern ethnographic datasets to address the MHH and suggest alternative ways in which it may still be relevant.

Introduction

A common view in the anthropological literature is that modern hunter-gatherers occupy ‘marginal,’ or poor quality habitats, compared to agriculturalists who have displaced them through numerical, political, or military means (Bigelow, 1972; Lee et al., 1968; Marlowe, 2005; Porter and Marlowe, 2007). This view, which we refer to as the marginal habitat hypothesis (MHH), suggests that contemporary foraging populations offer poor ecological models for Pleistocene hunter-gatherers (Porter and Marlowe, 2007). While this claim is commonplace in the anthropological literature, there has been little empirical investigation of the issue (Speth, 2010). Moreover, the term “marginal” has been used imprecisely and variably. Marginality has been used in an absolute sense in referring to habitats with low primary productivity (Marlowe, 2005; Porter and Marlowe, 2007) or those that are arid, cold, or in dense rainforest (Headland, 1987). The term has also been used in a relative sense to contrast the apparently impoverished habitats occupied by mobile foragers to the richer habitats of neighboring agriculturalists (Bigelow, 1972; Wilmsen, 1989).

For some organisms, good or bad (i.e., optimal or marginal) habitats can be relatively straightforward to define using measures such as primary productivity (PP) or net primary productivity (NPP), the latter reflecting the total energy available in a given habitat per year beyond the vegetation’s maintenance costs (McNaughton et al., 1989; Van Horne, 1983). Yet annual productivity can produce both food products and non-edible biomass that may not directly reflect available food energy (Kelly 1995, Porter and Marlowe 2007). Moreover, humans are biologically dependent on high-quality diets, achieved in part through highly targeted foraging on high-risk, high-reward food items, in addition to the development of complex food acquisition and processing strategies to increase caloric yield and decrease the costs of digestion (Carmody and Wrangham, 2009; Kaplan et al., 2000; Leonard et al., 2007; Wrangham, 2009).

Even with such complications, NPP have been widely and successfully applied in ethnographic studies as a proxy of habitat quality (Binford, 2001; Codding and Jones, 2013; Kelly, 2013), including the one study that has quantitatively tested the MHH, Porter and Marlowe (2007). This study merged data from the Standard Cross Cultural Sample (SCCS) (Murdock and White, 1969) with NASA satellite data on NPP to compare habitats occupied by hunter-gatherers to those occupied by horticulturalists, intensive agriculturalists, and pastoralists. The authors found that, on average, hunter-gatherers did not occupy significantly lower NPP habitats compared to other subsistence types. On this basis, Porter and Marlowe rejected the MHH (Porter and Marlowe, 2007).

Our goal in this paper is to revisit the MHH, with additional data and improved methods. To avoid confusion, we choose not to use the terms ‘marginal’ and ‘optimal’ when possible, and instead refer to habitat quality as reflected by a standardized measure of environmental productivity, NPP. First, we extend the analyses of Marlowe (2005) and Porter and Marlowe (2007) by incorporating several methodological modifications that account for the possibility that their findings were driven by latitude or by the spatial scale of NPP measurement (*Methods* and *Materials*). Second, we consider another means of assessing NPP as a proxy for habitat quality, population density (PD). To more accurately infer habitat quality for humans, it is important to consider how environmental energy is related to key demographic outcomes, such as PD. In principle, habitat quality should be reflected in both food availability (as indexed by NPP) and population density (Begon et al., 1996; Krebs, 1972). NPP and PD are positively associated among some modern (Chown et al., 2003; Luck, 2007) and pre-historic human populations (Codding and Jones, 2013), although there is also evidence to suggest that PD declines, in areas of high NPP (Balmford et al., 2001). While we expect that terrestrial NPP is useful in predicting general food availability, we also acknowledge that habitat quality is also influenced by non-food factors, including climate, competition, parasites, predators, and seasonality, etc. (Tallavaara et al., 2017).

Currently, we lack an understanding of how humans translate environmental productivity into demographic success in different ecological contexts. While the relationship between environmental productivity and population density has been extensively discussed within archaeological and anthropological discussions of the origin of agriculture (Boserup, 1976; Butzer, 1982; Netting, 1968), it has not been tested at a global scale with quantitative data. Similarly, the association between NPP and PD has not been explored among those human populations that are most relevant to reconstructing the recent ecological history of our species: populations across the globe who engage in pre-industrial subsistence strategies such as horticulture, intensive agriculture, pastoralism, and foraging. Given the capacity for human culture and technology to shape human-environment interactions, we propose that the assessment of habitat quality is improved by including population-specific details such as subsistence type and PD. With this aim, we examined how the relationship between NPP and PD varies by subsistence strategy, which provides a further basis for evaluating the MHH. In particular, if the relationship between NPP and PD varies with subsistence type, then terms such as ‘marginal’ and ‘optimal’ would seem to be of limited value when making comparisons across subsistence types (i.e. ‘foragers occupy marginal habitats compared to agriculturalists’).

Third, we discuss the limitations of using modern ethnographic datasets to address the MHH and suggest alternative ways in which the MHH may still be relevant.

Methods

We used ethnographic data from 186 pre-industrial societies of the SCCS (see *Materials* section below) to examine the relationship among NPP, subsistence type, and PD. First, we used environmental data from NASA on the average mean (NPP_{mean}) and max (NPP_{max}) of occupied habitats (based upon SCCS latitude and longitude) to test the MHH, which states that foragers tend to occupy less productive habitats than farming populations (*Objective 1*). Second, we modified this analysis to include latitude, thus accounting for global variation in biome distributions (*Objective 2*). Finally, reflecting the positive relationship between habitat productivity and carrying capacity noted elsewhere, we explore how NPP_{max} and PD are related for each subsistence type (*Objective 3*). We estimate the probability of societies having low, medium, or high PD as a function of NPP, testing NPP as a predictor of habitat quality for societies of each subsistence type, and incorporating PD as a marker of demographic success. To test the reliability of NPP measures, we used NPP_{max} in addition to NPP_{mean}. We also A) included a number of additional environmental and behavioral factors as model covariates, B) used a circular projection of foraging radius (rather than grid), C) sampled habitats based on both a 15 km and 120 km radius (testing NPP_{mean} and NPP_{max} over areas more representative of logistical and residential scales), and D) expanded NASA Moderate Resolution Imaging Spectroradiometer (MODIS) NPP data from 5 to 15 years to reduce error associated with annual variation).

Materials

We used data from four publicly available primary sources to determine how NPP is related to population density across four pre-industrial subsistence types. The SCCS (Murdock and White, 1969) was created as a means of addressing problems of autocorrelation in cross-cultural research (*i.e.* Galton's Problem), selecting a subset of pre-industrial societies from the *Ethnographic Atlas* (Murdock, 1967). SCCS societies are representative of cultural, geographic, linguistic, and regional variation, and are thus a collection of independent data points with good ethnographic coverage. From the SCCS we sourced fishing contribution to diet, latitude, longitude, population density, societal mobility, and study year[1]. We obtained mean annual precipitation (mm, MAP) and effective temperature (ET) from Porter and Marlowe (2007). We additionally followed their subsistence classifications, which were derived from SCCS measures as follows (the prefix 'v' followed by numbers refer to variable columns in the SCCS):

Foragers: local diet < 10% agriculture (v3 < 4), < 10% animal husbandry (v5 < 4), and trade < 50% and ≤ any single local source (v1 < 6); excludes equestrian hunters (v858 ≠ 5 [Mounted Hunting]).

Pastoralism: (v858 = 5 [Mounted Hunting] or 6 [Pastoralism > 33%]).

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[1] Murdock and White (1969) reported the approximate year of modern ethnographic study in *Appendix A*, which is included here in Table 1. We note that "modern" is a relative term. Many of the societies in the SCCS were studied in the mid-nineteenth to mid-twentieth centuries. However, data for some SCCS societies were drawn from observations conducted centuries ago (e.g. Aztec, Babylonian, Hebrew, Inca, Khmer, Roman).

Horticulture: (v858 = 7-10 [7 = Shifting Cultivation with digging sticks or wooden hoes, 8 = Shifting Cultivation with metal hoes, 9 = Horticultural Gardens or Tree Fruits, 10 = Advanced Horticulture with metal hoes]; and foragers reliant upon trade for > 50% of diet [v1 ≥ 4]).

Intensive agriculture: (v858 = 11 [Intensive Agriculture with no plow] or 12 [Intensive Agriculture with plow]).

Subsistence strategies reflect differential efficiency of energy extraction from the environment based on differences in resource abundance and distribution, technology, and degree of agricultural intensification, all of which may lead to variation in carrying capacity (Ellen, 1982, 1994; Redding, 1988; Rindos, 1984). We adopted the subsistence definitions used by Porter and Marlowe (2007). Forager (hunter-gatherer) populations are those primarily dependent on energy extracted directly from the natural environment, and thus not reliant upon plant cultivation, animal husbandry, or products acquired via trade. Following the definition used by both the SCCS and Porter and Marlowe (2007), our ‘forager’ designation does not preclude food storage behaviors. Horticulture is classified as either the practice of shifting cultivation or the keeping of gardens and/or fruit trees, or as populations of foragers who are themselves reliant upon trade for more than 50% of their subsistence (Porter and Marlowe, 2007). This definition varies slightly from the more common definition of horticulture as a mixed strategy of hunting-and-gathering and gardening characterized by sustained fallow periods (Keegan, 1986). Intensive agriculturalists may irrigate, use plows, and tend to exercise direct control over the reproduction of domesticated plants (Murdock and White, 1969; Porter and Marlowe, 2007). Finally, pastoralists consume domesticated animal byproducts such as meat, milk, and blood, and frequently also trade for starch-rich plant products (Murdock and White, 1969; Porter and Marlowe, 2007).

For information on biome classifications, we sourced data sets on world ecoregions from The Nature Conservancy, including the Marine Ecoregions Of the World (MEOW) (Conservancy, 2012; Spalding et al., 2007), and the Terrestrial Ecoregions Of the World (TEOW) (The Nature Conservancy, 2009). NPP data (MOD17A3 algorithm) from NASA’s MODIS Satellite (Running et al., 2015) were obtained from Numerical Terra Dynamic Simulation Group at the University of Montana (http://www.ntsg.umt.edu/project/mod17).

Derived variable calculations

We calculated average maximum (NPP_{max}) and mean (NPP_{mean}) NPP within 15 km and 120 km radii of each society's latitude and longitude coordinates, using NPP data averaged over a 15 year period (2000 - 2014). As NASA reports NPP as the g C/m^2/year for 1km^2 areas, NPP_{max} and NPP_{mean} represent two different ways of summarizing annual productivity over a populations' habitat. We sampled NPP using radii rather than square grids, as radii provide a better approximation than grids to the central-place foraging patterns of pre-industrial human societies (Binford, 1980; Kelly, 2013; Orians and Pearson, 1979). Shortest Euclidean distance from each society to a marine ecoregion (DME) was calculated from GIS shapefiles of MEOW.

The SCCS "Population Density" variable (v64) is reported in an ordinal, discretized form on a statute mile basis, though the denominator at low density is not constant, and several PD levels are potentially overlapping. This inconsistency led us to reduce the original population density categories from seven to three levels, representing a more easily comparable ordinal ranking: low (<1 person / sq. mile), medium (≥ 1 & < 25 people / sq. mile), or high (≥ 25 people / sq. mile). We opted for three levels in part because it was not feasible to fit a model with 186 observations to a categorical response variable with seven levels. Furthermore, population densities of low, medium, and high are much more intuitive, particularly when comparing across four subsistence types and habitat productivity gradients.

The SCCS societal mobility variable "Fixity of Settlement" (v61) was re-coded into a binary "permanent" (which retained the SCCS "Permanent" bin, n= 102) versus "impermanent" (collapsing the additional five SCCS non-"Permanent" levels, n=84) indicator variable (MOBILE). The SCCS "Principal Subsistence Category" variable (v820) was used to generate a binary "fishing" versus "non-fishing" indicator variable (FISH). We singled out fishing as the sole subsistence indicator variable because our primary environmental quality indicator, terrestrial NPP, is inherently blind to non-terrestrial sources of food production such as fish. We also adjusted latitude and/or longitude for 28 societies, correcting erroneous values from the SCCS. Four separate issues necessitated these adjustments: 1) some societies were reported with only approximate spatial locations; 2) for island or coastal dwelling societies small errors in spatial location placed society centroids in a marine environment; 3) obvious erroneous entries (i.e., Kenuzi Nubians); and 4) historical factors causing dramatic alteration of habitat (such as the Aswan Dam Project for Egyptians). The SCCS data and revised coordinates, as well as all variables and societies used in our analyses, are available in a Zenodo repository (Worthington and Cunningham, 2018). Revised Latitude and Longitude coordinates are denoted by an asterisk ("*") in the Summary Table 2.1. The original values as used by Porter and Marlowe (2007) are available in the Zenodo repository.

Data analysis

Data analyses were conducted for both a combined (warm and cold) sample of all SCCS societies and a warm subsample, delineated using the effective temperature (ET) variable. Porter and Marlowe (Porter and Marlowe, 2007) used a cutoff of $ET \geq 14$ for the warm subsample, which corresponds to approximately 40-45° degrees absolute latitude. This is suggested to correspond to a difference between higher and lower densities of underground plant storage organs (such as tubers and corms) eaten by human foragers: warm areas are expected to have higher densities (Marlowe, 2005). All analyses and results presented in the main text use the combined (warm and cold) sample. Contrasts between the combined and warm subsamples are presented in the Supplementary Materials (*Figure SM 2.2 a* and *b*).

Objective 1. To evaluate the MHH, we tested whether subsistence types differ based on the average mean and max NPP of the habitats they occupy. We used general linear models (GLMs) to predict average NPP_{max} and NPP_{mean} for each subsistence type (*Figure 2.3*). NPP_{max} is our primary focus, though comparisons of NPP_{max} and NPP_{mean} are presented in Figure 2.3 and

Figure SM 2.3. All NPP values are reported in units of grams Carbon/m^2 /year (g C/m^2 /year). Six environmental variables were used as explanatory variables in models: mean annual precipitation (MAP), effective temperature (ET), absolute latitude (AbLat), distance to marine ecoregion (DME), binary degree of mobility (MOBILE), and binary reliance on fished resources for protein in diet (FISH). In addition, we used GLMs to estimate average NPP_{max} and NPP_{mean} values across subsistence types for both a combined sample of warm and cold climate societies (on the basis of ET) and separately for warm climate societies. In the models, we controlled for MAP, AbLat, DME, MOBILE, and FISH. Pairwise comparisons of average NPP between subsistence types were adjusted for family-wise error using the sequential Bonferroni method (Holm, 1979).

Objective 2. To further explore the relationship between average NPP_{max} and latitude across subsistence types, we used GLMs to predict average NPP_{max} as a function of AbLat (*Figure 2.3*). Absolute latitude was used due to the general decline in solar radiation with increasing distance from the equator, and the associated expected decline in NPP with increasing latitude. Given the SCCS bias towards populations in the Northern Hemisphere (Marlowe, 2005), AbLat allowed for the comparison of populations based on distance from the equator, and proximity to the poles independent of North or South. As with Objective 1a, control variables were excluded from models in a block if statistically non-significant (SM Text).

Objective 3. We used ordinal logistic regression models to estimate the probability of societies having low, medium, or high PD as a function of NPP_{max} and NPP_{mean} and subsistence type, while controlling for ET, MAP, AbLat, DME, MOBILE, and FISH. The assumption of proportional odds was checked graphically by plotting the mean of each predictor variable versus levels of the response variable and comparing this to the expected value of the predictor variable for each response value under the proportional odds assumption.

Table 2.1 - *Summary Data Table*

SCCS ID	Society Name	Study Year	Subsistence	Longitude	Latitude	ET	NPP Mean (15km)	NPP Max (15km)	NPP Mean (120km)	NPP Max (120km)	NPP (P&M 2007)	Population Density	Climate	Mobility Binary	Biome Simple
1	Nama Hottentot	1860	Pastoralism	17	-27.5	16.18	122.2	198	161.5	958.2	204	Low	Warm	Impermanent	Desert
2	Kung Bushmen	1950	Foraging	20.58	-19.833 *	16.67	291.2	415.5	349.8	505.5	472	Low	Warm	Impermanent	Savanna/Grassland
3	Thonga	1895	Horticulture	32.333 *	-25.833 *	18.5	850.1	1063	882.5	1794.2	667	High	Warm	Impermanent	Forest
4	Lozi	1900	Intensive agriculture	23.5	-16	18	635.7	739.9	609.6	1149.1	756	Medium	Warm	Impermanent	Wetland
5	Mbundu	1890	Horticulture	16.5	-12.25	17.2	780.1	1267	818	1496	1041	Medium	Warm	Permanent	Savanna/Grassland
6	Suku	1920	Horticulture	18	-6	NA	863.1	1290	916.9	1304.8	865	Medium	Warm	Impermanent	Savanna/Grassland
7	Bemba	1897	Horticulture	30.5	-10.5	17.43	811.8	1234.5	770.3	1289.7	1039	Medium	Warm	Impermanent	Savanna/Grassland
8	Nyakyusa	1934	Intensive agriculture	34	-9.5	15.71	945.8	1384.2	793.4	1405	1106	High	Warm	Impermanent	Wetland
9	Hadza	1930	Foraging	35.18	-3.75	20.91	511.1	810.8	651.5	1629.1	607	Low	Warm	Impermanent	Savanna/Grassland
10	Luguru	1925	Horticulture	37.667 *	-6.833 *	22	854.6	1486.3	878	1688.2	912	High	Warm	Permanent	Savanna/Grassland
11	Kikuyu	1920	Pastoralism	37.167 *	-0.667 *	15.82	785	1282	675.2	1504.8	1150	High	Warm	Permanent	Savanna/Grassland
12	Ganda	1875	Horticulture	32.5	0.333 *	18.8	1393.7	1807.5	1387.7	2066.9	1341	High	Warm	Permanent	Savanna/Grassland
13	Mbuti	1950	Foraging	28.333 *	1.5	19.45	1318.2	1358.5	1299.1	1489.7	1445	Low	Warm	Impermanent	Forest
14	Nkundo Mongo	1930	Horticulture	19.167 *	-0.75	19.6	1067.9	1162.7	1062.6	1231.5	1570	Medium	Warm	Permanent	Forest
15	Banen	1935	Horticulture	10.8	4.667 *	18.73	894.2	1024	849.7	1071.7	1136	Medium	Warm	Permanent	Forest
16	Tiv	1920	Horticulture	9	7.25	21.43	434.9	659.1	500.1	922.5	624	High	Warm	Permanent	Savanna/Grassland
17	Ibo	1935	Horticulture	7.333 *	5.5	22.67	573.8	812.2	583.1	860.1	718	High	Warm	Permanent	Forest
18	Fon	1890	Horticulture	1.91	7.2	22	411.8	586.7	442.7	720.6	698	High	Warm	Permanent	Savanna/Grassland
19	Ashanti	1895	Horticulture	-1.5	7	21.33	606.4	738.8	590.9	849.2	931	High	Warm	Permanent	Forest
20	Mende	1945	Horticulture	-12	7.833 *	21.64	548	711.6	523.4	934.5	702	High	Warm	Permanent	Forest
21	Wolof	1950	Horticulture	-15.333 *	13.75	19.14	157	243.3	182.1	962.4	420	High	Cold	Permanent	Savanna/Grassland
22	Bambara	1902	Intensive agriculture	-7	12.5	22	126.5	218	126.5	303.2	312	Medium	Warm	Permanent	Savanna/Grassland
23	Tallensi	1934	Intensive agriculture	-0.567 *	10.66	NA	233.7	297.8	223.6	409.5	432	High	Warm	Permanent	Savanna/Grassland
24	Songhai	1940	Intensive agriculture	-0.03 *	16.26 *	19.14	0.6	19	4.4	59	44	Medium	Warm	Permanent	Tundra
25	Pastoral Fulani	1951	Pastoralism	7.5	15	19.33	43.4	73.3	41.9	100.1	104	Medium	Warm	Impermanent	Savanna/Grassland
26	Hausa	1900	Intensive agriculture	7.5	10.5	21.08	309	381.6	291.6	523.1	546	High	Warm	Permanent	Savanna/Grassland
27	Massa (Masa)	1910	Intensive agriculture	15.5	10.5	22.27	105.6	198.9	112	291.4	332	High	Warm	Permanent	Savanna/Grassland
28	Azande	1905	Horticulture	28.25	5.083 *	20.67	584.7	819.3	609.6	968.5	831	Medium	Warm	Permanent	Savanna/Grassland

Table 2.1 - Summary Data Table (Continued)

SCCS ID	Society Name	Study Year	Subsistence	Longitude	Latitude	ET	NPP Mean (15km)	NPP Max (15km)	NPP Mean (120km)	NPP Max (120km)	NPP (P&M 2007)	Population Density	Climate	Mobility Binary	Biome Simple
29	Fur (Darfur)	1880	Intensive agriculture	24.9 *	12 *	19.41	135.7	200.6	151.4	313.5	116	Medium	Warm	Permanent	Savanna/Grassland
30	Otoro Nuba	1930	Intensive agriculture	30.667 *	11.333 *	22.31	130.5	193.1	121.1	258.9	465	Medium	Warm	Permanent	Savanna/Grassland
31	Shilluk	1910	Horticulture	32.1 *	9.89 *	22.67	200.4	289.9	212.8	431.2	559	High	Warm	Permanent	Savanna/Grassland
32	Mao	1939	Horticulture	34.667 *	9.267 *	23.33	687	995.2	621.8	1304.6	1102	Medium	Warm	Permanent	Savanna/Grassland
33	Kaffa (Kafa)	1905	Intensive agriculture	36.5	7.267 *	22.31	1287.4	1502.1	1132.9	1754.5	1465	High	Warm	Permanent	Savanna/Grassland
34	Masai	1900	Pastoralism	36.75	-3.5	13.56	535.6	1609.8	595.2	1666.3	878	Medium	Warm	Impermanent	Savanna/Grassland
35	Konso	1935	Intensive agriculture	37.5	5.25	23.33	498.7	879.7	588.8	1616.3	656	High	Warm	Permanent	Savanna/Grassland
36	Somali	1900	Pastoralism	47.25	9	19.23	39.2	60.9	50.2	92.1	184	Medium	Warm	Impermanent	Savanna/Grassland
37	Amhara	1953	Intensive agriculture	37.75	12.5	20.67	421.3	686.9	440.3	1311.9	840	High	Warm	Permanent	Savanna/Grassland
38	Bogo	1855	Pastoralism	38.75	15.75	18	157.2	345.5	85.4	507.9	312	Medium	Warm	Impermanent	Forest
39	Kenuzi Nubians	1900	Intensive agriculture	30.52 *	19.15 *	17.08	39.4	133.1	27.7	133.1	27	NA	Warm	Permanent	Desert
40	Teda	1950	Pastoralism	17.5	20.5	18.7	0	0	34.4	59.8	0	Low	Warm	Impermanent	Desert
41	Tuareg	1900	Pastoralism	6.5	23	16.08	17.2	19.6	18.5	37.5	0	Low	Warm	Impermanent	Desert
42	Riffians	1926	Intensive agriculture	-3.25	34.917 *	15.6	369.6	720.8	366.8	1485.3	222	High	Warm	Permanent	Forest
43	Egyptians	1950	Intensive agriculture	32.65 *	25.7 *	16.52	50.6	197.8	51.5	197.8	196	High	Warm	Permanent	Wetland
44	Hebrews	621 B.C.E.	Intensive agriculture	35.2 *	31.76 *	16.1	316.1	809.7	342.6	1476	147	High	Warm	Permanent	Forest
45	Babylonians	1750 B.C.E.	Intensive agriculture	44.43 *	32.47 *	15.94	16	91.9	22.9	112.6	159	High	Warm	Permanent	Desert
46	Rwala Bedouin	1913	Pastoralism	38.5	33.25	15.23	47.8	57.9	43.6	115.6	68	Low	Warm	Impermanent	Desert
47	Turks	1950	Intensive agriculture	34.25	39.333 *	13.73	242.1	450.4	236.3	723.4	238	High	Warm	Permanent	Forest
48	Gheg Albanians	1910	Intensive agriculture	20.167 *	42	14.15	648	934	655.9	1771.8	443	High	Warm	Impermanent	Forest
49	Romans	110	Intensive agriculture	13.5	41.667 *	17.43	1026.5	1815.6	893.9	1915.2	503	High	Warm	Permanent	Forest
50	Basques	1934	Intensive agriculture	-1.667 *	43.25	13.48	839	1445.5	761.9	1670.8	590	Medium	Warm	Permanent	Forest
51	Irish	1932	Intensive agriculture	-10	53.5	11.88	749.4	1346.7	859.4	1403.8	672	High	Cold	Permanent	Forest
52	Lapps	1950	Pastoralism	21.5	68.7	10.48	208.5	404.6	221.5	595.7	111	Medium	Cold	Impermanent	Forest
53	Yurak Samoyed	1894	Pastoralism	51.5 *	68	10.19	219.5	234.4	202.2	512.9	77	Low	Cold	Impermanent	Tundra
54	Russians	1955	Intensive agriculture	41.333 *	52.667 *	10.93	379.5	621.8	392.8	862.6	256	Medium	Cold	Permanent	Forest
55	Abkhaz	1880	Pastoralism	40.77	43.125 *	NA	988.7	1461.2	664.7	1635.1	740	High	Cold	Permanent	Forest
56	Armenians	1843	Intensive agriculture	44.5	40	12.06	407.8	743.1	352.5	1117	288	High	Cold	Permanent	Savanna/Grassland

Table 2.1 - Summary Data Table (Continued)

SCCS ID	Society Name	Study Year	Subsistence	Longitude	Latitude	ET	NPP Mean (15km)	NPP Max (15km)	NPP Mean (120km)	NPP Max (120km)	NPP (P&M 2007)	Population Density	Climate	Mobility Binary	Biome Simple
57	Kurd	1951	Intensive agriculture	44.5	36.5	16.19	184	283.8	161.7	421.5	172	High	Warm	Permanent	Forest
58	Basseri	1958	Pastoralism	53	29	14.87	36.5	94.4	39	143	69	Medium	Warm	Impermanent	Forest
59	Punjabi (West)	1950	Intensive agriculture	74	32.5	16.34	443.1	541.5	419.5	1408.7	399	High	Warm	Permanent	Desert
60	Gond	1938	Horticulture	80.917 *	19.625 *	18.73	160	361.1	210.6	450.6	453	Medium	Warm	Impermanent	Forest
61	Toda	1900	Pastoralism	76.5	11.5	19.85	655	860.6	616.9	1234.1	1102	High	Warm	Impermanent	Forest
62	Santal	1940	Intensive agriculture	87.167 *	23.5	17.27	284.6	355.2	320.1	829	419	High	Warm	Permanent	Forest
63	Uttar Pradesh	1945	Intensive agriculture	83	25.917 *	17.04	355.2	411.4	395.2	727.8	428	High	Warm	Permanent	Forest
64	Burusho	1934	Intensive agriculture	74.583 *	36.433 *	15.33	26.4	131.4	58.3	370.7	90	Medium	Warm	Permanent	Tundra
65	Kazak	1885	Pastoralism	75.5	42.5	12.79	305.2	874.8	273	874.8	209	Medium	Cold	Impermanent	Savanna/Grassland
66	Khalka Mongols	1920	Pastoralism	96.083 *	47.167 *	10.78	76.2	274.8	94.8	431.7	127	Medium	Cold	Impermanent	Desert
67	Lolo	1910	Intensive agriculture	103.5	27.5	10.57	642.7	1366.3	684.7	1736.6	484	Medium	Cold	Permanent	Forest
68	Lepcha	1937	Intensive agriculture	89	27.5	12.67	482.9	869	648.8	1816	883	High	Cold	Permanent	Savanna/Grassland
69	Garo	1955	Horticulture	91	26	17.58	887.7	1630.1	1018.4	1796.4	819	High	Warm	Permanent	Forest
70	Lakher	1930	Horticulture	93	22.333 *	18.57	887.7	992	836.5	1071.3	974	Medium	Warm	Permanent	Forest
71	Burmese	1965	Intensive agriculture	95.667 *	22	18.89	444.6	728.5	541.3	1111.6	411	High	Warm	Permanent	Forest
72	Lamet	1940	Horticulture	100.667 *	20	15.65	1162.3	1275.6	1095.9	1354.7	1106	Low	Warm	Impermanent	Forest
73	Vietnamese	1930	Intensive agriculture	106.25	20.5	18.47	556.4	1034.5	683.8	1316.4	598	High	Warm	Permanent	Forest
74	Rhade	1962	Horticulture	108	13	22	674.4	957.5	733.1	1076	1081	High	Warm	Impermanent	Forest
75	Khmer	1292	Intensive agriculture	103.833 *	13	NA	304.4	893.2	587.5	988.7	648	High	Warm	Permanent	Forest
76	Siamese	1955	Intensive agriculture	100.85	14	16.33	536.7	940.6	532.2	1031.2	657	High	Warm	Permanent	Forest
77	Semang	1925	Foraging	101.25	5	17.11	747.8	808.4	728.4	1001.8	1334	Low	Warm	Impermanent	Forest
78	Nicobarese	1870	Horticulture	93.75	7	24.4	707.6	875.1	633.6	1013.1	1545	High	Warm	Permanent	Forest
79	Andamanese	1860	Foraging	92.67 *	12 *	23.6	840.5	1191.7	828.3	1220.1	1545	Medium	Warm	Impermanent	Forest
80	Vedda	1860	Foraging	81.25	7.75	22.67	569.8	904.7	588.1	1076.2	741	Low	Warm	Impermanent	Forest
81	Tanala	1925	Intensive agriculture	48	-22	19.71	1420.9	1843.1	1475.9	1950.4	1199	Medium	Warm	Impermanent	Forest
82	Negri Sembilan	1958	Intensive agriculture	102.25	2.583 *	18	735.6	909.1	723.2	1046	986	High	Warm	Permanent	Forest
83	Javanese	1954	Intensive agriculture	112.22	-7.7	21.64	844.8	1403.6	825.4	1512.6	865	High	Warm	Permanent	Forest
84	Balinese	1958	Intensive agriculture	115.333 *	-8.5	23.6	1290.9	1519.9	1130.4	1539.2	1723	High	Warm	Permanent	Forest

Table 2.1 - Summary Data Table (Continued)

SCCS ID	Society Name	Study Year	Subsistence	Longitude	Latitude	ET	NPP Mean (15km)	NPP Max (15km)	NPP Mean (120km)	NPP Max (120km)	NPP (P&M 2007)	Population Density	Climate	Mobility Binary	Biome Simple
85	Iban	1950	Horticulture	113	2	25.11	886.8	980.1	881.5	1014	1074	Medium	Warm	Impermanent	Forest
86	Badjau	1963	Foraging	120	5.2 *	25.11	973.4	1339.8	956.1	1372.9	1727	Low	Warm	Impermanent	Forest
87	Toradja	1910	Horticulture	121	-2	24.22	883	1051.7	910.2	1185	1051	Medium	Warm	Permanent	Forest
88	Tobelorese	1900	Horticulture	127.85 *	2	25.11	943	1247.3	936.3	1263.7	1592	Medium	Warm	Permanent	Forest
89	Alorese	1938	Horticulture	124.667 *	-8.333 *	24.4	1090.5	1381.8	896.3	1421	1380	High	Warm	Permanent	Forest
90	Tiwi	1929	Foraging	131	-11.375 *	22.67	764.3	1174.3	696.4	1328.6	1307	Low	Warm	Impermanent	Savanna/Grassland
91	Aranda	1896	Foraging	133.5	-24.25	16	100.3	141.6	98.3	310.7	189	Low	Warm	Impermanent	Desert
92	Orokaiva	1925	Horticulture	148	-8.5	22.36	1257.4	1376.1	1312.2	1589.6	1374	Medium	Warm	Permanent	Forest
93	Kimam	1960	Intensive agriculture	138.5	-7.5	20.67	1065.3	1497.2	1286.3	1605.4	941	Low	Warm	Permanent	Forest
94	Kapauku	1955	Horticulture	136	-4	24.22	1260.8	1425.3	1217	1510.1	1108	High	Warm	Permanent	Forest
95	Kwoma	1937	Horticulture	142.667 *	-4.167 *	27	1406.1	1564.1	1391	1634.7	946	High	Warm	Permanent	Forest
96	Manus	1929	Horticulture	147.167 *	-2.167 *	26	765.6	1105.6	697.2	1136.7	1520	High	Warm	Permanent	Forest
97	New Ireland	1930	Horticulture	152.885 *	-4.33 *	25.2	1115.9	1260.3	1064.7	1357.1	1552	Medium	Warm	Permanent	Forest
98	Trobrianders	1914	Horticulture	151.07	-8.489 *	24.4	995.3	1377.5	980.3	1470.3	1382	High	Warm	Permanent	Forest
99	Siuai	1939	Horticulture	155.55 *	-6.5 *	26	1182.2	1284.5	1127.8	1419.6	1283	High	Warm	Permanent	Forest
100	Tikopia	1930	Horticulture	168.821 *	-12.302 *	21.33	398.3	931.9	398.3	931.9	338	High	Warm	Permanent	Savanna/Grassland
101	Pentecost	1953	Horticulture	168.2 *	-15.8 *	21.33	978.3	1349.7	1038.8	1426.3	1405	Medium	Warm	Permanent	Forest
102	Mbau Fijians	1840	Horticulture	178.583 *	-18	NA	1012.3	1412	1142.3	1472.8	1392	High	Warm	Permanent	Forest
103	Ajie	1845	Intensive agriculture	165.667 *	-21.333 *	19.85	1151.5	1545.5	1180.9	1613.7	1092	Medium	Warm	Permanent	Forest
104	Maori	1820	Horticulture	174.2 *	-35.35 *	14	1542.4	1830.9	1566.1	1871.3	1482	Low	Warm	Permanent	Forest
105	Marquesans	1800	Horticulture	-140.167 *	-8.917 *	26	1017.4	1514.3	893.1	1519.7	1062	High	Warm	Permanent	Forest
106	Western Samoans	1829	Horticulture	-172.43 *	-13.75	20.4	942.9	1211.8	889.1	1292.2	1204	High	Warm	Permanent	Forest
107	Gilbertese	1890	Horticulture	172.983 *	3.373 *	28	503.7	1121.4	424.7	1164.5	295	High	Warm	Permanent	Forest
108	Marshallese	1900	Horticulture	171.033 *	7.146 *	26	129.8	203.1	265.1	460.5	1293	High	Warm	Permanent	Forest
109	Trukese	1947	Horticulture	151.615 *	7.356	26	359.9	946.6	424.4	1046.1	1527	High	Warm	Permanent	Forest
110	Yapese	1910	Horticulture	138.09 *	9.5	26	703.2	1269.6	699.3	1269.6	1685	High	Warm	Permanent	Forest
111	Palauans	1947	Horticulture	134.57 *	7.5	26	632	1104.8	550.6	1122.3	1613	High	Warm	Permanent	Forest
112	Ifugao	1910	Intensive agriculture	121.167 *	16.833 *	22.67	1115.2	1386.5	1019	1492.7	868	High	Warm	Permanent	Forest

Table 2.1 - Summary Data Table (Continued)

SCCS ID	Society Name	Study Year	Subsistence	Longitude	Latitude	ET	NPP Mean (15km)	NPP Max (15km)	NPP Mean (120km)	NPP Max (120km)	NPP (P&M 2007)	Population Density	Climate	Mobility Binary	Biome Simple
113	Atayal	1930	Horticulture	120.75	24.333 *	17.56	933.8	1271.8	830.4	1283.2	895	Medium	Warm	Impermanent	Forest
114	Chinese	1936	Intensive agriculture	120.083 *	31	NA	540.4	883.5	581.2	1377.9	537	High	Cold	Permanent	Forest
115	Manchu	1915	Intensive agriculture	125.5	50	12.29	327	480.8	318.9	678.4	357	High	Cold	Permanent	Forest
116	Koreans	1947	Intensive agriculture	126.417 *	37.6	10.78	665.5	1080.7	649.1	1207.3	399	High	Cold	Permanent	Forest
117	Japanese	1950	Intensive agriculture	133.667 *	34.667 *	14.14	837.5	1560.1	878	1740.4	634	High	Warm	Permanent	Forest
118	Ainu	1880	Foraging	143	42.833 *	12.25	641	943	737.4	1288.7	496	Low	Cold	Impermanent	Forest
119	Gilyak	1890	Foraging	142.8 *	54.06 *	10.84	455.8	640.9	420.5	828	299	Low	Cold	Impermanent	Forest
120	Yukaghir	1850	Foraging	153.5	64.75	9.64	288.2	445.3	273.4	578.8	179	Low	Cold	Impermanent	Forest
121	Chukchee	1900	Pastoralism	180	66.5	10.19	71.1	167.2	129.7	313.8	78	Low	Cold	Impermanent	Forest
122	Ingalik	1885	Foraging	-159.5	62.5	10.38	360.3	537.3	363.7	706.6	200	Low	Cold	Impermanent	Forest
123	Aleut	1800	Foraging	-163.75 *	54.9 *	10.38	388.8	967	348.7	982.4	364	Medium	Cold	Impermanent	Tundra
124	Copper Eskimo	1915	Foraging	-112 *	67.5 *	8.77	110.5	202.6	108.9	202.6	85	Low	Cold	Impermanent	Tundra
125	Montagnais	1910	Foraging	-74	50	11.76	469.7	655.7	464	727.2	344	Low	Cold	Impermanent	Forest
126	Micmac	1650	Foraging	-63.02 *	46.22 *	12.53	622.8	934.9	763	1362.2	378	Low	Cold	Impermanent	Forest
127	Saulteaux	1930	Foraging	-95.5	52	11.39	484	609.7	497	828.4	591	Low	Cold	Impermanent	Forest
128	Slave	1940	Foraging	-122	62	10.74	422.9	551.3	382.7	730.7	483	Low	Cold	Impermanent	Forest
129	Kaska	1900	Foraging	-131	60	10.74	268.3	373.1	256.3	433.8	214	Low	Cold	Impermanent	Forest
130	Eyak	1890	Foraging	-145.5 *	60.5	10.96	388.8	650	238.9	783.3	202	Low	Cold	Impermanent	Forest
131	Haida	1875	Foraging	-132.5	54	11.28	660.7	803.9	645.4	1184.8	516	Low	Cold	Impermanent	Forest
132	Bellacoola	1880	Foraging	-126.5	52.333 *	11.85	345.5	883.5	365.8	1114.5	217	Medium	Cold	Permanent	Forest
133	Twana	1860	Foraging	-123.25	47.433 *	13.05	781.8	1386.7	824.6	1574.9	726	High	Warm	Impermanent	Forest
134	Yurok	1850	Foraging	-124	41.5	12.86	1151.6	1792.7	924.3	1973.7	907	Medium	Cold	Permanent	Forest
135	Pomo (Eastern)	1850	Foraging	-123	39	14.19	1163.1	1566	992	2345.5	847	Medium	Warm	Impermanent	Forest
136	Yokuts (Lake)	1850	Foraging	-119.5	35	14.92	292.1	729.8	548.1	2154.3	452	Medium	Warm	Impermanent	Forest
137	Paiute (North.)	1870	Foraging	-119	43.5	12.67	221.1	661	212.7	826.1	226	Low	Cold	Impermanent	Desert
138	Klamath	1860	Foraging	-121.667 *	42.625 *	11.6	550.9	690.8	491.9	1392.5	449	Low	Cold	Impermanent	Forest
139	Kutenai	1890	Foraging	-116.667 *	49	12.32	534.3	679.4	523.6	992.6	333	Low	Cold	Impermanent	Forest
140	Gros Ventre	1880	Pastoralism	-108	48	11.78	245.4	417.5	250.9	780.9	285	Low	Cold	Impermanent	Savanna/Grassland

Table 2.1 - Summary Data Table (Continued)

