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The cost of cooking for foragers

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ABSTRACT

Cooked food provides more calories to a consumer than raw food. When our human ancestors adopted cooking, the result was an increase in the caloric value of the diet. Generating the heat to cook, however, requires fuel, and accessing fuel was and remains a common problem for humanity. Cooking also frequently requires monitoring, special technology and other investments. These cooking costs should vary greatly across multiple contexts. Here I explain how to quantify this cooking trade-off as the ratio of the energetic benefits of cooking to the increased cost in handling time and examine the implications for foragers, including the first of our ancestors to cook. Ethnographic and experimental return rates and nutritional analysis about important prey items exploited by ethnohistoric Numic foragers in the North American Great Basin provide a demonstration of how the costs of cooking impact different types of prey. Foragers should make choices about which prey to capture based on expectations about the costs involved to cook them. The results indicate that the caloric benefit achieved by cooking meat is quickly lost as the cost of cooking increases, whereas many plant foods are beneficially cooked across a range of cooking costs. These findings affirm the importance of plant foods, especially geophytes, among foragers, and are highly suggestive of their importance at the onset of cooking in the human lineage.

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1. Introduction

Cooking food conferred an energetic advantage to our hominin ancestors, as it does to the vast majority of humans today (Wrangham et al., 1999; Wrangham and Conklin-Brittain, 2003; Groopman et al., 2015). The discovery and adoption of cooking drove the evolution of many morphological and behavioral aspects of our species, eventually becoming a universal necessity among humans (Wrangham et al., 1999; Wrangham and Conklin-Brittain, 2003; Wrangham and Carmody, 2010; Organ et al., 2011; Groopman et al., 2015; Hardy et al., 2015; Parker et al., 2016). Although the ubiquity of cooking across human societies suggests strong benefits, the costs of cooking are often unexplored. These costs may have important opportunity trade-offs on a variety of fitness-related activities, especially in foraging contexts. For foragers, cooking necessitates not only the location and acquisition of prey items (i.e., potentially edible plants and animals) but also the location and acquisition of fuels and the time to prepare and cook those items, as well as any associated cooking tools. These investments of time are one way to estimate the cost of cooking and should determine whether an item is eaten raw or cooked or whether the item is eaten at all. The benefits of cooking have

frequently been noted (Wrangham et al., 1999; Wrangham and Conklin-Brittain, 2003; Carmody and Wrangham, 2009; Wrangham and Carmody, 2010; Carmody et al., 2011; Organ et al., 2011; Groopman et al., 2015; Barkai et al., 2017) and leveraged to explain the adoption of cooking in human evolution. The costs of cooking have received much less attention (refer to the studies by Henry, 2017; Henry et al., 2018, for some exceptions). Some have also noted the importance of firewood in more recent archaeological contexts (Heizer, 1963), the need for which presents a potentially significant cooking cost. Researchers such as Heizer (1963) and more recently Henry et al. (2018), suggest an economic approach, which explicitly defines the costs and benefits of cooking, with important implications for how we understand forager diets and ecological relationships. One such aspect is the importance of cooked geophytes (i.e., plants with starchy underground storage organs [USOs]) as a staple in human evolution (Vincent, 1985; O'Connell et al., 1999; Marean, 2010; Singels et al., 2016; De Vynck et al., 2016a; Larbey et al., 2019; Botha et al., 2020; Wadley et al., 2020).

In this article, I argue that the costs associated with cooking, which vary widely across ecological and social circumstances, should play a major role in our understanding of forager diets, including those present when the use of fire was adopted by the genus *Homo*. I propose a method for calculating the benefits of

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cooking and how the costs of acquiring those benefits will limit when cooking occurs. I derive this method from the microeconomic logic of behavioral ecology, utilizing elements of the prey choice model (Charnov, 1976a).

The Numic foragers of the North American Great Basin traditionally relied on geophytes as part of their subsistence. Because sufficient foraging data are available across a suite of prey types in that region, I use the Great Basin as a demonstration of how considering both the benefits and costs of cooking should inform our understanding of diet breadth, particularly when geophytes are available. This example is broadly generalizable to any foraging context or assessment of human prey choice, including those present at the onset of cooking as part of the human subsistence strategy. Finally, I discuss the implications of this cooking trade-off for understanding the relative importance of prey types in forager diets, with a special emphasis on geophytes.

2. Methods

2.1. Cooking affects postencounter return rates

Calculating the costs and benefits of cooking can be framed simply by considering how cooking will impact the postencounter return rate for a prey item. The postencounter return rate refers to the rate of energy capture per time spent handling a prey item, after it is encountered in the course of foraging. The postencounter return rate of any prey item i can be expressed (following Charnov, 1976a) as follows:

$$e_i/h_i \quad (1)$$

where e_i is the caloric value of prey item i (here considered in kilocalories/kilogram) and h_i is the postencounter handling cost associated with capturing and consuming prey item i (here considered in hours/kilogram).

The benefits of cooking can be measured as an increase in the bioavailability of calories contained in the materials of a prey item for the consumer. Here, I represent that change in bioavailability as a change in the value of e_i . Details about how I derive the cooked and raw values of e_i are found in section 2.2.