SCCS ID	Society Name	Study Year	Subsistence	Longitude	Latitude	ET	NPP Mean (15km)	NPP Max (15km)	NPP Mean (120km)	NPP Max (120km)	NPP (P&M 2007)	Population Density	Climate	Mobility Binary	Biome Simple
141	Hidatsa	1836	Intensive agriculture	-101	47	12.46	392.8	456.4	371.3	663.9	300	Low	Cold	Impermanent	Savanna/Grassland
142	Pawnee	1867	Horticulture	-100	42	12.74	307.1	500.5	341.3	627.5	332	Low	Cold	Impermanent	Savanna/Grassland
143	Omaha	1860	Horticulture	-96.5	41.433 *	13.11	328.4	487.2	357.2	552	388	Medium	Warm	Impermanent	Savanna/Grassland
144	Huron	1634	Horticulture	-79	44.5	12.67	561.4	697.1	561.4	1130	301	High	Cold	Impermanent	Forest
145	Creek	1800	Horticulture	-86	32.933 *	14.74	778.3	1430.9	800.8	1458.6	503	Medium	Warm	Impermanent	Forest
146	Natchez	1718	Horticulture	-91.417 *	31.5	15.76	540.4	1182	649.6	1508	577	Medium	Warm	Permanent	Forest
147	Comanche	1870	Pastoralism	-101.5	34	14.74	213.1	328.5	226.4	455.5	320	Low	Warm	Impermanent	Savanna/Grassland
148	Chiricahua	1870	Pastoralism	-109.5	32	14.8	132.9	348.9	124	429.7	280	Low	Warm	Impermanent	Desert
149	Zuni	1880	Intensive agriculture	-108.75	35.667 *	13.35	113.1	195	149.2	525.8	200	Medium	Warm	Permanent	Forest
150	Havasupai	1918	Intensive agriculture	-112.167 *	35.833 *	12.67	171.6	415.3	167.5	507.3	195	Low	Cold	Impermanent	Desert
151	Papago	1910	Intensive agriculture	-112	32	15.93	85.5	147.3	80.2	270.8	146	High	Warm	Impermanent	Desert
152	Huichol	1890	Horticulture	-105	22	13.2	914.5	1247.2	701.7	1493.6	696	Medium	Warm	Permanent	Forest
153	Aztec	1520	Intensive agriculture	-99.167 *	19	16.77	1068.3	1824.8	859	1954.2	1193	High	Warm	Permanent	Forest
154	Popoluca	1940	Horticulture	-94.833 *	18.25	21.08	852.5	1155.7	804.5	1532.3	724	High	Warm	Permanent	Forest
155	Quiche	1930	Horticulture	-91	15	19.23	781.6	1449.2	942.1	1599.9	1299	High	Warm	Permanent	Forest
156	Miskito	1921	Horticulture	-83.25 *	15	23.6	1261.8	1533.5	1006.4	1657.4	1217	Medium	Warm	Permanent	Wetland
157	Bribri	1917	Horticulture	-83.25	9	21.2	814	957.8	842.1	1245.8	847	NA	Warm	Permanent	Forest
158	Cuna (Tule)	1927	Horticulture	-78.5	9.25	26	842.3	1095.6	852.4	1195.5	713	High	Warm	Permanent	Forest
159	Goajiro	1947	Pastoralism	-71.75	11.917 *	26	312.8	807.7	517.3	1585.8	542	Low	Warm	Impermanent	Desert
160	Haitians	1935	Intensive agriculture	-72.167 *	18.833 *	22.67	879.4	1258.6	912.2	1765.1	812	High	Warm	Permanent	Forest
161	Callinago	1650	Intensive agriculture	-61.35 *	15.45 *	22.36	1402.9	1591.9	1246.4	1654	1821	Medium	Warm	Impermanent	Forest
162	Warrau	1935	Foraging	-62	9.078 *	14.8	1154.4	1323.3	1115	1590.8	908	Low	Warm	Impermanent	Forest
163	Yanomamo	1965	Horticulture	-65	2.417 *	27.14	1058.4	1119.1	1051.1	1200.8	1118	Low	Warm	Impermanent	Forest
164	Carib (Barama)	1932	Horticulture	-60.167 *	7.417 *	25.2	1237.8	1286.9	1237.1	1461.9	966	Low	Warm	Impermanent	Forest
165	Saramacca	1928	Horticulture	-55.75	3.5	25.2	1017.2	1068.2	1016.8	1085.6	1032	Medium	Warm	Permanent	Forest
166	Mundurucu	1850	Horticulture	-56.5	-6.5	22.8	916.3	964.3	910.4	1042.2	1231	Low	Warm	Permanent	Forest
167	Cubeo (Tucano)	1939	Horticulture	-70.5	1.25	27.14	839.7	993.3	845.4	1076.3	1055	Low	Warm	Permanent	Forest
168	Cayapa	1908	Horticulture	-79	1	27.14	1120.8	1219.9	927.5	1385.1	1049	Medium	Warm	Permanent	Forest

Table 2.1 - Summary Data Table (Continued)

SCCS ID	Society Name	Study Year	Subsistence	Longitude	Latitude	ET	NPP Mean (15km)	NPP Max (15km)	NPP Mean (120km)	NPP Max (120km)	NPP (P&M 2007)	Population Density	Climate	Mobility Binary	Biome Simple
169	Jivaro	1920	Horticulture	-78	-3	22.36	1675.7	1763.2	1495.4	1892.5	1541	Low	Warm	Impermanent	Forest
170	Amahuaca	1960	Horticulture	-72.25	-10.333 *	20.91	1916.2	1991.3	1904.4	2260	959	Low	Warm	Impermanent	Forest
171	Inca	1530	Intensive agriculture	-72	-13.5	11.45	521.9	1179.9	878.9	2383.7	485	Medium	Cold	Permanent	Savanna/Grassland
172	Aymara	1940	Horticulture	-65.75	-16	10	2048.9	2088.7	1917.3	2250.7	1131	High	Cold	Permanent	Forest
173	Siriono	1942	Foraging	-63.5	-14.5	19.33	1144.5	1282.5	1130.6	1676.9	459	Low	Warm	Impermanent	Forest
174	Nambicuara	1940	Horticulture	-58.75	-13	21.08	835.9	1109.8	877	1152	821	Low	Warm	Impermanent	Savanna/Grassland
175	Trumai	1938	Horticulture	-53.667 *	-11.833 *	21.33	785.6	960.3	766.4	1007.8	584	Low	Warm	Permanent	Forest
176	Timbira	1915	Horticulture	-46	-6.5	22.36	491.8	756.2	509.1	841.2	498	Medium	Warm	Impermanent	Savanna/Grassland
177	Tupinamba	1550	Horticulture	-44.5	-22.792 *	24.4	1705.6	1847.2	1342.3	1852	942	Low	Warm	Impermanent	Forest
178	Botocudo	1884	Foraging	-42.5	-19	18	1145.5	1633.2	1076.2	1735.1	790	Low	Warm	Impermanent	Forest
179	Shavante	1958	Foraging	-51.5	-13.5	21.33	711.1	1037.8	675	1103.7	340	Low	Warm	Impermanent	Savanna/Grassland
180	Aweikoma	1932	Foraging	-50	-28	14.44	1316.8	1815.4	1490.3	1855.4	1060	Low	Warm	Impermanent	Forest
181	Cayua	1890	Horticulture	-55	-23.5	18	874.1	1370.9	920.1	1515.9	611	Low	Warm	Impermanent	Forest
182	Lengua	1889	Horticulture	-58.5	-23	18.94	465	691.3	458.4	919.5	579	Low	Warm	Impermanent	Savanna/Grassland
183	Abipon	1750	Pastoralism	-59.5	-28	16.4	366	582.1	394	825	715	Low	Warm	Impermanent	Savanna/Grassland
184	Mapuche	1950	Intensive agriculture	-72.583 *	-38.5	14	1037.3	1656	1158.4	2023.9	765	High	Warm	Permanent	Forest
185	Tehuelche	1870	Pastoralism	-68	-40.5	14.39	133.2	191.8	134.8	499.1	287	Low	Warm	Impermanent	Savanna/Grassland
186	Yahgan	1865	Foraging	-69.4 *	-55.5	9.47	383.5	991.5	448.6	1050	178	Low	Cold	Impermanent	Forest

Table 2.1: Summary Data Table. *Primary data used to test the MHH are shown in Table 2.1. We have also included the NPP score used by Porter and Marlowe (2007) in their test of hunter-gatherer habitat marginality. Latitude and longitude coordinates marked with an asterisk (*) have been modified from the original values listed in the SCCS and used by Porter and Marlowe in their determination of NPP. Certain variables listed here (such as Absolute Latitude, Population Density, Fishing Binary, and Mobility Binary) are original derived variables, based upon SCCS variables (as described in the Methods section; see the Derived variable calculations sub-section).*

These data are sourced from:

1) The Standard Cross Cultural Sample (SCCS), Columns: $^{A, B, C, E, F, M, Q, \text{ and } R}$.

2) Porter and Marlowe, 2007), Columns: $^{D, L, N, O, \text{ and } P}$.

3) NASA Moderate Resolution Imaging Spectroradiometer (MODIS) NPP data (MOD17A3 algorithm) from Numerical Terra Dynamic Simulation Group at the University of Montana, Columns: $^{H, I, J, \text{ and } K}$.

4) Marine Ecoregions Of the World (MEOW): http://maps.tnc.org/files/metadata/MEOW.xml, Column: ^{S}.

5) Terrestrial Ecoregions Of the World (TEOW): http://maps.tnc.org/files/metadata/TerrEcos.xml, Column: ^{S}.

Results

Figure 2.2 shows the worldwide distribution of the 186 societies classified according to occupied biome, subsistence type, and climate. The distribution of subsistence types within the SCCS is shown in the inset of Figure 2.2. Horticulturalists are the most prevalent (38.7%), followed by intensive agriculturalists (29.6%), foragers (19.4%), and pastoralists (12.4%).

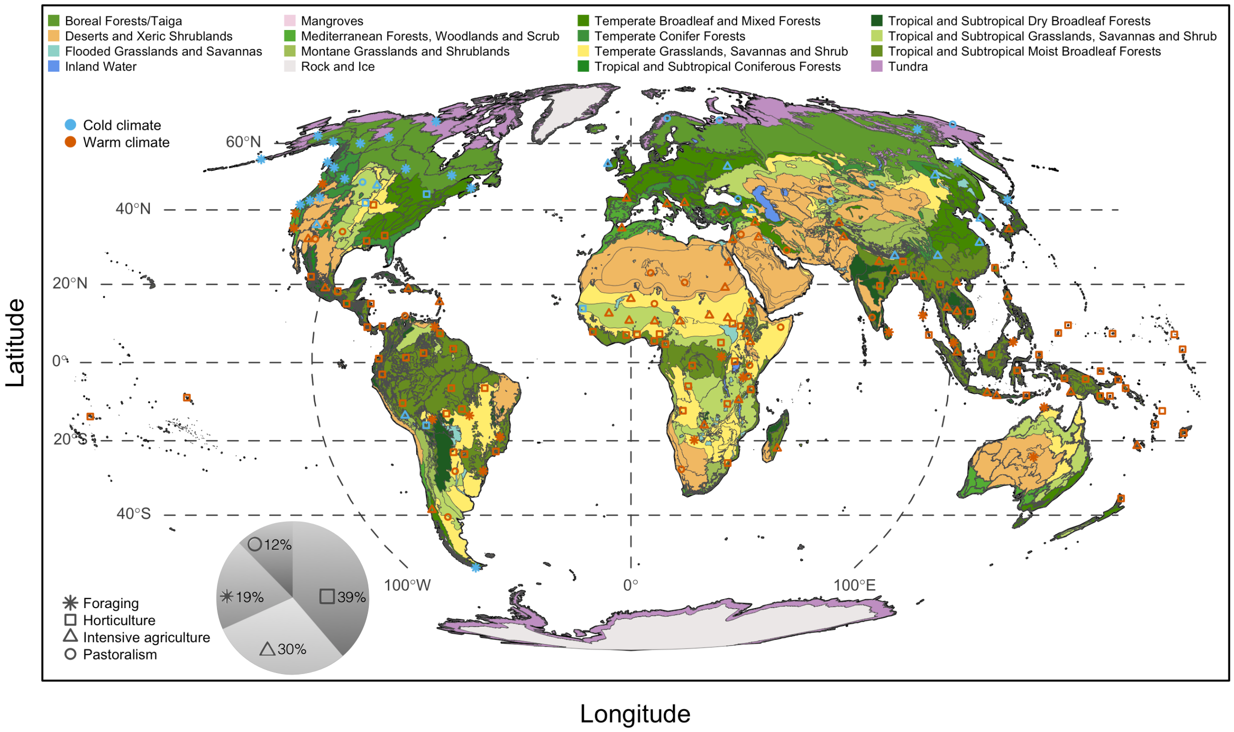

Figure 2.2: *Pre-industrial societies of the SCCS coded by terrestrial ecosystem. World map showing terrestrial biotic ecosystems and locations of 186 societies from the SCCS in a Mollweide equal area projection. Societies are grouped by climate (Warm (ET >13) and Cold (ET<13)) and subsistence type (Foraging, Horticulture, Intensive Agriculture, and Pastoralism). Inset pie chart indicates the representation (%) of societies in each subsistence type. Map polygons sourced from NASA shape files (https://github.com/nasa/World-Wind-Java/tree/master/WorldWind/testData/shapefiles) with terrestrial biotic ecosystem polygons from The Nature Conservancy shape files (http://maps.tnc.org/gis_data.html).*

Objective 1 - Variation in NPP (by subsistence type)

In a final GLM accounting for environmental variables (SM text), with subsistence modes in four separate categories, we found that pastoralists occupied habitats of significantly lower average NPP_{max} than any other subsistence type (mean difference ≥354 g C/m^2 /year, 95% CI: 85 - 624, $p \leq 0.0022$; *Figure 2.3 A*). We found no evidence that average NPP_{max} differed among foragers, intensive agriculturalists, and horticulturalists (mean difference ≤138, 95% CI: -70, 346, $p \geq 0.24$; *Figure 2.3 B*). Neither of these results changed substantively when we lumped farming types into combinations of two or three types (*Figure 2.3 C*), when we used NPP_{mean} rather than NPP_{max}, when we used a 120km radius rather than a 15km radius (*SM Text and Figure SM 2.1*), or when we divided societies by warm only and combined climates (SM *Figure 2.2a & 2.2b*).

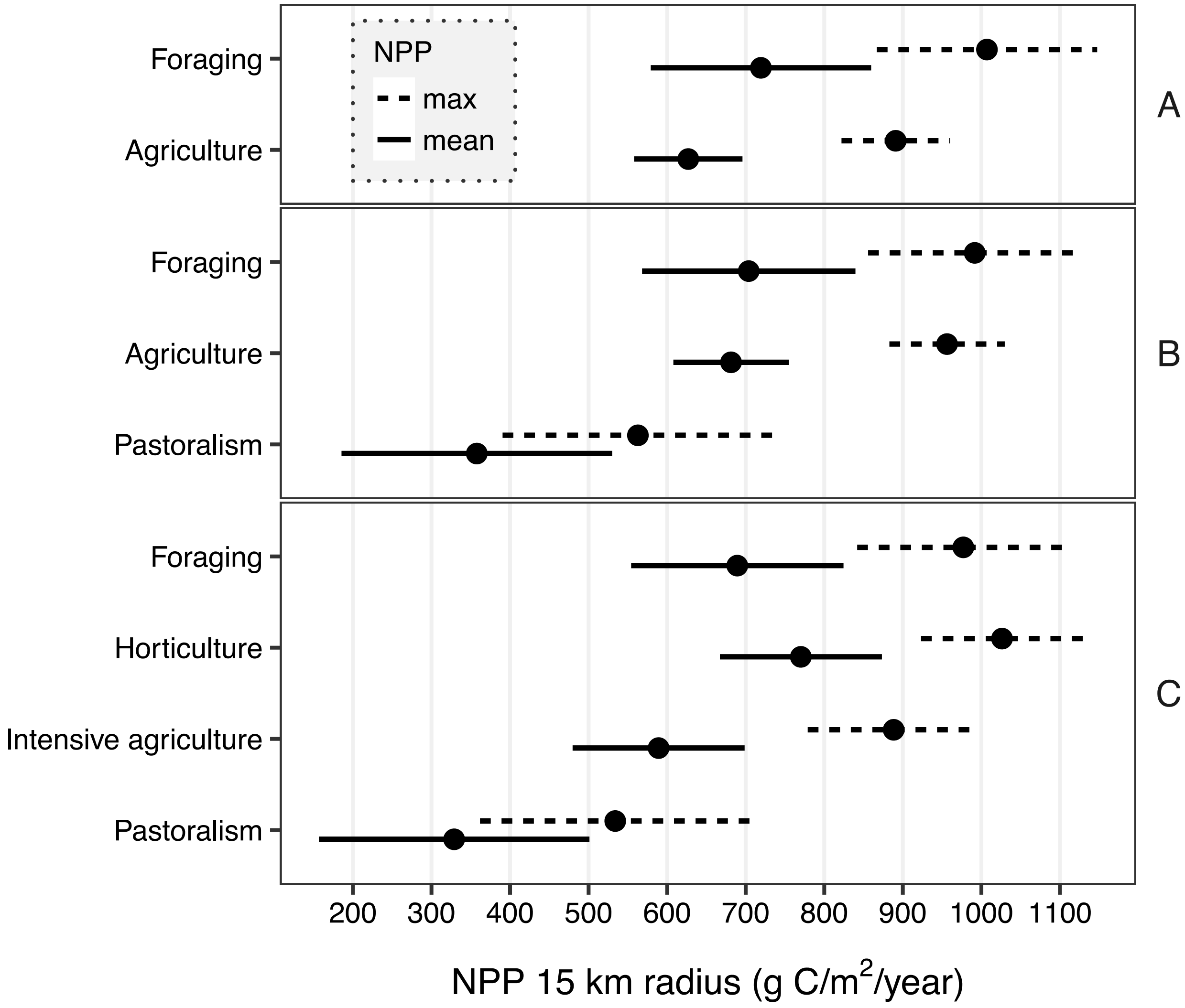

Figure 2.3: *Predicted NPP_{max} and NPP_{mean} by subsistence type. 15 km radius. Warm and cold climate societies are combined. Error bars represent 95% confidence intervals. Panels represent: (A) binary, (B) ternary, and (C) quaternary subsistence classifications.*

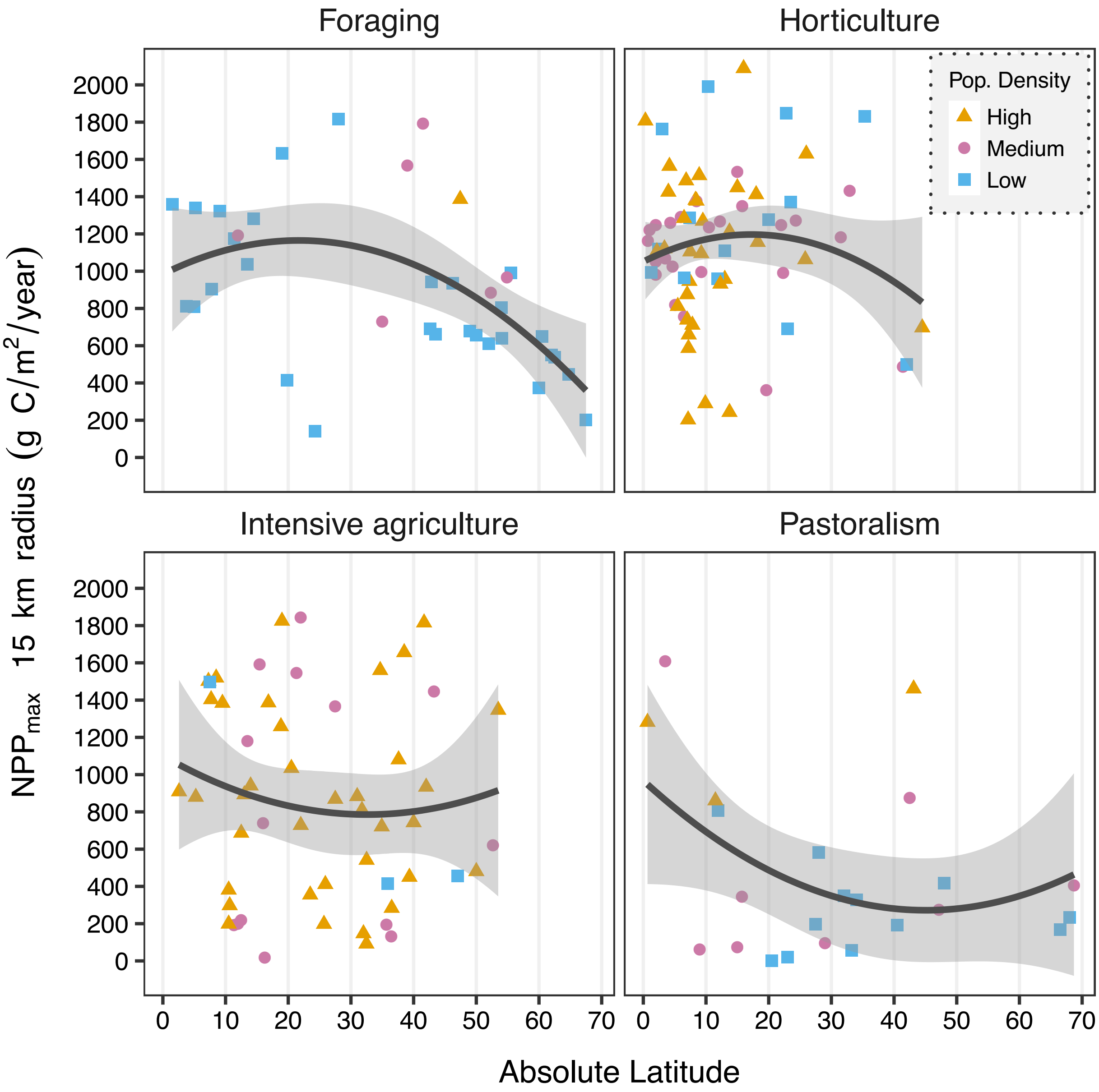

Figure 2.4*: Predicted NPP$_{max}$ versus absolute latitude by subsistence type.*
15 km radius. Lines and error ribbons represent point and 95% confidence interval predictions from a general linear model, respectively. Points correspond to observed NPP$_{max}$ and PD as reported in the SCCS and are colored by PD. Latitudinal distribution covers only the observed range of each subsistence type.

Objective 2 - Variation in NPP (by subsistence type) across latitude

To assess the relationship between average NPP$_{max}$ and latitude, we used GLMs to predict average NPP$_{max}$ as a function of AbLat (*Figure 2.4*). Foragers and pastoralists have latitudinal ranges extending up to almost |70°|, while horticulturalists and intensive agriculturalists have abbreviated ranges not extending much beyond |50°| latitude (*Figure 2.4*). In our final model accounting for environmental variables, NPP_{max} had a positive relationship with MAP ($p = 0.014$), with a 10-centimeter increase in precipitation increasing NPP_{max} by 11.2 g C/m^2 /year on average. Subsistence modes had different curvilinear relationships between NPP_{max} and AbLat (test of linear and quadratic AbLat interactions with subsistence mode, $F_{(3,\ 160)} = 3.4$, $p = 0.020$). Foragers and pastoralists exhibited contrasting concave and convex associations, respectively ($t_{(162)} = 2.5$, $p = 0.012$), with foragers displaying a (concave) trend towards increased NPP_{max} at mid latitudes, and lower relative NPP_{max} at relatively low and especially high latitudes. Pastoralists, by contrast showed a convex trend, in which they were more likely to occupy habitats with relatively higher NPP_{max} habitats at low equatorial latitudes. Horticulturalists also differed from pastoralists ($t_{(162)} = 2.4$, $p = 0.019$) in having a slightly concave relationship. We did not find evidence that intensive agriculturalists differed from the other three subsistence modes. There was very high variation in NPP at most latitudes, though the exception to this variation was for high latitude foragers, who had relatively predictable NPP. None of these results changed when we used a 120km radius rather than a 15km radius (*SM Figure 2.3*).

Objective 3 - Probability of subsistence strategies achieving low, medium, and high PD across NPP_{max} gradients

Finally, we sought to explain how population densities for each subsistence type were related to NPP_{max}. We used an ordinal logistic regression model to estimate the probability of societies having low (<1 person / sq. mile), medium (≥ 1 & < 25 people / sq. mile), or high (≥ 25 people / sq. mile) population density as a function of NPP_{max} and subsistence type, while controlling for all environmental variables. We found that the relationship between NPP_{max} and PD differed among subsistence modes (test of interaction between NPP_{max} and subsistence mode, likelihood ratio $\chi^2_{(3)} = 8.6$, $p = 0.035$). With each 500 g C/m^2 /year unit increase in NPP_{max} the odds of population density becoming larger by one unit (from low to medium or from medium to high) changed by 193% (95% CI: 91%, 349%) for foragers, -36% (95% CI: -6%, -56%) for horticulturalists, 40% (95% CI: -6%, 111%) for intensive agriculturalists, and 156% (95% CI: 33%, 393%) for pastoralists. Horticulturalists (*Figure 2.5*, second row from top) were the only subsistence type to exhibit a decreased probability of achieving high PD at high NPP_{max}, though they also had a low probability of having low PD at low NPP_{max}. Results were not markedly affected by our using a 120km radius rather than a 15km radius (SM Figure 2.4). In summary of Objective 3, we found that as NPP_{max} increased, the probability that population density would increase varied among subsistence types. Foragers and pastoralists had the most predictably positive relationship between population density and NPP. The NPP-PD relationships for horticulturalists and intensive agriculturalists were much less dramatic, as evidenced by their more modest odds ratios.

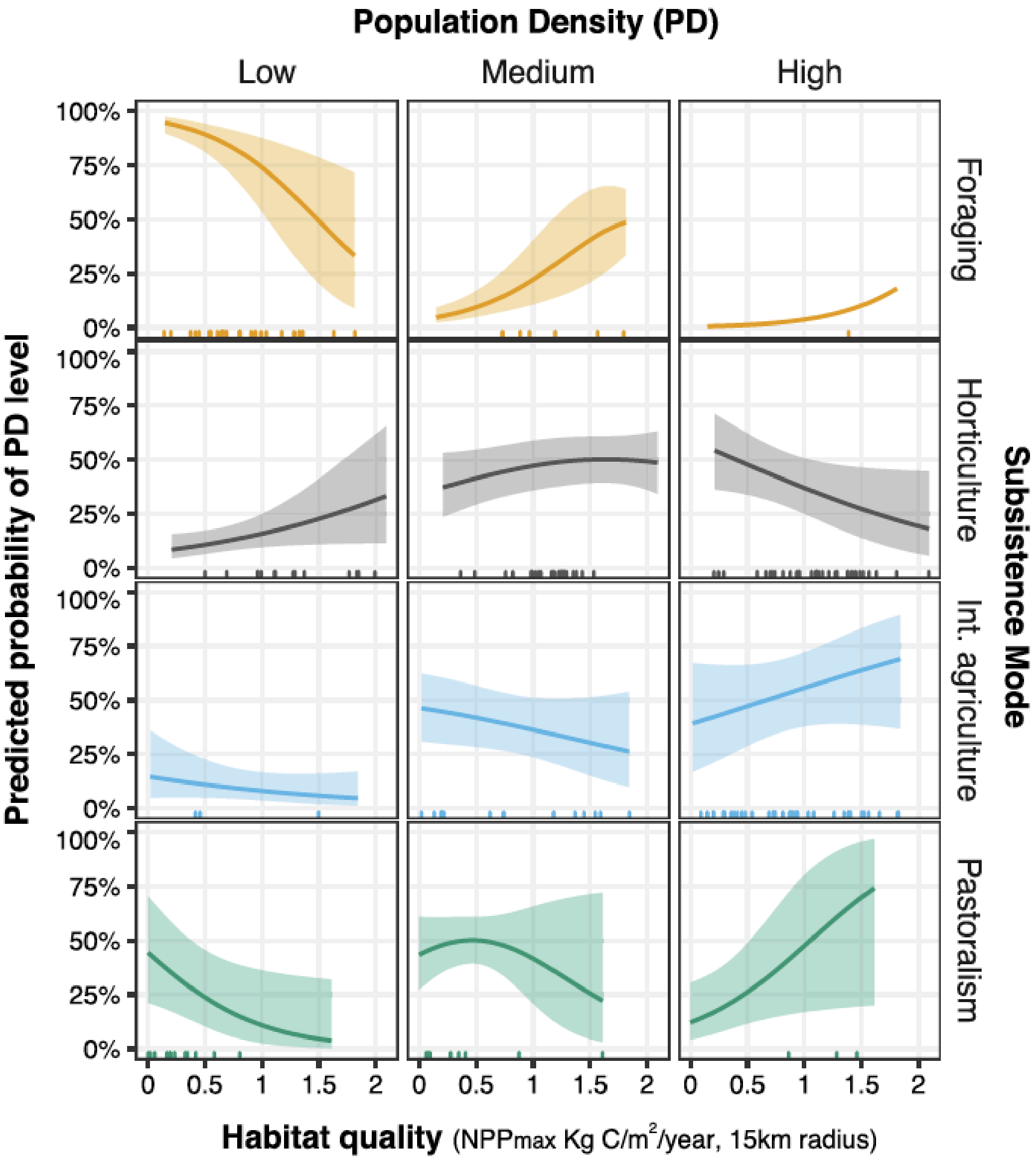

Figure 2.5: *Probability of population density level as predicted by NPP_{max}, by subsistence type. 15 km radius. Rows correspond to subsistence type. Columns correspond to levels of PD.*

Discussion

We sought to understand how the association between habitat net primary productivity (NPP) and population density (PD) varied for four subsistence types practiced by pre-industrial human societies. Our first goal (Objective 1) was to thoroughly assess the marginal habitat hypothesis (MHH). The MHH suggests that ethnographic foragers occupied low productivity habitats because agriculturalists would have possessed the social power and technology to exclude foragers from high productivity habitats (Marlowe, 2005; Porter and Marlowe, 2007). Contrary to the predictions of the MHH, Porter and Marlowe (2007) found that the foraging populations (n= 36, Mean NPP = 600 ± 431) represented in the SCCS did not live in significantly worse habitats than agriculturalists (n= 150, Mean NPP = 737 ± 455), based on their comparison of Mean NPP. They concluded by rejecting the MHH and stating that the ethnographic record, while not perfect, does not provide a biased picture of forager subsistence and social organization based on a history of interaction with agriculturalists.

The necessary caveats to our updated and more detailed analysis are the same as in Porter and Marlowe's (2007). The modern environmental data are not contemporaneous with ethnographic data, and subsequent changes in land use practices may have radically altered landscapes between these periods of data collection. Nevertheless, this point is not likely to introduce any systematic bias given that shifts in land usage patterns are no more likely for populations of one subsistence type than another (Porter and Marlowe, 2007). Furthermore, our use of both NPP_{max} and larger 120 km radius projections allowed for an estimation of maximal regional productivity (relative to NPP_{mean} and 15 km radii). Yet, these parameters failed to produce significantly different results than the smaller average models. These points suggest that there is no evidence of systematic bias between subsistence types with regards to changing land use patterns.

We also sought to check Porter and Marlowe's (2007) conclusions by considering a wider variety of variables in our analyses. We adopted more realistic circular projections of habitat use (representing both logistical and residential geographic areas at 15 km and 120 km radii), increased MODIS NPP data from 5 to 15 years, and conducted analyses based on both NPP_{mean} and NPP_{max}. Despite these methodological modifications which were intended to account for the ability of human populations to bias their subsistence activities to the most productive areas of their habitat and range, our findings are similar to those of Porter and Marlowe (2007). Foragers, intensive agriculturalists, and horticulturalists did not occupy habitats of significantly different quality, whereas pastoralists occupied the lowest quality habitats. This analysis appears to confirm that the available evidence does not support the MHH.

Porter and Marlowe (2007) suggested that the MHH may derive in part from the prominence in the literature of deserts occupied by societies such as the !Kung in southern Africa (in a hot desert) or the Inuit in the Arctic (a cold desert), populations inhabiting both productivity and latitudinal extremes. It is worth noting that the SCCS is biased towards populations in the Northern Hemisphere (Marlowe, 2005), with 132 Northern SCCS societies compared to only 54 in the South (although 57 societies are situated within 10° North or South of the equator). Previous work attempted to control for latitudinal effects using effective temperature (ET) (Marlowe, 2005; Porter and Marlowe, 2007).

To improve upon these efforts, our second goal (Objective 2) was to assess human population distribution using explanatory models that account for the effects of latitude and other key covariates on the global pattern of subsistence occupation. In particular, we sought to model the distribution of pre-industrial human settlement as a function of NPP_{max} and absolute latitude. The results for Objective 2 were similar to those of Objective 1. Our results accordingly lend credence to the claim of Porter and Marlowe (2007) that the prominence of certain societies in the anthropological literature may have contributed to a false impression of typical hunter-gatherer habitats. For example, the !Kung (for whom NPP_{max} was measured at 415.5 g C/m^2/year) are often cited as an example of a hunter-gatherer society occupying low quality habitat. In our model, the NPP_{max} value for the !Kung was roughly one third of the predicted value for a forager at AbLat ~20°, falling as an extreme outlier to the 95% confidence interval (*Figure 2.4*, upper left panel at 20° latitude). The !Kung society's occupation of a low productivity habitat at low latitude is thus unusual compared to other foragers in the SCCS.

Our third goal (Objective 3) was to assess and quantify the NPP-PD relationship across subsistence types in order to test our hypothesis that subsistence type moderates the NPP-PD relationship. We hypothesized that variation in PD derives from differences in the extractive efficiency of technologies and domesticates across subsistence types; therefore, including data on PD with environmental variables would provide a more complete picture of 'habitat quality' for pre-industrial humans than would either NPP_{mean} or NPP_{max} alone. We acknowledge that the inter-relationships among environment, technology, and population density are complex (Boserup, 1976), and that numerous mechanisms may be involved in translating environmental energy to PD. For example, disparities in fecundity, mortality, food production and security among subsistence types may all contribute to the divergent population demographic trends. Regardless of the exact mechanism, subsistence types represent cohesive cultural packages with respect to modes of food acquisition, processing, and storage (Ellen, 1982).

To test our hypothesis we modeled the probability of achieving low, medium, or high PD for each subsistence type, across the full range of the observed NPP_{max} gradient (*Figure 2.5*). We assessed the within-subsistence type ordinal PD shift from low to medium, and medium to high, as a function of NPP_{max}. In particular, we address historical claims of marginality. If the NPP-PD relationship varies with subsistence type, this would indicate that 'marginality' is not a useful comparative term. As our findings below indicate, subsistence modes do in fact show unique NPP-PD relationships. We now briefly address the findings regarding each subsistence type.

Foragers

As we expected, NPP was a reasonably good predictor of habitat quality for ethnographic foragers, as PD in foraging societies appeared to be environmentally constrained (*Figure 2.5*, top row). The positive association between NPP and PD suggests that habitat quality (as indicated by NPP) may indeed be a meaningful tool to assess the merits of the MHH, at least for foragers. Foragers at low NPP_{max} had a high probability of having low PD. In fact, foragers in habitats with $NPP_{max} \leq 1{,}000$ (g C/m^2/year) had a ~75% chance of having low PD (*Figure 2.5*, top left panel). At this productivity threshold ($NPP_{max} = 1{,}000$ g C/m^2/year) foragers had a ~20% probability of having medium PD (*Figure 4*, top middle panel). In the most productive habitats, foragers still only had a 50% probability of having medium PD, and a greater than 25% probability of still only having low PD. Though foragers maintained a relatively low probability of achieving even medium PD even in habitats with medium to high productivity, they did display a strong positive relationship between NPP and PD overall, across their entire range of NPP habitats. Unlike the other three subsistence types, foragers did not appear capable of achieving medium or high PD at low NPP_{max}.

High PD was achieved only among the Twana of the Pacific NW, who occupied the fifth most productive foraging habitat on the basis of NPP_{max}. These complex hunter-gatherers were able to achieve greater PD than other foragers due to their specialization on aquatic resources (anadromous fish) (Ames, 1994; Schalk, 1977). While the Twana were classified as high PD in our ordinal rankings, it should be noted that their PD as reported in the SCCS (26-100 persons / sq. mile) was much less than the PD (101-500 persons / sq. mile; >500 persons / sq. mile) achieved by some non-foraging societies, though all three population density levels were binned as high PD within our model. Exploitation of abundant marine resources is the main hunting and gathering strategy in high-latitude low-NPP regions, as shown by the SCCS. Thus 13 foraging societies live at a latitude greater than 50°, of which 11 relied on fished resources. The two exceptions – the Slave and Montagnais foragers – were heavily dependent on seasonally abundant large game such as moose in the seasonal boreal and taiga forests of Canada.

Non-foragers

Unlike foragers, farmers in low productivity environments were capable of supporting medium and high PD. If farmers and foragers can maintain different PD in the same habitat, and PD is in fact an adequate measure of demographic success, then the concept of 'marginality' requires further context to explain this pattern. Intensive agriculturalists (*Figure 2.5*, third row from top) and pastoralists (*Figure 2.5*, bottom row) demonstrated an overall positive NPP-PD association, like that of foragers. However, unlike foragers, these subsistence types were capable of maintaining medium and high PD even in habitats with low productivity. For intensive agriculturalists, the probability of a society having low PD never exceeded 25%, despite the fact that these populations frequently occupied low NPP_{max} habitats, indicating that low

NPP_{max} habitats can be successfully inhabited with technological intensification. Pastoralists had a relatively high probability (~50%) of supporting low PD in low NPP_{max} compared to intensive agriculturalists, whereas foragers maintained a probability of 75% or higher of supporting low PD in such habitats. This is because pastoralists were much more likely than foragers to have medium PD even in low productivity habitats, at a rate approaching that of intensive agriculturalists.

Horticulturalists (*Figure 2.5*, second row from top) appeared to face fundamental geographic constraints, occupying the narrowest latitudinal range of all subsistence types (from 0 to 45° absolute latitude). In high NPP_{max} habitats horticulturalists demonstrated a negative NPP-PD relationship, the only instance of a negative trend across all subsistence types. Tropical environments with short and predictable dry seasons are best suited for swidden agriculture, and swiddening techniques are implausible in temperate environments and grasslands (Ellen, 1982). Swiddening in humid rainforests generates high rates of nutrient draining that increase the fallow period and group dispersion (Ellen, 1982), thus limiting PD. Horticulturalists thus exhibit indirect support for the idea that rainforest habitats may actually be food-limited human habitats, despite their uniquely high levels of productivity (Bailey and Headland, 1991; Hart and Hart, 1986; Headland and Bailey, 1991).

Revisiting the MHH

The fundamental question surrounding the MHH is whether modern foragers bias our picture of the hunting and gathering lifeway during the Pleistocene, because, as Porter and Marlowe (2007) suggested, “pre-Holocene foragers living in more productive habitats may have had a considerably higher population density, resulting in different social organization” (p. 59).

In light of our findings, we can revisit what we mean by low-quality habitats for foragers. It is clear that tundra/taiga/polar habitats at high latitudes represent low-quality environments, and these habitats were exclusively occupied and exploited by foragers and pastoralists. Arid deserts also represent a low productivity environment, and yet non-foragers in these habitats were still capable of achieving relatively high PD. To a lesser extent, tropical rainforests (occupied principally by horticulturalists and foragers) may also represent low quality (on the basis of NPP-PD dynamics) habitats. While foragers do occupy these habitats, there is also no doubt that they would have occupied other habitats in the past. High-productivity riverine, lacustrine, deltaic, and flood plain aquatic habitats (i.e., Amazon, Ganges, Mississippi, Nile, and Yangtze Rivers) remain underrepresented in any analysis based on societies of the SCCS because these habitats have long been occupied by post-industrial societies. Foragers are similarly absent from South Africa's Cape Floral Region in the SCCS, a productive marine habitat proposed to have played a significant role as a refugia during a critical climatic period in the evolution of *Homo sapiens* (Marean, 2010, 2011).

Could Pleistocene African foragers have frequently achieved higher PD in higher quality habitats?

Among ethnographic foragers, achieving high PD is associated with an exceptional circumstance owing to geography: reliance on marine food sources. Foragers only achieved medium or high PD on seven occasions (out of a total 36 foraging societies), and six of these seven populations relied upon fished resources (the Eastern Pomo the lone exception). In tropical Pleistocene Africa, such high PD would have been unlikely, as marine productivity (unlike terrestrial NPP) increases with latitude (Huston and Wolverton, 2009), and African hunter-gatherers living in intact terrestrial ecosystems did not achieve higher PD levels. Furthermore, foragers at low and mid latitudes were largely absent from low NPP_{max} habitats. Thus, if high PD was achieved among Pleistocene foragers, it may have been achieved in a fundamentally different manner from modern foragers.

Conclusion

Consistent with a previous study (Porter and Marlowe, 2007), we did not find quantitative support for the MHH, as the habitats of ethnographic foragers did not evince consistently low NPP. The limitations of the ethnographic record, including the possibility that some non-foraging pre-industrial societies were also forced out of higher quality habitats, precludes a more definitive test of the MHH. Even by the earliest days of ethnographic observation, post-industrialized societies had left their mark on the distribution of smaller scale societies. Yet one distinctive ecological feature of foragers is that their population densities were better predicted by NPP than were non-foragers, especially within low productivity habitats. We suggest the tendency of foragers living in low-NPP habitats to have low PD may have contributed to the widespread perception that forager habitats are marginal.

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Chapter 3

CHAPTER 3

COMPARISON OF WETLAND AND DRY SAVANNA POST-ENCOUNTER FORAGING ENERGETICS BY WOMEN IN THE OKAVANGO DELTA

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Comparison of wetland and dry savanna foraging energetics by women in the Okavango: significance for human evolution.

Introduction

Humans have long been considered to have evolved in savanna habitats, but savannas include numerous possible types that differ with respect to food production. Savanna habitats cover approximately 20% of the earth's land area and are generally characterized by an open canopy (Sankaran et al., 2005). Despite this, savannas may differ considerably in tree cover, with tree density ranging from 100-3300 trees per hectare, which overlaps with tree cover in many riparian forests (~100 trees/ha) (Jibrin, 2013; Scholz et al., 2008). In this paper we consider how wet and dry savannas would have led to differences in foraging success for early hominins.