The cost of cooking can be measured as an increase in handling time (h_i ; described in detail in section 2.3). Handling time includes a suite of activities, including but not limited to pursuing, digging, grinding, and butchering. It is important to note that as this analysis focuses on postencounter return rates, time spent in search of prey items is neither a component of h_i nor a factor in considering the cost and benefit of cooking as formulated here. In studies of human diets, handling time does not conventionally incorporate the cost of digestion; however, some have suggested it should (Boback et al., 2007; Carmody and Wrangham, 2009; Wrangham and Carmody, 2010). On the other hand, nonhuman foraging studies often incorporate the cost of digestion, with some noting the special constraint digestive costs pose to maximizing energy intake (Burrows and Hughes, 1991; Hirakawa, 1997; Knutsen and Salvanes, 1999; Jeschke et al., 2002; Van Gils et al., 2005; Papanikolaou et al., 2014). Because of this omission, h_i is underreported in the prey data used in this article. For example, time to chew before swallowing is not included in h_i . Cooking should decrease the handling costs of digestion, but because I do not attempt to quantify that decrease in h_i here, the cost of cooking as an increase in h_i is overestimated. Therefore, the results presented in the following should be taken conservatively.

The North American Great Basin (Fig. 1) is a region where experimental and ethnographic research has gathered data sufficient for estimating how the costs and benefits of cooking apply to a

foraged diet. Ethnohistoric and experimental studies of Numic hunter-gatherers provide an extensive reporting on the diets of Great Basin foragers (Table 1; Kaldy et al., 1980; Norton et al., 1984; Couture et al., 1986; Simms, 1987; McCarthy, 1993; Barlow and Metcalfe, 1996; Smith et al., 2001; Byers and Ugan, 2005; Smith and McNees, 2005; O'Connell, personal communication, 2008). Macronutrient composition not available in the anthropological foraging literature is drawn from the USDA FoodData Central online database (2019). All data and sources are presented in Table 2. I discuss the Great Basin ecological and cultural context further in section 2.4. With the data presented in Tables 1 and 2, I calculate the benefits of cooking and then demonstrate how those benefits decrease variably for each prey type across a range of cooking costs. In section 2.5, I introduce *Perideridia gairdneri*, the common yampah root, used here as a model species both to illustrate how the analysis is conducted and to demonstrate variation in the benefits of cooking.

2.2. Cooking improves the energetic yield of food

Cooking alters food chemically and physically in ways beneficial to consumers by “advanc[ing] the digestion process, so that more energy and nutrients can be obtained from any one mouthful of food,” (Wandsnider, 1997:2) while also reducing food-borne pathogens and facilitating storage for some prey items. While numerous benefits from cooking could be assessed as an energetic gain, here I focus on the increase in digestibility, or the increase in the bioavailability of calories in a cooked item. I represent this increase in bioavailability in terms of energetic yield, defined as the caloric value of the prey item to the consumer. This analysis does not capture any other aspects of the utility of cooking, such as the value of detoxifying or removing parasites from food, improved chewing efficiency or decreased costs of digestion (Zink et al., 2014). It should thus be noted that the results of this analysis underrepresent the true value not only of cooking but also of small controlled fires in general.

Much work is still needed to determine the relationship between the characteristics of food and consumers and the bioavailability of calories and macronutrients, including how cooking or other forms of processing affect bioavailability (Carmody and Wrangham, 2009; Schnorr et al., 2015; Henry et al., 2018). The analysis presented here serves as an approximation, while acknowledging that calculating the actual caloric value of macronutrient absorption, cooked or raw, is more complex. Previous research establishes macronutrient absorption, measured as the difference between the amount of macronutrient materials consumed and those excreted in feces, as a useful proxy for bioavailability (Groopman et al., 2015). By extension, I assume that when food material experiences an increase in absorption between raw and cooked materials, it experiences a concomitant increase in energetic yield to the consumer. I include a brief discussion on this issue in section 4.3.

Cooking alters the energetic yield of food by increasing the bioavailability of constituent macronutrients in variable amounts, depending on how those macronutrients react to the application of heat (Carmody and Wrangham, 2009). The increase in energetic yield awarded by cooking is estimated here by drawing on experimentally derived values of the difference in digestibility between raw and cooked materials (Wrangham et al., 1999; Carmody and Wrangham, 2009). Previous studies suggest that cooking results in an increase in bioavailability of three constituent macronutrients: starches (Carmody and Wrangham, 2009; Carmody et al., 2011), proteins (Boback et al., 2007) and lipids (Groopman et al., 2015). A cooking transform (C_i), the estimated proportionate caloric gain resulting from the physical and chemical changes

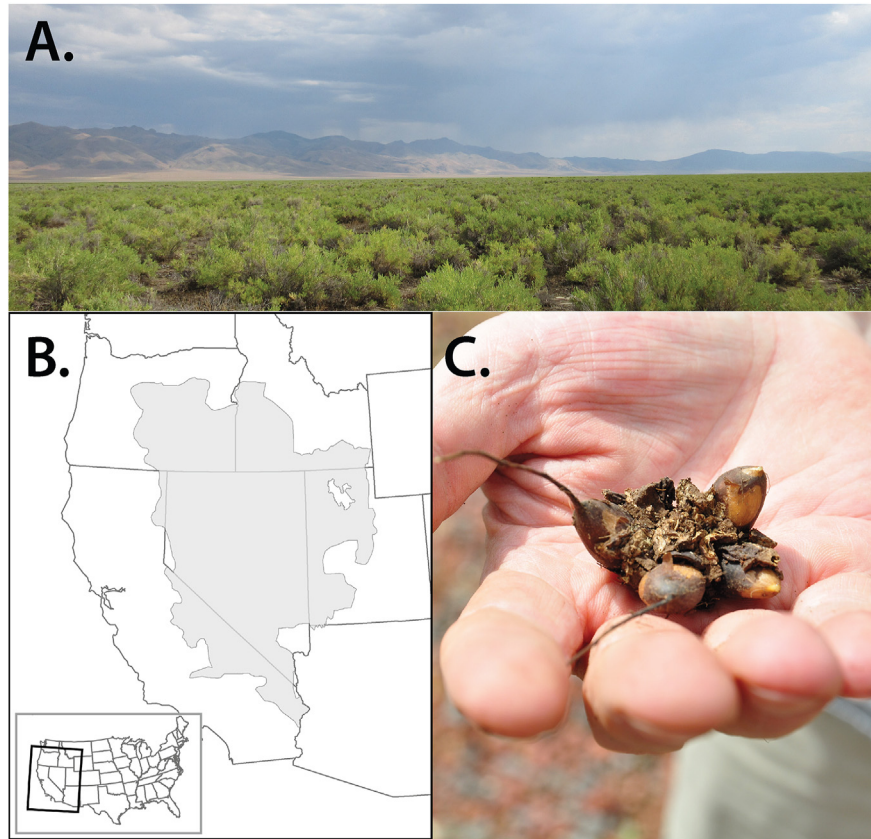


Figure 1. Images showing details of the Great Basin example. A) A view across Grass Valley in the central Great Basin, shown as an example of the distribution of woody shrubs and grasses dominating the valley floor, with wooded hills in the distance (photo taken by K. Magargal). B) A map showing the extent of Numic forager territory (shaded in gray) in the Great Basin region in the Western United States (adopted from the study by Parker et al., 2018). C) A handful of the edible roots of *Perideridia* sp. (photo courtesy of L. Louderback and J. F. O'Connell).

caused by cooking prey item i for each type of macronutrient, is given in Table 3.

Importantly, many wild foods have not undergone carbohydrate composition analysis sufficient to isolate starches from other types of carbohydrates, so in the analysis presented here, the cooking transform for starches is applied to the entire carbohydrate portion of the prey item. This may result in an overestimate of the benefit of cooking. However, it is also likely that fiber, which provides caloric value (Oku and Nakamura, 2014) and which is altered by cooking (Zia-ur-Rehman et al., 2003), contains more bioavailable calories when cooked. A sensitivity analysis useful in conceptualizing the results of varying the amount of carbohydrates made more digestible via cooking is provided in section 3.1.

The total energetic content of materials is often measured via bomb calorimetry, and thus, for edible materials, this can be considered the maximum potential energetic yield. I use this value to approximate the cooked value for the prey items (Atwater and Snell, 1903). Further discussion about this approximation is provided in section 4.3. To avoid variation in lab protocols (which are often left unmentioned in the nutritional analysis of wild foods where energetic yield is reported), I calculate the energetic yield of a cooked item using the Atwater method. This method approximates the maximum energy contained in the materials using the '4-9-4' method; the carbohydrate and protein components are assigned a value of 4 kcal/g and the lipid component is assigned 9 kcal/g (Atwater and Snell, 1897; Nichols, 1994). I then divide the cooked caloric value of macronutrients affected by cooking by the

C_i for that macronutrient. The calculation for the raw energetic yield of each prey item can be expressed as follows:

$$\frac{e_i^{\text{carbohydrate}}}{C_i^{\text{carbohydrate}}} + \frac{e_i^{\text{protein}}}{C_i^{\text{protein}}} + \frac{e_i^{\text{lipid}}}{C_i^{\text{lipid}}} \quad (2)$$

where $e_i^{\text{carbohydrate}}$ is the caloric value of carbohydrates in a kilogram of prey item i , e_i^{protein} is the caloric value of proteins in a kilogram of prey item i , e_i^{lipid} is the caloric value of lipids in a kilogram of prey item i , $C_i^{\text{carbohydrate}}$ is the cooking transform for the type of carbohydrate in prey item i , C_i^{protein} is the cooking transform for proteins, and C_i^{lipid} is the cooking transform for lipids.

To perform these calculations, I used the R v. 4.0.3 programming environment (R Core Team, 2019). Importantly, because different food items contain different proportions of the macronutrients in question, the increase in energetic yield conferred by cooking varies considerably across specific prey items as well as broad categories of prey types. I categorize prey items into types following Simms (1987) into nuts, roots, seeds, small game, and large game because the macronutrient composition of prey items in these categories tend to be more similar than between the categories. Grouping prey items in this way allows for broad summaries of how the cooking trade-off will affect types of prey items not just in the Great Basin but across the world. All R code used to produce the

Table 1

The scientific name, common name, and prey type for the sample of Great Basin prey items used in the analysis.