The environmental context of the earliest hominins presumably bore specific ecological features that help explain some of the key differences between themselves and the shared last-common ancestor (LCA). This landscape has been reconstructed variously as a rainforest, woodland, dry savanna, wetland savanna, or some combination thereof, with most researchers favoring a 'savanna environment,' broadly defined (Bender et al., 2012; Domínguez-Rodrigo et al., 2014; White et al., 2009). Presuming the LCA had a chimpanzee-like digestive system (Wrangham and Pilbeam, 2001), it could only have survived the shift to living among those non-rainforest habitats that provided sufficient amounts of preferred and/or fallback foods year-round (i.e. fruits and leaves, respectively; Laden and Wrangham (2005)). This condition eliminates many candidate African habitats and emphasizes the importance of permanent water sources, including lakes, rivers, and deltas that facilitate the regular maintenance of tissues edible to a chimpanzee-like ape. In particular, dry savannas suffer from the disadvantage of lower fruit abundance than rainforests, and other energy- and fat-rich food sources such as nuts and seeds may be available only seasonally (Peters, 1987; Peters et al., 1984).

Shallow-water deltaic environments have been proposed as candidate ecosystems for facilitating the hominin shift from a rainforest environment to a more savanna-like habitat (Verhaegen et al., 2007; Wrangham, 2005; Wrangham et al., 2009). In fact, a controversial recent publication has argued that a "Makgadikgadi–Okavango palaeo-wetland" located in Northwest Botswana may have offered not only a refuge to anatomically modern humans, but also a homeland for the earliest populations of modern *Homo* *sapiens sapiens* (Chan et al., 2019). While this paper has quickly been challenged, several other lines of evidence indicate the favorable habitat quality of deltaic environments. In particular, the underwater storage organs (UWSOs) of water-lilies, semiaquatic emergent, and floodplain herbs are abundant year-round in delta regions and tend to bear mechanically and nutritionally favorable qualities, as outlined in Wrangham's 'Delta Hypothesis' (Wrangham, 2005; Wrangham et al., 2009). Reflecting this favorable energetic environment, baboon populations (*Papio cynocephalus ursinus*) exhibit high population densities (Hamilton et al., 1976) and growth rates (Johnson, 2003) in the Okavango of Botswana relative to baboon populations in other environments. The baboons have also been shown to use shallow water habitats to exploit UWSOs and underground storage organs (USOs) as fallback foods (Wrangham et al. 2009). Similarly, human population densities around deltaic regions are high (Ericson et al., 2006), and widespread historical ethnographic sources describe the prolific harvesting of foods among shallow-water deltaic habitats (Brock et al., 1983; Garver et al., 1988; Ritchie, 2012; Tindale, 1974).

Despite these lines of support for the importance of shallow-water deltaic environments (Wrangham, 2005), there has been little systematic study of human foraging behavior among delta habitats. In contrast, dry savanna habitats have received more in-depth study, particular through long-term research on the subsistence ecology of !Kung (Lee, 1979; Lee and DeVore, 1976; Lee et al., 1968) and Hadza hunter-gatherers (Marlowe, 2010; Woodburn, 1966, 1968) from southern and East Africa, respectively. However, debate persists regarding whether the !Kung and Hadza live in 'marginal' habitats and whether their environments represent suitable analog habitats for paleoenvironmental reconstructions (Cunningham et al., 2019; Porter and Marlowe, 2007). Recent evidence suggests that while ethnographic hunter-gatherers in general do not occupy lower productivity habitats (on the basis of net primary productivity (NPP)), the !Kung do inhabit habitats with very low NPP when compared to other hunter-gatherer populations, including the Hadza (Cunningham et al., 21019). Given the lack of studies of foraging in wet savanna and the uncertain status of the dry-savanna habitats occupied by hunter-gatherers, the relative merits of foraging among dry savanna and nearby wetland areas remain unclear. The ultimate aim of this research is therefore to determine whether well-watered habitats would have been associated with greater foraging success for females of foraging populations than nearby dry habitats.

Our study focuses on the Okavango Delta, a habitat abundant in plant items edible by humans (Westlake, 1982; Wrangham et al., 2009). The Okavango is located in Botswana a country with a rich legacy of human foraging research and study (Cashdan, 1986; Lee, 1979; Lee and DeVore, 1976). The goal of the study was to compare foraging success in adjacent wet and dry habitats. This necessitated finding out how much food women obtained per hour of foraging, how nutritionally beneficial the foods were, and how much energy the women expended while foraging. To achieve this, we asked the following questions:

1. **(*Q1*) How do return rates differ between habitats?**

   We hypothesized that Wet and adjacent Dry habitats differ in terms of foraging success. A prediction of the Delta Hypothesis is that foraging in deltaic habitats should entail reduced search and harvesting time, and higher nutritional rewards. We address this prediction by presenting search time (pre-encounter), handling (post-encounter) time, total foraging time, and post-encounter return rates (kcal/hour).

2. **(*Q2*) Which foods are targeted in each habitat?**

   We describe dietary species richness and diet composition in Wet and Dry areas across the annual cycle. The Delta Hypothesis suggests that wetland habitats maintain relatively consistent production of edible foods across the annual cycle. Thus wetland (Wet) habitats are likely to generate less seasonal variation, and perhaps reduced dietary species richness than Dry habitats. We present summaries of diet composition in the form of plant parts and species collected in both Wet and Dry habitats.

3. **(*Q3*) What are the nutritional properties of foods in each habitat?**

   We compare the nutritional properties of foods in each environment in order to draw comparisons with other candidate hominin foods described in previous studies (De Vynck et al., 2016; Schoeninger et al., 2001). The Delta Hypothesis predicts that numerous foods in Wet deltaic habitats bear favorable nutritional properties compared to those in Dry habitats. Due to the importance of calories in both models from optimal foraging and reproductive ecology, we focus on the calorie as the primary measure of nutritional value. We also present data on four key macronutrients (total non-structural carbohydrates (TNC), free simple sugars (FSS), lipid, and crude protein (CP)), the basic components from which calories are determined.

4. **(*Q4*) How do the energetic costs of searching and harvest differ between habitats?**

   We use direct measurements of energy expenditure to characterize the costs of searching for and harvesting food in each habitat. The Delta Hypothesis suggests that in wetlands vegetation is more abundant, particularly in dry periods of the year. Similarly, high sunlight and water regimes should result in aquatic species having less well defended plant tissues (Vermeij, 2016). As a result, food resources should be easier to find in wet habitats, resulting in lower energetic search costs compared to dry habitats. We present data comparing the Wet and Dry returns as a function of their post-encounter energetic foraging efficiency ratios (post-encounter kcal acquired/kcal expended handling).

We performed focal follows on Okavango women who engaged in semi-experimental foraging tasks in relatively dry mosaic grass and woodland habitat, as well an alternative alluvial floodplain habitat, across an annual cycle that was characterized by significant variations in rainfall. Foraging sessions (days) are broken down into two component parts: pre-encounter (which includes walking – searching and traveling, poling or paddling of ‘mokoro’ traditional canoes, wading, etc.) and post-encounter (active food collection and handling). Travel by vehicle to foraging grounds is not included in these analyses. During foraging, we estimated instantaneous energy expenditure via heart rate monitors calibrated to energy expenditure measured using open-respirometry. We also recorded details of foraging behavior (e.g. activity and posture) on a continuous basis (Altmann, 1974). We identified foraging returns to the species level and most plant samples were subsequently analyzed for nutritional quality. We focus on women’s foraging because among traditional societies such as hunter-gatherers, the collection of plant foods typically falls under the domain of womens' work (Marlowe, 2005, 2007), a pattern of behavior which also holds true among our study groups in the Okavango.

Methods and Materials

Ecological context of study villages

The North West District of Botswana, also referred to as Ngamiland, is home to the Okavango Delta, a large inland delta draining the Kavango (or, Okavango) River, which originates in the highlands of Angola where it is known as the Rio Cubango. The two study villages were Seronga (S 18° 48' 46.8", E 22° 24' 57.6") and Gudigwa (S 18° 35' 56.4", E 22° 54' 43.2", sometimes spelled Gudingwa).

The village of Seronga is located 95 km South West of the Mohembo Ferry Crossing, which is itself 10 km north of the border town of Shakawe, the nearest town. Shakawe featured a petrol station, a grocery store, and a bank/ATM, but resources are frequently unavailable or out of service. Most resources available for purchase in (or closer to) Seronga originated in Shakawe, and were sold for a significant profit, inflating price for local villagers. The Okavango Trust ran a cooperative market in Seronga, re-selling a limited selection of market goods, consumables, and foods. Gudigwa was even more remote than Seronga, situated a further 60 km down the road. Many villagers in Gudigwa traveled to or received resources from Seronga, but few people in either village made the trip to Shakawe with any regularity. Informants reported that there has been a decline in the reliance on foraged food as the result of a number or factors including government food rations and subsidies, the presence of staple foods from small markets, and reduced game and resources near permanent settlements.

In both villages, residents tended to shift between multiple residences, driven in part by seasonal subsistence activities. Most villagers had a residence in or near the village center. This may be reed and stick-walled dwellings with thatch roofs (materials generally foraged for), or if the family had sufficient means, a mud brick structure with corrugated tin roof. For some, this was a primary residence, though for many this residence was used only for stays before or after travel to a neighboring village, for convenience when attending an activity in the village, to be closer to the village primary school, or some other activity that necessitated staying near the village center and road. Families also tended to have a plot used for farming, which often included a small hut or shaded roof structure that was used to escape the hottest part of the day, or to provide some shelter when overnighting. Finally, if families were wealthy enough to own cattle, or if the men worked as cattle keepers for wealthier cattle owners, there might have been a third residence, known as the cattle post. For many with cattle, the cattle post served as the primary residence, as the cattle are a great source of wealth and pride, and required tending and defense from predators (Bock, 1998; Eigner, 2012).

While not truly a residence, some individuals from both villages also spent a few nights a year "camping," especially those with proximity to the delta. Women said that their families would travel by mokoro (canoe) out into the delta, and spend time on floodplain "islands" engaging in subsistence activities. Women would use this opportunity to cut and collect thatch grass and reeds for tending to their homes' walls and roofs, as well as collecting food items to eat while in the bush. Men would set up long nets, catching large quantities of fish to be smoked and preserved for later consumption or sale. These sorts of activities seem to have been more prevalent in the recent past, particularly prior to the government's cessation of all citizen hunting activities, including the issuance of Special Game Licenses (SGLs) for Remote Area Dwellers (RADs), such as many Bugakwe or "Basarwa" ("bushmen") of the Okavango and the North-West District. Such stories of camping in the bush with family were told with a sense of warm nostalgia, or fondness of time spent with older relatives as children.

Climate and weather

The climate in this region is classified as hot semi-arid or steppe climate (type "BSh"), typical of hot mid-latitude tropics and subtropics, according to the widely used Köppen climate classification system. Seronga, with an altitude of 986m, has an average annual temperature of 22.1°C and annual precipitation totaling only 459 mm (https://en.climate-data.org/location/214830/). Gudigwa, with an altitude of 964m, has an average annual temperature of 22.1°C and annual precipitation totaling only 496 mm (https://en.climate-data.org/location/914559/). The totals reflect those produced by climate models available from climate-data.org. While these rainfall totals represent average annual rainfall totals, actual rainfall was measured at each village during the period of field study.

Daily weather data were recorded using three weather stations (Davis Instruments Wireless Vantage Pro2™ (Davis Instrument, Hayward, CA, USA)) located in or near Seronga and Gudigwa, and near where the women foraged for wild foods. Precipitation in the region was highly seasonal, with no rain typically falling in the winter month of July, and rainfall peaking in the summer month of February. During the study period (August 2014-July 2015) the rains displayed the expected bi-modal distribution (Batisani and Yarnal, 2010; Driver and Reason, 2017), with virtually no rain falling in the month of January (as seen in *Figure 3.1*). June and July were on average the coldest months, while temperatures peaked in October and November. The trends fit the broader regional monthly patterns, as experienced in Maun (WorldWeatherOnline, 2019).

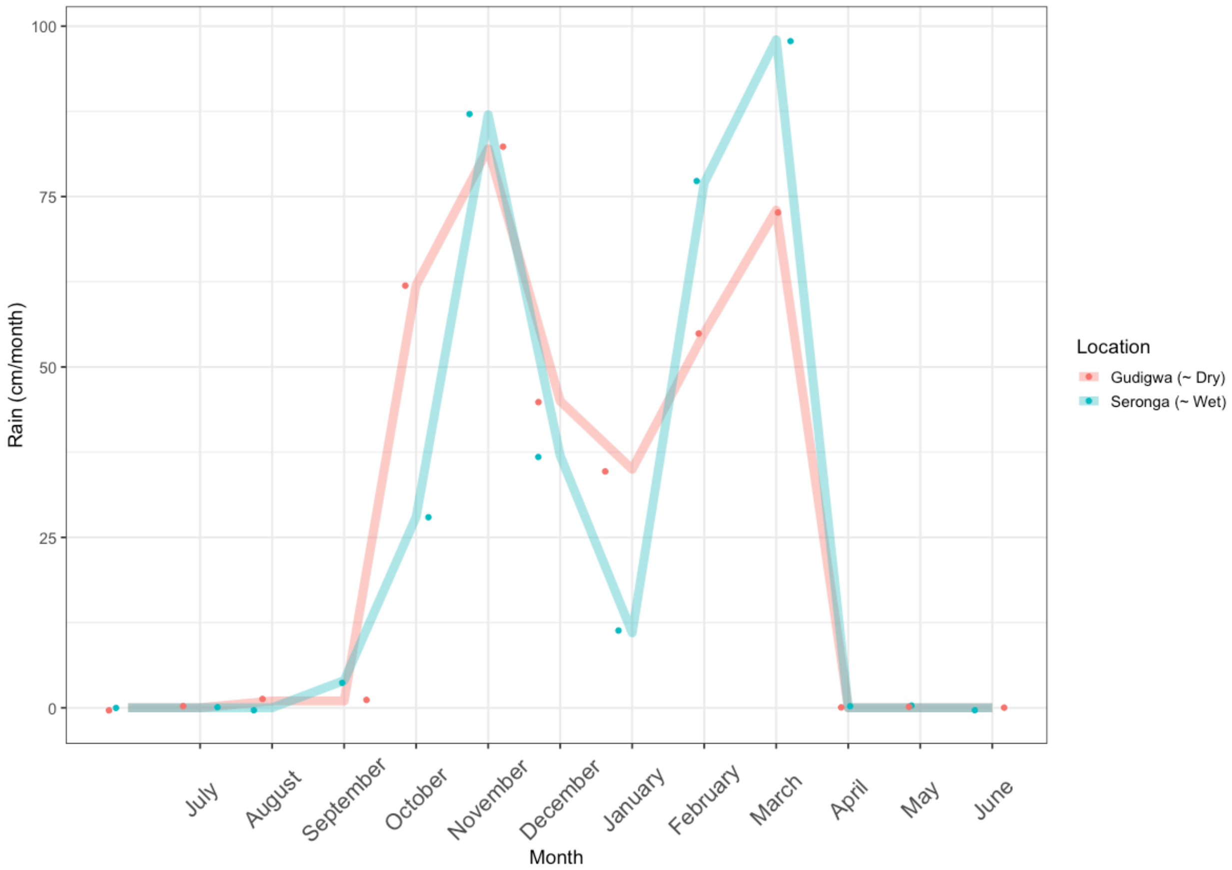

Figure 3.1: *Rainfall in Seronga (blue) and Gudigwa (red) from July 2014-July 2015. There was a bimodal distribution of rain during the period of field study that was abnormal. Locals remarked that the rains had "failed," and many chose not to plant crops this year.*

Floodwaters from the Angola Highlands carried via the Okavango River tended to reach the Delta between May and August, depending on the amount of rainfall in Angola, the amount of local rainfall, and the position in the Delta itself. Seronga, situated at the base of the so-called "panhandle," is in close proximity to the primary floodplain and the main river channel itself. Thus, it is located in an area where its inhabitants have year-round access to its waters. Gudigwa, on the other hand, is both east and slightly north, at the very northern most tip of the eastern delta margin. Floodwaters reached this area later, and with less amplitude than in Seronga. In the southern panhandle, where Seronga is located, the flooding season coincides with the rainy season, and maximal flow rates can reach 620 m^3s^{-1} (see *Figure 3.2*). The dry season generally persists from August through December, and during this time the Okavango flow can drop to 114 m^3s^{-1} (King et al., 2009).

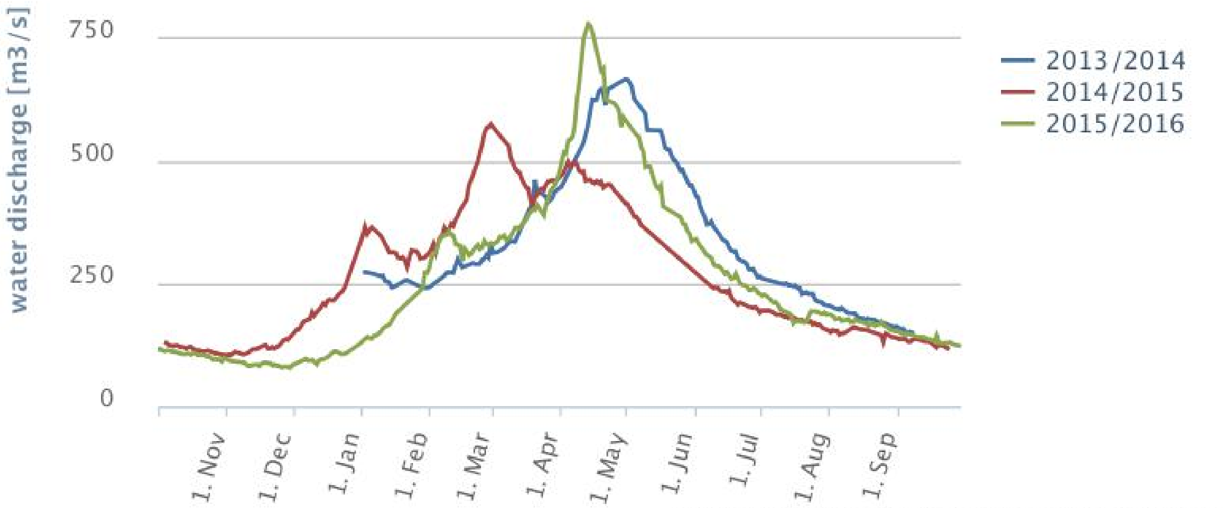

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Figure 3.2: *Water discharge in Mohembo from November 2013 - September 2016. Flood data sourced from the Okavango Research Institute's flood level monitoring site:* *http://okavangodata.ub.bw/ori/monitoring/water/*

Subject recruitment and retention

Ten women were recruited from two Okavango villages—Seronga and Gudigwa—in the Northwest Ngami District. Participation involved one foraging day per month for each woman. Subjects were compensated for their participation on each foraging day (once per month), regardless of the amount of foraging returns or the time spent foraging. Subjects were free to leave the study at any time. Participation by study subjects was relatively constant through the year but did include some attrition (*Figure 3.3*). If subjects left the study, a replacement subject in that village was recruited. In total, the study involved the participation of 24 women. In Gudigwa, two months (August and December) included 11 foraging subjects, while all others included 10 women. In Seronga, all months had 10 focal individuals, except for the final month (July 2015) in which only 9 subjects completed focal foraging sessions. After we dropped the subjects that did not complete the Cosmed VO2 calibration tasks, data in our analysis contained a subset of the total individuals (21 of 24).

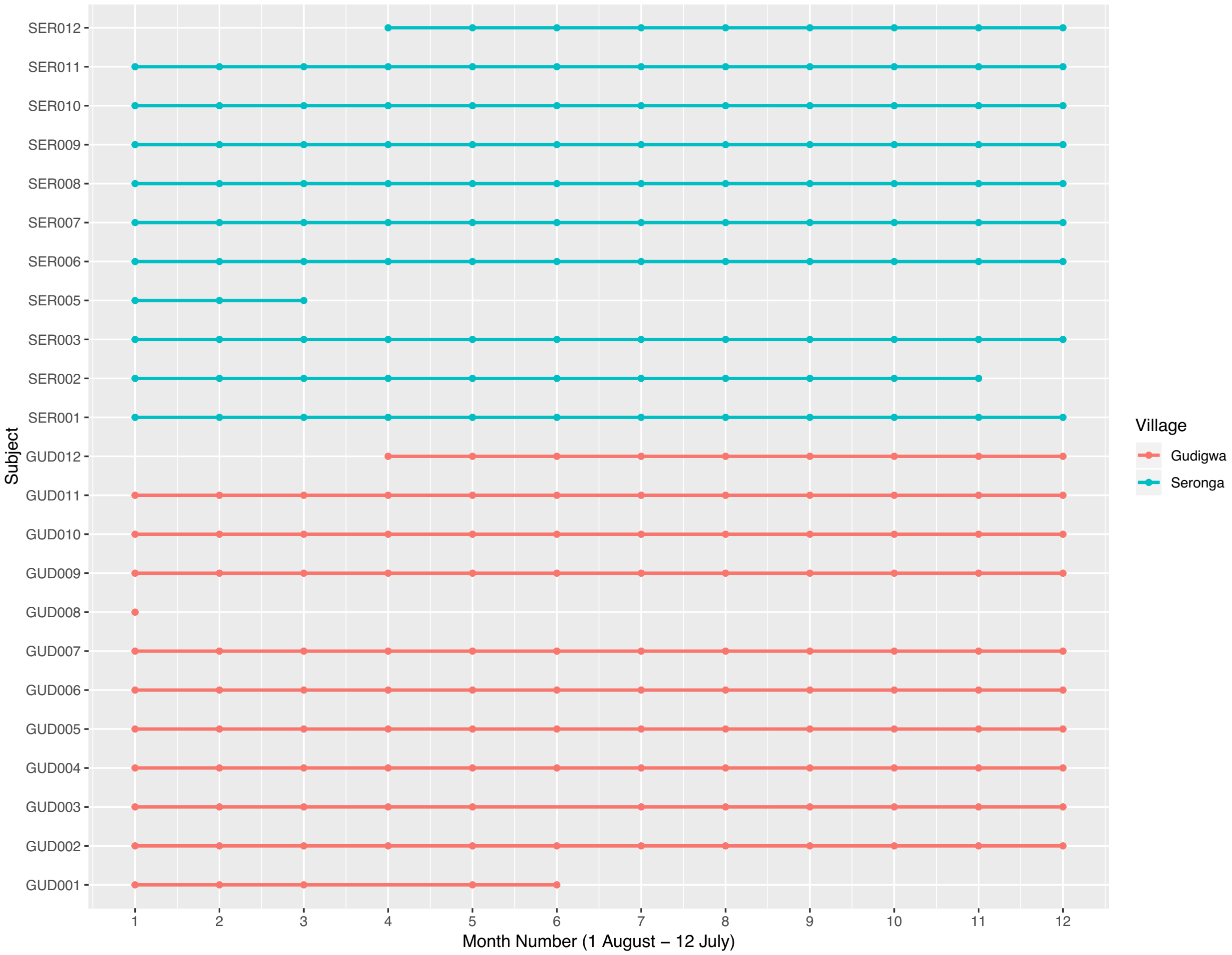

Figure 3.3: *Subject participation by month in Seronga (blue) and Gudigwa (red).*

Anthropometric data

Age was self-reported by individuals, to the best of their ability. Height was measured using a Seca 213 Portable Stadiometer (Seca Company, Hamburg, Germany). Weight was measured using a Tanita BC-558 Ironman Segmental Body Composition Monitor (Tanita Corp., Arlington Heights, IL, USA). We also collected anthropometric data using the Tanita BC-558 Body Composition Monitor. These additional variables included body fat (%), water content (%), muscle content (kg), bone content (kg), and approximate daily caloric need (cal/day), a composite variable derived by the Tanita BC-558 from user-entered age, sex, height, and weight input. Summary information on anthropometry is shown in *Table 3.4.*

Table 3.4 - *Subject anthropometry.*

Mean:	**Gudigwa**	**Seronga**	**Welch Two Sample t-test**
Age	47.7 y	44.1 y	t = 0.55473, df = 17.452, p-value = 0.5861
Height	158.0 cm	164.6 cm	t = -3.0016, df = 17.822, p-value = 0.0077
Weight	64.2 kg	62.1 kg	t = 0.40294, df = 15.648, p-value = 0.6924
BMI	25.7	22.9	t = 1.5144, df = 14.821, p-value = 0.151
Body Fat %	33.70%	31.20%	t = 0.83925, df = 17.146, p-value = 0.4129
Children	5.73 ± 2.24	4.82 ± 3.43	------
Daily Caloric Need	1275.27 ± 194.46	1287.18 ± 134.62	------

Calibration and energetic measurements

Due to logistical limitations of conducting open respirometry with subjects during real-time foraging, we relied on heart rate-VO2 regressions to estimate the energetic expenditure of subjects during foraging activities. To accomplish this, it was first necessary to calibrate heart rate and VO2 on an individual basis (Keytel et al., 2005; Leonard, 2003, 2010). We conducted physical tests to generate subject-specific regressions between heart rate and energy expenditure using the 'flex heart rate method' (Leonard 2001).

Subjects completed a battery of simple activities and postures while wearing a portable open-circuit respirometry system **(**Cosmed K4 b^2, Chicago, IL, USA) that measures breath-by-breath oxygen consumption (mL/min/kg). During the tests, the subjects wore two heart rate monitors: a Polar heart rate monitor (Polar Electro Oy, Kempele, Finland) associated with the Cosmed system, and one associated with the Garmin Forerunner 310XT (Garmin Ltd., Olathe, KS, USA) GPS watch. Heart rate data from the Garmin (HR_Garmin) and Polar (HR_Polar) heart rate belts were highly correlated (r^2=0.95 for all pooled data). We used the Polar-derived values to determine the heart rate-VO2 regressions, but during foraging tasks the Garmin-derived values were used.

Calibration measurements were conducted once, during the fourth study month (November 2014). Subjects who quit the study prior to this point or joined the study later did not complete the calibration test (N=3). Foraging data, but not energetic cost data, from these subjects were included in the final analysis.

During the tests, we focused on three resting activity levels by asking subjects to lie in a supine position, to sit upright, and to stand upright for five minutes. Subjects then walked at three speeds corresponding to 60, 90, and 120 steps per minute for 2-3 minutes. Finally subjects completed a 30 cm box ("Chester") step test (Sykes and Roberts, 2004) at two rates (15 and 30 steps/min) corresponding to Chester stages I and III.

We calculated the average of the three resting activities, which were typically virtually identical. The energy expenditure value corresponding to this average was then used for any heart rate data points below the 'flex point', which was defined as half of the distance between the highest resting point and the lowest active point (Leonard 2001). For points above the 'flex point', we fit a linear regression to the heart rate (Polar) versus energy expenditure data. Using these individual-specific values and equations for resting and active states, we could then estimate energy expenditure during women's foraging without direct measurements of VO2.

Foraging sessions

Focal follows were conducted over 13 months, from July 2014 through July 2015. Data from the first month (July 2014) is not included in these analyses, as this month was used to pilot methods and acquaint subjects with the study methodology. On a given foraging day, women were asked to choose a starting location for their foraging session. The starting location was variable, and women often asked to be driven to a location within a reasonable distance to begin their trial. The starting point of each foraging trial is marked on *Figure 3.5*. Note that the colors do not necessarily relate to whether the foraging activities took place in a Wet or Dry foraging location (though, they was a high correlation between village and location). Wet habitats were classified as rivers, areas with standing water (such as flooded plain, or islands surrounded by river or flooded plains. These classifications were made as a judgment by the researcher during the foraging bout, and the foraging location was recorded at multiple times throughout the session, with each change in activity or posture.

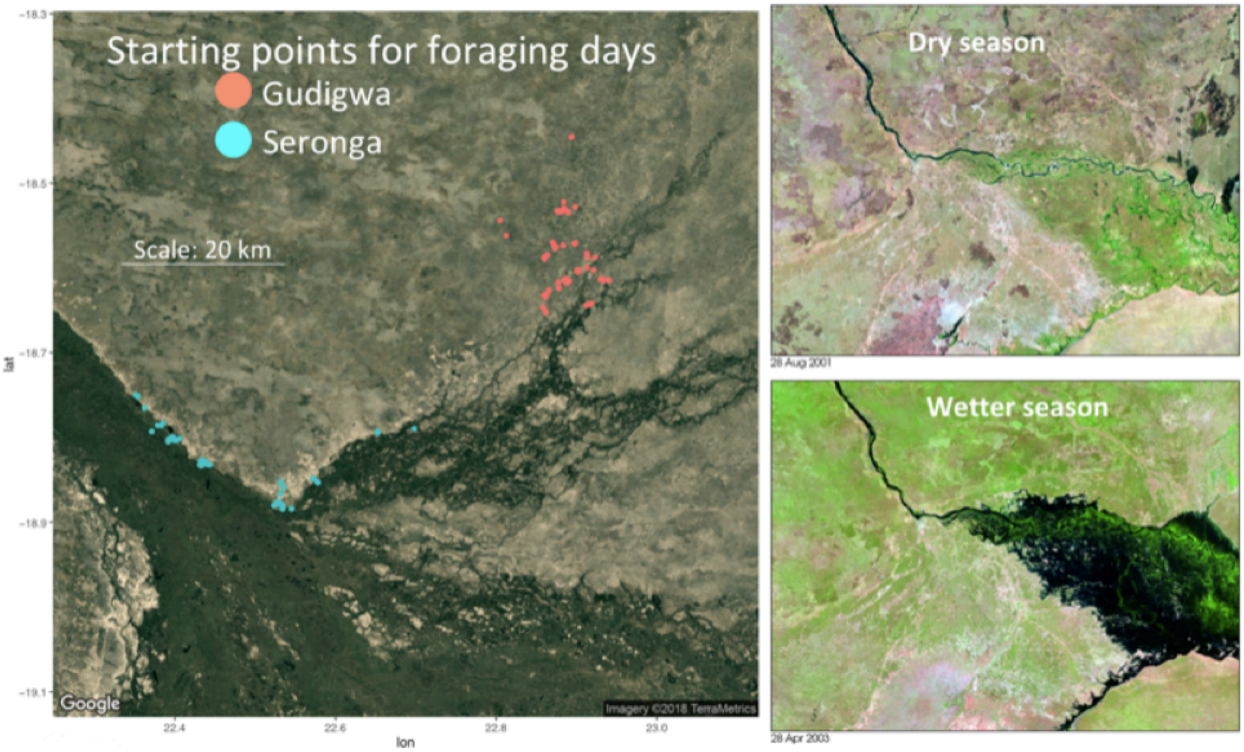

Figure 3.5: *Starting points for foraging sessions in Seronga (blue) and Gudigwa (red); panel showing relative change in water level in August (dry season) and April (wet season).*
Maps courtesy of Google via TerraMetrics (left) and NASA MODIS (right inset).

Each subject was followed for one foraging session per month. Unfortunately, with this sampling frequency, we cannot adequately control for between-individual skill variation. To achieve such control typically requires high sample sizes (Hill and Kintigh, 2009), but the remote nature of the field site along with time and budgetary constraints prevented more frequent focal observations each month. Women typically foraged as pairs of freely chosen foraging partners from their village. Partners were often friends, neighbors, or relatives. Sometimes additional individuals would occasionally accompany subjects. Data recording (heart rate measurement and focal observation) began once foraging was initiated (*Figure 3.5*), which was explicitly stated or obvious (i.e. we had driven to a foraging location).

Travel was defined as time spent on foot and does not include time in the vehicle en route to foraging locations. Women in Gudigwa chose to drive to foraging grounds much more frequently than did women in Seronga, and yet the (non-vehicle) travel and search time (pre-encounter) from the start of foraging until the first instance active food collection (post-encounter) was still greater in the Dry (predominantly Gudigwa) than Wet (predominantly Seronga) habitats (see *Figure 3.6*). For this reason, we do not believe that pre-foraging driving (as used in other human behavioral ecological studies) to be a significant source of bias in our foraging outcomes (Bird and Bird, 2017; De Vynck et al., 2016).

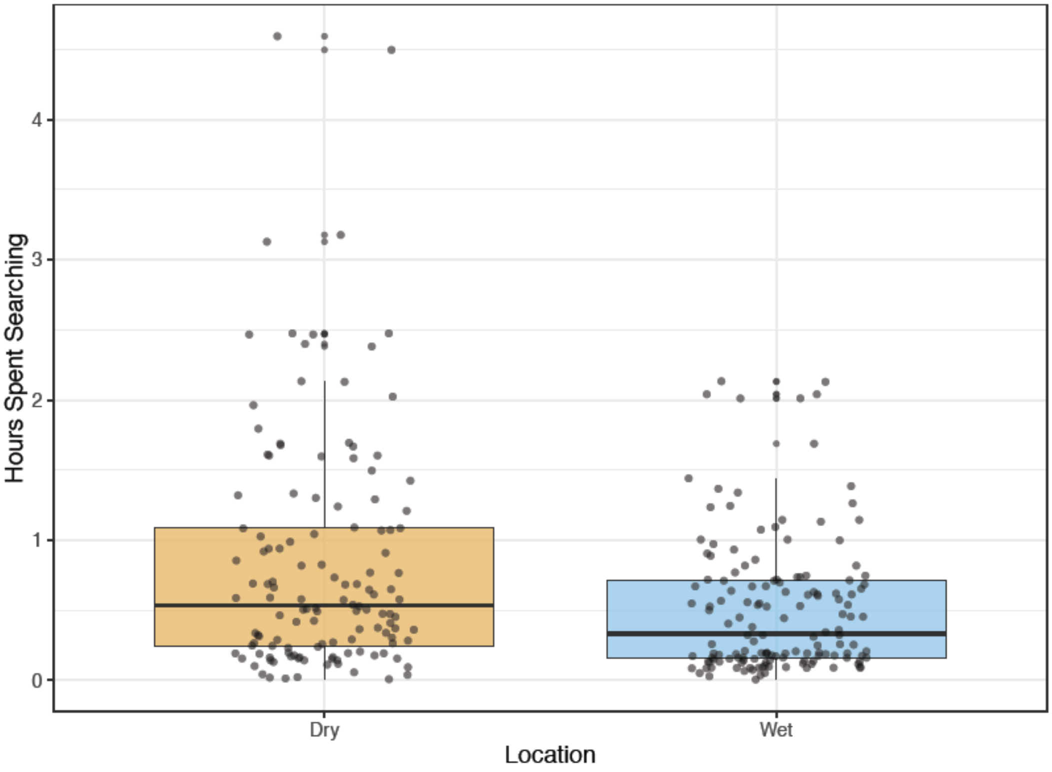

Figure 3.6: *Pre-Encounter Search Time to First Food Collection (Post-Encounter), by Habitat.*

A pair of researchers collected data on each of the two female subjects throughout simultaneous focal follows. Each subject wore a Garmin heart rate and GPS monitor throughout the foraging session. Researchers did not prompt or direct the subjects, and as such the behavior and level of coordination between women was entirely self-determined by the study participants. Researchers collected detailed observations on all foraging activities, including body posture, activity ID, and the objects with which that subjects engaged during the foraging session (see complete *Ethogram* in the *Supplementary Materials Table SM 3.1* for all information collected). We defined foraging as time spent searching, pursuing, and harvesting wild foods. Post-field processing of wild food done in the home was generally not observed. Additional social (partner ID, individuals accompanying foragers, children, etc.) and environmental data (wet or dry habitat) providing further context for the foraging session were also recorded. Women were free to communicate with one another. Foraging activity was divided into pre- and post-encounter periods, which represent search and handling, respectively. Subjects chose when to finish the foraging session. Garmin GPS and heart rate monitors were removed at this time, women were compensated and the foraging session was concluded.

The Garmin Forerunner 310XT monitor was worn by the focal subjects throughout the foraging session. This device collected continuous data on GPS position, altitude, second-by-second heart rate, and a running measure of distance traveled. Focal observations recorded by the researchers were noted to the nearest five seconds. The Garmin heart rate data was later collapsed to this resolution (every 5 seconds). We filtered the data by excluding the first two minutes of any new activity to allow the individual to achieve a steady-state if possible. We then averaged the converted O2 values for the duration of that particular activity.

We calculated several quantities. We calculated the net acquisition rate (R_n ; (Smith, 1979)), which includes the time spent foraging (T_a)*:* $R_n = (E_a – E_e)/T_a$. Previous work (Smith 1979, Ydenberg 1994) has assumed that fitness is a function of the net energy acquired (E_n), where: $En = E_a - E_e$. We also calculated the ratio (F) of energy gained (E_a) to energy spent (E_e) per unit time foraging (energy efficiency; Smith, 1979; Stephens & Krebs, 1986; Ydenberg, Welham, Schmid-Hempel, Schmid-Hempel, & Beauchamp, 1994), where $F = E_a/E_e$.)

We analyzed these quantities across the annual cycle, treating each individual foraging 'bout' as an independent data point for gross and net return rates. Each resource collected during a bout composed a single row entry. We used generalized linear mixed models (GLMMs) to calculate the determinants of foraging productivity. The distribution of return rates (kcal/hr) for the 309 bouts was strongly right-skewed and was log-transformed to satisfy assumptions of normality. Categorical predictor variables included location (Wet/Dry), month of year, plant species, and plant part, and subject ID was incorporated as a random factor. We used model selection criterion (based on lower AIC values) to arrive at the final model, which included all the categorical predictor variables listed above.

Food collection and nutritional analyses

When possible, foraging returns were collected following each individual foraging bout within a foraging session. At the end of the foraging session, the total fresh weight of foods recovered was recorded. A subsample of each food item recovered was taken for future nutritional analyses (generally around ~100g). Samples were then processed at the research station, and the usable fraction was determined (by removing pits, shells, aFR4etc. that would not be consumed). The samples were dried at 100° C, labeled, and bagged for future analysis.

Field samples of foraged foods were returned to the Harvard University Nutritional Ecology Laboratory (NEL) in the dried and bagged state, following importation to the United States under an active USDA APHIS import permit. These samples were analyzed for ash, crude protein (CP), fiber (NDF, ADF, and lignin), free simple sugar (FSS), lipid content, and moisture content (or the field dry matter). Total non-structural carbohydrate (TNC) levels were determined by difference; %TNC = 100 - %Lipid - %CP - %Ash - %NDF. Some samples were also sent out for additional analysis of starch content, though those values are not reported in this analysis. Here, starch is included in the TNC measure, which has been corrected to account for FSS values reported independently. All nutritional analyses followed well-established procedures, described in detail by Conklin-Brittain (2006). While Conklin-Britain (2006) modeled nutritional value for ape foods based on three levels of fiber digestibility, we used the lowest of these, zero, as humans have an estimated hind gut volume of only 20%, compared to 52% in apes (Milton and Demment, 1988). While this decision might have influenced total caloric measures for some fiber-rich foods, the effect was likely minimal; a comparison of “No” and “High” levels of fiber digestibility produced reductions in r^2 values for plant parts at differing levels (decrease r^2 values shown in parenthesis): USOs (0.013), Piths (0.046), Fruits (0.074), and Seeds (0.141). As such, our final values were unlikely to significantly underestimate food value, though these effects are likely to affect caloric values of seeds, fruits, and piths than more than underground storage organs.

For each foraging session, a daily total of foods by species gathered by each subject were calculated based on the nutritional analyses conducted in the NEL – allowing for a daily measure of foraging productivity. These data included the total fresh usable weight, the caloric value, as well as the macronutrient composition, and species and plant part information. This dataset, referred to as “Nut” (for Nutrition), also contained key variables that allowed these foraging returns to be linked to the broader foraging, energetic, postural, and behavioral dataset, known as the “Master” file, including Date, Subject ID, Location, and Village. The Nut and Master files were linked for analysis in R to create a “final_table” file, which contained 276 comprehensive and complete observations.

Ethics statement

Ethical considerations and permissions were reviewed and granted by the Institutional Review Boards of Harvard University (protocol number CR-23935-01), the University of Botswana (Ref No. RES/IRB/1508, protocol number SKMBT-42150114154100), and the Republic of Botswana Ministry of Health (protocol number PPME 13/18/1 VIII (503)). Plant samples imported to the United States were done so with the permission of the US Department of Agriculture (USDA permit number PCIP-15-00799).

Results and Preliminary Discussion

Data analyses were based on 276 unique foraging sessions across 22 female subjects. Foraging bouts ranged from less than 1 to nearly 400 minutes, with a mean of 87.2 minutes, when combined across all foraging locations. Almost all tests reported below involve a comparison between Wet and Dry foraging locations. There were 146 bouts in Wet foraging locations, and they ranged from .5 to 249.8 minutes, with a mean of 70.0 minutes. Total foraging time was longer in Dry foraging locations (n=130), with bouts ranging from 4.6 to 399.0 minutes, with an average time of 106.6 minutes. The total energetic gain over the study period during the research was 569,094 kcal from 399.5 foraging hours, or ~50 (8 hour) person-days, i.e. a mean rate of caloric production of 1,424.5 kcals/h across all observations, including both searching (travel to food patches) and foraging within patches.

Q1: Wet vs Dry Foraging: Search time (pre-encounter)

We first assessed productivity on the basis of caloric production per hour of foraging search time. We found significant differences in Wet and Dry habitat (pre-encounter) search times (t(df=200.67)= 3.75, p<0.001; Mean(Wet)= 1860.3 seconds, Mean(Dry)= 3004.3 seconds).