Scientific name	Common name	Prey type
<i>Pinus monophylla</i>	Single-leaf pinyon	Nut
<i>Quercus gambelii</i>	Gambel oak	Nut
<i>Allium textile</i>	Textile onion	Root
<i>Calochortus nuttallii</i>	Sego lily	Root
<i>Camassia quamash</i>	Camas	Root
<i>Cymopterus bulbosus</i>	Bulbous spring parsley	Root
<i>Lewisia rediviva</i>	Bitterroot	Root
<i>Lomatium canbyi</i>	Canby's biscuitroot	Root
<i>Lomatium cous</i>	Cous biscuitroot	Root
<i>Lomatium hendersonii</i>	Henderson biscuitroot	Root
<i>Perideridia gairdneri</i>	Common yampah	Root
<i>Schoenoplectus</i> spp.	Bulrush roots	Root
<i>Achnatherum hymenoides</i>	Ricegrass	Seed
<i>Salicornia</i> spp.	Pickleweed	Seed
<i>Atriplex canescens</i>	Fourwing saltbush	Seed
<i>Atriplex confertifolia</i>	Shadscale	Seed
<i>Carex</i> spp.	Sedge	Seed
<i>Descurainia pinnata</i>	Tansymustard	Seed
<i>Distichlis spicata</i>	Saltgrass	Seed
<i>Helianthus</i> spp.	Sunflower	Seed
<i>Hordeum jubatum</i>	Foxtail barley	Seed
<i>Leymus cinereus</i>	Great Basin wild rye	Seed
<i>Leymus salina</i>	Salina wild rye	Seed
<i>Muhlenbergia asperifolia</i>	Scratchgrass	Seed
<i>Poa</i> spp.	Bluegrass	Seed
<i>Schoenoplectus</i> spp.	Bulrush seeds	Seed
<i>Anatidae</i> spp.	Duck	Small game
<i>Centrocercus urophasianus</i>	Sage-grouse	Small game
<i>Lepus</i> spp.	Jackrabbit	Small game
<i>Sylvilagus</i> spp.	Cottontail rabbit	Small game
<i>Thomomys</i> spp.	Ground squirrel	Small game
<i>Antilocapra americana</i>	Pronghorn	Large game
<i>Odocoileus hemionus</i>	Deer	Large game
<i>Ovis canadensis</i>	Bighorn	Large game

Data are organized by prey type, then scientific name. All scientific nomenclature is drawn from the [USDA Agricultural Research Center \(2019\)](#). Reference to specific prey items in other parts of the text are by genus or genus and species only. See [SOM Table S1](#) for full botanical citations for plant species.

calculations and the resulting figures is provided in [Supplementary Online Material \(SOM\)](#).

2.3. The costs of cooking limit its utility

The cost of cooking can be measured in terms of handling time (h_i). Cooking can be considered a processing technique, where a variety of activities are conducted in the course of applying heat to a prey item. These activities are various and may include collection and processing of fuels such as firewood, construction and maintenance of cooking technology such as pottery or roasting pits and additional processing of prey items specifically associated with cooking. A wide range of ecological and social conditions are likely to influence what form cooking takes and how much cooking costs, leading to broad variation in choices related to both cooking and prey choice. Where handling costs are low, for example in a forest where wood is abundant and of high quality for cooking, a forager is more likely to cook a prey item because the overall rate of caloric return is increased via cooking. In other words, where the cost of cooking is low, the benefits are more likely to outweigh the costs. Where the cost of cooking is high, such as open tundra where little fuel can be found, or damp rainforest where it is difficult to start and maintain a fire, a forager might choose to consume the item raw or to bypass the item altogether. The cost of cooking should be considered as the net difference in handling time in a cooked versus raw prey item. Some outcomes from cooking may actually reduce certain forms of handling costs. For example, some research

suggests that cooking reduces chewing costs ([Dominy et al., 2008; Carmody and Wrangham, 2009](#)), although this likely varies considerably and may not be true for all prey items. For example, [Schoeninger et al. \(2001\)](#) find that the same amount of indigestible fibers is present in some tubers consumed by the Hadza, regardless of whether they are in cooked or raw form.

The ratio of cooking benefit (increase in e_i) to cooking cost (increase in h_i) will dictate the postencounter return rate for a raw versus cooked prey item. Considering the postencounter return rate for a suite of potential prey items, while also considering the costs and benefits of cooking those prey items, provides a new tool for gaining insight into human dietary choices. The following sections consider an example from the North American Great Basin using data from prey items important to the Numa.

2.4. Prey items and variation in the costs of cooking in the Great Basin

While studies from around the world detail nutritional and foraging data, including early hominin sites in Africa, research conducted in the North American Great Basin is unique in providing the macronutrient breakdowns and estimated handling times for a large suite of prey items required for the present analysis. For this reason, I conducted a sample analysis of the cooking trade-off using prey items from the Great Basin. The Great Basin of Western North America is part of a region characterized by what geologists call 'basin and range', a large region of alternating mountain ranges and valleys, some of which hydrologically flow between each other, but none that allow water to escape to the ocean ([Grayson, 2011](#)). Topographic factors heavily influence the vegetal variation (and thus, the abundance of cooking fuel) between basin and range, with lower elevations dominated by nonwoody grasses, forbs and woody shrubs, and middle and higher elevations dominated by woodlands of pinyon (*Pinus monophylla*) and juniper (*Juniperus* sp.). [Figure 1A](#) shows an example of vegetation variation, and [Figure 1B](#) shows a map of the region.

Numic people traditionally moved between the basins and ranges of the Great Basin seasonally, with variation in this pattern captured by whether the group's landscape use was characterized more by residential or logistic mobility ([Steward, 1938; Thomas, 1973; Binford, 1980; Zeanah, 2002](#)). This pattern of land use would have presented different problems for building and maintaining cooking fires in each season, presenting an example of how the costs of cooking may vary. Below, I consider how the seasonal shift in diet may be influenced by the costs and benefits of cooking. I also use a set of prey items from the Great Basin as an example to examine the overall importance of types of prey in light of the cooking trade-off.

2.5. To cook or not: *Perideridia* spp. as a specific example of the cooking trade-off

The starchy roots of *Perideridia* spp. (including *P. gairdneri*, *P. bolanderi* and *P. oregana*) were an important food source for many prehistoric peoples across Western North America ([Kelly, 1932; Steward, 1938; Couture et al., 1986; Herzog, 2014](#)). *Perideridia* sp. root is pictured in [Figure 1C](#). *Perideridia* spp. root can be eaten raw or cooked and is traditionally cooked by Numic people via roasting over coals, pit roasting or pounding into a mash and boiling ([Kelly, 1932; Fowler, 1989](#)). What might account for this variation in preparation strategies? Here, I use *P. gairdneri* as a specific example to illustrate the trade-off inherent in cooking. Estimates of the cooked caloric yield (e_i), pre-cooking handling time (h_i), encounter rates (λ_i), and the percentage of the relevant constituent macronutrients are given in [Table 2](#).

Table 2

Values for Great Basin prey items drawn from the literature or calculated.

Scientific name	Cooked e_i (kcal/kg)	h_i (no cooking cost) (h)	Cooked $\frac{e_i}{h_i}$ (no cooking cost, $\frac{\text{kcal}}{\text{hr}} \cdot \frac{\text{kg}}{\text{kg}}$)	Encounter rate	% protein	% lipids	% carbohydrate	Starch type
<i>Achnatherum hymenoides</i>	2773	6.9 ^a	401.884058	2.2 ^a	12.61 ^b	1.54 ^b	71.18 ^b	S
<i>Salicornia</i> spp.	4017.7	16.2 ^a	248.0061728	1.7 ^a	27.28 ^c	10.13 ^c	50.37 ^c	S
<i>Allium textile</i>	937.4	2.7 ^d	347.1851852	5.9 ^a	2.83 ^e	0.18 ^e	20.2 ^e	U
Anatidae spp.	2064.8	0.369 ^f	5595.663957	0.5688 ^f	17.42 ^g	15.2 ^g	0 ^g	NA
<i>Antilocapra americana</i>	1077.9	0.06 ^a	17,965	0.25 ^a	22.38 ^h	2.03 ^h	0 ^h	NA
<i>Atriplex canescens</i>	3080.9	2.5 ^a	1232.36	6.4 ^a	7.7 ^a	0.01 ^a	69.3 ^a	S
<i>Atriplex confertifolia</i>	2872.9	2.7 ^a	1064.037037	5.9 ^a	3.9 ^a	0.01 ^a	67.9 ^a	S
<i>Calochortus nuttallii</i>	922	13.42 ⁱ	68.70342772	5.9 ^d	1.75 ⁱ	0 ^j	21.3 ^j	U
<i>Camassia quamash</i>	1428	2.7 ^d	528.8888889	5.9 ^d	4.97 ^j	0 ^j	30.73 ^j	U
<i>Carex</i> spp.	2647	12.8 ^a	206.796875	1.75 ^a	10.6 ^a	0.3 ^a	54.9 ^a	S
<i>Centrocercus urophasianus</i>	1116.8	0.246 ^f	4539.837398	0.8531 ^f	25.94 ^k	0.88 ^k	0 ^k	NA
<i>Cymopterus bulbosus</i>	1179.5	0.78 ^e	1512.179487	5.9 ^d	1.87 ^e	0.63 ^e	26.2 ^e	U
<i>Descurainia pinnata</i>	3624.5	2.8 ^a	1294.464286	2 ^a	27.2 ^a	0.05 ^a	63.3 ^a	S
<i>Distichlis spicata</i>	2604	15.8 ^a	164.8101266	0.55 ^a	12.61 ^b	1.54 ^b	71.18 ^b	S
<i>Helianthus</i> spp.	3690	7.2 ^a	512.5	2.15 ^a	20.78 ^l	51.46 ^l	20 ^j	S
<i>Hordeum jubatum</i>	3123	11.2 ^a	278.8392857	1.3 ^a	13.4 ^a	0.3 ^a	64 ^a	S
<i>Lepus</i> spp.	1080.4	0.0861 ^f	12,548.19977	0.3978 ^f	21.79 ^m	2.32 ^m	0 ^m	NA
<i>Lewisia rediviva</i>	3890	2.7 ^a	1440.740741	5.9 ^a	10 ⁿ	1 ⁿ	85 ⁿ	U
<i>Leymus cinereus</i>	2850	5.9 ^a	483.0508475	2.65 ^a	8.8 ^a	1.4 ^a	59.3 ^a	S
<i>Leymus salina</i>	2790	2.6 ^a	1073.076923	7 ^a	12.5 ^a	0.6 ^a	55.9 ^a	S
<i>Lomatium canbyi</i>	1220	2.7 ^d	451.8518519	5.9 ^d	2.5 ^j	0 ^j	28 ^j	U
<i>Lomatium cous</i>	1240	2.7 ^a	459.2592593	5.9 ^d	1 ^j	0 ^j	30 ^j	U
<i>Lomatium hendersonii</i>	1824.8	2.7 ^d	675.8518519	5.9 ^d	2.17 ^j	0 ^j	43.45 ^j	U
<i>Muhlenbergia asperifolia</i>	2463	9.4 ^a	262.0212766	1.55 ^a	12.61 ^b	1.54 ^b	71.18 ^b	S
<i>Odocoileus hemionus</i>	1512.9	0.08 ^a	18,911.25	0.03 ^a	21.78 ^o	7.13 ^o	0 ^o	NA
<i>Ovis canadensis</i>	1031.9	0.055 ^a	18,761.81818	0.425 ^a	20.6 ^p	2.31 ^p	0 ^p	NA
<i>Perideridia gairdneri</i>	4059.7	0.75 ^q	5412.933333	5.9 ^d	6.35 ^r	1.61 ^r	79.25 ^r	U
<i>Pinus monophylla</i>	6342	4.5 ^a	1409.333333	6.85 ^a	8.3 ^c	57 ^c	22 ^c	S
<i>Poa</i> spp.	3412	6.8 ^a	501.7647059	1.55 ^a	12.61 ^b	1.54 ^b	71.18 ^b	S
<i>Quercus gambelii</i>	1040.5	3.4 ^s	306.0294118	9.1 ^a	1.59 ^a	6.17 ^a	10.54 ^a	S
<i>Schoenoplectus</i> spp (roots)	651	2.1 ^a	310	16.25 ^a	0.2 ^a	0.3 ^a	15.4 ^a	U
<i>Schoenoplectus</i> spp (seeds)	3103	3.4 ^a	912.6470588	9.55 ^a	6.5 ^a	6.3 ^a	56.9 ^a	S
<i>Sylvilagus</i> spp.	1080.4	0.1263 ^f	8554.235946	0.3267 ^f	21.79 ^m	2.32 ^m	0 ^m	NA
<i>Thomomys</i> spp.	1138.1	0.185 ^a	6151.891892	0.775 ^a	21.23 ^t	3.21 ^t	0 ^t	NA