Testing one aspect of the first research question (Q_1), that Wet habitats would allow reduced foraging times by foragers, we concluded that search and handling times in Wet habitats were in fact reduced compared to Dry foraging locations. Search (pre-encounter) times were higher in the Dry habitat than in the Wet habitat (t(df=200.7)=-3.75, p<0.001, mean(Wet)=0.52 hrs, mean(Dry)=0.83 hrs), though again there was a lot of skew in the Wet habitat data, so the median was lower in the Wet habitat, as seen in *Figure 3.7*.

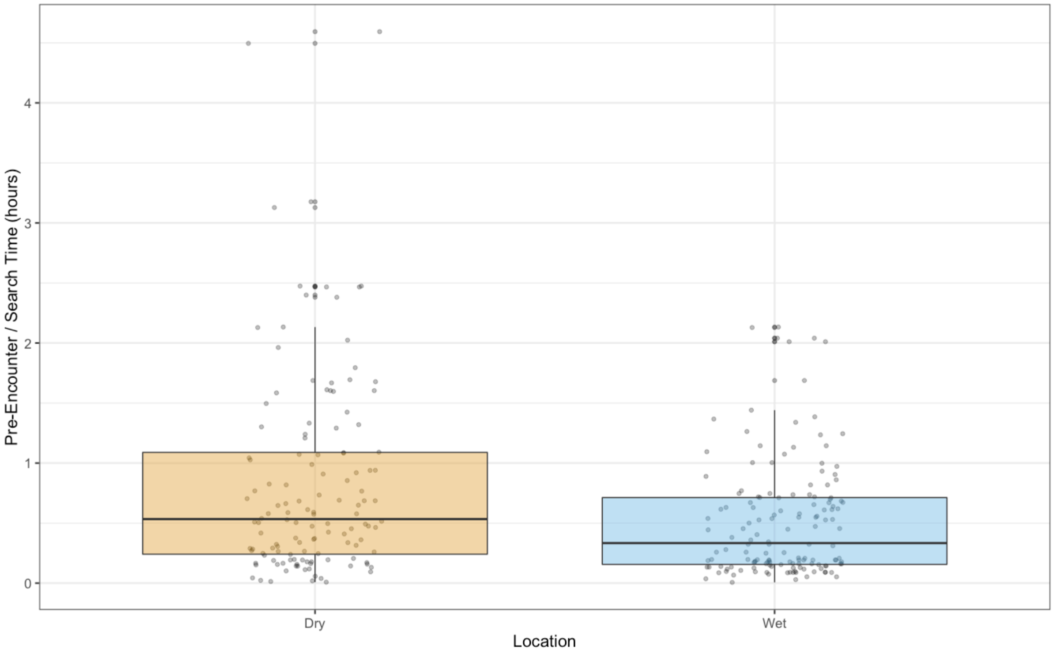

Figure 3.7: *Search (pre-encounter) time by habitat. Time spent searching was higher in Dry (orange) than Wet (blue) foraging locations.*

Q1: Wet vs Dry Foraging: Handling time (post-encounter)

Time spent harvesting and handling foods (post-encounter) were generally short (roughly one half-hour), and this differed between habitats (t(df=166.6)=-2.94, p=0.003, Time(Wet)=0.65 hrs, Time(Dry)=0.94 hrs), but the medians were virtually identical (as shown in *Figure 3.8*).

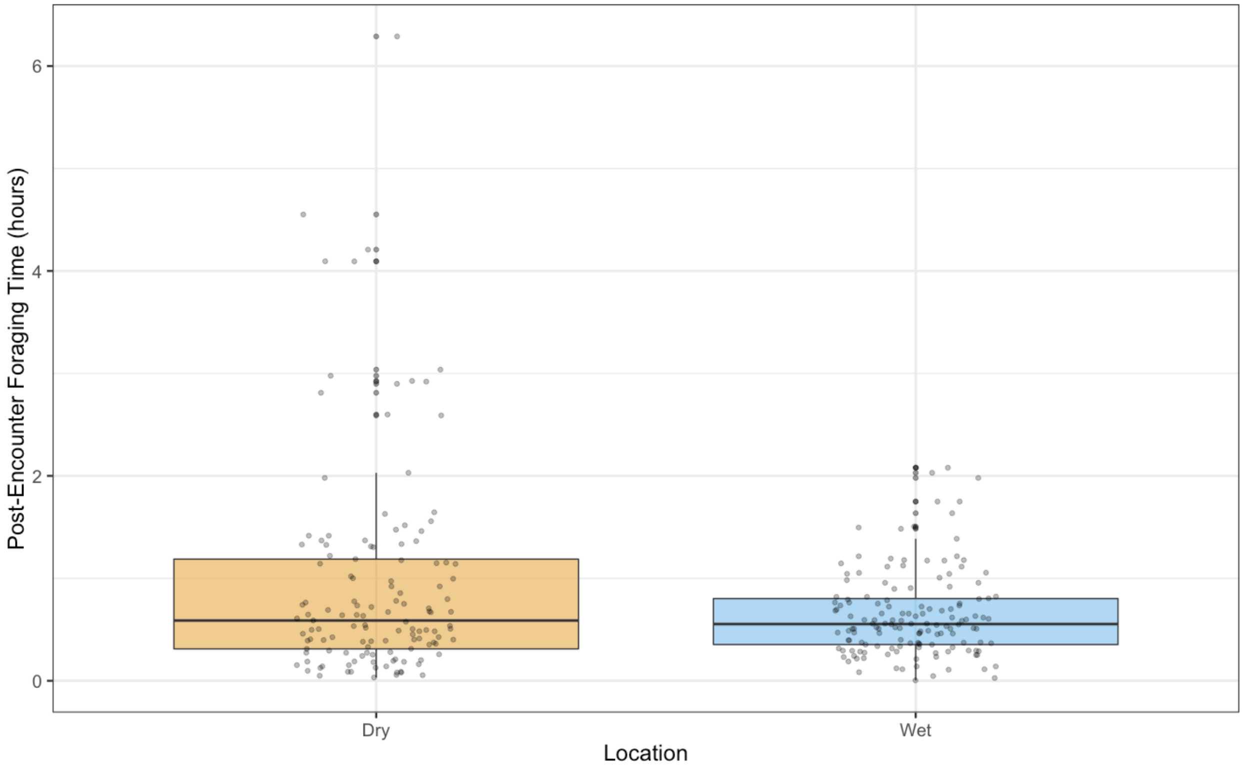

Figure 3.8: *Time spent handling (post-encounter foraging) was higher in Dry (orange) than Wet (blue) foraging locations.*

Q1: Wet vs Dry Foraging Return Rates: Overall Foraging Time (pre- & post- encounter)

Overall, the search time data appeared to show that more time was spent foraging in Dry habitats, but the differences were relatively modest. This suggests that Dry habitat foods required more searching, while Wet habitat foods were perhaps more abundant and easily accessed. Total foraging time was higher in Dry habitats than Wet habitats (t(df=172.5)=-4.63 p<0.001, mean(Wet)=1.17 hrs, mean(Dry)=1.78 hrs) (see *Figure 3.9*).

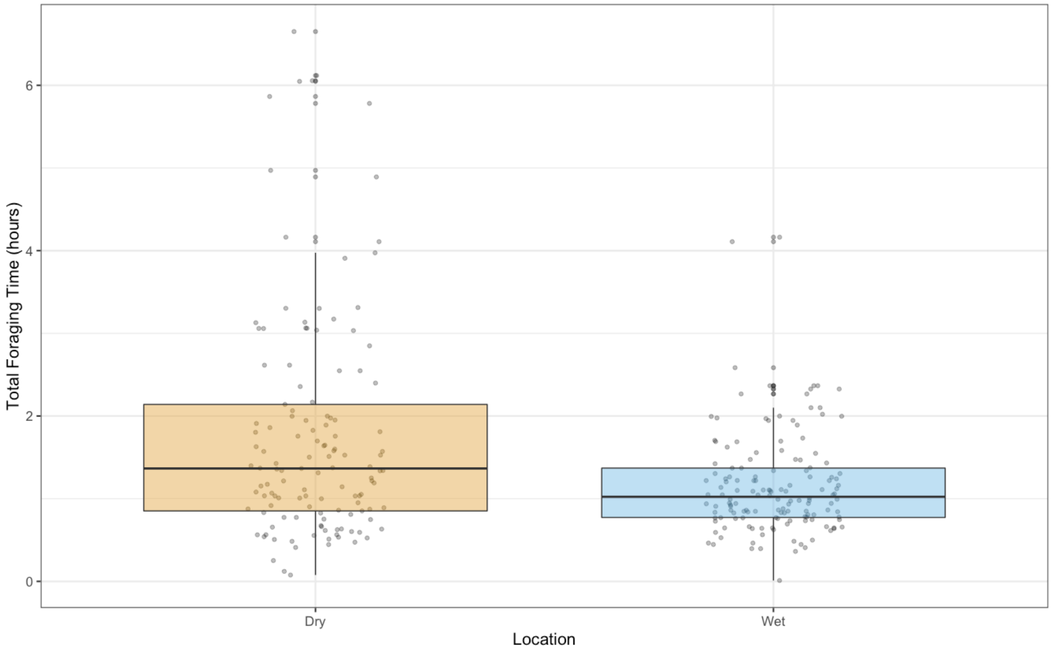

Figure 3.9: *Total time spent foraging was higher in Dry (orange) than Wet (blue) foraging locations.*

To better visualize and understand the dynamics of Wet and Dry foraging effort, as assessed by total foraging time, we visualized foraging time by habitat and study month (August 2014 – July 2015). *Figure 3.10* shows that there is indeed a seasonal component of total foraging time.

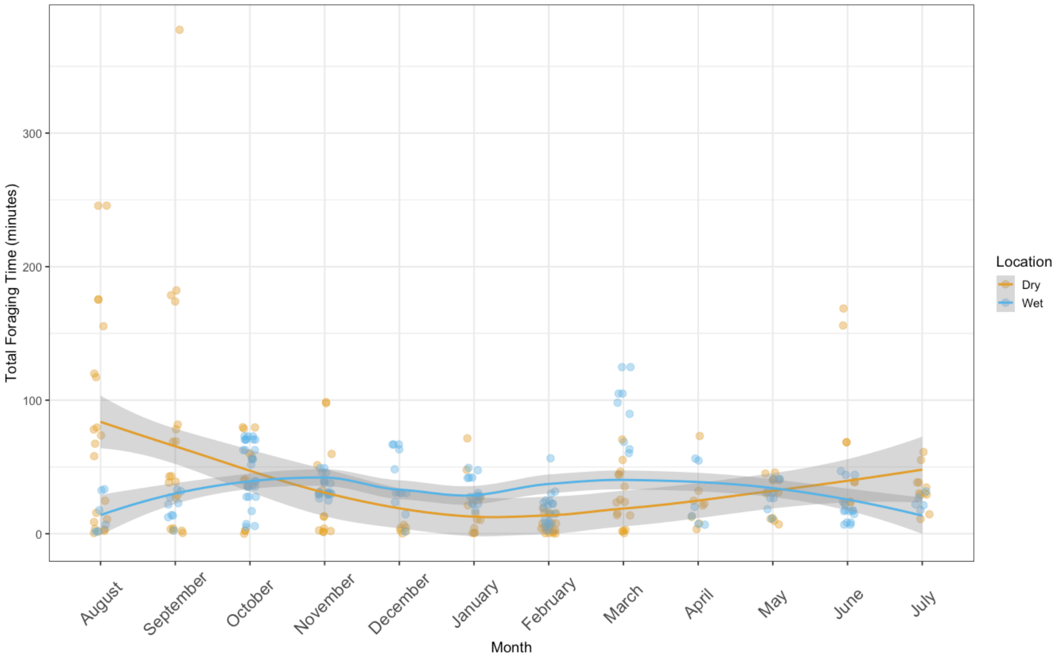

Figure 3.10

Figure 3.10 (Continued): *Total time spent foraging by month. Foraging times were on average higher in Dry (red) than Wet (blue) foraging locations during the winter months of July, August, and September.*

Q1: Wet vs Dry Foraging: Post-encounter return rates

Comparison of median values showed that the handling (post-encounter) return rates from Wet habitat foraging had a relatively skewed distribution (median (Dry) = 2320.9 kcal/hr, median(Wet) = 558.7 kcal/hr) (see *Figure 3.11*), with Dry habitats having displayed higher returns. Results were similar when we assessed productivity on the basis of mean post-encounter return rates (kcal/hr). Based on a t-test (with individual foraging bouts as the unit of analysis, and not controlling for any other variables), Dry locations were significantly more productive than Wet locations (t(df=284)=-5.3, p<0.001; Mean(Wet)=1428.3 kcal/hr, Mean(Dry)=2956.6 kcal/hr). In other words, after women had arrived at their chosen food patches those in the drier habitat produced almost twice as many calories per hour of foraging as those in the wetter habitat.

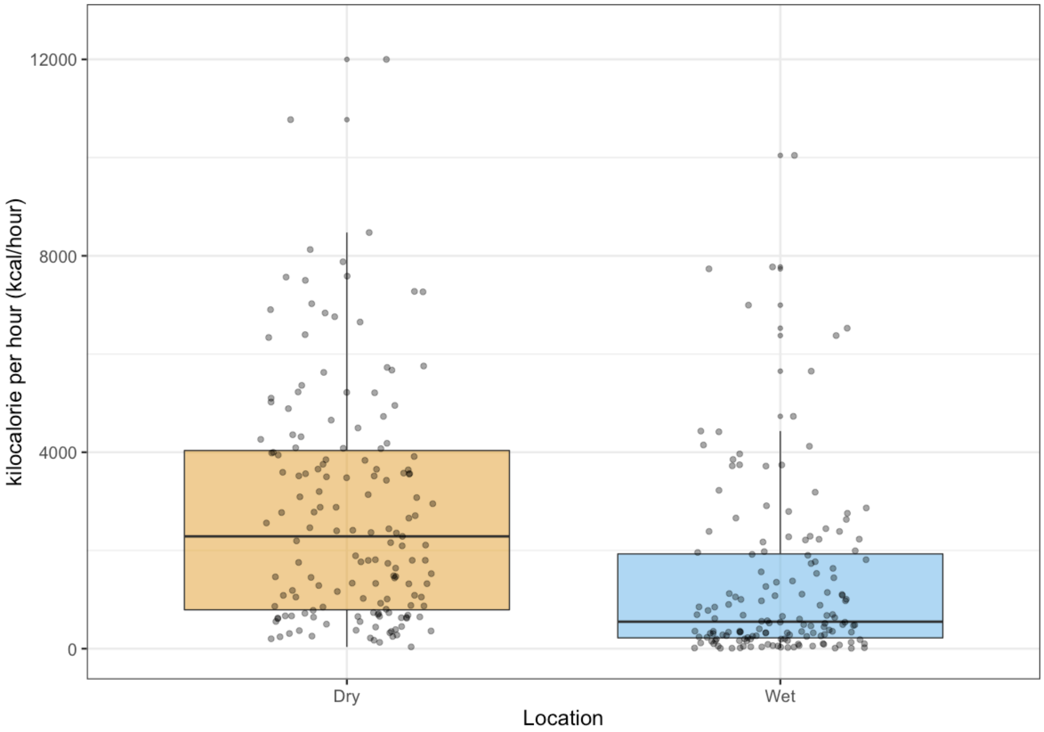

Figure 3.11: *Post-encounter return rates (kcal/hour) show that Dry habitat foraging is generally more productive than Wet habitat foraging.*

To provide further information on the differences reported in *Figure 3.11*, violin plots show where points are clustered in each location. *Figure 3.12* shows that in the Wet foraging location there was a pronounced cluster at return rates of lower than 600 kcal/hr. To find out whether these low-return foods that were frequently produced in wet habitats tended to be a distinct type, we repeated this graphical presentation by separating USOs (including UWSOs) and non-USOs. *Figure 3.13* shows that in Wet habitats, the low-productivity cluster was composed primarily of USOs.

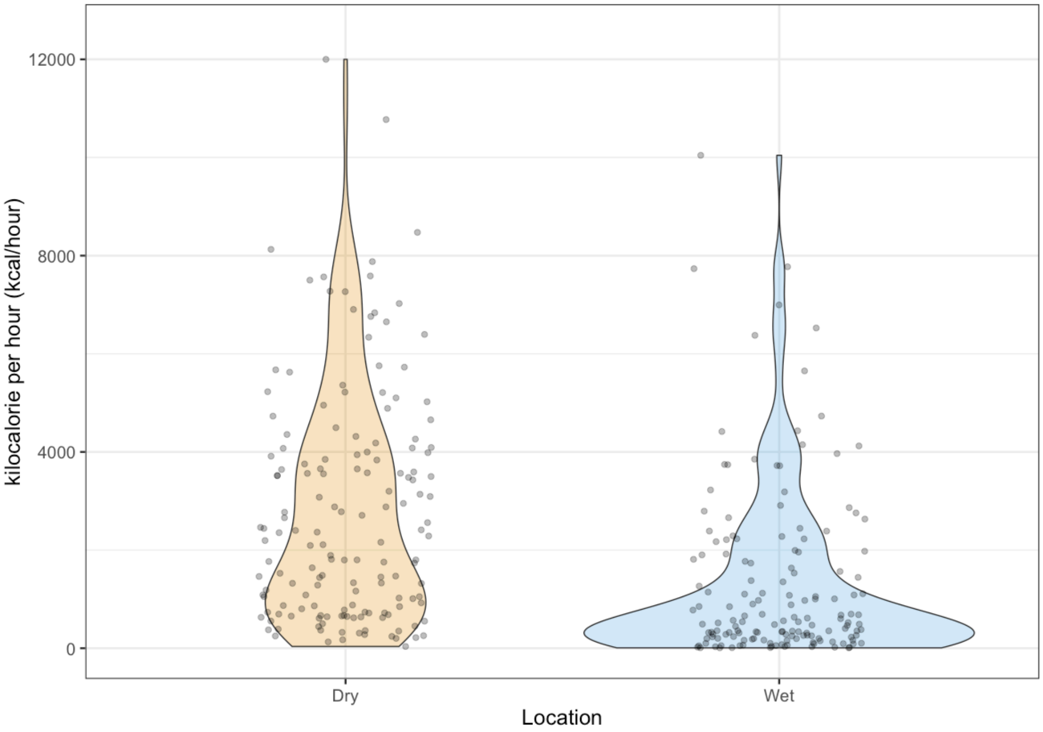

Figure 3.12: *Post-encounter return rates (kcal/hour) violin plots reveal the large cluster of points at low return rates in Wet habitats.*

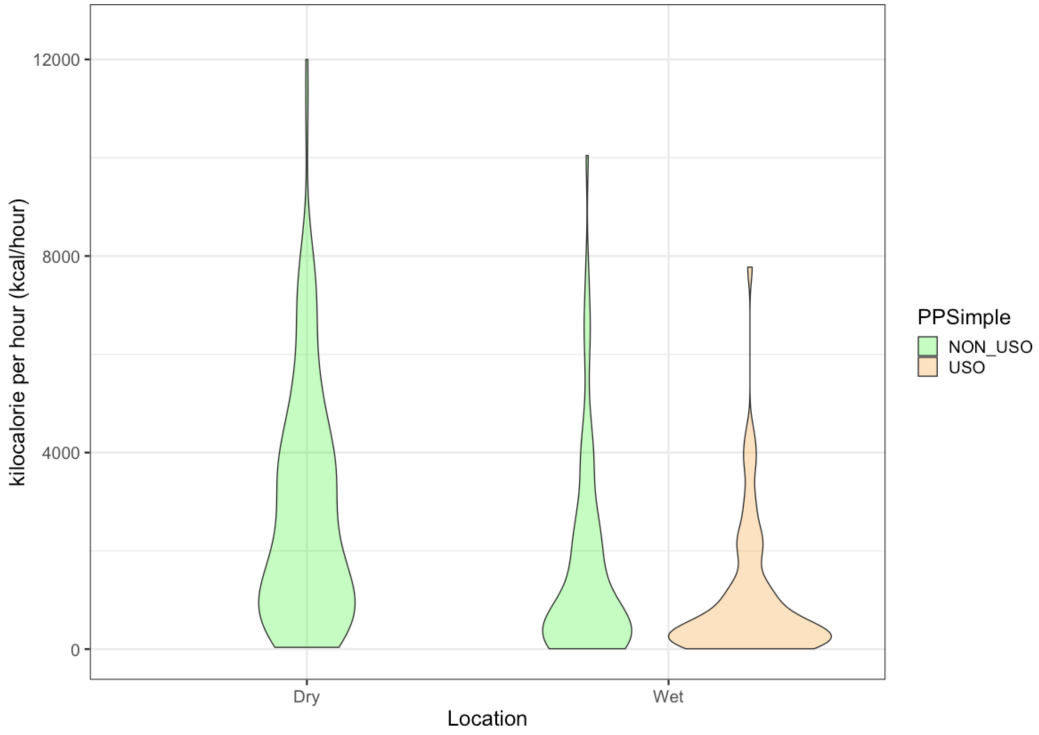

Figure 3.13: *Post-encounter return rates (kcal/hour) violin plots reveal the large cluster of points at low return rates in Wet habitats, sorted by simple plant part.*

Given that dry habitats yielded higher rates of food production per hour of foraging, we considered how the difference was affected by seasonal variation. To account for the many potential confounding variables that may affect habitat profitability, we tested foraging returns with a linear mixed model (*see Figure 3.14*).

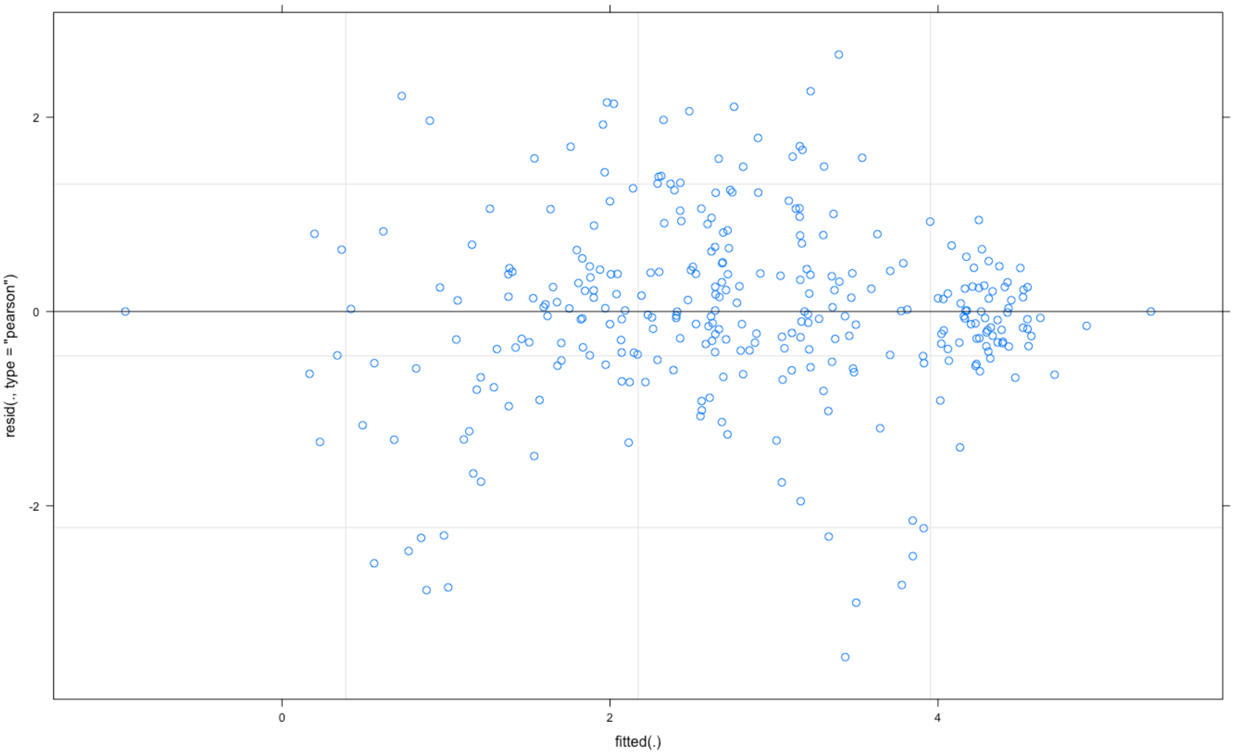

Figure 3.14: *Linear Mixed Model: Calories/Minute As a function of Month, Location, Plant Part, and Subject.*

This analysis tells us the determinants of foraging rate (kilocalories captured per unit time). We added in variables to determine the goodness of fit. Adding in variables beyond the null model did improve the fit by a considerable margin. Variables and factors included in our best-fit model (expanded upon below in *Tables 3.15 & 3.16*) included “location,” “plant part,” and month. Note that in mixed models p-values are not presented. Month, location, species, and plant part all significantly affected foraging rate, when accounting for repeated sampling of the same individuals,' and this best fit model had the lowest AIC value (Null = 1123, Best Fit Test= 983) compared to alternative models tested.

Table 3.15 - ***Linear Mixed Model Fitting and Models.***

Linear mixed model fit by REML ['lmerMod']:

Formula: kcal.min ~ as.factor(MonthNum) + as.factor(Location) + as.factor(Species) + as.factor(PlantPart) + (1 | Subject)

Null Model Test (*kcal/min by Subject)*:

Formula: lmer(kcal.min ~ (1|Subject))

AICc(Null) = 1122.67

Linear Mixed Model Best Fit: (*kcal/min by Month by Location by PlantPart by Subject)*:

Formula: kcal.min ~ as.factor(MonthNum) + as.factor(Location) + as.factor(PlantPart) + (1 | Subject)

AICc(Model) = 983.1

Table 3.15: *'Null Model' versus 'Linear Mixed Model: Best Fit', with associated AIC model scores. REML criterion at convergence: 851.7*

Table 3.16: ***Linear Mixed Model - Fixed Effects***

Fixed Effects	Estimate	Std. Error	t value
(Intercept)	3.60934	0.65109	5.544
as.factor(MonthNum)2	0.11428	0.30714	0.372
as.factor(MonthNum)3	-0.61881	0.32457	-1.907
as.factor(MonthNum)4	-0.24945	0.32446	-0.769
as.factor(MonthNum)5	-0.32853	0.40865	-0.804
as.factor(MonthNum)6	-0.47365	0.39475	-1.2
as.factor(MonthNum)7	-0.43315	0.40604	-1.067
as.factor(MonthNum)8	0.36757	0.4347	0.846
as.factor(MonthNum)9	-0.03847	0.49284	-0.078
as.factor(MonthNum)10	-0.01403	0.35613	-0.039
as.factor(MonthNum)11	-0.08078	0.36042	-0.224
as.factor(MonthNum)12	0.23641	0.384	0.616
as.factor(Location)Wet	0.55271	0.76125	0.726
as.factor(Species)Antidesma venosum	-4.94529	1.69819	-2.912
as.factor(Species)Berchemia discolor	-4.36526	1.37938	-3.165
as.factor(Species)Cirina forda	1.1958	1.22218	0.978
as.factor(Species)Cyperus papyrus	-4.87484	1.61191	-3.024
as.factor(Species)Cyperus sp.	-2.49789	1.245	-2.006
as.factor(Species)Dialium engleranum	-3.33309	1.46248	-2.279
as.factor(Species)Diospyros chamaethamnus	-2.00307	1.35338	-1.48
as.factor(Species)Diospyros mespiliformis	-3.97101	1.51795	-2.616
as.factor(Species)Diospyros virgata	-2.8328	1.30428	-2.172
as.factor(Species)Ficus sycomorus	-2.49882	1.69405	-1.475
as.factor(Species)Garcinia livingstonei	-3.22692	1.63884	-1.969
as.factor(Species)Gonimbrasia belina	0.0567	0.98665	0.057
as.factor(Species)Grewia avellana	-4.20003	1.32043	-3.181
as.factor(Species)Grewia bicolor	-3.37507	1.33088	-2.536
as.factor(Species)Grewia falcistipula	-3.73236	1.35297	-2.759
as.factor(Species)Grewia flavescens	-4.88944	1.33256	-3.669
as.factor(Species)Grewia retinervis	-4.48975	1.28377	-3.497
as.factor(Species)Guibourtia coleosperma	0.76852	0.62187	1.236
as.factor(Species)Nymphaea lotus	-4.22982	1.48073	-2.857
as.factor(Species)Nymphaea nouchali var. caerulea	-5.51422	1.43335	-3.847
as.factor(Species)Ochna pulchra	-3.51271	1.46052	-2.405
as.factor(Species)Parinari capensis	-0.75725	1.63183	-0.464
as.factor(Species)Parinari curatellifolia	-2.50129	1.43882	-1.738
as.factor(Species)Phoenix reclinata	-4.3537	1.54522	-2.818
as.factor(Species)Raphionacme burkei	-0.01485	0.95858	-0.015
as.factor(Species)Rhus tenuinervis	-3.44191	1.30348	-2.641
as.factor(Species)Sclerocarya birrea	-2.2017	1.85981	-1.184
as.factor(Species)Syzigium cordatum	-4.52844	1.63884	-2.763
as.factor(Species)Syzigium guineense	-4.32631	1.46985	-2.943
as.factor(Species)Typha capensis	-4.96921	1.63768	-3.034
as.factor(Species)Vangueria sp.	-2.47538	1.34541	-1.84
as.factor(Species)Ximenia americana	-3.43714	1.31784	-2.608
as.factor(Species)Ximenia caffra	-2.78094	1.27844	-2.175
as.factor(PlantPart)Fruit	2.94828	1.12958	2.61
as.factor(PlantPart)Nut	1.97059	1.67123	1.179
as.factor(PlantPart)Pith	3.37254	1.28916	2.616
as.factor(PlantPart)Rhizome	3.63753	1.11444	3.264
as.factor(PlantPart)Rhizome (Imm.)	2.29823	1.15579	1.988
as.factor(Species)Ximenia caffra	-0.47882	0.75849	-0.631

Calories/Minute As a function of Multiple Factors

Seasonal variation by foraging location

In an attempt to further understand habitat-specific return rates, we assessed Wet and Dry post-encounter return rates on a monthly basis. *Figure 3.17* shows that from September through January the foraging returns in Dry habitats were higher than those in Wet habitats. In the other months of the year the confidence intervals overlapped.

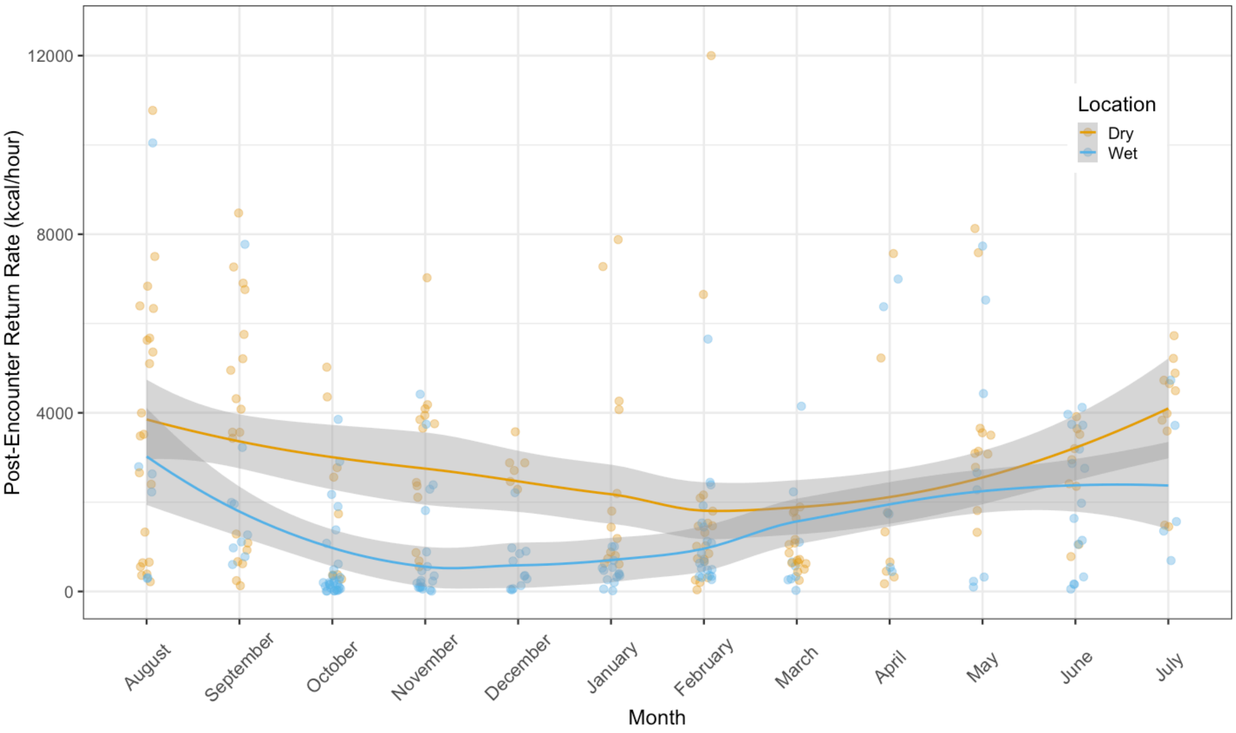

Figure 3.17: *Post-encounter return rates (kcal/hr) by month, in Dry (orange) and Wet (blue) foraging locations. Modeled lines include a shaded 95% confidence interval based on the within habitat monthly variation in post-encounter return rates. The Wet habitat was never more productive at the month level than the Dry habitat. For roughly half of the year, the Dry habitat was in fact more productive than the Wet.*

The observed monthly variation might be explained by the seasonal effect of rain and flood events. Rains arrived late during this field season, and the region received around ~420 mm of rainfall in the year of study (average rainfall is ~475mm). The majority of rain fell between January (month 6) and May (month 10). July (month 12) and August (month 1) typically represent the dry period, with the annual flood period in the panhandle reaching lowest levels around that time. The bimodal distribution of rain as seen in *Figure 3.1*, however, was atypical.

What explains the increased profitability of Dry habitats?

Having determined that post-encounter return rates were higher in Dry habitats than in Wet habitats (contrary to our prediction), we wanted to explore our data to determine what produced the observed habitat differences, and why Wet habitats were not more profitable than Dry ones.

Differences in habitat profitability (indicated by higher return rates) could in theory result from (Q_1) decreased search and handling times, as well as (Q_2) habitat specific differences in species and plant part distribution, which might produce (Q_3) differences linked to the caloric density or yield from certain plant parts. Habitat variability could be reduced in a number of ways, influenced by the presence and distribution of water availability of other abiotic factors. The year-round presence of water available to delta plants might have led to reduced seasonality in plant productivity, although productivity was not assessed directly. Furthermore, floodplains commonly used as foraging locations by women present may act as one large patch, reducing subsequent search time. Women can simply collect aquatic resources while moving within a patch, rather than moving between them, as is necessary with trees or bushes in Dry foraging locations.

Q2: Wet vs Dry Differences in Plant Parts and Species

In order to determine whether differences in habitat profitability were connected to search and handling time (Q_1) or aspects of food properties (Q_2) and caloric density (Q_3), we looked for additional indicators of differences between Wet and Dry foraging locations. We found significantly reduced dietary species richness breadth in the Wet location as indicated by the results of a Wilcoxon signed rank test (V = 63, p-value = 0.0079). Species richness for Wet and Dry habitats are shown in *Figure 3.18* for each month of study.

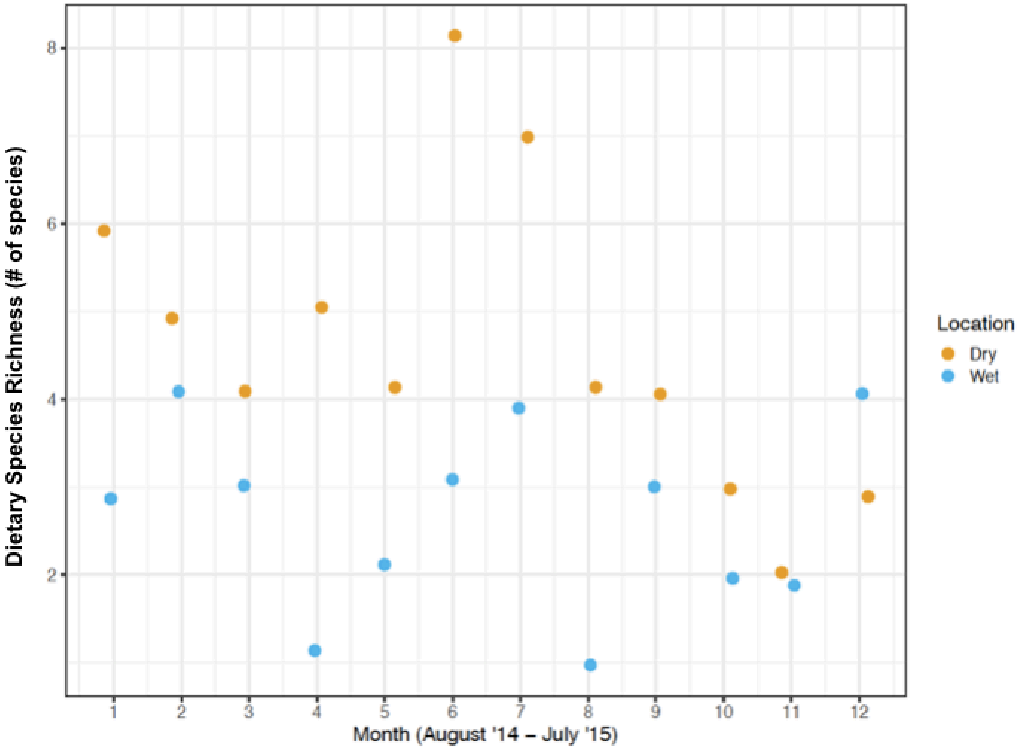

Figure 3.18: *Dietary Species Richness in Wet and Dry foraging locations, by month.*

Furthermore, women foraging in Wet habitats appeared to have generally targeted fewer plant parts (*Figure 3.19*) and species (*Figure 3.20*). Figure 3.19 demonstrates that the majority of foraging bouts in Wet habitats focused on just three plant parts: pith, fruits, and USOs. In the Dry habitat, foraging efforts appeared to be more evenly distributed across six dominant plant parts (arils with seeds, flowers, larvae, nuts, pith, fruits, and tubers). *Note: while larvae are not a plant part, they are picked off of plants such as mopane in a manner consistent with fruit picking.*

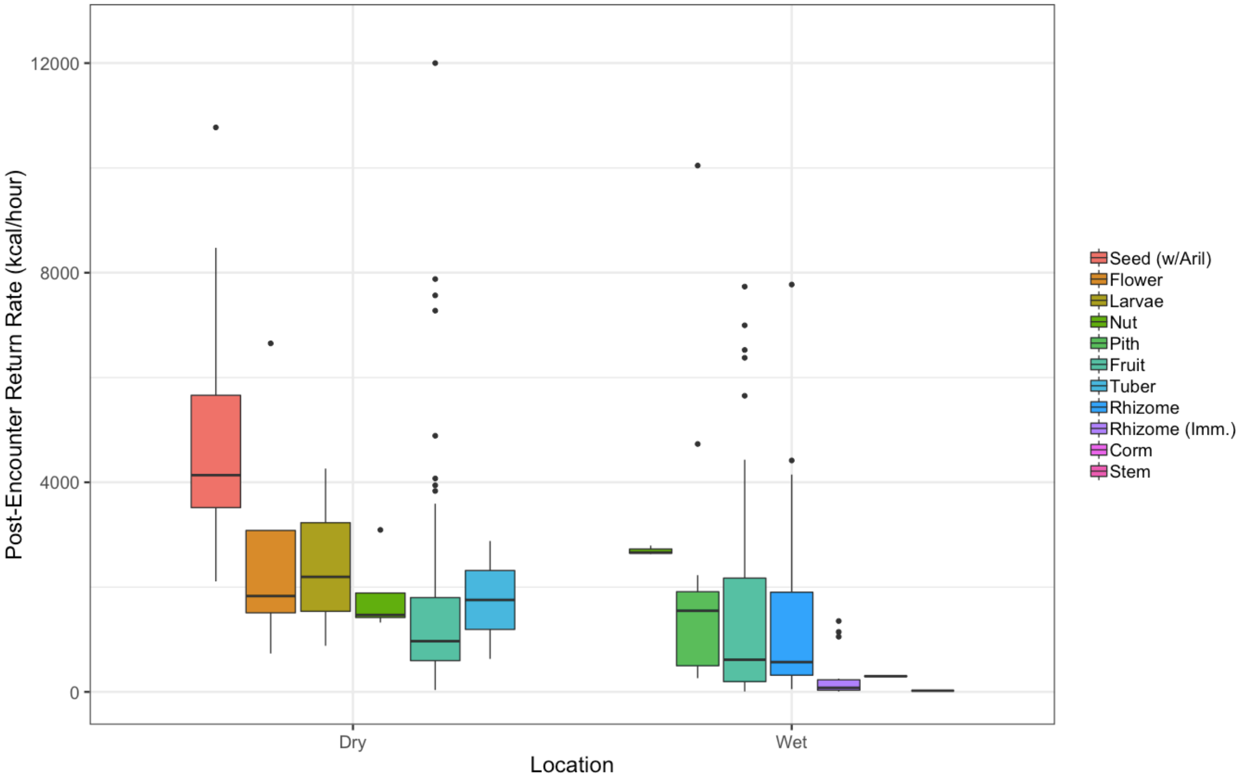

Figure 3.19: *Post-encounter return rates (kcal/hr) by plant part (in rank order), in Dry and Wet foraging locations. Seeds with arils appear to have driven high Dry habitat return rates. Wet habitat returns were dominated by USOs (primarily rhizomes from Nymphaea sp.), despite the fact that the return rates for USOs were comparable to piths and fruits. Overall, returns in the Wet habitat were fairly modest.*

Q3: Plant Parts and Species differ in caloric density

Although difficult to see, *Figures 3.19 & 3.20* show a similar finding - that seeds with arils (especially *Guibourtia coleosperma*) yielded very high return rates. USOs were associated with modest return rates. So while dietary species richness is low in Wet habitats, foragers often focused on moderate to low return UWSOs and USOs, while in Dry habitats foragers accessed more calorically dense foods, such as seeds with arils and nuts (*Q_3*).