NA = not applicable, in cases where the prey item does not contain starch.

Starch types are made by association with Table 3, where U is underground storage organ and S is seed. Data are ordered alphabetically by scientific name. The cooked e_i column was calculated using the Atwater method using the % of proteins, lipids, and carbohydrates. The cooked (no cost) $\frac{e_i}{h_i}$ is calculated by dividing the cooked e_i by the reported h_i (Atwater and Snell, 1897; Nichols, 1994).

^a Simms (1987).^b USDA FDC ID 168890 ('red hard winter wheat').^c Barlow and Metcalf (1996).^d Substituted from bitterroot.^e Smith and McNeese (2005; their table 4).^f Byers and Ugan (2005; their table 7).^g USDA FDC ID 174468 ('whole wild duck').^h USDA FDC ID 175292 ('Game meat, antelope, raw').ⁱ Smith et al. (2001). Handling time derived by reported 3 people taking 8.5 h to obtain 1.9 kg of sego bulbs. Handling calculated as 8.5/(1.9/3).^j Couture et al. (1986).^k USDA FDC ID 172831 ('ruffed grouse').^l USDA FDC ID 170562 ('Seeds, sunflower seed kernels, dried').^m USDA FDC ID 174347 ('game rabbit').ⁿ Norton et al. (1984).^o USDA FDC ID 172602 ('Game meat, deer, ground, raw').^p USDA FDC ID 175303 ('Game meat, goat, raw').^q O'Connell, personal communication (2008).^r Kaldy (1980).^s McCarthy (1993).^t USDA FDC ID 172523 ('Game meat, squirrel, raw').

3. Results

3.1. A close look at cooking a Great Basin staple: *Perideridia* sp.

The benefits of cooking *P. gairdneri* root (as well as the rest of the Great Basin prey items) are described in terms of e_i and e_i/h_i in Table 4. Cooking *P. gairdneri* root changes the caloric yield (e_i) from ~2281 kcal/kg to ~4060 kcal/kg, a ~1779-kcal/kg increase.

Therefore, the benefit of cooking *P. gairdneri* root can be measured as an increase in bioavailable calories of ~1779 kcal/kg. Of course, cooking is likely to come with a time cost (measured here as an increase to h_i), which is likely to vary. If the cost of cooking *P. gairdneri* is zero, the cooked postencounter return rate is ~5413 kcal/h, a ~2372-kcal/h increase from the raw postencounter return rate of ~3041 kcal/h. However, as the cost of cooking increases, the postencounter return rate of cooked *P. gairdneri*

Table 3

Average percentage of caloric gain for each type of macronutrient for which cooking is known to have an effect.

Macronutrient type	Average increase in digestibility from raw to cooked	C_i	Reference
Starch: cereal/seed	23%	1.23	Carmody and Wrangham (2009) ^a
Starch: USO/tuber	91%	1.91	Carmody and Wrangham (2009) ^b
Starch: legume	14%	1.14	Carmody and Wrangham (2009) ^c
Protein	12.70%	1.13	Boback et al. (2007) ^d
Lipid	3.71%	1.04	Groopman et al. (2015) ^e

Starches are broken down into starch type, calculated based on values as given in the study by Carmody and Wrangham (2009: 382, their table 3). The cooking transform, C_i , is a multiplier derived from these percentages of increase in digestibility. Calculations of the raw values of prey items are found by dividing the starch, protein and lipid components of that prey item by the concomitant C_i and summing them, as shown in equation (2) of the main text.

^a The value for seed starch is an average of the three reported.

^b USO starch is taken from the value for potato reported from Englyst and Cummings (1987).

^c For reference, the value for legume starch derived from Sun et al. (2006) as compiled by Carmody and Wrangham (2009) is also tabulated here, although it does not apply to any prey items used in the analysis. Readers should be cautioned that this value was measured in pigs, not humans.

^d An increase in the caloric value of proteins is taken from Boback et al. (2007: 654), and was also applied by Henry et al. (2018).

^e An increase in the caloric value of lipids is taken from Groopman et al. (2015, their table 2).

decreases. It is no longer worth cooking any prey item when the cost of cooking is great enough that the cooked postencounter return rate is lower than the raw postencounter return rate. The cost of cooking, in hours per kilogram, where the postencounter return rate equals the raw value, is here termed the cooking cost limit. The cooking cost limit for *P. gairdneri* is ~0.59 h/kg. If it costs more than

this amount of time per kilogram to cook *P. gairdneri* root, the resource should be consumed raw or bypassed altogether. This is shown graphically in Figure 2A.

The cooking transform (C_i) used here, derived from experiments using modern grocery store potatoes, may indeed be an overestimate of the increase in caloric bioavailability, as the grocery

Table 4

Table showing calculated values for prey items.

Scientific name	Raw e_i (kcal/kg) ^a	Raw $\frac{e_i}{h_i}$ (kcal/hr) ^b	Cooking cost limit (hrs/kg) ^c	$\Delta \frac{e_i}{h_i}$ (kcal/hr) ^d
<i>Achnatherum hymenoides</i>	2299.6	333.3	1.42	68.6
<i>Salicornia</i> spp.	3480.3	214.8	2.5	33.2
<i>Allium textile</i>	538.8	199.6	2	147.6
<i>Anatidae</i> spp.	1932	5235.8	0.03	359.8
<i>Antilocapra americana</i>	967.9	16,131.4	0.01	1833.6
<i>Atriplex canescens</i>	2527.1	1010.8	0.55	221.5
<i>Atriplex confertifolia</i>	2347	869.3	0.6	194.8
<i>Calochortus nuttallii</i>	508	37.9	10.94	30.8
<i>Camassia quamash</i>	819.5	303.5	2	225.4
<i>Carex</i> spp.	2186.5	170.8	2.7	36
<i>Centrocercus urophasianus</i>	994.4	4042.2	0.03	497.6
<i>Cymopterus bulbosus</i>	669.4	858.2	0.59	654
<i>Descurainia pinnata</i>	3025.7	1080.6	0.55	213.9
<i>Distichlis spicata</i>	2140.3	135.5	3.42	29.4
<i>Helianthus</i> spp.	3085.9	428.6	1.41	83.9
<i>Hordeum jubatum</i>	2581.6	230.5	2.35	48.3
<i>Lepus</i> spp.	972.1	11,290.3	0.01	1257.9
<i>Lewisia rediviva</i>	2220.6	822.5	2.03	618.3
<i>Leymus cinereus</i>	2361.1	400.2	1.22	82.9
<i>Leymus salina</i>	2312.3	889.3	0.54	183.7
<i>Lomatium canbyi</i>	674.9	250	2.18	201.9
<i>Lomatium cous</i>	663.7	245.8	2.34	213.5
<i>Lomatium hendersonii</i>	986.8	365.5	2.29	310.4
<i>Muhlenbergia asperifolia</i>	2037.8	216.8	1.96	45.2
<i>Odocoileus hemionus</i>	1388	17,349.9	0.01	1561.3
<i>Ovis canadensis</i>	929.1	16,892.9	0.01	1869
<i>Perideridia gairdneri</i>	2280.8	3041	0.59	2371.9
<i>Pinus monophylla</i>	5941.9	1320.4	0.3	88.9
<i>Poa</i> spp.	2810.7	413.3	1.45	88.4
<i>Quercus gambelii</i>	933	274.4	0.39	31.6
<i>Schoenoplectus</i> spp.	355.6	169.3	1.74	140.7
<i>Schoenoplectus</i> spp.	2625.7	772.3	0.62	140.4
<i>Sylvilagus</i> spp.	972.1	7696.7	0.01	857.5
<i>Thomomys</i> spp.	1029.3	5563.7	0.02	588.1

^a The raw e_i is calculated by dividing the cooked macronutrient components by the appropriate C_i from Table 3, then summed, as given in equation (2).

^b A raw $\frac{e_i}{h_i}$ (postencounter return rate) is calculated by dividing the raw e_i by the precooking handling times reported in Table 2. This represents the maximum possible postencounter return rate, where cooking cost is zero, but decreases as cooking cost increases.

^c The cooking cost limit for each prey item is the maximum amount of handling time dedicated to cooking that is worth investing. If cooking a prey item requires more time than the cooking cost limit, the postencounter return rate is less than for the raw item, and so the item should not be cooked.

^d The $\Delta \frac{e_i}{h_i}$ column shows the difference in postencounter return rate acquired by cooking each prey resource at no cooking cost.

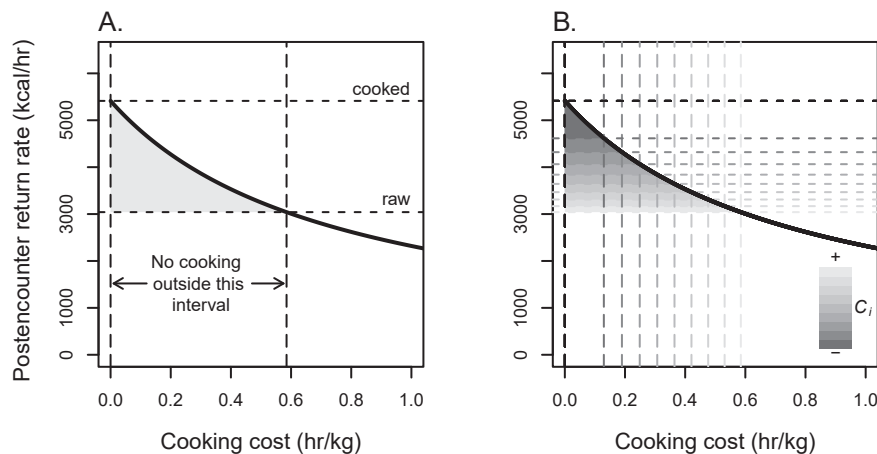


Figure 2. A) Image showing how the postencounter return rate of *Perideridia gairdneri* shifts across a range of cooking costs. Dashed horizontal lines mark the raw and cooked postencounter return rate values. Dashed vertical lines denote the interval of potential cooking costs worth paying to cook *P. gairdneri*, with the shaded region representing all potential cooked values. The right-most vertical dashed line is the cooking cost limit. B) Graphical representation of the sensitivity analysis on C_i that shows how the postencounter return rate and the cooking cost limit both decrease as C_i decreases. Darker shades of gray represent the same relationship as in panel A, but for C_i decreasing at 10% intervals.