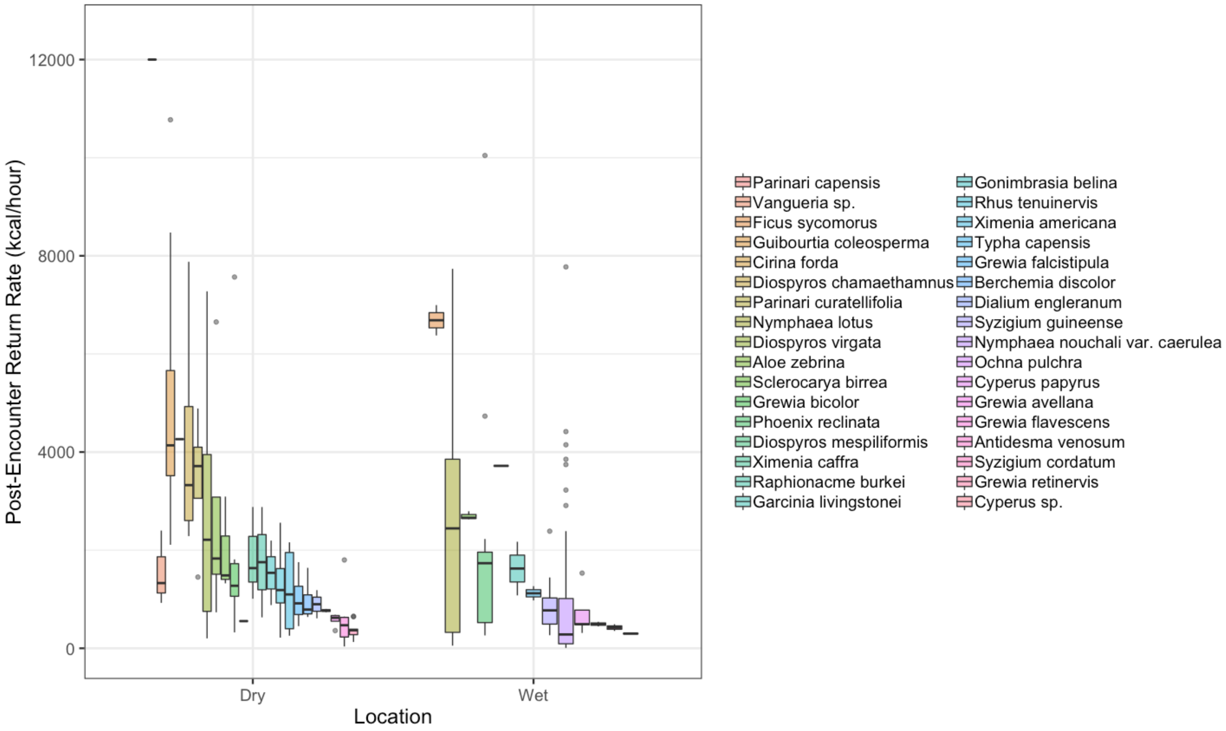

Figure 3.20: *Post-encounter return rates (kcal/hr) by species (in rank order), in Dry and Wet foraging locations.*

Food composition as a driver of profitability

Given the reduction in overall foraging time in Wet foraging locations, and the indication the Wet habitats may also exhibit reduced variation (via both seasonal change and diet breadth restrictions), it appears that differences in measured profitability (based on kcal/hr return rates) may be chiefly explained by the increased nutritional quality of foods specific to the Dry foraging locations. Comparisons of plant parts (*Figure 3.19*) and species (*Figure 3.20*) support the claim that in general, seeds with arils, flowers, and nuts were particular to Dry habitats, while USOs such as tubers and rhizomes (especially *Nymphaea spp.*), and stems were much more common in Wet locations. When we analyzed the macronutrient composition of the foods recovered, explanations emerge.

Following up on the previous figures showing the kcal/hour foraging rate by plant part*, Figure 3.21* shows how plant parts varied in their macronutrient composition, which played a direct role in determining the caloric value of foods. High lipid content of both seeds (with arils) and nuts (foods restricted largely to Dry foraging locations) played the major role in determining the higher foraging productivity of Dry habitats.

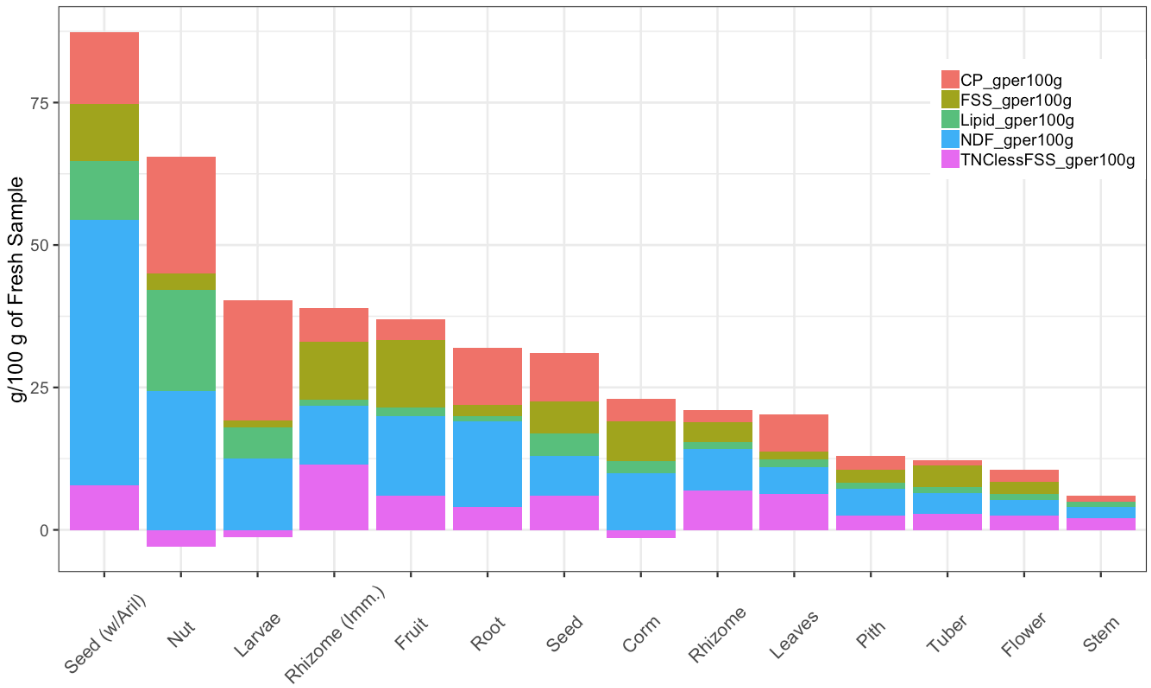

Figure 3.21: *Macronutrient composition by plant part. Plant part is listed on the horizontal access, and the five key macronutrients are stacked and coded by color. Total non-structural carbohydrate (TNC) less Free Simple Sugars (FSS) a measure of digestible non-sugar carbohydrates, are purple. Crude Protein (CP) is red; FSS is colored brown; Lipid is green; Neutral Detergent Fiber (NDF) is blue. NDF, while not factored into nutritional analyses in this model, also has the potential to reflect some level of starch erroneously captured during the fiber analysis. (Negative TNC values should be interpreted as zero).*

However, it is worth noting that the immature rhizomes of water lily species (*Nymphaea sp.)* were relatively calorically dense, and that USOs in general are of moderate food utility, providing an intermediate caloric return relative to the other resources in our dataset. Also, this figure shows about what we would expect, with pith, flowers, and stems being of low food utility.

Q4: Foraging Costs: Post-Encounter Energetic Foraging Efficiency Ratios

Certain food resources required particular postures to be assumed during foraging pursuit. As we know from the heart rate and respirometry calibration tasks, postures varied in their energetic costs. We analyzed post-encounter foraging costs (expressed as VO2/min/kg) by plant part to see the cost of foraging for particular resources. In *Figure 3.22* we see that the Dry habitat tended to have higher Energetic Foraging Efficiency scores than did Wet habitats. Tellingly, the efficiency ratios (post-encounter kcal produced / kcal expended handling) were generally higher in the Dry habitats than in Wet, complementing the higher on average caloric returns, and mirroring the results previously reported for the traditional post-encounter return rates (kcal/hr).

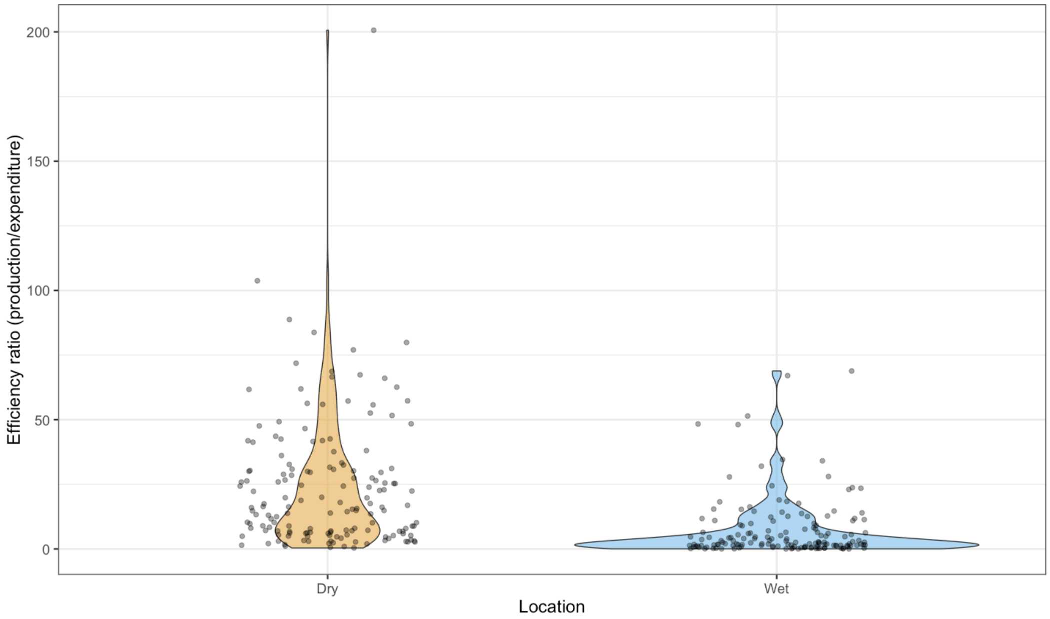

Figure 3.22: *Energetic Foraging Efficiency Ratio in Dry (orange) and Wet (blue) foraging locations.*

Foraging costs (handling) differed slightly by habitat type. *Figure 3.23* shows that the foraging cost, expressed as the volume of oxygen consumed by the forager (VO2 ml O_2/kg/min), differed slightly by plant part and foraging location. The Wet habitat was slightly more costly to forage in than the Dry habitat – furthering the productivity gap, when combined with the higher on average caloric return of the Dry habitat.

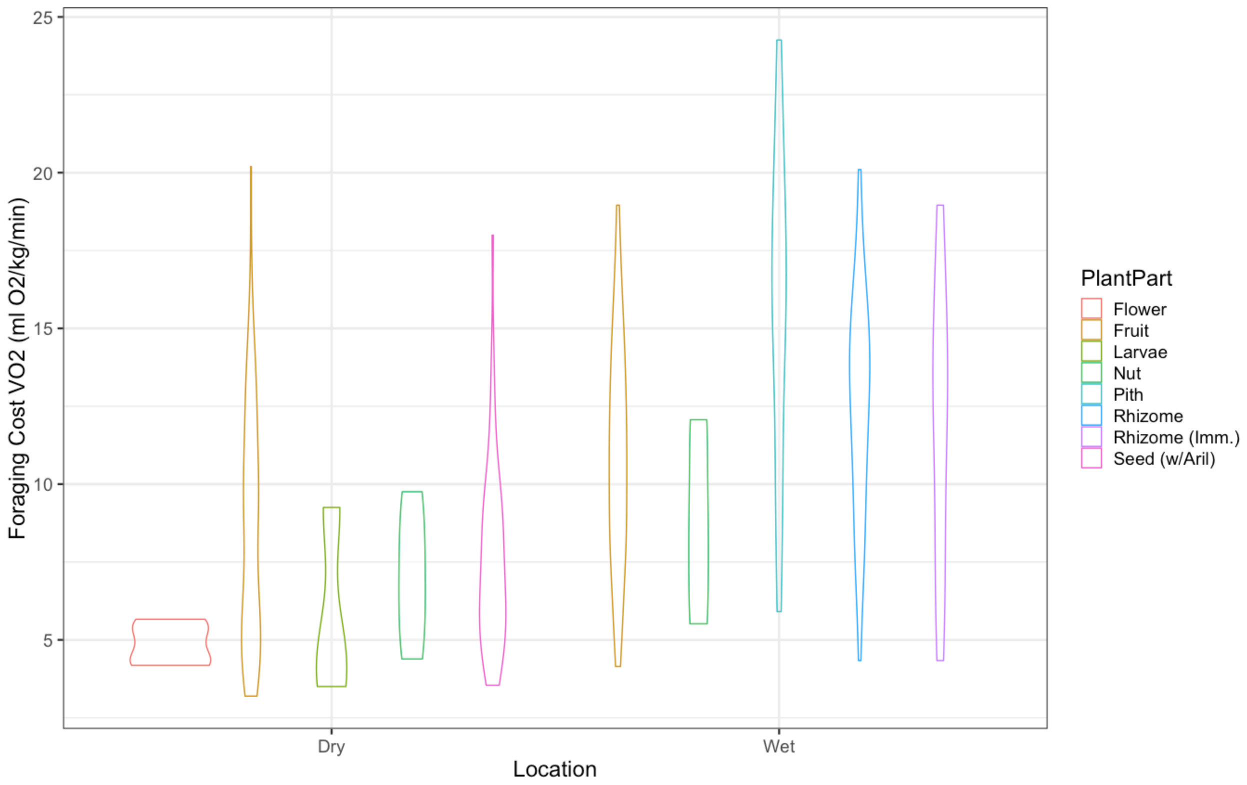

Figure 3.23: *Costs of foraging for different plant parts (handling) in Dry (left) and Wet (right) foraging locations.*

Post-Encounter Energetic Foraging Efficiency Ratios

As with *Figure 3.17*, *Figure 3.24* shows that the Dry foraging locations were slightly more profitable for foragers in most months, though there was slightly less variation present in the analysis of energetic foraging efficiency than post-encounter return rates alone. Overall the dry habitat had greater returns per unit (kcal) of effort.

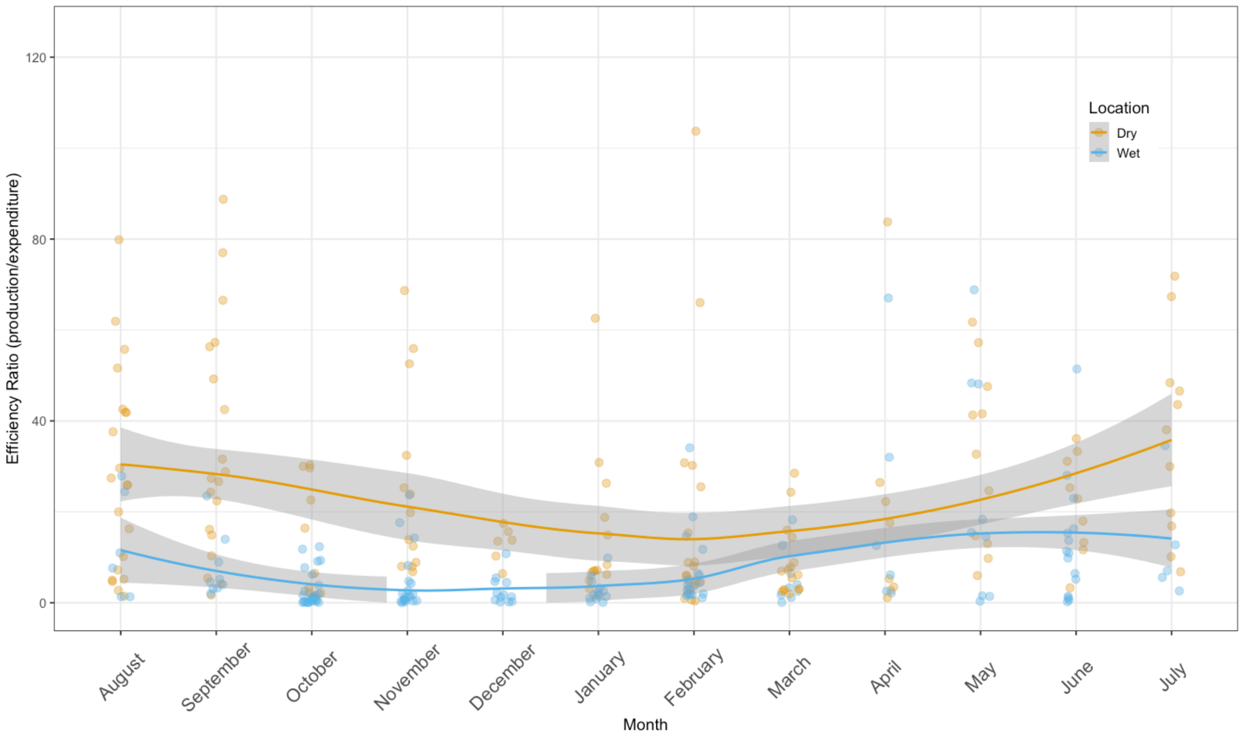

Figure 3.24: *Post-encounter Energetic Foraging Efficiency Ratio by month and in Dry (orange) and Wet (blue) foraging locations.*

Discussion

Using the Okavango Delta and its surrounding dry savanna woodland as a model habitat, we compared foraging success in adjacent Wet and Dry habitats. In each habitat, we assessed how much food women obtained per hour of foraging, how nutritionally beneficial the foods were, and how much energy the women expended while foraging.

We found evidence indicating that Dry habitats were more productive than Wet ones, based on the post-encounter foraging returns and post-encounter Energetic Foraging Efficiency models we produced. While we found that Dry habitats tended to be more productive than Wet habitats on the basis of caloric return rates, we did find that certain aspects of wetland foraging were associated with positive indicators of habitat quality. In particular, search time, handling time, and diet species richness were all reduced in wetland habitats compared to Dry. While greater diet species richness and biodiversity are typically associated with increased dietary quality in the diets of subsistence populations (Lachat et al., 2018), a narrowed focus may indicate specialization on key productive resources.

Having determined that Dry habitats produced on-average higher return rates than Wet habitats, we sought further context by studying the caloric and energetic productivity of each habitat type. We determined that much of the high productivity of the Dry habitat can be attributed to the profitability of certain plant parts, namely nuts and arils, which occur more frequently in Dry habitats than Wet. By comparison, USOs, UWSOs, and pith were targeted with much more regularity in Wet habitats than Dry. The relatively high caloric post-encounter return rates of the Dry habitat stand as one striking result of this analysis.

The higher productivity of the Dry habitats on average means that access to Dry habitats is valuable, but it does not necessarily undermine the idea that access to Wet habitats is important also. For the women of Seronga (living in easy range of Wet locations), the Okavango is a better-integrated habitat than for the women of Gudigwa (confined to Dry areas). Women from Seronga benefit from the complementarity of Wet and Dry habitats. They have the ability to access two distinct foraging habitats with mere short logistical forays, and can choose to access both on a single day, in any season. Women in Gudigwa, by contrast, do not have the choice to forage in Wet habitats for much of the year.

Search and handling costs were generally higher in Wet habitats – perhaps a dual effect of the physical resistance to locomotion in water (necessitating wading and poling), as well as a thermoregulatory effect of having to counteract the cooling of the body by cool surface waters. These increased costs likely counteracted the significant reduction in time spent searching and handling in Wet habitats. Similarly, the nutritional properties of foods gathered in each habitat tended to differ only minimally, again with the exception of lipid-rich foods gathered in the Dry habitat.

The expectation, derived largely from the premise laid out in the Delta Hypothesis, was that Wet habitats would be more profitable. However, it must be noted that this study was not a definitive test of the Delta

Hypothesis, as the comparisons presented here between wet and dry habitats focus on post-encounter return rates, As such, there are key predictions from the Delta Hypothesis regarding encounter rates, patch density, and plant regeneration that are not addressed by the methods used here. The quantitative analysis presented here did however show that on the basis of post-encounter return rates, Dry savanna woodland habitats of the Okavango Delta displayed greater foraging success as indicated by the returns of local women. In an attempt to merge the benefits of foraging (in the form of caloric return rates) and foraging costs, we developed a new measure of post-encounter energetic foraging efficiency, which we call the Energetic Foraging Efficiency Ratio (post-encounter production/ handling expenditure). By accounting for subject-specific activity costs, we reconstructed return rates in a manner that accounted for the cost of acquisition. While this did not dramatically change the profitability or ranking of resources in either habitat, it was interesting to see the costs of specific foraging behaviors. While the more detailed accounting of foraging success represented by Energetic Foraging Efficiency is a theoretically salient index, the simple fact of the matter is that it did not change the outcome. This is interesting, as it suggests that the standard and much more easily attained index of profitability, post-encounter return rate, is an adequate measure of foraging success under most circumstances and conditions.

We suggest that future study efforts into the Delta Hypothesis should find a way to compare habitats for other measures of productivity such as food abundance (enough for a whole village?), rates of food source recovery (quicker regrowth in Wet?), as well as the cost of searching from mobile camps (rather than fixed settlements). Future work could benefit from an experimental framework in which women are asked to forage in both a Wet and a Dry location on several days per month (rather than choosing only one). This approach would produce pair-matched return rates (in every month and habitat). It may also buffer future studies from any potential differences in ethnographic knowledge possessed by women occupying different villages – as such inequities likely exist. Women in Gudigwa, as noted in the Introduction, tended to have a greater reliance on wild foods, and likely retained greater skills and knowledge with regards to these resources. Study design could account for some of this in the future.

Paradoxically, women from Seronga live at the intersection of Wet and Dry habitats; yet, despite the ease with which women in Seronga could have biased their foraging activities to Dry habitats, they showed a clear preference for foraging in Wet habitats (*Figure 3.25*). Given the higher on-average caloric post-encounter (and overall) return rates from the Dry habitats, this remains a point that warrants further study. One must account for the way in which women in Seronga had access to both Wet and Dry in every month, while women in Gudigwa did not. Perhaps, with these modifications to study design, future efforts to test the Delta Hypothesis more comprehensively may be able to answer why it was that women in Seronga tended to prejudice their foraging activities towards the Wet delta habitat – despite the empirical evidence showing that Dry habitats tended to be more productive.

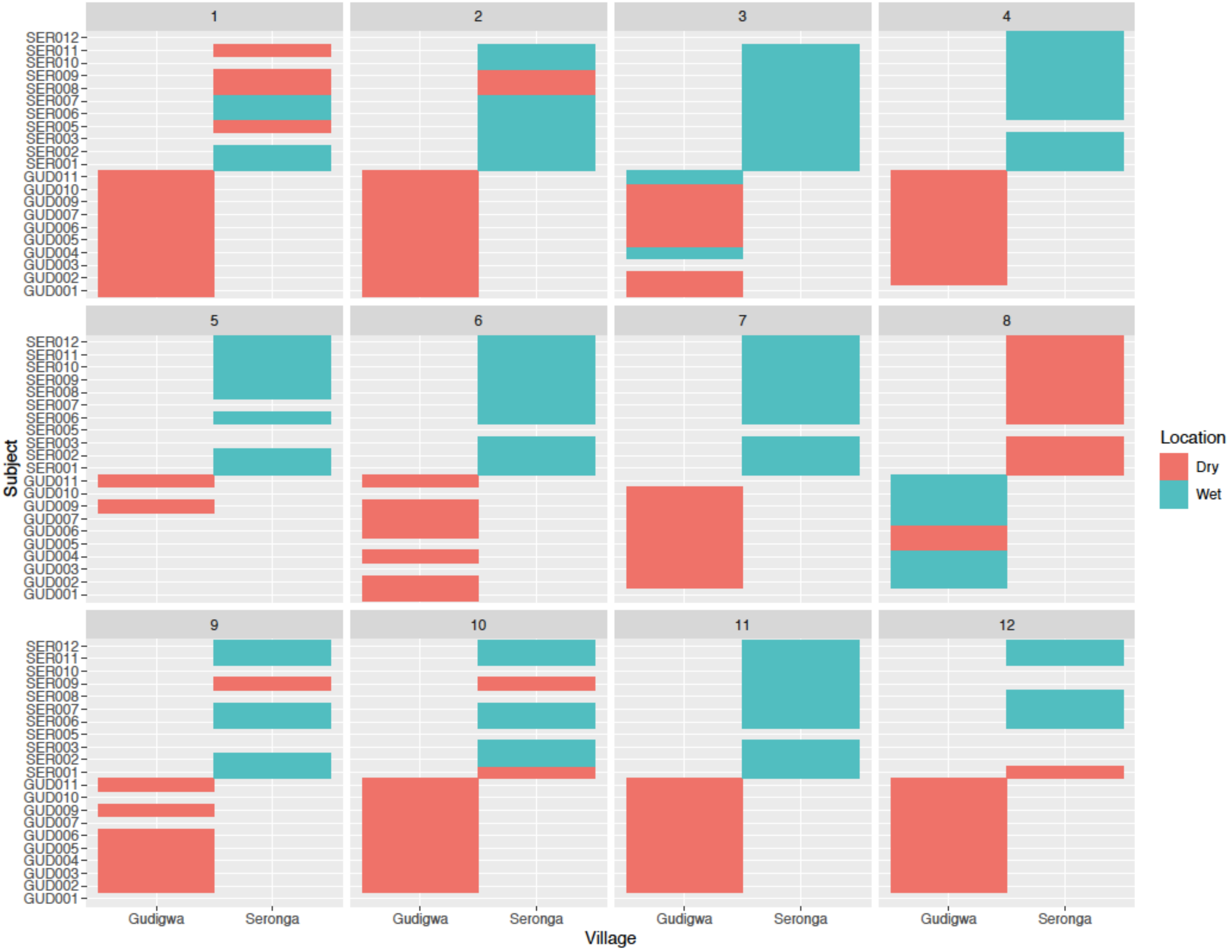

Figure 3.25: *Monthly foraging habitat choice, by subject and village. Despite year-round access to Dry habitats, women in Seronga generally chose to forage in Wet habitats. No statistical tests or surveys of female subjects were conducted to determine why they chose Wet habitats more frequently than Dry. However, this would be a natural starting point for subsequent study with this population.*

Ultimately, there is an irony to this work, as we set out to study women's foraging because of our belief that it was women's work that allowed men to take foraging risks. Women frequently underwrite the daily caloric costs of the family. However, Delta and Wet foraging may reflect a different side of the sexual division of foraging labor. It may be that in Wet habitats, men are able to procure more fat and protein with regularity and reduced variance than in Dry habitats (we did not study this here), and that in Wet habitats it is merely carbohydrates that are needed from women. While women in Dry habitats frequently collected lipid-rich arils, seeds and nuts it might be that men are collecting enough fats and protein from fish and aquatic game that there is less emphasis on these efficiency-maximizing foods by women in Wet foraging locales. In much of Africa, game is notably lean throughout much of the year (Speth, 2010), suggesting that lipids acquired by women may be particularly valuable in these habitats.

Conclusion

Most foraging populations today do not rely solely on wild foods for their survival. In truth, very few societies have survived independent of agriculturalists and pastoralists in the past century. Rather than merely dismissing the utility of these societies as models for human foraging, we must accept that this is the state of the field, and that it is likely that within the next few decades all human societies will be more inter-connected to those societies that surround them. There is a challenge to studying such societies, with wild and indigenous knowledge rapidly declining, and less routine foraging behaviors exhibited. The research model employed here – sponsored foraging trips – may be one way moving forward to experimentally compare foraging returns in different habitats, populations, and societies. I hope this paper can serve as one such jumping off point, presenting some methods and approaches for studying human behavior in a changing and interconnected global community.

Acknowledgements

I would like to thank the women who participated as research subjects, as well as the communities in the Okavango Panhandle that hosted me. Seronga was particularly welcoming during the 10 months I personally spent in Botswana. The Poler's Trust offered me a home base for me and for my research throughout the course of the fieldwork detailed here.

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CHAPTER 4

THE STARCH CONTENT OF UNDERGROUND STORAGE ORGANS (USOs) FROM DIVERSE AFRICAN HABITATS

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The starch content of underground storage organs (USOs) from diverse African habitats

Abstract

Underground storage organs (USOs) are widely acknowledged as an important food resource throughout human evolution, but their nutritional properties remain poorly characterized. Here we analyze a novel dataset on the concentration of non-resistant starch in African USOs eaten by foragers in five habitats relevant to human evolution. We found that rainforest tubers were high in starch, at levels comparable to the starch content of cultivated USOs. In contrast, USOs from more arid climates (collectively referred to as savanna) tended to be relatively starch-poor, in line with previous findings. Although starch from savanna USOs can be an important component of savanna forager diets (such as the Hadza and Ju/'hoansi), our results suggest that non-resistant starch is not the only variable responsible for USOs being chosen. Within a wet savanna habitat (Okavango Delta), starch content of water lilies (*Nymphaea spp*.) co-varied positively with protein (CP) and simple sugars (FSS), and negatively with indigestible forms of fiber (NDF and Lignin). These findings suggest that water lily rhizomes may have been a high quality food item for human foragers. The variation that we found in starch content emphasizes that the value of wild food resources can differ across habitats.

Introduction

Underground storage organs (USOs, including tubers, rhizomes, bulbs, corms, and other modified roots) have played a central role in a number of hypotheses regarding human behavior and dispersal (Hawkes 2003; O'Connell, et al. 1999), and social organization (Hawkes, 2003; O'Connell et al., 1999; Wrangham, 2009). USOs are plant vegetative parts that store nutrients, minerals, and water in below ground structures (Andersen, 1987). They have been implicated as crucial food sources during hominin and human evolution (Sponheimer et al., 2005; Sponheimer and Lee-Thorp, 2003): archaeological, morphological, and geochemical evidence suggest that hominin exploitation of USOs dates at least to the origins of *Australopithecus* and the advent of open-habitat foraging (Dominy et al., 2008; Hardy et al., 2015; Hatley and Kappelman, 1980; Laden and Wrangham, 2005; Peters and O'Brien, 1981; Ungar and Sponheimer, 2011; Yeakel et al., 2007). Hominins likely consumed USOs as part of an increasingly high-quality diet, presenting a contrast to living apes and most other primate species.

The only primates known to eat USOs often are certain terrestrial Old World primates, namely savanna baboons (*Papio cynocephalus*) and gelada monkeys (*Theropithecus gelada*) (Dunbar and Bose, 1991; Whiten et al., 1987; Wrangham et al., 2009). Importantly, USO consumption is largely absent from great ape diets (Conklin-Brittain et al 2002). In contrast, USOs are a staple food source among many hunting and gathering populations, both ethnographic (Kelly, 1995; Lee et al., 1968; Marlowe, 2005) and contemporary (Marlowe, 2010; Marlowe and Berbesque, 2009; Vincent, 1985a, b; Yasuoka, 2009, 2013). Humans may bear a derived genetic legacy related to habitual starch consumption as a result of dependence on USOs, exhibiting global variation in salivary amylase copy number that has been claimed to track dietary starch levels in hominoid evolution (Pajic et al., 2019; Perry et al., 2007; Perry et al., 2006), though uncertainties about the functional significance of amylase impose caution on this evolutionary hypothesis (Fernández and Wiley, 2017).

USOs bear favorable distinctive ecological and nutritive properties that support their exploitation by many human populations, and that would have made them appealing food sources to early hominins. They are abundant across African habitats, they are generally available year-round, and they are more dense in digestible energy than leaves. USOs may bear high levels of starch (Hardy et al., 2015; Hladik et al., 1984), and have been suggested to contain relatively low levels of indigestible fiber compared to other primate foods (Conklin-Brittain et al., 2002). These factors suggest that the dietary quality of early hominins that exploited USOs would have been raised compared to a diet based primarily on fruits and leaves, as observed among African apes – perhaps especially upon moving into dryer and more open “xeric” habitats where USOs can abound (Pate and Dixon, 1982; Vincent, 1985b).

Despite the prominence of USOs in scenarios of human evolution, empirical studies of their nutrient value remain limited. To date, investigators have described USO starch concentration (Hladik, et al. 1984; Schoeninger et al. 2001), and distribution and abundance for two human forager populations in Africa, the Baka and the Hadza (Vincent 1985a; Vincent 1985b; Yasuoka 2009; Yasuoka 2013; Yasuoka 2010). The mechanical properties of USOs have been preliminarily investigated with Hadza tubers (Dominy et al. 2008). Geophyte availability has also been assessed in the Cape *fynbos*, a setting that has received much attention for its role in the evolution of modern humans (De Vynck et al., 2016; Procheş et al., 2008; Singels et al., 2016). Wetland savannas, which have been proposed to be important sources of USOs during times of food scarcity and during human migrations, have largely been ignored by anthropologists despite a high co-occurrence with hominin fossil bearing sites (Wrangham et al., 2009). As a result of the limited scope of this research, the dietary quality of USOs and its variation among habitats remains poorly understood. Wild rainforest yams in the genus *Dioscorea* have been reported to have starch content similar to domesticated tubers (Hladik et al., 1984; Yasuoka, 2010), foods considered to be energy-dense staple food sources for many modern industrial human populations (Zeeman et al., 2010). In contrast, Schoeninger et al. (2001) described savanna USOs collected by Hadza hunter-gatherers in Tanzania as being of relatively low-caloric value, based on a small set (n=7 specimens across three species) of fiber-rich and low-to-moderate starch samples. These two contemporary foraging populations from which we have data on starch concentration present two very different pictures of USO starch content.

Starch is highlighted in the diet of foragers and modern domesticated diets alike because it is one of the main storage molecules used by plants, particularly for energy stored below ground in geophytes. A polymeric carbohydrate, starch is composed of the polysaccharides amylopectin and amylose. Starch is generally highly bio-available. In fact, 60-70% of human caloric intake is estimated to derive from starch (Robyt, 2008). Starch digestibility is largely affected by the ratio of amylose:amylopectin and the physical structure of starch granules (Englyst and Englyst, 2005). Amylose can form very compact structures that make glucosidic bonds much more inaccessible to digestive enzymes. Such difficulty digesting has led to the classification of some starches as ‘resistant forms’ (i.e. resistant starch, or RS). Other starches are described as ‘rapidly’ and ‘slowly digestible starch’ (RDS & SDS respectively). Together RDS and SDS represent the fraction of native starches likely to be completely digested by humans, particularly through the use of simple food processing techniques (Englyst and Englyst, 2005). We focus on these two forms of non-resistant starch. Unless otherwise noted, all further references to starch are to the non-resistant starches measured in this study.

The role of USOs in scenarios of human evolution extends beyond the time of early hominins to the emergence of our own genus *Homo* and subsequent modern human migration patterns across the globe. Charred remains of edible USOs (*Hypoxis spp.*) dated to 170kya in South Africa (Wadley et al., 2020) provide direct evidence of early USO exploitation by anatomically modern humans.

Wet savanna (deltaic and lacustrine) habitats have been proposed to offer important fallback resources in the form of water-associated USOs to humans and baboons alike. Plant parts from water lilies, semiaquatic emergent, and floodplain herbs are hypothesized to have nutritionally favorable qualities (Wrangham, 2005; Wrangham et al., 2009). Wadley et al. (2020) noted that *Hypoxis angustifolia* rhizomes proliferate in wetter (mixed savanna) habitats today, and claimed that such resources “*would have provided reliable and familiar carbohydrate sources for mobile groups.”* Humans and savanna baboons (Wrangham et al. 2009) alike exploit the USOs from the Okavango Delta region (see Chapter 3, which uses foraging data to contextualize the data on macronutrient content presented here).

Other than dry savannas, the best data available on the starch content of wild USOs comes from rainforest habitats. Recent evidence shows that rainforest yams in lowland central Africa can occur in such high abundance that they offer significant yield potential for Baka hunter-gatherers in Cameroon (Sato, 2001; Yasuoka, 2006, 2009, 2010, 2012, 2013). During long-term foraging expeditions by Baka bands (up to 2-3 months) known as “molongo,” wild yams accounted for 62% total household energy intake (Yasuoka 2009). Prior to the documentation of molongo returns for the Baka, researchers suggested that carbohydrates could actually be quite scarce in rainforests. Yasuoka’s (2009) findings demonstrate that rainforest populations can derive a majority of their calories from wild yams during at least a few months. However, it is unclear whether this is due to the timing of molongo expeditions, perhaps coinciding with seasonal peaks in *Dioscorea spp*. nutritional quality, or more general patterns of yam availability and quality. For most rainforest foraging populations, over half of calories consumed come from starchy foods (USOs and grains) acquired from local agricultural groups through the trade of forest products (Bahuchet et al., 1991; Bailey et al., 1989; Headland and Bailey, 1991). This has led to the idea that rainforest foragers could not obtain sufficient calories from the rainforest habitat alone, a debate dubbed the “wild yam question” (Bahuchet et al., 1991; Headland, 1987; Headland and Bailey, 1991; Headland and Reid, 1989).

The major question motivating the present study is whether the reported differences in USO starch concentration between Central African rainforest (Central African Republic and Gabon) and East African savanna (Tanzania) are representative of starch content across other rainforest and savanna habitats. Here, we report on the starch content of wild USOs samples from both underground and underwater plants from several new study countries in sub-Saharan Africa. We adopt the basic binary habitat structure of Laden and Wrangham (2005), identifying two contrasting tropical ecosystems – rainforest (R) and savanna (S). Our data come from two sources. First, we present data on starch concentrations from USOs foraged by populations across five ecologically distinct habitats, including Botswana (S), Namibia (S), South Africa (S), Tanzania (S), and Uganda (RF) (we refer to this as our “novel dataset”). Two of these populations, the Hadza of Tanzania and the Ju/'hoansi (!Kung) of Namibia, have rich traditions of previous study by anthropologists. Previously, anthropologists have broadly considered savanna and rainforest habitats as two distinct location groupings that ought to correlate with USO abundance, density, and perhaps food quality (Laden and Wrangham, 2005). We apply this binary habitat classification to the all study countries from which samples were included. Second, we compiled published data on starch content of USOs across one savanna and five rainforest habitat types, including some common USO food species (such as the sweet potato), from both anthropological and food science literature (we refer to this as our “published dataset”). Given that many USO discussions are centered around starch content and availability, and the lack of general understanding regarding USO starch availability by habitat type, we have chosen to take a narrow focus in this study and to concentrate on the non-resistant starch content of USOs.

Kelly (2013) noted in his review of human foraging that women in ethnographic and contemporary foraging populations generally acquire more plant resources than do men. Female foragers are expected to maximize energy intake for themselves and their offspring, while limiting variance, within a set of constraints (Hurtado et al., 1985; Hurtado et al., 1992). Bliege Bird et al. (2009) found that Martu women prefer foods that improved the probability of providing “*a successful daily harvest*” (pg. 120). For many women in African foraging societies, USOs provide a common solution balancing the demands of meeting energetic needs and constraints (Hawkes, 2003; Lee et al., 1968; Marlowe and Berbesque, 2009; O'Connell et al., 1999; Schoeninger et al., 2001; Vincent, 1985a). By providing quantitative information about starch concentrations, we hope to improve our understanding of how USOs would have contributed to hominin foraging success, particularly for women who spend much more time pursuing USO plant foods.

Materials and Methods

Study sites

We use data collected in five habitats by various research teams whose collection efforts spanned some 13 years. Table 4.1 shows the study sites, their habitat types, and the research effort. A. Cunningham conducted fieldwork in three of the locations presented in this study: Botswana, South Africa, and Uganda.

Fieldwork in Botswana was conducted in the North West District, in and around the Okavango Delta. Women from two study villages (Seronga and Gudigwa) foraged for wild foods during monthly focal follows between August 2014 and July 2015. Women were recruited with input from local village leaders, who suggested participants with knowledge and experience collecting and using wild plant resources.

Fieldwork in South Africa occurred in August 2013, and was focused on the region around Stilbaai, in the Hessequa Municipality of the Western Cape. Women were recruited from 5 settlements near five vegetative zones participated in experimental foraging bouts. While some women had limited knowledge of wild plant utility, most lacked a true working familiarity with edible wild resources – reflecting the loss of indigenous knowledge in the current generation. Given this lack of local expertise, women were instructed to target species known or suspected to be edible based on previous work in the area (De Vynck et al., 2016; Singels et al., 2016).

Fieldwork in Uganda occurred in two field seasons, from December 2010 to January 2011, and from June to July 2011 (during the two annual dry seasons). The sampling of yams from Uganda 6 months apart was notable given the seasonal variation in yams referenced by Yasuoka (2009) and Dounias (2001). Subjects were identified with the assistance of the Batwa Development Program (BDP). Twa men and women from the village of Byumba gathered yams in designated plant resource harvest areas of Mixed Use Zones (MUZs) adjacent to Bwindi Impenetrable National Park (Byarugaba, 2010; Byarugaba et al., 2007). AJC measured participants' energy expenditure while they foraging for USOs. Participants typically searched for only two classes of food while moving through the forest – wild yams, and honey. The primary aims of this work were related to energy expenditure and tuber roasting experiments, but only unroasted USOs were analyzed for starch concentration.

Research in Tanzania was conducted by M. Firestone, who collected data as part of his Harvard University undergraduate thesis under the direction of R. Wrangham (Firestone, 2003). From September 2002 to October 2003, Firestone accompanied researchers working with Frank Marlowe (Marlowe, 2010) on foraging trips with Hadza hunter-gatherers. Hadza participants were part of a long-term research study lead by Marlowe. Subjects collected and processed wild plant foods from the area around Lake Eyasi. Firestone preserved samples for nutrient analysis at Harvard. In addition, a large collection of samples were collected by N. Conklin-Brittain and A. Crittenden in 2004 and 2005, in collaboration with F. Marlowe. A. Crittenden preserved samples in the field and conducted the non-starch nutritional analyses at Harvard in 2006-2007.

Firestone also spent October 2002 to January 2003 working with the Ju/'hoansi (!Kung), in the NyaeNyae Conservation area of Eastern Namibia. Firestone was primarily interested in forager cooking habits as they pertained to USOs, though he also collected raw (uncooked) plant samples for comparison.

Table 4.1 - ***Sample origins for unpublished data.***

Study Country (S or RF)	Habitat type	Annual rainfall (mm)	Elevation (m)	Foraging population	Sample collector	Dates collected	# of species
Botswana (S)	Zambezian Flooded Woodland; Köppen: Mid-Latitude Steppe and Desert Climate	520	980	Yei Bugakhwe	AJC	Aug 2014 – Jul 2015	6
South Africa (S)	Cape Floral Fynbos; Köppen: Marine West Coast Climate	1200	100	Khoe-San descendants	AJC	Aug 2013	9
Uganda (RF)	Albertine Rift Afromontane Forest; Köppen: Tropical Monsoon	2400	1500	Twa	AJC	Dec 2010 - Jan 2011, Jun – Jul 2011	3
Tanzania (S)	East Africa Acacia Savanna; Köppen: Oceanic Subtropical Highland Climate	515	1400	Hadza	*1* MF *2* ANC	*1* Sep - Oct 2002, *2* 2005, 2006	4
Namibia (S)	Kalahari Xeric Savanna; Köppen: Mid-Latitude Steppe and Desert Climate	450	1150	Ju/'hoansi	MF	Oct 2002 – Jan 2003	12

Table 4.1: *Study Country shows where fieldwork was conducted, and where plant samples were collected. "S": savanna; "RF": rainforest. Rainforest is primarily evergreen forest, while savanna includes all other tropical and subtropical terrestrial habitats (Laden and Wrangham (2005). Annual rainfall and elevation are from https://en.climate-data.org/. Foraging populations include contemporary groups that collected samples included in starch analyses. Sample collector initials: (AJC) Andrew Cunningham, (ANC) Alyssa Crittenden, (MF) Matthew Firestone. Number (#) of species refers to species included in starch analyses reported in this chapter.*

Plant parts

USOs analyzed here included the following types: aerial tubers (bulbils), bulbs, corms, rhizomes, roots, and tubers (*Figure 4.2*). We follow the identification and terminology structure of Dominy et al. (2008), who in turn based classification on definitions and descriptions established in the botanical field (Manning et al., 2002; Pate and Dixon, 1982). Aerial tubers are potato-like tuber structures that grow off a stem; bulbs are modified and compacted shoots and scales or layers, such as onions; corms are a simple swollen and compacted stems; rhizomes are horizontal stems which are ever-growing; tubers are thickened roots of either perennial or adventitious origin.

Two samples collected by M. Firestone were simply labeled as 'root', indicating an informal designation for a woody underground component that did not identify as a readily definable USO of another sort. One such sample, from the species *Vigna frutescens*, was likely a tuber. It is a preferred USO species for Hadza foragers, referred to by them as //Ekwa (Marlowe, 2010; Marlowe and Berbesque, 2009; Schoeninger et al., 2001). The other 'root' collected by Firestone was from Namibia, and lacks enough additional information to reclassify. One additional species from South Africa, *Annesorhiza nuda*, was a small taproot (not a true tuber). As such, it is classified simply as a 'root'. The roots from *Annesorhiza nuda*, as well as some corms (*Chasmanthe sp.* and *Ferraria sp.*), harvested by women in South Africa contained both newer growth and USOs developed during previous years' growth. Because local women lacked the ethnobotanical knowledge to determine utility for these species, we only included the fresh (most recent year's) plant part in this analysis.

Field Collection of USO Samples

Food samples were collected by local research participants or were harvested directly by the researchers. In all cases, fresh samples were preserved in the field in the same fashion. Whole plant samples were weighed for fresh weight (FW). Because handling and processing techniques differed among observed foragers, there is some variation in our sample in the level of pre-collection modification. The level of post-procurement processing is noted in the supplementary materials (*Table SM 4.1, Column "notes"*). Such processing was performed to reduce food items to an edible portion by removing the inedible parts such as woody peels, (bitter) leaves, thorns, etc. The edible fraction was weighed by either the observer or forager. Fresh samples (whole or usable/edible portion) were then sliced and dried at ~40° C (drying method was subject to variation between research team). After drying to constant weight, samples were again weighed to determine the field dry matter (% FDM). Individual dried samples were labeled and packaged for return to US-based universities and laboratories, where they were analyzed and stored.

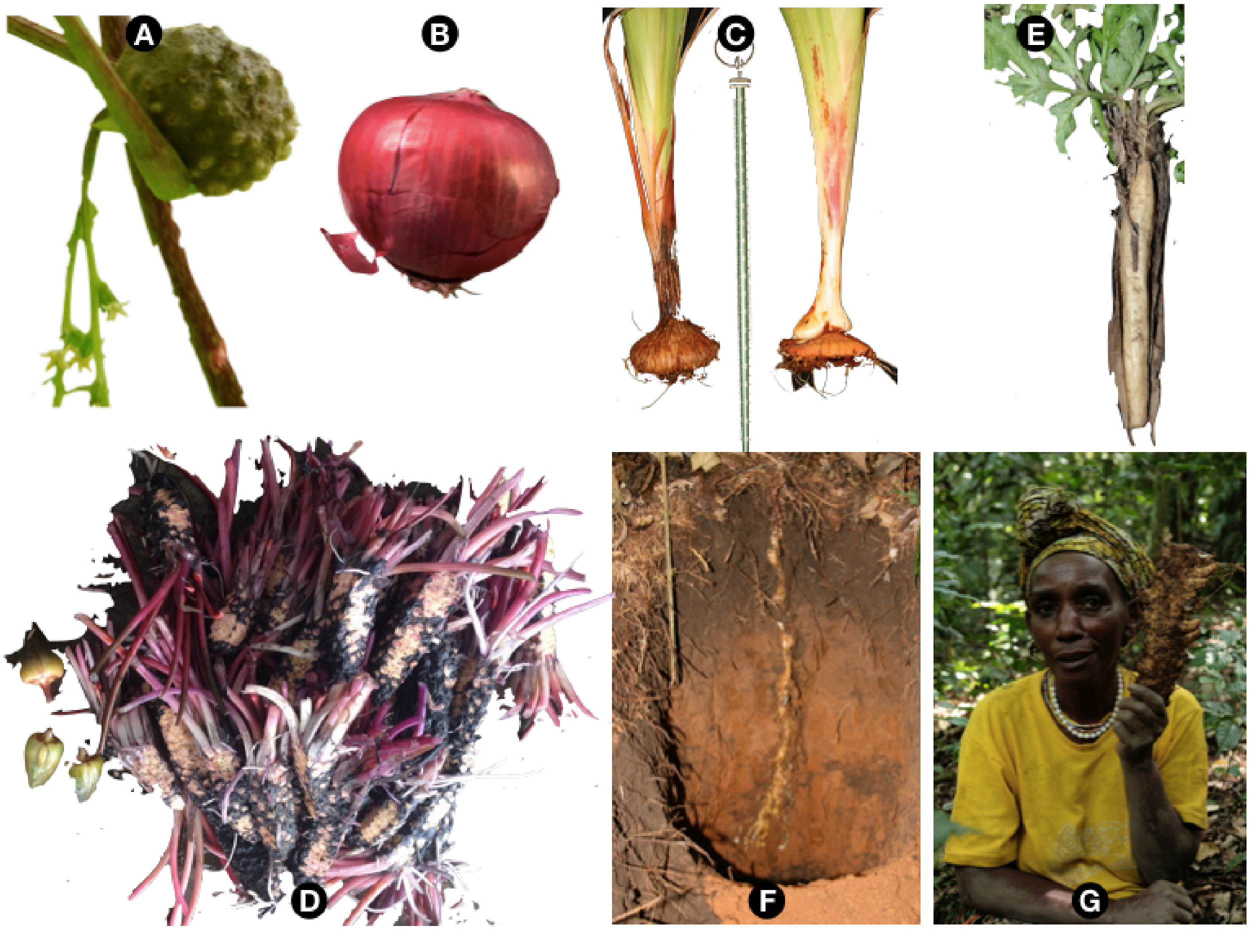

Figure 4.2: *Types of USO collected in various study locations. Photos representing the different USO plant parts collected and analyzed in this study. (A)* ***aerial tuber*** *of Dioscorea bulbifera [copyright Wikimedia Commons/Dinesh Valke]. (B)* ***bulb*** of the common domesticated red onion *Allium cepa. (C)* ***corm*** *(terminal brown swelling with tunic) of Watsonia sp. in South Africa. (D)* ***rhizome*** *trimmed of roots pile from Nympahaea nouchali from Botswana; note the three green fruits to the left. (E)* ***roots*** *of Anneshoriza nuda (photograph by B.-E. van Wyk from (Sobiyi, et al. 2019). (F)* ***tuber*** *of Dioscorea praehensilis in ground in Uganda. (G) Twa woman holding "ebihama" –* ***tuber*** *of Dioscorea praehensilis in Uganda***.** *Photos C, D-G by AC.*

Starch analyses

All starch analyses included in our novel dataset were carried out in at the Nutritional Ecology Lab (NEL$_1$) at CUNY Hunter, coordinated and supervised by J. Rothman. The starch results presented here from the NEL$_1$ at CUNY Hunter, were validated by a subset of analyses run in the Harvard Nutritional Ecology Lab

(NEL_2) by A. Cunningham and N. Conklin-Britain. Samples from Botswana, Namibia, South Africa, and Tanzania were all returned to NEL_2 for analyses related to other pilot projects or studies, distinct from their current use related to starch. Samples from Uganda were collected with the intention of analyzing starch content. We obtained permissions from the original collectors, members of the current research team, and/or the custodian of the samples who brought them to the NEL_2 to utilize superfluous samples for starch analysis.

Megazyme (Wicklow, Ireland) Total Starch Assay kits (AACA Method #s: 996.11, 76.13; ICC Standard Method #: 168) were used to assay non-resistant starch in dried and milled plant samples on a dry weight basis (%DW). USO samples were ground to pass a #40 mesh screen, and then weighed to 100 mg and analyzed in duplicate. Samples were “washed” with aqueous ethanol (80% by volume) to remove non-starch D-glucose and maltodextrins, and then processed using the “Standard Assay Procedure (AA/AMG)” (alpha amylase/amyloglucosidase, AACC Method 76-12). This method of analysis has been used by others to assess non-resistant starch availability for USOs known to be consumed by humans (Carmody, et al. 2011; Carmody 2012). It should be noted that this method involves incubation of samples at temperatures exceeding the temperature of the human body (~37° C), including 6 minutes of boiling, and a combined 50 minutes at 50° C, in effect cooking all samples. According to this procedure, starch (a polysaccharide) was initially hydrolyzed by thermostable alpha amylase, which digests polysaccharide chains of amylose into smaller subunits. These are then further cleaved by amyloglucosidase, converting disaccharides into the monosaccharide glucose. Glucose is then quantified using spectroscopy. Glucose and control starch samples (maize and wheat) were used to validate and normalize results.

Starch assay procedure presented numerous problems, for both Nutritional Ecology Laboratories involved in this research, despite previous use of the Megazyme Total Starch kits by both labs. A. Cunningham ran 560 starch assays in the summer of 2016, including a number of control and validation runs.
Analyses from this period showed variation in quantification of maize and wheat starch standards between runs, despite low technical duplicate variations within runs. N. Conklin-Brittain independently ran

samples in the NEL_2, and found similar variation. Starch controls (e.g. Maize 96%) sometimes underestimated starch content by 20% or more, illustrating incomplete starch capture. J. Rothman and the NEL_1 also had initial challenges applying this methodology. Early runs in the NEL_1 displayed very low starch concentrations. Both NEL labs encountered these issues over a 12-18 month period, particularly during hot summer months in the Northeast USA (Cambridge, MA and New York, NY).

J. Rothman and the NEL_1 re-ran samples late in the fall of 2017, after fully replenishing everything in the lab that was used for testing starch. These updates included new Megazyme kits, new reagents, new glassware, new water bath (that could be set to higher than 100C), and re-calibrations on the spectrophotometer. Starch assays finally produced reasonable and consistent results. Samples presented in this analysis from the novel dataset are from starch assays conducted in the fall/winter of 2017 and spring of 2018. Despite validation and previous success, the Megazyme Total Starch assay procedure presented significant technical challenges to two established laboratories with long histories of analyzing wild primate and human foods. This laboratory procedure was thus more problematic than commonly expected, being sensitive to unknown factors responsible for variation in results between runs.

Nutritional analyses

Standard nutritional assays (Conklin-Brittain, et al. 1998; Wrangham, et al. 1998) for dry matter and ash, crude protein (CP), free simple sugars (FSS), lipids, fiber (soluble, and non-soluble) were collected for some samples included in this analysis, and will be published at a later date as they relate to individual field sites and studies. A small subset of those analyses are included here, showing co-variation of starch content with free CP, FSS, soluble fiber (neutral-detergent fiber, or NDF), and lignin among samples in our best studied USO, water lily rhizomes *(Nymphaea nouchali*). These data are presented as a preliminary investigation. Comprehensive nutritional data for the Hadza sample will be published independently by A. Crittenden and collaborators. Nutritional analyses for samples in Botswana will be published by A. Cunningham and collaborators. Additional nutritional data from M. Firestone for the Hadza and Ju/'hoansi are available in his thesis. Two main factors limited our ability to present further macronutrient data. First, for many species there was insufficient sample material. Second, of those that were assayed for additional nutrients, most are destined for publication elsewhere by the primary researchers. Furthermore, starch has the potential to confound and contaminate some measures of nutrients – particularly fiber – that are used to calculate total non-structural carbohydrates (TNC).

Seasonal Variation

USOs, like all plant parts, can vary in their food quality as a function of development stage and seasonality (Dafni, et al. 1981; Dounias 2001; Flores and Flores 1997; Procheş, et al. 2006). While our dataset is small, and disperse across a wide geographic region, we preliminarily address the issue of seasonal variation in starch content using our most robust and heavily sampled specimens. Water lily rhizomes (n=34) from Botswana were collected over the course of a 12-month continuous study period. We consider how the starch content of water lily rhizomes resources from Botswana (S) varied by month.

Data analysis

Analyses were conducted in R version 3.5.1. We present summary statistics (mean and standard deviation (SD)) for each study location, with samples organized by species and plant part. Given methodological differences in how starch analyses were conducted, we first present these data separately, then use the pooled novel and published datasets in our analyses.

We used linear mixed-effects model (LMM) to calculate the determinants of starch content (%DW), a continuous variable ranging between 0 and 1. Categorical predictor variables including habitat (“LocationBinary” = Rainforest “RF” or Savanna “S”), plant part, and domestication status (“SampleOrigin” = Wild “W” or Cultivated “C”) were included as fixed effects. Plant species was incorporated as a random effect. To determine which predictor variables should be included in the final model, we used model selection criterion to compare models containing various combinations of the predictor variables. Specifically, we used a corrected Akaike information criterion (AICc) for low sample size, with lower values indicating a better-supported model. We also included a null model (which included only species) in the candidate set. Note that in mixed models p-values are not presented. Instead, information-theoretic criterion are used to directly compare the strength of different linear models against each other. Despite the low sample sizes and uneven sampling in our study, we hope that this study can be a catalyst to encourage more complete sampling of USOs across habitats, nutrients, and plant parts.

Seasonal variation was assessed for a subsample of water lily rhizomes by examining the correlation between starch content (%DW) and collection month. Nutritional co-variances are also offered for non-resistant starch and (CP), free simple sugars (FSS), and fiber (lignin and NDF (neutral detergent fiber)). We also include a visual inspection of harvesting incidents by study month.

Ethics

Ethical permissions relating to the use of human subjects were obtained by each research team, from sponsoring universities including Dartmouth College (IRB CPHS # 22410 for work in Uganda), Harvard University (IRB CR-23935 for work in Botswana and South Africa), the University of Botswana (RES/IRB/1508 for work in Botswana), and both Harvard University (permits held by M. Firestone) and the University of California San Diego (permits held by A. Crittenden and team for work in Tanzania). Work in Uganda was additionally covered by permits from the Uganda National Council for Science and Technology (permit no. HS 617), and the Uganda Wildlife Authority (permit no. UWA/FOD/RES/50). Work in South Africa was covered by permits from CapeNature (0028-AAA008-00121). Permits the Tanzanian Commission for Science and Technology (COSTECH) covered work in Tanzania among the Hadza (collectively held by Frank Marlowe, with whom MF and ANC worked). A. Crittenden also obtained USDA import permits for these samples. Additionally, A. Cunningham held USDA permits for the legal import of dried plant materials for the purpose of lab analyses (USDA APHIS Permit P37-14-01357).

Results

For many samples (where sample mass allowed), we conducted replicate measurements in the lab for the same plant part on the same specimen (species and study country) from different samples. In these cases, these values were averaged to avoid pseudo-replication. In our novel dataset, we sampled 107 USO samples from a total of 32 species (*for reference, Laden and Wrangham (2005) identified 104 edible*

USO species). For each species, mean starch (% DW) values, standard deviation (SD), and sample size (SS) are reported in Table 4.3.

Table 4.3 - ***Mean starch content of African USOs (unpublished values)*****.**

Study Country (S or RF)	Species	Name	Plant Part	SS (#)	Mean Starch (% DW)	SD
Uganda (RF)	*Dioscorea bulbifera*	Amatugu	Aerial Tuber	2	58.9	10.6
South Africa (S)	*Babiana sp.*	Bobejaantjie	Corm	2	71.8	1.0
South Africa (S)	*Chasmanthe sp.*	Oranjevlamblom	Corm	2	51.0	4.3
South Africa (S)	*Ferraria sp.*	Spinnekopblom	Corm	2	49.4	3.4
South Africa (S)	*Watsonia sp.*	Pypie	Corm	1	22.5	NA
South Africa (S)	*Annesorhiza nuda*	Anyswortel	Root	4	56.8	2.4
Namibia (S)	unknown	N/won/washe	Root	1	6.8	NA
Uganda (RF)	*Dioscorea praehensilis*	Ebihama	Tuber	14	60.7	16.6
Namibia (S)	unknown	/'Han	Tuber	1	53.8	NA
Uganda (RF)	*Dioscorea preusii*	Ebikwa	Tuber	5	53.0	27.3
Tanzania (S)	*Vigna macrorhyncha*	Do'oako	Tuber	1	46.8	NA
Namibia (S)	*Trochomeria macrocarpa*	N=wara!ko!ko	Tuber	1	46.1	NA
Namibia (S)	unknown	Nchun	Tuber	1	34.4	NA
Tanzania (S)	*Vigna frutescens*	//Ekwa	Tuber	4	46.1	17.16
Namibia (S)	*Vigna dinteri*	Sha	Tuber	1	22.9	NA
Botswana (S)	*Raphionacme burkei*	Legoshira	Tuber	1	22.3	NA
Tanzania (S)	*Vatoraea pseudolablab*	Shumuako	Tuber	2	13.1	11.3
Namibia (S)	unknown	//Kore	Tuber	1	12.9	NA
Namibia (S)	*Asclepiadaceae sp.*	!Xo!Kama	Tuber	1	11.7	NA
Namibia (S)	*Hydnora sp.*	//Hokxam	Tuber	1	10.1	NA
South Africa (S)	*Cyphia sp.*	Baroe	Tuber	6	9.4	5.5
Tanzania (S)	*Eminia atenullifera*	Makalita	Tuber	6	7.6	2.9
South Africa (S)	*Pelargonium lobatum*	Kaneelbol	Tuber	3	5.5	1.8
Namibia (S)	unknown	Gwe	Tuber	1	3.4	NA
Botswana (S)	*Nymphaea lotus*	Tswii	Rhizome	6	53.0	5.1
Botswana (S)	*Nymphaea nouchali var. caerulea*	Tswii	Rhizome	28	33.9	15.1
South Africa (S)	*Typha capensis*	Papkuil	Rhizome	2	13.9	2.7
Botswana (S)	*Typha capensis*	Tjita	Rhizome	1	9.4	NA
Botswana (S)	*Cyperus papyrus*	Koma	Rhizome	1	4.2	NA
Namibia (S)	unknown	Uhru	Bulb	1	54.9	NA
Namibia (S)	unknown	!Goro	Bulb	1	3.6	NA
Namibia (S)	*Eulophia sp.*	=Dau	Bulb	1	0.5	NA

Table 4.3: *Mean starch content of USOs arranged by plant part (pooled by study country and species). Study country as in Table 4.1. Data are reported on a dry weight basis (%DW). This table presents all new starch analyses presented in this study.*

Our published dataset added starch values for 64 USO samples (all of which were tubers) from 15 species, to our final comparative dataset (Chen et al., 2003; Fakir et al., 2012; Hladik et al., 1984; Ravindran et al., 1995; Schoeninger et al., 2001; Wanasundera and Ravindran, 1994). Table 4.4 presents the mean starch (%DW) values, standard deviation (SD), and sample size (SS) by study country and species for these published values. Four species from the published USO samples were in common with species analyzed in our novel dataset.

Table 4.4 - *Mean starch content of published USOs.*

Study Country (S or RF)	Species	Name	Plant Part	SS (#)	Mean Starch (%DW)	SD	Source
Bangladesh (RF)	*Manihot esculenta*	Cassava	Tuber *	7	84.9	2.4	Fakir et al. 2012
Gabon (RF)	*Dioscorea semperflorens*	Yam	Tuber	1	81.3	*NA*	Hladik et al. 1984
Sri Lanka (RF)	*Dioscorea alata*	Yam	Tuber *	7	79.5	3.7	Wanasundera & Ravindran 1994
Central African Republic (RF)	*Dioscorea semperflorens*	Yam	Tuber	1	78.8	*NA*	Hladik et al. 1984
Central African Republic (RF)	*Dioscorea mangenotiana*	Yam	Tuber	1	75.9	*NA*	Hladik et al. 1984
Central African Republic (RF)	*Dioscorea alata*	Yam	Tuber *	4	74.9	3.4	Hladik et al. 1984
Central African Republic (RF)	*Dioscorea cayenensis-rotundata*	Yam	Tuber *	5	73.7	1.4	Hladik et al. 1984
Central African Republic (RF)	*Dioscorea minutiflora*	Yam	Tuber	1	73.4	*NA*	Hladik et al. 1984
Gabon (RF)	*Dioscorea burkilliana*	Yam	Tuber	3	73.2	4.4	Hladik et al. 1984
Sri Lanka (RF)	*Ipomoea batatas*	Sweet Potato	Tuber *	16	72.1	4.12	Ravindran et al. 1995
Central African Republic (RF)	*Dioscorea burkilliana*	Yam	Tuber †	1	71.2	*NA*	Hladik et al. 1984
Central African Republic (RF)	*Dioscorea dumetorum*	Yam	Tuber †	1	68.2	*NA*	Hladik et al. 1984
China (RF)	*Ipomoea batatas*	Sweet Potato	Tuber	3	67.4	*9.1*	Chen et al. 2003
Gabon (RF)	*Dioscorea dumetorum*	Yam	Tuber	2	65.7	3	Hladik et al. 1984
Central African Republic (RF)	*Dioscorea praehensilis*	Yam	Tuber	1	58.3	*NA*	Hladik et al. 1984
Gabon (RF)	*Dioscorea bulbifera*	Yam	Tuber	1	57.6	*NA*	Hladik et al. 1984
Gabon (RF)	*Dioscorea cayenensis-rotundata*	Yam	Tuber	1	53.6	*NA*	Hladik et al. 1984
Gabon (RF)	*Dioscorea preussii*	Yam	Tuber	1	48.4	*NA*	Hladik et al. 1984
Tanzania (S)	*Vigna frutescens*	//Ekwa hasa	Tuber	5	26	18.2	Schoeninger et al. 2001
Tanzania (S)	*Ipomoea transvaalensis*	Panjuko	Tuber	1	23.9	*NA*	Schoeninger et al. 2001
Tanzania (S)	*Eminia entennulifa*	Makaritako (or Makalita)	Tuber	1	19.6	*NA*	Schoeninger et al. 2001

Table 4.4: *Published mean starch content (%DW) for 64 samples from 15 tuber species, collected from locations in Africa and Asia. Study location includes the binary habitat marker identifying each row as either savanna (S) or rainforest (RF). Within the Plant Part column, " * " denotes samples from cultivated (i.e. domesticated) varietals of the species named. " † " denotes a mix of wild and cultivated varietals for a given species. Tubers lacking a * or † indicate wild varietals. Our aim in assembling Tables 2 and 3 is to collate all available data on starch concentrations in wild USOs exploited by African foraging populations, together with a few representative agricultural USOs.*

Starch Content Across Populations

Figure 4.5 presents mean starch content for each species and USO plant part by study site, and includes both the novel and published data sets. The four savanna sites (Botswana, Namibia, South Africa, and Tanzania) showed a similar range of values across USO species, from a low of less than 10% to a high of more than 50%. Hadza samples from the novel (Tanzania) and published (Tanzania*) data sets from the overlapped considerably in their starch content, though the novel samples displayed a much greater range.

In order to find out whether the high within-site variation in USO starch content was due to differences in the USO types being exploited, Figure 4.5 shows violin plots for the most frequently represented USO type in each study country. The range of starch concentrations was similarly high regardless of whether the USO type was a tuber (Tanzania, Namibia), corm (South Africa), bulb (Namibia) or rhizome (Botswana). By contrast, all non-savanna sites had USO starch values higher than 50%. All but one of these USOs were tubers (the lone exception was an aerial tuber).

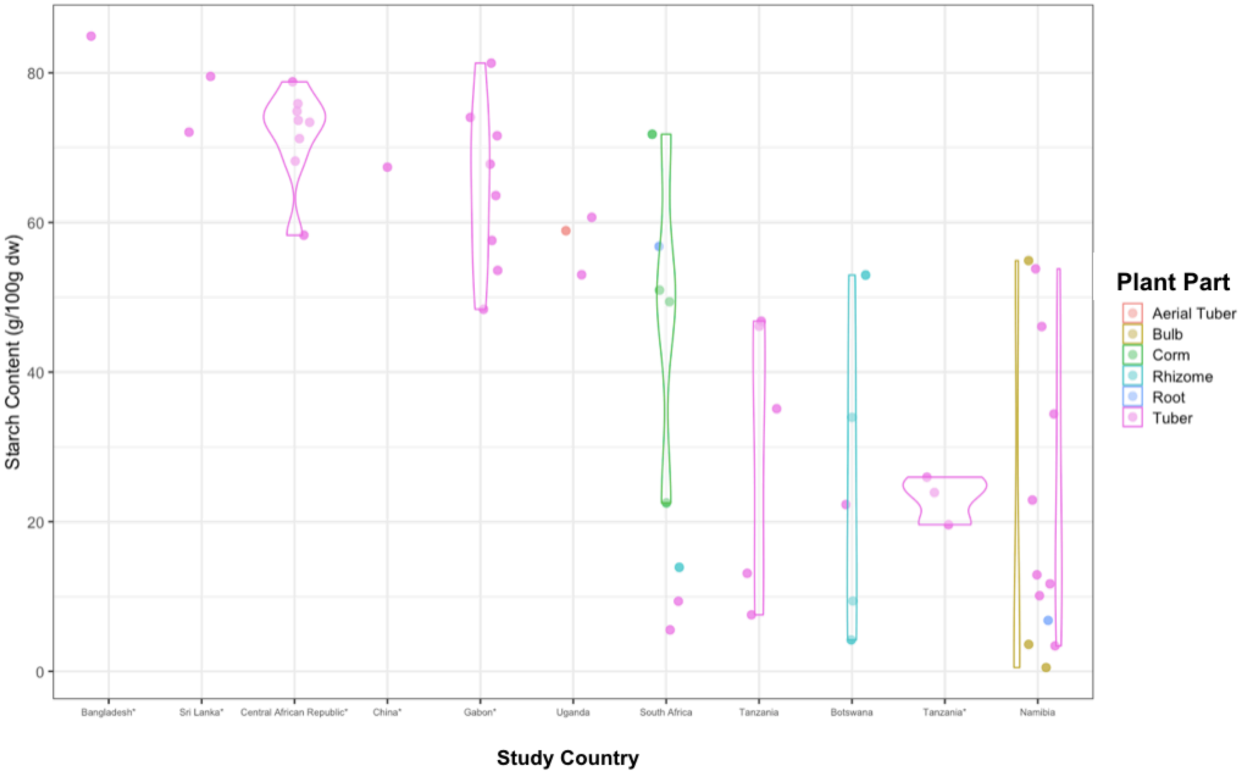

Figure 4.5: *Starch content by study country***.** *The mean starch content (%DW) of USO samples from both the novel and published datasets. Single points reflect the mean species value of starch. Published starch values are denoted by a * after the study country name. Novel starch findings are presented by study country name only. Violin plots indicate the sampling distribution within each plant part, for the most frequent USO types within each study country.*

To better understand the predictors of starch content, we modeled the relationship between starch content and several fixed-effect predictor variables in a linear mixed effects model, with plant species included as a random effect (Table 4.6). Models 1, 2, and 3 were better-performing than the null model (Model 4). We found strong support for one candidate model, which included species as a random effect and our binary habitat variable. Plant part was not supported as an important predictor. It is perhaps not surprising that domestication status was not included in the final model, given the lack of published starch content for savanna USOs. Regression results (y= -0.41x + 0.68) show that species from savanna USOs (S habitat mean = 27.3 %DW) are half as starchy as rainforest USOs (RF habitat mean = 68.2 %DW). The output of this mixed model suggests that there was a strong correlation (Corr. Intr.; r= -0.834) between the intercepts (intercept) and the slopes (x) among the binary locations (S and RF) considered here. Based on these results, both cultivated and wild rainforest USOs have significantly higher starch content than wild savanna USOs. These distinctions are visualized in *Figure 4.7*.

Table 4.6 - ***Model results predicting starch content (%DW).***

Model	Fixed effects	Random effects	AICc	deltaAICc
1 (Best)	LocationBinary	Species	-35.10	-
2	PlantPart + LocationBinary	Species	-16.02	19.07848
3	PlantPart + SampleOrigin + LocationBinary	Species	-9.10	25.99824
4 (Null)	None	Species	-8.37	26.72913
5	SampleOrigin	Species	-3.68	31.42295
6	PlantPart	Species	10.96	46.06587
7	PlantPart + SampleOrigin	Species	16.24	51.34068

Table 4.6: *Seven models containing linear combinations of fixed and random effects were ranked by AICc values. DeltaAICc values show strong support for the highest-ranking model which contained only the fixed effect LocationBinary, which distinguishes savanna vs. rainforest habitat.*

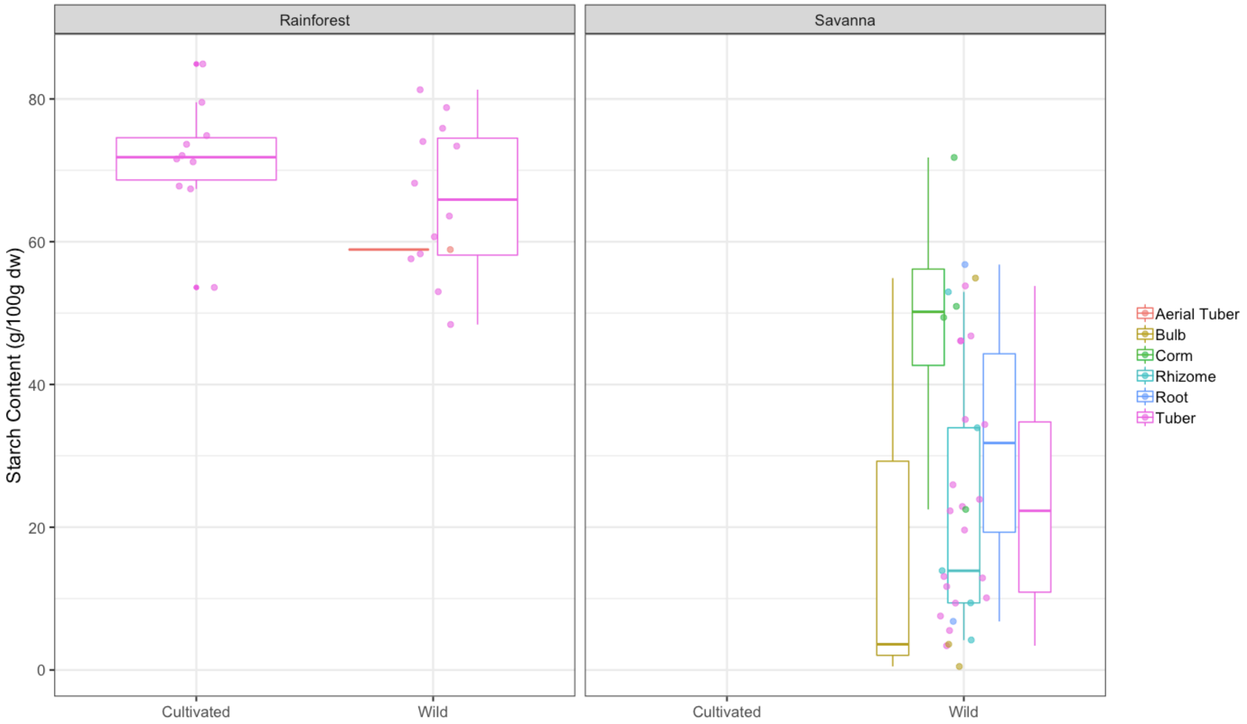

Figure 4.7: *Starch content by habitat (S or RF) for wild (W) and cultivated (USOs). Starch content (%DW) presented by habitat, sorted by plant part and sample origin. Rainforest USOs (limited to only tubers and aerial tubers) display high average starch content. Savanna USOs in our sample were much more diverse by plant part, though completely limited to wild specimens. Rainforest USOs did not differentiate on the basis of wild or cultivated sample origin.*

Results derived from an in-depth review of samples from Botswana

Nutritional co-variation with starch

Protein ($r^2 = 0.19$) and free soluble sugars (FSS) ($r^2 = 0.36$) both displayed positive correlations with starch concentration, while our two measure of fiber, NDF ($r^2 = 0.30$) and Lignin ($r^2 = 0.50$) demonstrated trade-offs, as indicated by negative correlations (*Figure 4.8*). All four relationships showed systematic patterns of co-variation, serving as an independent check on the validity of the Megazyme starch methodology.

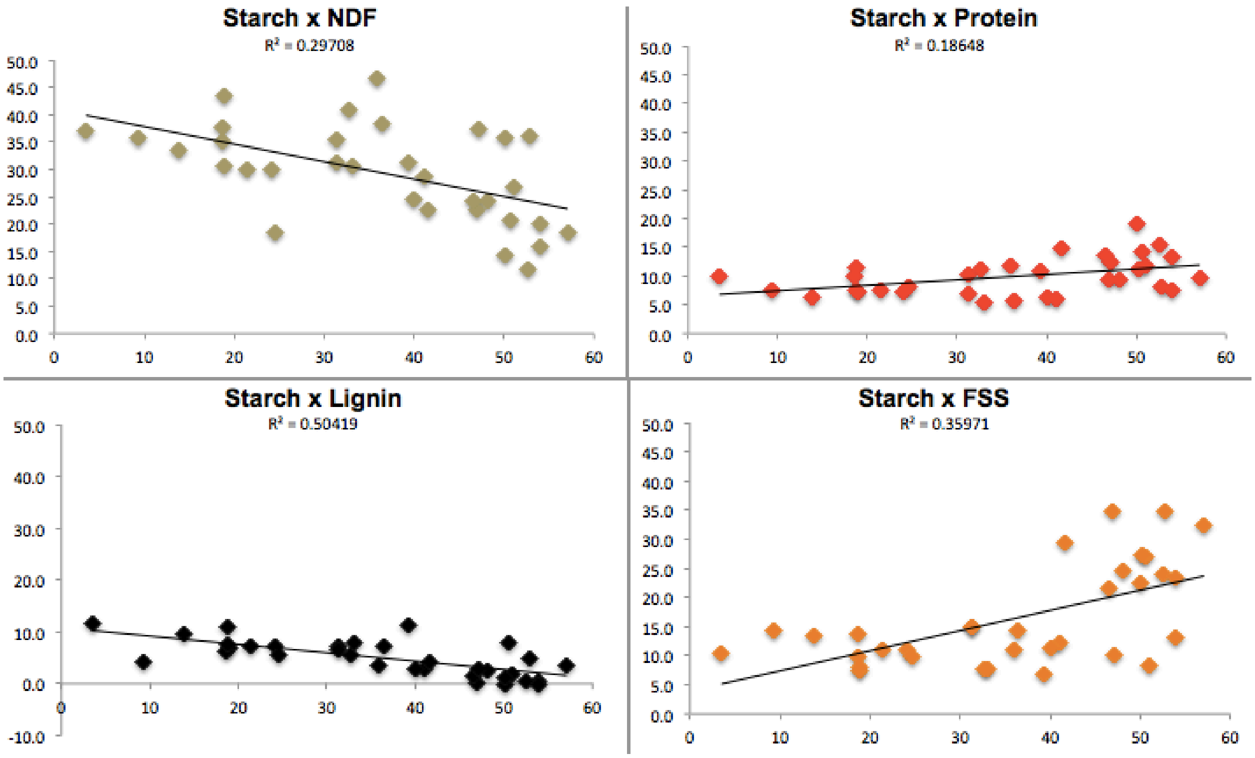

Figure 4.8: *Starch co-variation with some key nutritional components. Here, we show how the starch measured (%DW) on the x-axis co-vary with (clockwise from top left) neutral detergent fiber (NDF), protein (CP), sugars (FSS), and lignin. Protein and FSS both displayed positive correlation with starch, while of fiber (NDF and Lignin) demonstrated trade-offs, with negative correlations.*

Seasonal Variation

Although our study consists of the largest sample size to date of the starch content of wild USOs (107 samples across 32 species and 5 study countries), results are still preliminary. Exploring variation across the seasons is challenging because it requires intensive sampling at a single locale for the same plant species and part. Nevertheless, we were able to conduct a small analysis that sheds light on this issue. Within our novel dataset, the largest single sample was of water lily rhizomes from *Nymphaea nouchali var caerulea* (n=28) from Botswana. Figure 4.9 displays starch data for rhizomes from both species of water lily (*Nymphaea spp.*) sampled over the course of the study year. There was high variability in starch content within months as well as across the year (low goodness-of-fit values) but no evidence of systematic change across seasons.

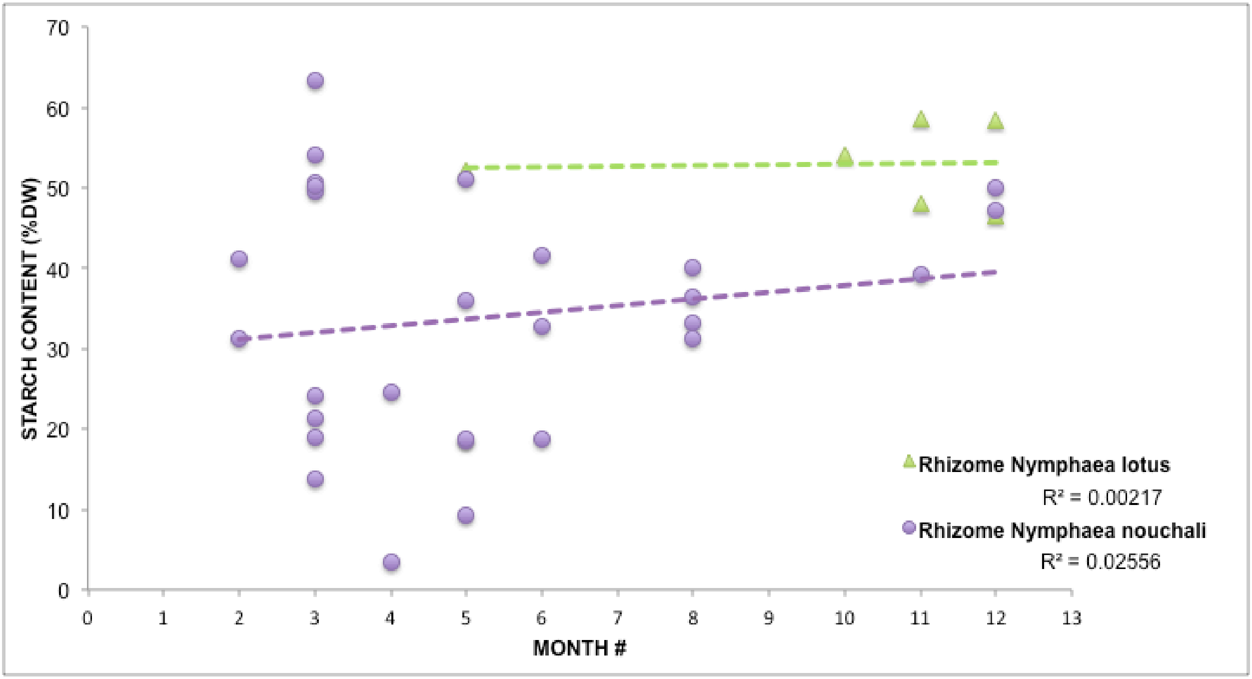

Figure 4.9: *Seasonal variation in water lily rhizome starch content. Starch content (%DW) is plotted by study month August 2014 – July 2015) for both species of water lily rhizomes included in our novel dataset. Nymphaea nouchali (n=28, purple,) rhizomes were collected throughout the year, whereas Nymphaea lotus (n=6, green) appeared to be harvested more in the later half of the year – which corresponds to the recession of local floodwaters and the onset of the local dry season.*

Discussion

We focused our analysis on non-resistant starch as a source of plant energy that would have been a component of USO quality to early hominins and early modern humans. To do so, we assessed the starch content of a variety of USOs from a range of habitats relevant to human evolution. Our investigation was premised on the concept that increases in dietary quality were important in human evolution, and that USOs were likely an important class of foods targeted by hominin foragers that increased dietary quality. To date, there has been some disagreement about the nutritional quality of wild USOs (e.g. Schoeninger et al 2001), but there have been few empirical data to bear on the issue. By providing novel data on starch content across a range of USOs, our results provide three advances in thinking about USOs as food items during human evolution.

First, our comparisons across habitats support the previously suspected difference in starch content between rainforest and savanna USOs. When accounting for repeated sampling at the species level, our statistical models showed that raw, unprocessed rainforest USOs had higher concentrations of starch (48.4 to 81.3 % DW) than savanna USOs (0.5 – 71.8 %DW). Rainforest USOs had so much starch that they rivaled cultivated USOs. It is also notable that we did not find examples of cultivated USOs from savanna habitats to include in the reference table for published starch values. Thus the starch content of potatoes (New World tubers from *Solanum spp.*) range between 60-80 (%DW), with a reported mean starch content of 75% for a sample of 11 *Solanum spp.* (Burlingame et al., 2009). In effect, wild rainforest yams are as energy dense as the domestic carbohydrate sources that foragers might trade for. This result adds a novel dimension to the 'wild yam question,' which pertains to the habitat quality of rainforests for hunter-gatherers. Despite many rainforest USOs being toxic in their raw form and requiring elaborate processing such as soaking, leaching, and boiling or roasting to remove the harmful alkaloids present in the flesh (Neuwinger, 1996), our results suggest that energy can be relatively accessible in rainforest USOs in the form of starch. We therefore suggest that when modern humans began to re-occupy rainforest habitats in the Pleistocene, tubers would have represented a crucial staple food, though questions remain about seasonal availability and overall harvest potential.

Second, again in support of previous work, our enlarged sample shows that savanna USO species were typically low to moderate in terms of their starch content. Given the prominence of savanna populations and their reliance on USOs in the literature, it is somewhat surprising that savanna USOs fared so poorly in terms of starch content. With respect to Hadza tubers, our work is largely concordant with that of Schoeninger et al (2001). The overlapping samples between our studies, those for the species *Vigna frutescens*, evinced low starch values (published mean starch = 26 %DW vs. novel mean starch = 46.1 %DW), though our mean value was nearly double that reported by Schoeninger et al. (2001). Other savanna species consumed by Hadza and Ju/'hoansi were similarly low in starch content, regardless of USO type. For instance, savanna bulbs (n=3) were relatively low in starch (median starch content <10 %DWB). Surprisingly, corms had the highest mean starch content (starch content = 22.5 to 71.8 %DWB) of the four species we tested.

The low starch values in Hadza tubers raise an interesting puzzle because those tubers are regularly exploited and appear to play an important role in Hadza socioecology. Hadza tubers account for 24.7% of food brought into camp by fresh weight (30% for women), and yet account for 38.8% of the calories adult women consume in camp (Marlowe, 2010). Women spend a considerable amount of their foraging time searching and digging for tubers (Marlowe 2010), rank tubers higher in diet preference than men (Berbesque and Marlowe, 2009), and contribute to the diet of others by providing tubers to family members well into menopause (Hawkes, 2003; O'Connell et al., 1999). One possibility is that there are other nutrients that add to the value of tubers that have not yet been quantified (e.g. see Wandsnider (1997) for fructans).

Two additional points might explain this puzzle. Berbesque and Marlowe (2009) state directly that the benefits of targeting USOs for Hadza women are that tubers are a “large” and “reliable” source of food. Tubers provide significant yields (large returns) for the time invested. Tubers constitute a reliable resource, they exhibit both availability and reduced variance compared to other savanna plant food resources. Tubers were collected by Hadza women less when berries were in season, indicating that tubers are staple fallback foods (Marlowe, 2010; Marlowe and Berbesque, 2009). There may simply be few other options on the savanna for carbohydrates when baobab and berries are not seasonally available. In short, Hadza tubers, despite the low starch levels indicated by our analysis, appear to contribute significantly to their survival.

The Hadza results call attention to the importance of processing techniques employed by savanna populations to reduce the consumption of indigestible fiber in the form of lignin and woody or fibrous strands, which would have reduced the mean starch content of tubers from Tanzania even further. Marlowe (2010) was explicit in his description of how the Hadza actively try to exclude tuber lignin and fiber from their diets. The exclusion of inedible fractions (such as woody peels) prior to consumption (or field collection for nutritional analyses) was also noted for some samples from Namibia. For example, many Hadza tubers such as //Ekwa are only briefly roasted, then peeled, wadged and expectorated (Marlowe, 2010; Schnorr et al., 2016). The samples returned to the lab for analysis often reflected this post-collection modification. This differed qualitatively from rhizomes and tubers from Botswana, tubers and corms South Africa, and wild yams from Uganda, which were frequently consumed in their entirety (AJC personal observation). A complete list of differences in the sample part analyzed is provided in Supplementary Table 1 (e.g. tuber pith, whole, or peel). Removing indigestible fiber and woody peels is important given the low to moderate starch content in Hadza tubers. Ingesting such high fiber loads would reduce dietary quality significantly. Previous work assessing the nutritional content and bioavailability of Hadza tubers have taken unique steps to account for the substantial fiber content of these tubers (Schnorr et al., 2015).

Despite the modern association with savanna habitats of populations like the Hadza of East Africa, it is worth remembering that Raymond Dart first highlighted savanna habitats as they pertained to *Australopithecus* in South Africa (Dart and Salmons, 1925). South African USOs sampled in our study included more diversity of plant parts (corms, tubers, rhizomes, and root) than any other of the other study countries. However, it is also known that South Africa (particularly the Cape Floral Region from where we collected samples) is the richest and most diverse USO habitat in the world (Cowling, 1995; De Vynck et al., 2016; Procheş et al., 2006; Singels et al., 2016). Corms from South Africa, noted for their high starch content, come in particularly small food package sizes. This point warrants consideration as it directly contradicts tuber benefits noted by those who study the Hadza. Future research into the actual return rates for such high quality and small sized resources should account for the hight starch content when modeling energy returns (De Vynck et al., 2016; Marean, 2010, 2011; Singels et al., 2016). In short, much remains to be understood about why savanna USOs tend to be an important food for foragers, despite their low starch concentrations.

Third, water lily rhizomes from the mosaic savanna habitat of the Okavango provide a deeper understanding of the connection between starch content and food quality. *Nymphaea spp.* in our novel data set from Botswana were of moderate quality on the basis of starch content (mean starch content of 35-55 %DW) – on par with the highest tubers from savanna populations such as the Hadza. We also found no evidence to indicate that their starch content, a proxy for food quality, changed systematically through the course of the year – indicating that these may be relatively predictable and stable resources.

The nutritional properties of water lily rhizomes stand out for a few reasons. First, they exhibited moderate starch density, which can be paired with evidence of productivity and utility as indicated by other sources. *Nymphaea spp.* occur at such densities in waterways that they are frequently classified as a 'noxious weed' – indicating the exceptionally high growth potential and biomass (Raja et al., 2010). And second, unlike Hadza tubers (many of which are in the family *Leguminosae*), Rainforest tubers (*Dioscoreaceae*), or potatoes (from the nightshade family, *Solanaceae*) which may be toxic in their raw state (Eaton, 2007; Neuwinger, 1996; Tagliabue et al., 1995), species in the family *Nymphaeaceae* are considerably less toxic and are frequently edible in their raw state (Rahmatullah et al., 2009; Raja et al., 2010). The wide distribution of key edible species such as wild water lilies would have provided a consistent resource for foragers moving great distances between habitats, across new continents, and through both generational and evolutionary time. *Nymphaea nouchali*, collected by foragers in the Okavango Delta of Botswana, is also be found and eaten as distantly as India and Bangladesh (Rahmatullah et al., 2009). Similarly, *Nuphar*, a genus in the *Nymphaeaceae* family, is known from archaeological sites in both North America and Europe (*N. lutea*), as well as in the Middle East (*N. luteum*) back to 790,000 years ago (Melamed et al., 2016). While members of the genus *Nuphar* are generally less palatable than *Nymphaea sp*., they are nonetheless represented in the archaeological record, perhaps having been processed with soaking and leaching and/or cooking (Henry et al., 2011; Mercader et al., 2008). Some other lacustrine and emergent non-USO plant resources known to be eaten by subsistence populations are assumed to be sources of dietary starch, such as the pith from the heart of palms, bulrush, and papyrus. All of these were present in Plio-Pleistocene habitats (Hardy et al. 2015), and were sampled by foragers in Botswana.

This study is admittedly limited by its focus on the content of starch in USOs. Data on macronutrients or micronutrients (e.g. salt, Andersen 1987), package size, and mechanical and chemical properties are crucial for assessing food quality. Nor did we assay samples for resistant starch, which like phytochemical defensives would have been made more digestible by cooking. With the control of fire and the advent of habitual cooking, most USOs would have presented even greater energetic rewards (Carmody and Wrangham, 2009; Wrangham, 2009), both by negating plant secondary compounds and altering physical structure (such as gelatinizing starch), contributing to increased digestibility and reduced digestive costs. Many of the omissions noted for our study were connected to the opportunistic sampling of samples remaining from previous studies. Despite containing one of the largest datasets of non-resistant starch in wild human foods ever reported in the anthropological literature, our dataset is still too small and too incomplete to probe the variety of ecological factors that dictate starch content. However, we hope that this work spurs further investigation of the factors that modulate USO food quality.

Subsequent work in this area must do more to account for the issues of food package size, resource density and distribution, return rates, and pre-consumption processing. A further investigation of other carbohydrates (resistant starch, simple sugars, soluble fiber, fructans, etc.) is required to better explain the dietary benefits of many savanna USOs. Such studies will reveal whether savanna USOs have a net value equivalent to those found in rainforests, or alternatively whether savanna USOs are inherently low-quality as dietary items. Additionally, food package size and return rates with consideration of yield are sure to be important factors when considering the savanna USO question, to build more accurate and robust models of USO dietary quality (Sayers and Lovejoy, 2014).

Here, we documented novel variation in starch content for wild foods relevant to the diets of hunter-gatherer populations across a spectrum of habitats. Our findings affirm that USOs vary widely in their starch content, which must in turn influence their food quality for human consumers. This has implications for dietary reconstructions in studies of human evolution, as savanna USOs in general were not as energy dense as rainforest tubers. Rainforest USOs (nearly all tubers), by comparison, were indistinguishable from cultivated USOs on the basis of non-resistant starch content. Aquatic USOs, specifically water lily rhizomes from *Nymphaea,* offered an intriguing exception to the general pattern of savanna USOs, and may be worthy of additional study attention. We hope that this study can be a catalyst to encourage more complete sampling of USOs across habitats, nutrients, and plant parts.

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CHAPTER 5

CONCLUSION

Contemporary foraging populations provide a lens by which we may view the first 95% of our species' subsistence. Humans of the past, like those of the present, faced daily decisions about what to eat. Diet composition and nutrition in turn had direct consequences on health, survival, and the evolution of our species. As anthropologists, we frequently look to dietary shifts as explanations for the monumental behavioral and biological changes recognized at key points in our history. In the pursuit of connecting these complementary points, I sought to address aspects of the human foraging spectrum at both global and individual levels, using insights gained from both ethnographic and contemporary hunting and gathering populations.

My thesis aimed to answer three questions about forager habitat quality and productivity. First, I addressed the question of whether ethnographic foragers lived in marginal habitats, using population density as a measure of how net primary productivity translated into a key demographic outcome (population density). These patterns, and the population dynamics that historically resulted, likely led to shifts towards alternative modes of subsistence in the Pleistocene and early Holocene. Second, I established a new site for foraging research in the Okavango Delta to compare the foraging returns of women in adjacent wet and dry savanna habitats. This work sought to push African behavioral and foraging ecology beyond dry upland savanna habitats, providing the first empirical test of wet savanna foraging. Within the mosaic environment of the Okavango, detailed evidence at the individual and habitat levels indicated how women fared in terms of their foraging efficiency, and the dietary composition that resulted from their efforts. Finally, continuing the theme of comparing adjacent habitat types, I compared the starch content of USOs from savanna and rainforest habitats. This third research topic substantially increased the number of wild foods with known starch content collected by African foragers, and confirmed the superiority of rainforest USOs relative to those from savanna habitats.

Foragers did not occupy marginal habitats

Colleagues and I demonstrated that ethnographic hunters and gatherers did not occupy so-called 'marginal' habitats compared to three other pre-industrial subsistence modes (*horticulture, intensive agriculture,* and *pastoralism*). This work substantiated and expanded upon the work of Porter and

Marlowe (2007). What did differ for each of these subsistence types were relationships between net primary productivity (NPP) and the probability of achieving a given (*low, medium,* or *high*) population density. In general, foragers were more likely than non-foraging societies to have low population density. Not surprisingly, foragers that occupied low NPP habitats were very likely to have low population density. Foragers occupying medium to high NPP habitats had the highest probability of attaining medium or high population density. Foragers achieving high population density had a remarkable commonality – reliance on marine resources. High latitude foraging populations in particular relied upon marine / fished resources. The link between high population density and a reliance upon marine resources suggests support for the claim by many that aquatic and coastal habitats may have been important to human foraging populations (De Vynck et al., 2016a; Kuliukas and Morgan, 2011; Marean, 2011; Marean et al., 2007; Wrangham, 2005; Wrangham et al., 2009). Rainforest hunter-gatherers in Africa did not achieve high population density, despite having high NPP. This lends demographic support to the general idea encompassed by proponents of the "wild yam question," though it is notable that this also reflects the general tendency of African foragers to have low population density. The overall NPP-PD dynamic for foragers were most similar to those observed for pastoralists.

The shared NPP-PD patterns of foraging and pastoralist societies are notable because these two subsistence modes had the widest geographical distribution. Globally, societies from these two subsistence types were found between 0° and nearly 70° absolute latitude. For high latitude human populations, both hunter-gatherers and pastoralists converge upon a similar dietary strategy, increased reliance upon animals and animal by-products. Tallavaara et al. (2017) also found strong evidence for a positive effect of NPP on hunter-gatherer PD. They noted that biodiversity likely drives PD in low NPP environments, whereas pathogens are likely the dominant stressor in high NPP environments, such as the tropics. These are valuable points to be considered alongside the results we report.

Foraging energetics of wetland and dry savanna habitats

Biodiversity has also driven arguments behind the relative importance of deltaic habitats. Wetlands, such as the Okavango, are known biological hotspots, drawing in large mammals, migratory birds, and other terrestrial game to areas that also provide ideal habitats for fish and aquatic prey species (Ramberg et al., 2006). Comparison of foraging in adjacent Wet and Dry habitats of the Okavango Delta, however, found that Dry habitats were more profitable when assessed on the basis of post-encounter return rates. These results appeared to be driven by the occurrence of certain resources that were relatively rich in lipids (seeds with arils and nuts) within the Dry habitats. Applying a new method that accounted for the energetic cost of foraging did not substantially change these results, as energetic foraging efficiency comparisons also favored the Dry habitat. However, a paradox remains. Why did women from Seronga, who live at the interface of Wet and Dry habitats, tend to favor the Wet floodplain and river habitat, when they had access to the more profitable (based on return rates) Dry habitats to the East?

Wet habitats exhibited reduced dietary species richness, had lower search and total foraging time, and were a much more common source of USOs. Habitats were similar in their production of fruits. Wet habitats were clearly a preferred habitat for the part-time foragers who had consistent access to both forms of savanna. This conforms to the predictions set forth the ‘Delta Hypothesis’ (Wrangham et al., 2009). Return rates however, skewed by the caloric richness of fats, favored Dry habitats. Much more work is needed in wet savanna habitats to reveal the complex dynamics at play. Future efforts should incorporate measures of biomass and resource regeneration, as well as research methods focused on key aspects of variability.

Throughout Africa, hominins have been found in association with species common to riparian woodlands and wetland habitats (Wrangham et al. 2009). Brunet et al. (2005) described the paleo-environment associated with *Sahelanthropus tchadensis* as likely to have been similar to the modern Okavango Delta. The deserts of Chad were once home to wetlands, gallery forests, and savannas, and hominid fossils were recovered in close proximity to large fish remains (over 1 m long)(Vignaud et al., 2002). Wrangham et al. (2009) noted an additional 24 hominid and hominin fossil-bearing sites, half of which were associated with floodplain or lake margin depositional habitats. Wet savannas are not merely some humorous playground of the aquatic ape theory. They remain key hotspots of biodiversity today, and are well represented within the hominin fossil record. It is time we devote the research attention and resources they deserve, to understanding how successfully human foragers are in exploiting their richness.

Starch content of savanna and rainforest USOs

Arid savannas are known to be rich in USO-producing species (Andersen, 1987; Vincent, 1985b). They present the sort of seasonal environment in which plants need to store water and nutrients for periodic shortages, and geophytes are an ideal solution to this environmental challenge. For human populations that consume USOs, the starch content of wild geophytes has been limited to those reported by Hladik et al. (1984) and Schoeninger et al. (2001). This thesis contributes samples from four new sources, increasing the habitat comparison of starch content from three countries to seven (ten, including published values for cultivated varieties). With an expanded reference collection of USO starch content come two important takeaways. First, rainforest USOs are higher in starch than are savanna USOs. Second, starch content from wild USOs have the ability to rival cultivated varieties in starch content, suggesting that USOs have the potential to be more than mere low-quality, starvation or fallback foods. Revised measures of starch content allow for more accurate modeling of energy availability. The complementary pieces of future models must include accurate measures of biomass, edible portion, and harvest rates.

Low biomass for rainforest USOs was at the heart of the “wild yam question,” despite recent evidence that indicates that wild yams can provide a majority of dietary calories in some months (Bailey and Headland, 1991; Headland and Bailey, 1991; Yasuoka, 2009, 2013). It has long been suggested that human populations living in the forest would be unable to find enough wild yam tubers (*Dioscoraea spp.*) to support their carbohydrate needs, particularly in primary forest habitats (Hart and Hart, 1986; Headland, 1987; McKey, 1996). Unlike rainforest habitats, data from multiple savanna habitats provide quantified estimates of USO biomass. Vincent reported USO biomass for the Hadza as ranging from 0.04 to 180 tonnes/hectare. *//Ekwa hasa*, a preferred Hadza tuber, ranged from 0.1 to 17 tonnes/hectare, with a range of 45 to 883 plants/hectare (Vincent, 1985a, b). She also reported ~97 plants/hectare for the Ituri Forest (Hart and Hart survey n.d.) though these values were not reported elsewhere to my knowledge, and the tonnage per hectare were not provided. Youngblood (2004) studied the geophyte species of the Upper Nama Karoo in South Africa's central plateau (~ 500 km north east of Mossel Bay), and reported yields that ranged from 7.8 – 60 tonnes/hectare. A recent study from Coastal South Africa found edible USO biomass from 0.22 to 0.66 tonnes/hectare (reported as <200 to >600 kg/hectare)(De Vynck et al., 2016b). This is the same population I worked with to collect plant samples in South Africa that were analyzed in Chapter 4 of this thesis. Collectively, these results suggest that there may be an inverse relationship between biomass and starch content. This is a point worthy of future consideration and study. Biomasses for aquatic and semiaquatic USOs are needed to fully appreciate their utility to human foragers.

Youngblood (2004) noted an observation that I too have made; South African USOs tended to be buried much less deep, and tended to be much less fibrous than those described by Vincent and others from the Hadza. This was also true of USOs I observed being foraged in Botswana and South Africa. Detailed measures of costs associated with foraging for USOs, comprehensive nutritional analyses, and more realistic models of digestibility may be needed to truly understand the potential of USOs for human consumers. My analysis also lacked data on starch content for cultivated USOs from savanna habitats. On this point, it should also be noted that savanna habitats are frequently areas where grains are cultivated as a source of starch, rather than USO yielding crops. This is an interesting point, given the natural richness and biodiversity noted for savanna USOs. It does not help that the origin for some domesticated USOs, such as the sweet potato, are still poorly understood, though Central America seems to be the most likely origin (Mu et al., 2018; O'Brien, 1972; Srisuwan et al., 2006).

Moving forward without 'pure' hunter-gatherers

This thesis demonstrated two additional means for researching human ecology and evolution without access to humans. New methods in remote sensing applied to the rich ethnographic record, allows for the modeling of complex aspects of behavioral change. Additionally, untold numbers of samples remain in university laboratories and museums, from a half-century or more of anthropological research into the ways and lifestyles of hunter-gatherers. There are nearly 400 dried and preserved plant samples from my time in Botswana alone. These offer both a ready and economical resource for future analyses into the human diet. Advances in paleobotanical research have already opened the door to a better understanding of pre-historic human diets (Henry et al., 2011, 2014; Henry et al., 2019; Mercader et al., 2008). Dried samples such as my collection offer a ready reference for researchers looking to identify edible species in dental calculus or stone tools.

Beyond ethnographic data, modern analytical methods, and the use of superfluous samples stored in labs and museums, I advocate for the continued embrace of experimental foraging experiments using part-time foragers. There are few isolated populations remaining that practice hunting and gathering without the influence of the modern domesticated and industrialized world, and anthropologists typically cannot reach those that are so isolated. Despite this, we continue to seek out populations that live in close proximity to the habitats that have been central to the evolution of our species. Contemporary populations still offer tremendous value to the scientific and anthropological communities. As colleagues of mine have done in South Africa (De Vynck et al., 2016) and elsewhere, paying local knowledgeable peoples to participate in foraging experiments is a means of continuing to collect important evidence from formative habitats. The erosion of traditional knowledge is a loss to be mourned. While such “sponsored” trips may not be as pure or ideal as working with fulltime hunter-gatherers, they are nonetheless valuable from a scientific perspective. Additionally, this approach to research provides economic benefits to peoples who are often in need – and where we the researchers stand to gain so much professionally from their participation. I worked with such part-time foragers in every country where I conducted research: Botswana, South Africa, and Uganda. While this can be difficult to sustain on a student’s research budget, I am thankful that I had the opportunity to sponsor research participants to engage in studies that connected them with their place, and their heritage.

Embracing the challenges and opportunities presented by the employment of part-time foraging subjects will allow the field of human behavioral ecology to move forward with more careful, controlled, and detailed explorations of behavior. This will be a viable research option for many students this century, as fewer and fewer peoples forage. This is the sad reality of vanishing subsistence mode, when paired with the prestige and professional advances that come from owning such access.

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SUPPLEMENTARY MATERIALS

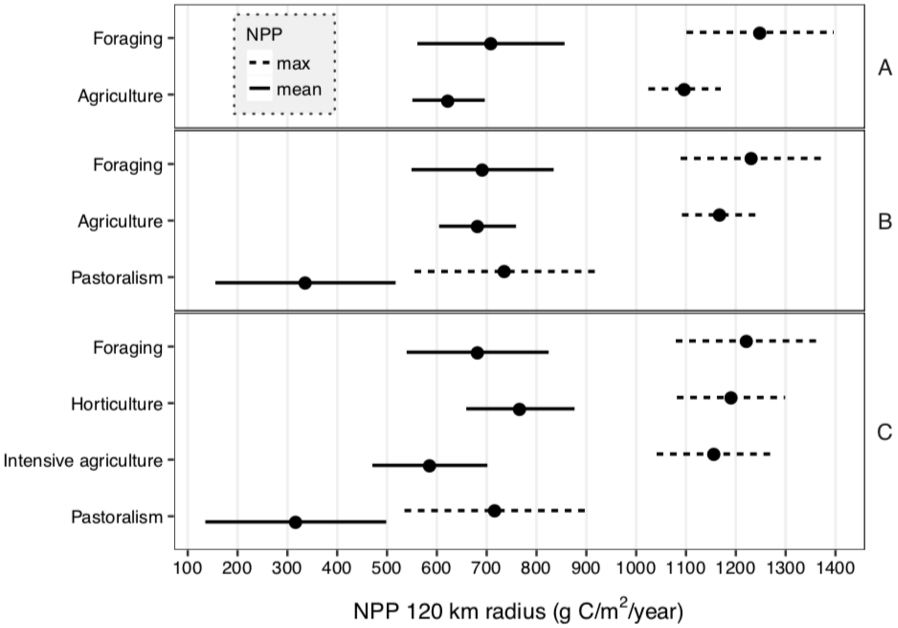

Figure SM 2.1: *Predicted NPP_{max} and NPP_{mean} (within 120 km radius) classified by subsistence type. Warm and Cold climate societies combined. Error bars represent 95% confidence intervals. Panels represent: (A) binary, (B) ternary, and (C) quaternary subsistence classifications.*

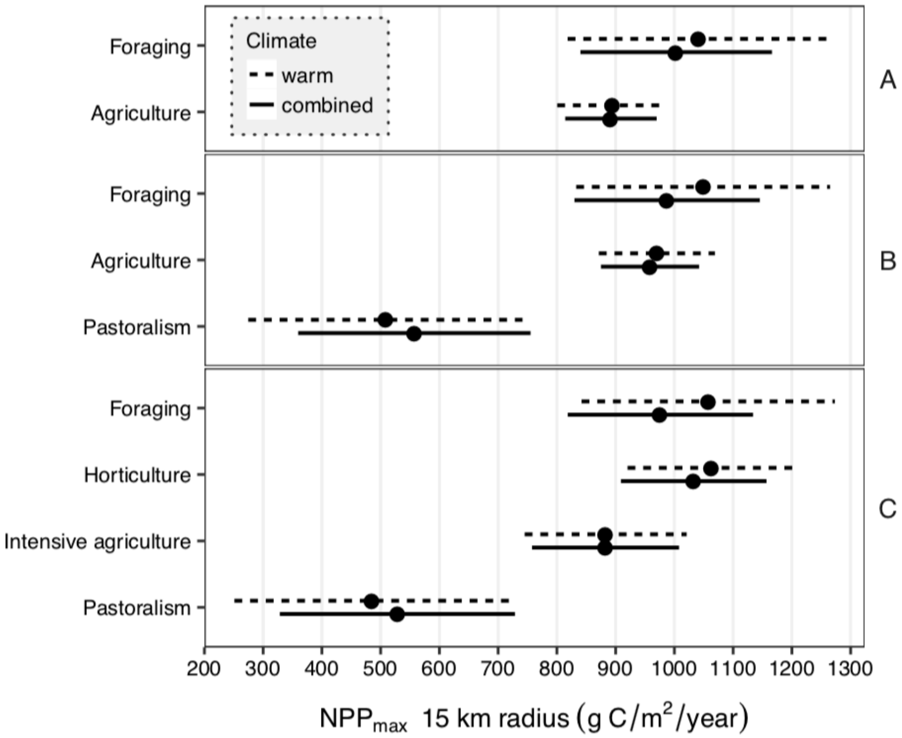

Figure SM 2.2a: *Predicted NPP_{max} (within 15 km radius) classified by subsistence type. Climate grouping (ET) indicated by line type for Warm climate (dashed line; ET>13) and Warm and Cold Combined climate (solid line) societies. Error bars represent 95% confidence intervals. Panels represent: (A) binary, (B) ternary, and (C) quaternary subsistence classifications.*

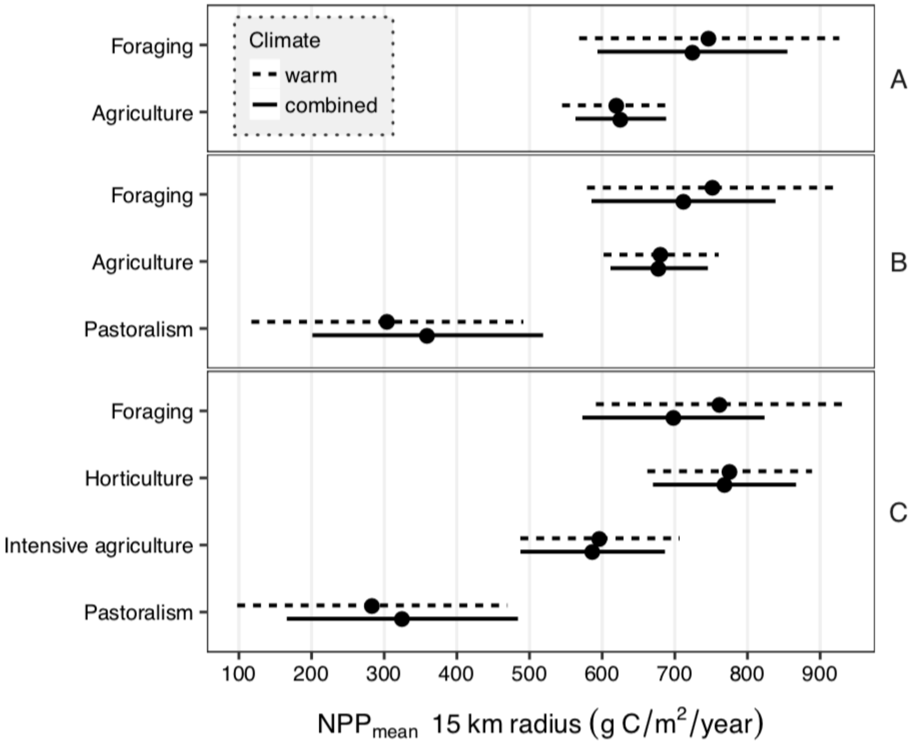

Figure SM 2.2b: *Predicted NPP$_{mean}$ (within 15 km radius) (within 15 km radius) classified by subsistence type. Climate grouping (ET) defined by line type for Warm climate (dashed line) and Warm and Cold Combined climate (solid line) societies. Error bars represent 95% confidence intervals. Panels represent: (A) binary, (B) ternary, and (C) quaternary subsistence classifications.*

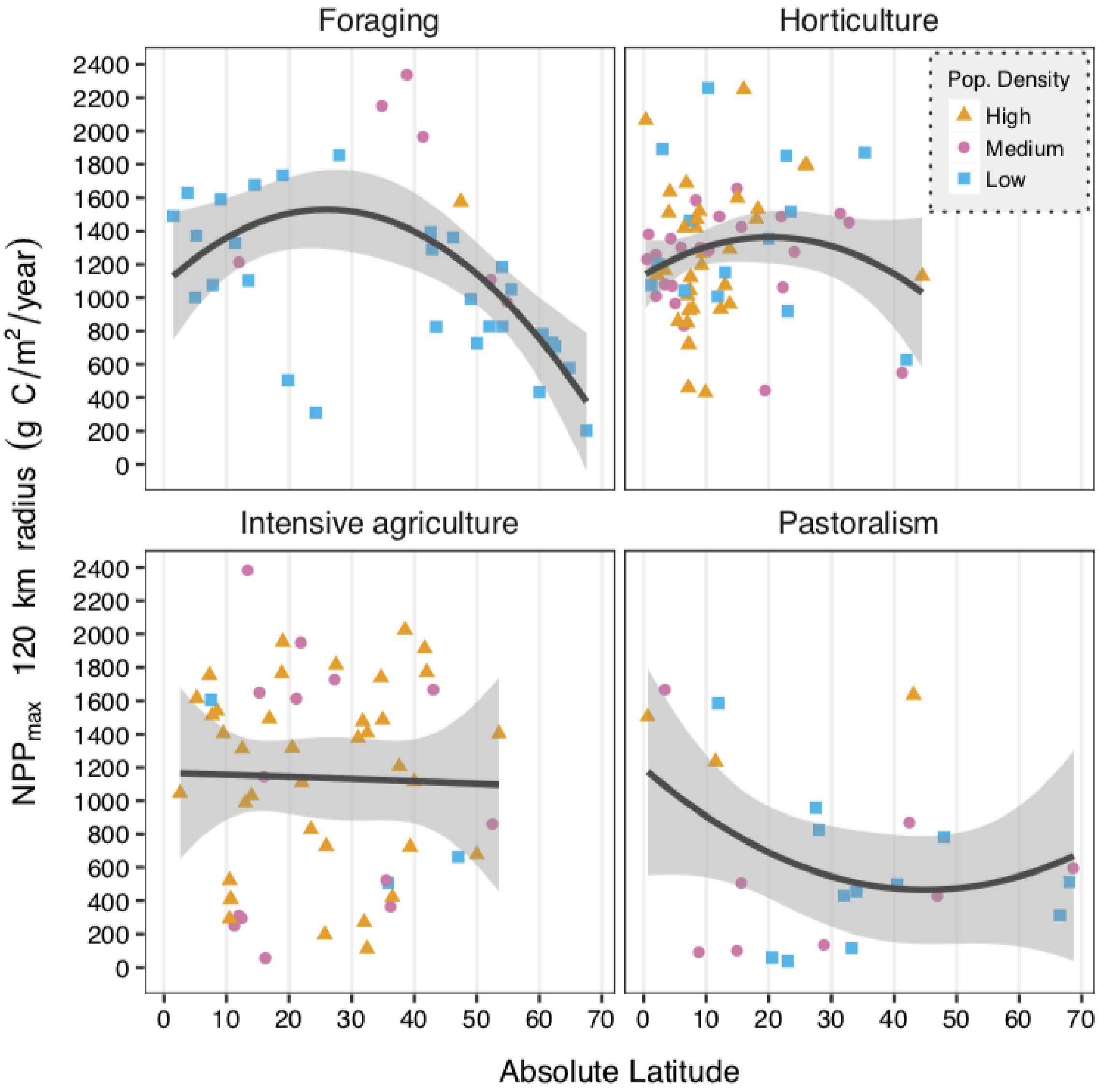

Figure SM 2.3: *Predicted NPP$_{max}$ (120 km radius) versus absolute latitude, classified by subsistence type. Lines and error ribbons represent point and 95% confidence interval predictions from a general linear model, respectively. Points correspond to observed NPP$_{max}$ and PD as reported in the SCCS and are colored by PD. Latitudinal distribution covers only the observed range of each subsistence type.*

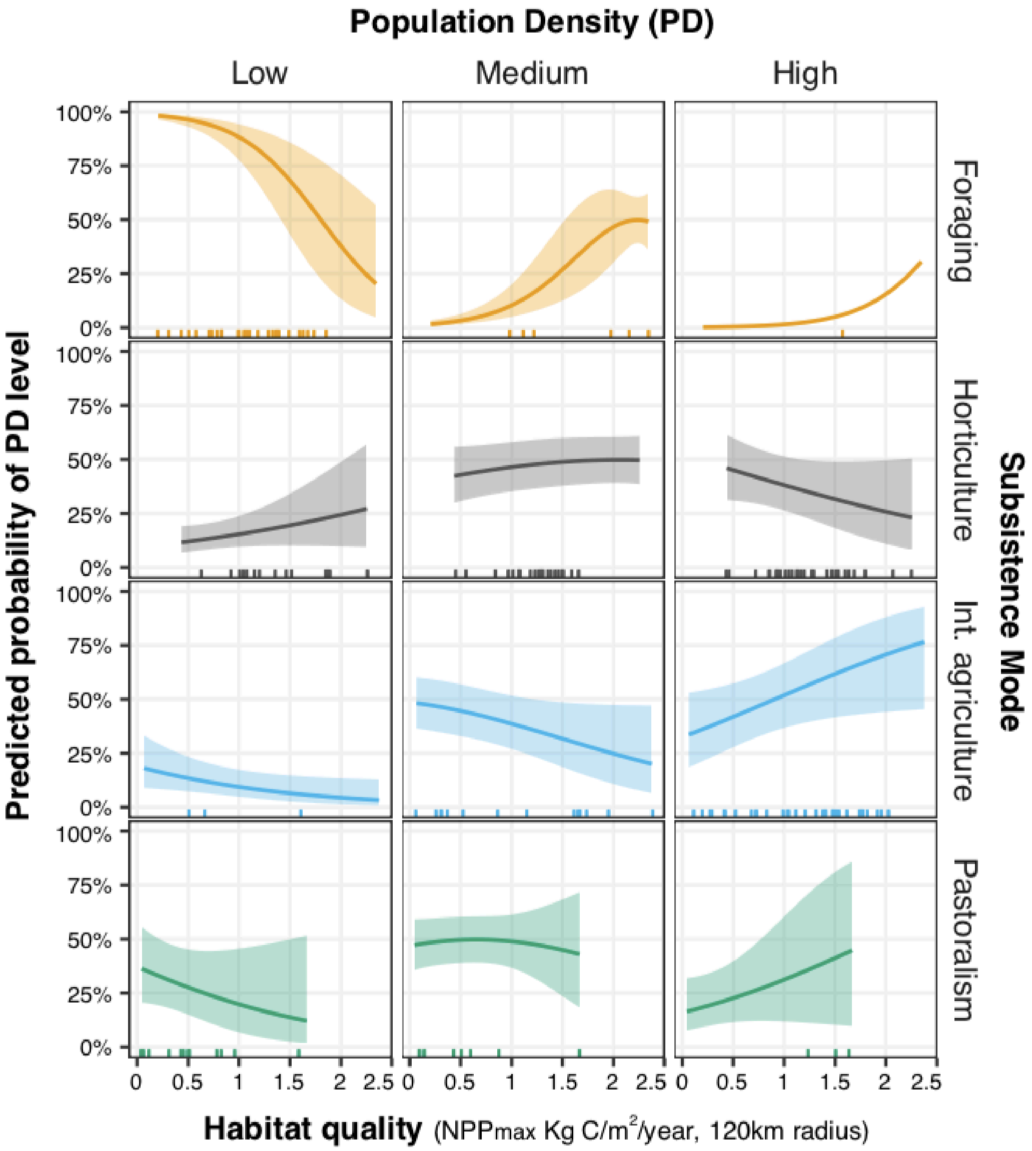

Figure SM 2.4: *Predicted probability of exhibiting low, medium, or high PD, versus NPP$_{max}$ (120 km radius). Rows correspond to subsistence type. Columns correspond to levels of PD.*

Contrast	**Estimate**	**SE**	**df**	***t*-ratio**	***p*-value**
Agriculture - Foraging	-116	80.6	347	-1.44	0.15

Table SM 2.5: *Predicted NPP$_{max}$ and NPP$_{mean}$ (within 15 km radius) classified into binary subsistence types. Warm and Cold climate societies combined. p-values are adjusted for multiple comparisons using the sequential Bonferroni method.*

Contrast	**Estimate**	**SE**	**df**	***t*-ratio**	***p*-value**
Foraging - Horticulture	-49	89.6	343	-0.55	0.63
Foraging - Intensive agriculture	89	88.0	343	1.01	0.63
Foraging - Pastoralism	443	109.9	343	4.03	0.0003
Horticulture - Intensive agriculture	138	78.5	343	1.76	0.24
Horticulture - Pastoralism	492	106.1	343	4.64	<0.0001
Intensive agriculture - Pastoralism	354	101.7	343	3.48	0.0022

Table SM 2.6: *Predicted NPP_{max} and NPP_{mean} (within 15 km radius) classified into ternary subsistence types. Warm and Cold climate societies combined. p-values are adjusted for multiple comparisons using the sequential Bonferroni method. p-value adjustment: sequential Bonferroni method for 6 tests.*

Contrast	**Estimate**	**SE**	**df**	***t*-ratio**	***p*-value**
Foraging - Agriculture	35	80.0	345	0.44	0.66
Foraging - Pastoralism	429	110.7	345	3.87	0.0003
Agriculture - Pastoralism	394	96.4	345	4.08	0.0002

Table SM 2.7: *Predicted NPP_{max} and NPP_{mean} (within 15 km radius) classified into quaternary subsistence types. Warm and Cold climate societies combined. p-values are adjusted for multiple comparisons using the sequential Bonferroni method. p-value adjustment: sequential Bonferroni method for 3 tests.*

SM Text (Chapter 2) Model Specifications:

Objective 1

$$\begin{gathered} NPP_{max\,i} = \beta 01 + \beta 1 horticulture_i \\ + \beta 2 pastoralism_i \\ + \beta 3 intensiveAgriculture_i \\ + \beta 4 MAP_i \\ + \beta 5 ET_i \\ + \beta 6 ET^2{}_i \\ + \beta 7 AbLat_i \\ + \beta 8 AbLat^2{}_i \\ + \beta 9 DME_i \\ + \beta 10 MOBILE_i \\ + \beta 11 FISH_i \\ + e_i \end{gathered}$$

(1) Using an ordinary least squares estimator, where *NPP*$_{max}$ is average maximum Net Primary Productivity within either a 15 km or 120 km radius of each society, *horticulture*, *pastoralism*, and *intensiveAgriculture* are dummy variables with foraging as the reference level, *MAP* is mean annual precipitation in millimeters, *ET* is effective temperature, *ET2* is effective temperature squared, *AbLat* is absolute latitude, *AbLat2* is absolute latitude squared, *DME* is distance to marine ecoregion, *MOBILE* is a dummy variable denoting degree of mobility, *FISH* is a dummy variable indicating degree of reliance on fished resources for protein in diet, and *e* is residual error.

Objective 2

$$\begin{gathered} NPPmax\ i = \beta 01 + \beta 1 horticulture_i \\ + \beta 2 pastoralism_i \\ + \beta 3 intensiveAgriculture_i \\ + \beta 4 MAP_i \\ + \beta 5 ET_i \\ + \beta 6 ET2_i \\ + \beta 7 AbLat_i \\ + \beta 8 AbLat^2{}_i \\ + \beta 9 DME_i \\ + \beta 10 MOBILE_i \\ + \beta 11 FISH_i \\ + \beta 12 horticulturei \times AbLat_i \\ + \beta 13 pastoralismi \times AbLat_i \\ + \beta 14 intensiveAgriculturei \times AbLat_i \\ + \beta 15 horticulturei \times AbLat^2{}_i \\ + \beta 16 pastoralismi \times AbLat^2{}_i \\ + \beta 17 intensiveAgriculturei \times AbLat^2{}_i \\ + e_i \end{gathered}$$

(2) Using an ordinary least squares estimator, where *NPP*$_{max}$ is average maximum Net Primary Productivity within either a 15 km or 120 km radius of each society, *horticulture*, *pastoralism*, and *intensiveAgriculture* are dummy variables with foraging as the reference level, *MAP* is mean annual precipitation in millimeters, *ET* is effective temperature, ET^2 is effective temperature squared, *AbLat* is absolute latitude, $AbLat^2$ is absolute latitude squared, *DME* is distance to marine ecoregion, *MOBILE* is a dummy variable denoting degree of mobility, *FISH* is a dummy variable indicating degree of reliance on fished resources for protein in diet, and *e* is residual error.

Objective 3

$$\begin{gathered}
\mathbf{P}(PDi = 1 \mid X\beta,\ e\ \ = \text{logistic}(\beta_0 1 + \beta_1 horticulture_i \\
+ \beta_2 pastoralism_i \\
+ \beta_3 intensiveAgriculture_i \\
+ \beta_4 NPP_{max\ i} \\
+ \beta_5 MAP_i \\
+ \beta_6 ET_i \\
+ \beta_7 ET^2{}_i \\
+ \beta_8 AbLat_i \\
+ \beta_9 AbLat^2{}_i \\
+ \beta_{10} DME_i \\
+ \beta_{11} MOBILE_i \\
+ \beta_{12} FISH_i \\
+ \beta_{13} horticulture_i \times NPP_{max\ i} \\
+ \beta_{14} pastoralism_i \times NPP_{max\ i} \\
+ \beta_{15} intensiveAgriculture_i \times NPP_{max\ i} \\
+ e_i\ )
\end{gathered}$$

(3) Using a maximum likelihood estimator (computed using iteratively reweighted least squares), where *PD* is an ordinal response variable indicating degree of population density with three categories: high, medium, and low as the reference level, *horticulture*, *pastoralism*, and *intensiveAgriculture* are dummy variables with foraging as the reference level, NPP_{max} is average maximum Net Primary Productivity within either a 15 km or 120 km radius of each society, *MAP* is mean annual precipitation in millimeters, *ET* is effective temperature, ET^2 is effective temperature squared, *AbLat* is absolute latitude, $AbLat^2$ is absolute latitude squared, *DME* is distance to marine ecoregion, *MOBILE* is a dummy variable denoting degree of mobility, *FISH* is a dummy variable indicating degree of reliance on fished resources for protein in diet, and *e* is residual error.

Table SM 3.1: Complete ethogram for foraging observations in Botswana

Context	Activity	Activity # / Code
General		
	Unknown	??
	Travel (Walking or Wading)	1 - WT
	Pause (Pause While Walking)	2 - WP
Food Related		
	Search (Walking or Wading)	3 - WS
	Picking Tree (Pick Fruit From Tree or Bush)	4 - PT
	Picking Ground (Pick Fruits/Foods From Ground)	5 - PG
	Digging - Hand	6 - DH
	Digging - Tool	7 - DT
	Pursue Larvae	9 - PH
	Pursue Honey	9 - PH
	Game/Prey pursuit	10 - PP
	Pursue Veg	11 - PV
	Process Veg (Food Processing - Vegetable)	12 - VP
	Process Game (Food Processing - Game)	13 - GP
	Food processing (mechanical)	14 - MP
	Food processing (thermal)	15 - TP
Miscellaneous Work		
	Tool manufacture	16 - TM
	Tool repair	17 - TR
	Homework (housekeeping)	18 - HW
	Groom Self (Washing or Cleaning Self)	19 - GS
	Groom Other (Washing or Cleaning Other)	20 - GO
	Active interaction with own children (Play or entertain own child)	21 - IK
	Active interaction with others children	22 - OK
	Carry Child	23 - CC
	Feed Nurse (Nurse Child)	24 - FN
	Feed Food (Feed Food to Child)	25 - FF
	Collect Wood	26 - CW
	Build Fire	27 -BF
	Collect Water	28 - WC
Leisure		
	Rest	29 - RE
	Rest / wait at vegetable	30 - RV
	Rest / wait at larvae	31 - RL
	Rest / wait at honey	32 - RH
	Rest / wait at game	33 - RG

Table SM 3.1 (Continued)

Context	Activity	Activity # / Code
	Sleep	34 - SL
Eating		
	Eat from Source	35 - ES
	Eat from Store (Non-Source)	36 - EN
	Eat from Other Source (Eat From Source Collected by Other)	37 - OE
	Eat from Other Otore (Eat From Other's Non-Source Store)	38 - ON
	Drink from Source	39 - DS
	Drink from Bottle (Or other Store)	40 - DB
Social		
	Talk Others (Talk to Others, May be on Phone)	41 - TO
	Talk Self	42 - TS
	Play Game	43 - PL
	Dance	44 - DA
Agricultural		
	Plough Field	45 - PF
	Hoe Field	46 - HF
	Plant Seed	47 - PS
	Weed Field	48 - WF
	Harvest Foods	49 - HV
	Water Crops / Ag Water	50 - AW
Additional - TBD		
	Void / toilet - short / long call	51 -VD
	Pull Mokoro	52 - PLM
	Paddle Mokoro Travel	53 - PDT (or PdS)
	Paddle Mokoro Search	54 - PDS (or PdS)
	Pole Mokoro Travel	55 - POT
	Pole Mokoro Search	56 - POS
	Push Mokoro	57 - PUM
	Ride In Mokoro	58 - RIM
	Drive (In Car)	59 - DR
Cooperation		
	Assistance - Give	60 - AG
	Assistance - Receive	61 - AR
Habitat		
	River / Delta	R
	Lake / Lagoon	L
	Flood Plain	F
	Sandveld / dry	S
	Pan	P

Table SM 3.1 (Continued)

Context	Activity	Activity # / Code
	Island	I
Posture		
	Supine / laying flat on back	LB
	Prone / laying flat on stomach	PR
	Laying on side	LS
	Kneel / knees on ground, weight on back of lower leg	KN
	Sit / buttocks on substrate	SB
	Squat / buttocks off ground, knees flexed	SQ
	Bend / flexed at waist, legs straight	BE
	Stand / weight on feet, back straight	ST
	Walk	WK
	Run	RU
	Dance	DA
	Climb / quadrupedal travel off-ground	CL
	Perch / stationary off-ground	PE
	Wade / walking in water > .25 m deep	WA
	Swim / travel in water horizontal, feet not touching	SW

Table SM 4.1: Complete list of samples and notes analyzed for starch content

sample_id	moisture	starch _dwb	starch _perc	perc_ fdm	wild_ cult	loc_bin	location	species	part	name	collector	source	notes	bag_notes
T-1-1-E	0.91	64.4	0.644	24.9	Wild	Savanna	Tanzania	Vigna frutescens	Tuber	//Ekwa	A. Crittenden	new	Whole	was classified as 'root' - reclass as tuber
T-2-3-A	0.91	56.6	0.566	24.9	Wild	Savanna	Tanzania	Vigna frutescens	Tuber	//Ekwa	A. Crittenden	new	Whole	was classified as 'root' - reclass as tuber
2t-2005	0.94	35.4	0.354	23.8	Wild	Savanna	Tanzania	Vigna frutescens	Tuber	!Ekwa	A. Crittenden	new	Whole	
3t-2005	0.94	28.1	0.281	24.9	Wild	Savanna	Tanzania	Vigna frutescens	Tuber	!Ekwa	A. Crittenden	new	Whole	
1t-2006	0.94	12.3	0.123	16.9	Wild	Savanna	Tanzania	Eminia atenullifera	Tuber	Makalita	A. Crittenden	new	Pith	
2t-2006	0.94	5.2	0.052	18.4	Wild	Savanna	Tanzania	Eminia atenullifera	Tuber	Makalita	A. Crittenden	new	Pith	
3t-2006	0.94	4.3	0.043	21.5	Wild	Savanna	Tanzania	Eminia atenullifera	Tuber	Makalita	A. Crittenden	new	Pith	
1l-2006	0.95	6.3	0.063		Wild	Savanna	Tanzania	Eminia atenullifera	Tuber	Makalita	A. Crittenden	new	Peel	
T-2-6	0.94	8.5	0.085	18.9	Wild	Savanna	Tanzania	Eminia atenullifera	Tuber	Makalito	A. Crittenden	new	Whole	Assume misspelling
T-2-7	0.93	8.7	0.087	18.9	Wild	Savanna	Tanzania	Eminia atenullifera	Tuber	Makalito	A. Crittenden	new	Whole	Assume misspelling
15w-2006	0.92	25.1	0.251		Wild	Savanna	Tanzania	Acacia nilotica	Bean	Mangwala	A. Crittenden	new	Whole	
6l-2006	0.93	35.1	0.351		Wild	Savanna	Tanzania	Coccinea surantiaca	Tuber	Matukwaya	A. Crittenden	new	Peel	
5t-2006	0.92	46.8	0.468	12.7	Wild	Savanna	Tanzania	Vigna macrorhyncha	Tuber	Shaehako	A. Crittenden	new	Pith	
18-2005	0.93	5.1	0.051	18.4	Wild	Savanna	Tanzania	Vatoraea pseudolablab	Tuber	Shumuako	A. Crittenden	new	Whole	
17ib-2005	0.93	21.1	0.211	40.1	Wild	Savanna	Tanzania	Vatoraea pseudolablab	Tuber	Shumuako	A. Crittenden	new	Bark	
N-1-3	0.94	3.4	0.034		Wild	Savanna	Namibia	unknown 1	Tuber	Gwe	M. Firestone	new	Whole	Not usually cooked
N-1-6	0.92	34.4	0.344		Wild	Savanna	Namibia	unknown 2	Tuber	Nchun	M. Firestone	new	Whole	
N-1-12	0.93	3.6	0.036		Wild	Savanna	Namibia	unknown 3	Bulb	!Goro	M. Firestone	new	Whole	Onion-like
N-2-2	0.92	0.5	0.005		Wild	Savanna	Namibia	Eulophia sp.	Bulb	//Dau	M. Firestone	new	Whole	Big and ripe
N-2-5	0.94	22.9	0.229		Wild	Savanna	Namibia	Vigna dinteri	Tuber	Sha	M. Firestone	new	Whole	Ripe
N-2-8	0.93	11.7	0.117		Wild	Savanna	Namibia	Asclepiadaceae sp.	Tuber	!Xo!Kama	M. Firestone	new	Whole	Potato-like
N-4-2	0.91	46.1	0.461		Wild	Savanna	Namibia	Trochomeria macrocarpa	Tuber	N=wara!ko!ko	M. Firestone	new	Whole	Good sample
N-4-7	0.92	6.8	0.068		Wild	Savanna	Namibia	unknown 4	Root	N/won/washe	M. Firestone	new	Whole	Water Root. Eaten for water
N-5-2	0.92	12.9	0.129		Wild	Savanna	Namibia	unknown 5	Tuber	//Kore	M. Firestone	new	Whole	
N-5-4	0.93	53.8	0.538		Wild	Savanna	Namibia	unknown 6	Tuber	/'Han	M. Firestone	new	Whole	Important Food Source

Table SM 4.1 (Continued)

sample_id	moisture	starch _dwb	starch _perc	perc_ fdm	wild_ cult	loc_bin	location	species	part	name	collector	source	notes	bag_notes
N-8-1	0.93	10.1	0.101		Wild	Savanna	Namibia	Hydnora sp.	Tuber	//Hokxam	M. Firestone	new	Whole	
N-8-2	0.93	54.9	0.549		Wild	Savanna	Namibia	unknown 7	Bulb	Uhru	M. Firestone	new	Whole	Good sample
SA061	0.95	22.5	0.225	40.2	Wild	Savanna	South Africa	Watsonia sp.	Corm	Watsonia sp.	A. Cunningham	new	Whole	
SA094	0.93	72.5	0.725	37.8	Wild	Savanna	South Africa	Babiana sp.	Corm	Babiana sp.	A. Cunningham	new	Whole	
SA092	0.93	71.1	0.711	44.1	Wild	Savanna	South Africa	Babiana sp.	Corm	Babiana sp.	A. Cunningham	new	Whole	
SA017	0.94	54	0.54	23.9	Wild	Savanna	South Africa	Chasmanthe sp.	Corm	Chasmanthe sp.	A. Cunningham	new	Whole	
SA018	0.94	47.9	0.479	24.1	Wild	Savanna	South Africa	Chasmanthe sp.	Corm	Chasmanthe sp.	A. Cunningham	new	Whole	
SA084	0.96	51.8	0.518	15.3	Wild	Savanna	South Africa	Ferraria sp.	Corm	Ferraria sp.	A. Cunningham	new	Whole	
SA085	0.95	47	0.47	16.1	Wild	Savanna	South Africa	Ferraria sp.	Corm	Ferraria sp.	A. Cunningham	new	Whole	
ANDY	0.95	48.4	0.484	12.4	Wild	Savanna	South Africa	Aponogeton distachyos	Flower	Aponogeton distachyos	A. Cunningham	new	Whole	
SA031	0.97	56.2	0.562	21.4	Wild	Savanna	South Africa	Annesorhiza nuda	Root	Annesorhiza nuda	A. Cunningham	new	Whole	
SA033	0.97	53.7	0.537	21.3	Wild	Savanna	South Africa	Annesorhiza nuda	Root	Annesorhiza nuda	A. Cunningham	new	Whole	
VEZA001	0.97	58.4	0.584	19.1	Wild	Savanna	South Africa	Annesorhiza nuda	Root	Annesorhiza nuda	A. Cunningham	new	Whole	
VEZA002	0.96	58.9	0.589	21	Wild	Savanna	South Africa	Annesorhiza nuda	Root	Annesorhiza nuda	A. Cunningham	new	Whole	
SA097	0.96	12	0.12	12.1	Wild	Savanna	South Africa	Typha capensis	Rhizome	Typha capensis	A. Cunningham	new	Whole	
SA077	0.95	5.7	0.057	17.4	Wild	Savanna	South Africa	Cyphia sp.	Tuber	Cyphia sp.	A. Cunningham	new	Whole	
SA080	0.96	4.5	0.045	19.9	Wild	Savanna	South Africa	Cyphia sp.	Tuber	Cyphia sp.	A. Cunningham	new	Whole	
ASZA002	0.96	12.9	0.129	20.6	Wild	Savanna	South Africa	Cyphia sp.	Tuber	Cyphia sp.	A. Cunningham	new	Whole	
SA072	0.95	18.1	0.181	22.8	Wild	Savanna	South Africa	Cyphia sp.	Tuber	Cyphia sp.	A. Cunningham	new	Whole	
VEZA002	0.95	10.6	0.106	18.8	Wild	Savanna	South Africa	Cyphia sp.	Tuber	Cyphia sp.	A. Cunningham	new	Whole	
SBZA001	0.96	4.4	0.044	14	Wild	Savanna	South Africa	Cyphia sp.	Tuber	Cyphia sp.	A. Cunningham	new	Whole	
VEZA001	0.95	6.1	0.061	48.5	Wild	Savanna	South Africa	Pelargonium lobatum	Tuber	Pelargonium lobatum	A. Cunningham	new	Whole	
VEZA004	0.94	3.5	0.035	42.2	Wild	Savanna	South Africa	Pelargonium lobatum	Tuber	Pelargonium lobatum	A. Cunningham	new	Whole	
VEZA005	0.93	7	0.07	47.3	Wild	Savanna	South Africa	Pelargonium lobatum	Tuber	Pelargonium lobatum	A. Cunningham	new	Whole	
SA098	0.96	15.8	0.158	14.3	Wild	Savanna	South Africa	Typha capensis	Rhizome	Typha capensis	A. Cunningham	new	Whole	
Ebihama 005	0.95	63.7	0.637	25.1	Wild	Rainforest	Uganda	Dioscorea praehensilis	Tuber	Dioscorea praehensilis	A. Cunningham	new	Whole	
Ebihama 007	0.93	75.1	0.751	40.1	Wild	Rainforest	Uganda	Dioscorea praehensilis	Tuber	Dioscorea praehensilis	A. Cunningham	new	Whole	
Ebihama 008A	0.92	75.9	0.759	31.7	Wild	Rainforest	Uganda	Dioscorea praehensilis	Tuber	Dioscorea praehensilis	A. Cunningham	new	Whole	
Ebihama 009b	0.93	65	0.65	25.6	Wild	Rainforest	Uganda	Dioscorea praehensilis	Tuber	Dioscorea praehensilis	A. Cunningham	new	Whole	

Table SM 4.1 (Continued)

sample_id	moisture	starch_dwb	starch_perc	perc_fdm	wild_cult	loc_bin	location	species	part	name	collector	source	notes	bag_notes
Ebihama 2	0.92	77.9	0.779	22.7	Wild	Rainforest	Uganda	Dioscorea praehensilis	Tuber	Dioscorea praehensilis	A. Cunningham	new	Whole	
Ebihama 5	0.93	58.2	0.582	29.3	Wild	Rainforest	Uganda	Dioscorea praehensilis	Tuber	Dioscorea praehensilis	A. Cunningham	new	Whole	
Ebihama 7	0.9	79.1	0.791	24.3	Wild	Rainforest	Uganda	Dioscorea praehensilis	Tuber	Dioscorea praehensilis	A. Cunningham	new	Whole	
Ebihama 8	0.93	72.6	0.726		Wild	Rainforest	Uganda	Dioscorea praehensilis	Tuber	Dioscorea praehensilis	A. Cunningham	new	Whole	
Ebihama 9	0.93	62.3	0.623	29.5	Wild	Rainforest	Uganda	Dioscorea praehensilis	Tuber	Dioscorea praehensilis	A. Cunningham	new	Whole	
Ebihama 11	0.93	69.5	0.695	10.7	Wild	Rainforest	Uganda	Dioscorea praehensilis	Tuber	Dioscorea praehensilis	A. Cunningham	new	Whole	
Ebihama 12	0.94	41.7	0.417		Wild	Rainforest	Uganda	Dioscorea praehensilis	Tuber	Dioscorea praehensilis	A. Cunningham	new	Whole	
Ebihama 14	0.94	28.4	0.284		Wild	Rainforest	Uganda	Dioscorea praehensilis	Tuber	Dioscorea praehensilis	A. Cunningham	new	Whole	
Ebihama 18	0.92	40.6	0.406		Wild	Rainforest	Uganda	Dioscorea praehensilis	Tuber	Dioscorea praehensilis	A. Cunningham	new	Whole	
Ebihama 19	0.93	39.6	0.396		Wild	Rainforest	Uganda	Dioscorea praehensilis	Tuber	Dioscorea praehensilis	A. Cunningham	new	Whole	
Ebikwa 1	0.91	73.5	0.735	23.5	Wild	Rainforest	Uganda	Dioscorea preusii	Tuber	Dioscorea odoratissima	A. Cunningham	new	Whole	
Ebikwa 4	0.92	66.8	0.668		Wild	Rainforest	Uganda	Dioscorea preusii	Tuber	Dioscorea odoratissima	A. Cunningham	new	Whole	
Ebikwa 6	0.93	34.9	0.349		Wild	Rainforest	Uganda	Dioscorea preusii	Tuber	Dioscorea odoratissima	A. Cunningham	new	Whole	
Ebikwa 7	0.95	13.9	0.139	8.9	Wild	Rainforest	Uganda	Dioscorea preusii	Tuber	Dioscorea odoratissima	A. Cunningham	new	Whole	
Ebikwa 8	0.91	75.9	0.759		Wild	Rainforest	Uganda	Dioscorea preusii	Tuber	Dioscorea odoratissima	A. Cunningham	new	Whole	
Amatugu 1	0.93	51.4	0.514	14.6	Wild	Rainforest	Uganda	Dioscorea bulbifera	Aerial Tuber	Dioscorea bulbifera	A. Cunningham	new	Whole	
Amatugu 2	0.93	66.4	0.664		Wild	Rainforest	Uganda	Dioscorea bulbifera	Aerial Tuber	Dioscorea bulbifera	A. Cunningham	new	Whole	
B 277	0.91	14	0.14	9.7	Wild	Savanna	Botswana	Cyperus papyrus	Pith	Cyperus papyrus	A. Cunningham	new	Whole	
B 072	0.92	6.3	0.063	14.3	Wild	Savanna	Botswana	Phoenix reclinata	Pith	Phoenix reclinata	A. Cunningham	new	Whole	
B 093	0.94	5.3	0.053	13.6	Wild	Savanna	Botswana	Phoenix reclinata	Pith	Phoenix reclinata	A. Cunningham	new	Whole	
B 096	0.92	31.3	0.313	24.2	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 099	0.92	41.1	0.411	30.1	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 104	0.92	9.4	0.094	8.3	Wild	Savanna	Botswana	Typha capensis	Rhizome	Typha capensis	A. Cunningham	new	Whole	
B 105	0.92	4.2	0.042	13.2	Wild	Savanna	Botswana	Cyperus papyrus	Rhizome	Cyperus papyrus	A. Cunningham	new	Whole	
B 107	0.94	24.1	0.241	18.4	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 108	0.91	50.6	0.506	47.7	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 110	0.92	21.4	0.214	17.4	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 111	0.91	37.1	0.371	23.8	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Fruit	Nymphaea nouchali	A. Cunningham	new	Whole	
B 112	0.93	18.9	0.189	13.6	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	

Table SM 4.1 (Continued)

sample_id	moisture	starch _dwb	starch _perc	perc_ fdm	wild_ cult	loc_bin	location	species	part	name	collector	source	notes	bag_notes
B 115	0.91	54	0.54	48.1	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 120	0.91	49.5	0.495	27.6	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 121	0.92	50.2	0.502	49.4	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 127	0.91	35.3	0.353	21.2	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Fruit	Nymphaea nouchali	A. Cunningham	new	Whole	
B 141	0.91	13.8	0.138	22.6	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 142	0.93	63.4	0.634	43.6	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 143	0.93	28.5	0.285	24.4	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Fruit	Nymphaea nouchali	A. Cunningham	new	Whole	
B 162	0.93	35.8	0.358	19.7	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Fruit	Nymphaea nouchali	A. Cunningham	new	Whole	
B 166	0.92	3.5	0.035	7.7	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 172	0.91	24.6	0.246	17.9	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 173	0.91	40.4	0.404	24.2	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Fruit	Nymphaea nouchali	A. Cunningham	new	Whole	
B 183	0.93	9.3	0.093	14	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 185	0.9	52.1	0.521	30.3	Wild	Savanna	Botswana	Nymphaea lotus	Rhizome	Nymphaea lotus	A. Cunningham	new	Whole	
B 186	0.93	18.6	0.186	12.8	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 187	0.93	5.7	0.057	14.8	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Fruit	Nymphaea nouchali	A. Cunningham	new	Whole	
B 190	0.92	35.9	0.359	21.6	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 219	0.91	18.8	0.188	21	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 222	0.91	51	0.51	50.9	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 236	0.94	22.3	0.223	17.5	Wild	Savanna	Botswana	Raphionacme burkei	Tuber	Raphionacme burkei	A. Cunningham	new	Whole	
B 245	0.91	32.7	0.327	19.8	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 246	0.92	54.3	0.543	26	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Fruit	Nymphaea nouchali	A. Cunningham	new	Whole	
B 249	0.9	53.4	0.534	25.9	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Fruit	Nymphaea nouchali	A. Cunningham	new	Whole	
B 250	0.91	18.7	0.187	15.6	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 252	0.9	41.6	0.416	39.7	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 258	0.92	2.7	0.027	15.7	Wild	Savanna	Botswana	Phoenix reclinata	Pith	Phoenix reclinata	A. Cunningham	new	Whole	
B 283	0.91	0.5	0.005	11.1	Wild	Savanna	Botswana	Aloe zebrina	Flower	Aloe zebrina	A. Cunningham	new	Whole	
B 284	0.92	3.8	0.038	21.3	Wild	Savanna	Botswana	Hibiscus sp.	Flower	Hibiscus sp.	A. Cunningham	new	Whole	
B 293	0.91	14.6	0.146	8.2	Wild	Savanna	Botswana	Cyperus papyrus	Pith	Cyperus papyrus	A. Cunningham	new	Whole	
B 304	0.91	36.4	0.364	24.9	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	

Table SM 4.1 (Continued)

sample_id	moisture	starch _dwb	starch _perc	perc_ fdm	wild_ cult	loc_bin	location	species	part	name	collector	source	notes	bag_notes
B 306	0.91	37.3	0.373	23.2	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Fruit	Nymphaea nouchali	A. Cunningham	new	Whole	
B 307	0.91	31.3	0.313	26	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 310	0.91	40	0.4	25.8	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 316	0.92	3	0.03	12	Wild	Savanna	Botswana	Aloe zebrina	Flower	Aloe zebrina	A. Cunningham	new	Whole	
B 325	0.91	33.1	0.331	50.6	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 333	0.93	0	0	13.4	Wild	Savanna	Botswana	Phoenix reclinata	Pith	Phoenix reclinata	A. Cunningham	new	Whole	
B 338	0.9	27.8	0.278	15.5	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Fruit	Nymphaea nouchali	A. Cunningham	new	Whole	
B 365	0.9	45.9	0.459	27.3	Wild	Savanna	Botswana	Nymphaea lotus	Fruit	Nymphaea lotus	A. Cunningham	new	Whole	
B 369	0.9	46.7	0.467	25.4	Wild	Savanna	Botswana	Nymphaea lotus	Fruit	Nymphaea lotus	A. Cunningham	new	Whole	
B 370	0.91	54	0.54	44.4	Wild	Savanna	Botswana	Nymphaea lotus	Rhizome	Nymphaea lotus	A. Cunningham	new	Whole	
B 379	0.91	39.3	0.393	44.9	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 380	0.92	2.5	0.025	12.1	Wild	Savanna	Botswana	Nymphaea lotus	Fruit	Nymphaea lotus	A. Cunningham	new	Whole	
B 381	0.9	58.7	0.587	44.5	Wild	Savanna	Botswana	Nymphaea lotus	Rhizome	Nymphaea lotus	A. Cunningham	new	Whole	
B 391	0.91	55.2	0.552	30.3	Wild	Savanna	Botswana	Nymphaea lotus	Fruit	Nymphaea lotus	A. Cunningham	new	Whole	
B 394	0.91	48.1	0.481	38.3	Wild	Savanna	Botswana	Nymphaea lotus	Rhizome	Nymphaea lotus	A. Cunningham	new	Whole	
B 415	0.94	6	0.06	16.5	Wild	Savanna	Botswana	Phoenix reclinata	Pith	Phoenix reclinata	A. Cunningham	new	Whole	
B 419	0.91	47.1	0.471	47.5	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 423	0.9	50.1	0.501	49.4	Wild	Savanna	Botswana	Nymphaea nouchali var. caerulea	Rhizome	Nymphaea nouchali	A. Cunningham	new	Whole	
B 424	0.91	33	0.33	23.8	Wild	Savanna	Botswana	Nymphaea lotus	Fruit	Nymphaea lotus	A. Cunningham	new	Whole	
B 425	0.9	46.5	0.465	46.3	Wild	Savanna	Botswana	Nymphaea lotus	Rhizome	Nymphaea lotus	A. Cunningham	new	Whole	
B 428	0.9	58.4	0.584	55.3	Wild	Savanna	Botswana	Nymphaea lotus	Rhizome	Nymphaea lotus	A. Cunningham	new	Whole	
		48.4	0.484		Wild	Rainforest	Gabon*	Dioscorea preussii	Tuber		Hladik et al. 1984	lit	Whole	
		68.2	0.682		Wild	Rainforest	Central African Republic*	Dioscorea dumetorum	Tuber		Hladik et al. 1984	lit	Whole	
		75.9	0.759		Wild	Rainforest	Central African Republic*	Dioscorea mangenotiana	Tuber		Hladik et al. 1984	lit	Whole	
		58.3	0.583		Wild	Rainforest	Central African Republic*	Dioscorea praehensilis	Tuber		Hladik et al. 1984	lit	Whole	
		69.9	0.699		Wild	Rainforest	Gabon*	Dioscorea burkilliana	Tuber		Hladik et al. 1984	lit	Whole	
		78.2	0.782		Wild	Rainforest	Gabon*	Dioscorea burkilliana	Tuber		Hladik et al. 1984	lit	Whole	
		57.6	0.576		Wild	Rainforest	Gabon*	Dioscorea bulbifera	Tuber		Hladik et al. 1984	lit	Whole	

Table SM 4.1 (Continued)

sample_id	moisture	starch _dwb	starch _perc	perc_ fdm	wild_ cult	loc_bin	location	species	part	name	collector	source	notes	bag_notes
		78.8	0.788		Wild	Rainforest	Central African Republic*	Dioscorea semperflorens	Tuber		Hladik et al. 1984	lit	Whole	
		81.3	0.813		Wild	Rainforest	Gabon*	Dioscorea semperflorens	Tuber		Hladik et al. 1984	lit	Whole	
		73.4	0.734		Wild	Rainforest	Central African Republic*	Dioscorea minutiflora	Tuber		Hladik et al. 1984	lit	Whole	
		63.6	0.636		Wild	Rainforest	Gabon*	Dioscorea dumetorum	Tuber		Hladik et al. 1984	lit	Whole	
		67.8	0.678		Cultivated	Rainforest	Gabon*	Dioscorea dumetorum	Tuber		Hladik et al. 1984	lit	Whole	
		53.6	0.536		Cultivated	Rainforest	Gabon*	Dioscorea cayenensis-rotundata	Tuber		Hladik et al. 1984	lit	Whole	
		73.1	0.731		Cultivated	Rainforest	Central African Republic*	Dioscorea cayenensis-rotundata	Tuber		Hladik et al. 1984	lit	Whole	
		72.1	0.721		Cultivated	Rainforest	Central African Republic*	Dioscorea cayenensis-rotundata	Tuber		Hladik et al. 1984	lit	Whole	
		75.4	0.754		Cultivated	Rainforest	Central African Republic*	Dioscorea cayenensis-rotundata	Tuber		Hladik et al. 1984	lit	Whole	
		74.8	0.748		Cultivated	Rainforest	Central African Republic*	Dioscorea cayenensis-rotundata	Tuber		Hladik et al. 1984	lit	Whole	
		72.9	0.729		Cultivated	Rainforest	Central African Republic*	Dioscorea cayenensis-rotundata	Tuber		Hladik et al. 1984	lit	Whole	
		73.6	0.736		Cultivated	Rainforest	Central African Republic*	Dioscorea alata	Tuber		Hladik et al. 1984	lit	Whole	
		76.7	0.767		Cultivated	Rainforest	Central African Republic*	Dioscorea alata	Tuber		Hladik et al. 1984	lit	Whole	
		70.7	0.707		Cultivated	Rainforest	Central African Republic*	Dioscorea alata	Tuber		Hladik et al. 1984	lit	Whole	
		78.5	0.785		Cultivated	Rainforest	Central African Republic*	Dioscorea alata	Tuber		Hladik et al. 1984	lit	Whole	
		71.6	0.716		Cultivated	Rainforest	Gabon*	Dioscorea burkilliana	Tuber		Hladik et al. 1984	lit	Whole	
		71.2	0.712		Cultivated	Rainforest	Central African Republic*	Dioscorea burkilliana	Tuber		Hladik et al. 1984	lit	Whole	
		51.1	0.511		Wild	Savanna	Tanzania*	Vigna frutescens	Tuber	//Ekwa hasa	Schoeninger et al. 2001	lit	Whole	
		25.8	0.258		Wild	Savanna	Tanzania*	Vigna frutescens	Tuber	//Ekwa hasa	Schoeninger et al. 2001	lit	Whole	
		35.1	0.351		Wild	Savanna	Tanzania*	Vigna frutescens	Tuber	//Ekwa hasa	Schoeninger et al. 2001	lit	Whole	
		12.8	0.128		Wild	Savanna	Tanzania*	Vigna frutescens	Tuber	//Ekwa hasa	Schoeninger et al. 2001	lit	Whole	
		4.95	0.0495		Wild	Savanna	Tanzania*	Vigna frutescens	Tuber	//Ekwa hasa	Schoeninger et al. 2001	lit	Whole	
		19.6	0.196		Wild	Savanna	Tanzania*	Eminia entennulifa	Tuber	Makaritako	Schoeninger et al. 2001	lit	Whole	
		23.9	0.239		Wild	Savanna	Tanzania*	Ipomoea transvaalensis	Tuber	Panjuko	Schoeninger et al. 2001	lit	Whole	

Table SM 4.1 (Continued)

sample_id	moisture	starch_dwb	starch_perc	perc_fdm	wild_cult	loc_bin	location	species	part	name	collector	source	notes	bag_notes
		75.6	0.756	24.4	Cultivated	Rainforest	Sri Lanka*	Dioscorea alata	Tuber		Wanasundera and Ravindran 1994	lit	Whole	
		77.1	0.771	29	Cultivated	Rainforest	Sri Lanka*	Dioscorea alata	Tuber		Wanasundera and Ravindran 1994	lit	Whole	
		82.8	0.828	25.2	Cultivated	Rainforest	Sri Lanka*	Dioscorea alata	Tuber		Wanasundera and Ravindran 1994	lit	Whole	
		83.3	0.833	30.1	Cultivated	Rainforest	Sri Lanka*	Dioscorea alata	Tuber		Wanasundera and Ravindran 1994	lit	Whole	
		76.5	0.765	22.9	Cultivated	Rainforest	Sri Lanka*	Dioscorea alata	Tuber		Wanasundera and Ravindran 1994	lit	Whole	
		77.1	0.771	22.5	Cultivated	Rainforest	Sri Lanka*	Dioscorea alata	Tuber		Wanasundera and Ravindran 1994	lit	Whole	
		84.3	0.843	34.5	Cultivated	Rainforest	Sri Lanka*	Dioscorea alata	Tuber		Wanasundera and Ravindran 1994	lit	Whole	
		83.2	0.832	41.4	Cultivated	Rainforest	Bangladesh*	Manihot esculenta	Tuber		Fakir et al. 2012	lit	Peeled	
		86.7	0.867	37.3	Cultivated	Rainforest	Bangladesh*	Manihot esculenta	Tuber		Fakir et al. 2012	lit	Peeled	
		85	0.85	40.9	Cultivated	Rainforest	Bangladesh*	Manihot esculenta	Tuber		Fakir et al. 2012	lit	Peeled	
		88	0.88	40.6	Cultivated	Rainforest	Bangladesh*	Manihot esculenta	Tuber		Fakir et al. 2012	lit	Peeled	
		87.1	0.871	41.5	Cultivated	Rainforest	Bangladesh*	Manihot esculenta	Tuber		Fakir et al. 2012	lit	Peeled	
		82.4	0.824	43.8	Cultivated	Rainforest	Bangladesh*	Manihot esculenta	Tuber		Fakir et al. 2012	lit	Peeled	
		81.9	0.819	45.3	Cultivated	Rainforest	Bangladesh*	Manihot esculenta	Tuber		Fakir et al. 2012	lit	Peeled	
Wariyapola		73.2	0.732	34.5	Cultivated	Rainforest	Sri Lanka*	Ipomoea batatas	Tuber		Ravindran et al. 1995	lit	Whole	
FA17		72.03	0.7203	36.3	Cultivated	Rainforest	Sri Lanka*	Ipomoea batatas	Tuber		Ravindran et al. 1995	lit	Whole	
Jewel		68.16	0.6816	36.7	Cultivated	Rainforest	Sri Lanka*	Ipomoea batatas	Tuber		Ravindran et al. 1995	lit	Whole	
B5		70.78	0.7078	32.8	Cultivated	Rainforest	Sri Lanka*	Ipomoea batatas	Tuber		Ravindran et al. 1995	lit	Whole	
Nemogold		72.18	0.7218	33.2	Cultivated	Rainforest	Sri Lanka*	Ipomoea batatas	Tuber		Ravindran et al. 1995	lit	Whole	
I16		75.65	0.7565	32.8	Cultivated	Rainforest	Sri Lanka*	Ipomoea batatas	Tuber		Ravindran et al. 1995	lit	Whole	
128		73.61	0.7361	31.2	Cultivated	Rainforest	Sri Lanka*	Ipomoea batatas	Tuber		Ravindran et al. 1995	lit	Whole	
129		66.1	0.661	30.6	Cultivated	Rainforest	Sri Lanka*	Ipomoea batatas	Tuber		Ravindran et al. 1995	lit	Whole	
LI		73.63	0.7363	34.4	Cultivated	Rainforest	Sri Lanka*	Ipomoea batatas	Tuber		Ravindran et al. 1995	lit	Whole	
L3		76.74	0.7674	36.1	Cultivated	Rainforest	Sri Lanka*	Ipomoea batatas	Tuber		Ravindran et al. 1995	lit	Whole	
L5		73.52	0.7352	37.2	Cultivated	Rainforest	Sri Lanka*	Ipomoea batatas	Tuber		Ravindran et al. 1995	lit	Whole	
L9		66.7	0.667	35.4	Cultivated	Rainforest	Sri Lanka*	Ipomoea batatas	Tuber		Ravindran et al. 1995	lit	Whole	
L11		76.32	0.7632	31.9	Cultivated	Rainforest	Sri Lanka*	Ipomoea batatas	Tuber		Ravindran et al. 1995	lit	Whole	
L16		74.17	0.7417	35.6	Cultivated	Rainforest	Sri Lanka*	Ipomoea batatas	Tuber		Ravindran et al. 1995	lit	Whole	
L17		77.34	0.7734	33.4	Cultivated	Rainforest	Sri Lanka*	Ipomoea batatas	Tuber		Ravindran et al. 1995	lit	Whole	

Table SM 4.1 (Continued)

sample_id	moisture	starch _dwb	starch _perc	perc_ fdm	wild_ cult	loc_bin	location	species	part	name	collector	source	notes	bag_notes
LS9		63.13	0.6313	34.1	Cultivated	Rainforest	Sri Lanka*	Ipomoea batatas	Tuber		Ravindran et al. 1995	lit	Whole	
		68.5	0.685	31.9	Cultivated	Rainforest	China*	Ipomoea batatas	Tuber		Chen et al. 2003	lit	Peeled	
		75.9	0.759	36.7	Cultivated	Rainforest	China*	Ipomoea batatas	Tuber		Chen et al. 2003	lit	Peeled	
		57.8	0.578	18.6	Cultivated	Rainforest	China*	Ipomoea batatas	Tuber		Chen et al. 2003	lit	Peeled	