store potato is different in important ways from *P. gairdneri* and most wild USOs. To capture how variation in C_i impacts the cooking cost limit, I performed a sensitivity analysis which treats the 91% increase in digestibility reported by Englyst and Cummings (1987, as reported in the study by Carmody and Wrangham, 2009) as a maximum and calculates alternative outcomes for *P. gairdneri* at decreasing 10% intervals of C_i . The result is shown graphically in Figure 2B. As the value of C_i decreases, so does the benefit of cooking and the cooking cost limit. At half the benefit of cooking ($C_i = 1.455$), the maximum potential increase in the postencounter return rate afforded by cooking is ~1573 kcal/h. The cooking cost limit drops to ~0.31 h/kg. Further details of the sensitivity analysis are provided in SOM.

For many plants, especially USOs such as *P. gairdneri*, the carbohydrate content varies seasonally. In addition to seasonal shifts, carbohydrate content is likely to vary greatly with ecological characteristics, or simply with stochastic differences between individual plants. To assess how variation in carbohydrate content affects the outcome of this analysis, I performed a second sensitivity analysis, shown graphically in Figure 3. In this analysis, I explored the relationship between C_i and the cooking cost limit as the carbohydrate component varies. As the carbohydrate component decreases, so does the cooking cost limit and the slope of the line that describes the cooking cost limit as a function of C_i . When $C_i = 1.91$ (its maximum value), and the carbohydrate content of *P. gairdneri* is 50% of the reported value given in Table 2, the cooked e_i is calculated as ~2229 kcal/kg and the raw e_i is calculated as ~1322 kcal/kg, both lower values than for 100% of the reported starch content. The maximum potential increase in the postencounter return rate afforded by cooking is then ~1209 kcal/h, less than half the potential maximum increase for 100% the reported carbohydrate content (which was noted earlier as ~2371 kcal/h). As the carbohydrate component of a prey item drops, so does the increase in digestibility afforded by cooking it, and so the cooking cost limit is also smaller. In this case, *P. gairdneri* with 10% the reported carbohydrate value has a cooking cost limit of ~0.51. Supplementary Online Material Figure S1 graphically represents the relationship between the cooking cost limit and postencounter return rate for

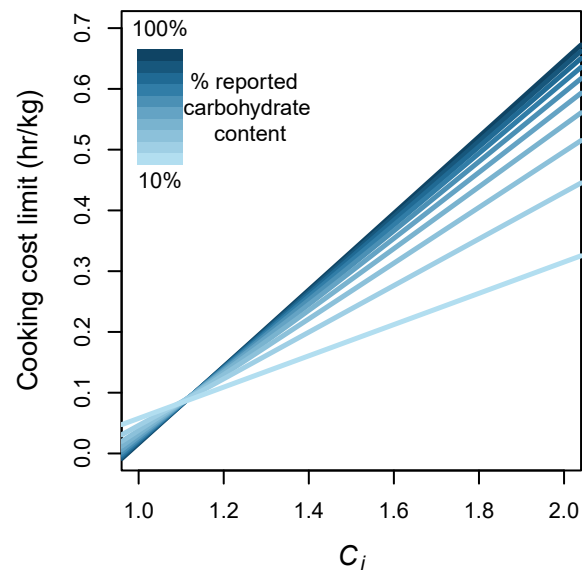


Figure 3. Graphical representation of the sensitivity analysis on carbohydrate content examining how the relationship between C_i and the cooking cost limit varies with carbohydrate content, using data from *Perideridia gairdneri*. As the percentage of carbohydrates decreases, so does the cooking cost limit. The cooking cost limit also changes less as a function of C_i as the percentage of carbohydrates decreases, as evidenced by the decreasing slope of the plotted lines. The darkest blue line represents the relationship between variables at 100% the reported carbohydrate value for *P. gairdneri*, with each lighter color representing a decreasing 10% interval. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

P. gairdneri with 50% the reported carbohydrate value, with the sensitivity analysis on C_i as described earlier. Supplementary Online Material Figure S1 can be compared with Figure 2 to further illustrate how variation in both C_i and carbohydrate content affects the outcomes of cooking (see SOM S1 for further details).

Similar variation in the content of protein and lipids would produce similar cooking outcomes, but to a lesser degree because

both those macronutrients have a lower C_i than carbohydrates. This analysis of how cooking outcomes vary with the proportion of carbohydrate contained in the prey item can also be interpreted in relation to differentiating between types of carbohydrates. As mentioned in section 2.2, I applied the C_i of starch to the total carbohydrate content in the prey item owing to limitations of the data set. Reframing this sensitivity analysis on carbohydrate content in terms of the starch component of the carbohydrates gives a fuller picture of the benefit of cooking. For example, rather than interpreting the details reported in the previous paragraph as the outcomes for a case where the carbohydrate content is 50% of the reported content, one could interpret those details as aligning for a case where 50% of the carbohydrate content of *P. gairdneri* is starch.

3.2. Examining cooking across prey types

Table 4 summarizes the benefits of cooking and the cooking cost limit for each of the 34 Great Basin prey items explored here. Across this suite of prey items, few benefit from paying a high cost of cooking, with a cooking cost limit of 2 hours or less per kilogram for most prey items (Fig. 4). Prey types show specific tendencies when considering cooking trade-offs. The postencounter return rate of large and small game increases the most with cooking on average, but only at very low cooking costs. This is because the protein and lipid components, which are the meat components made more bioavailable by cooking, have a smaller C_i than carbohydrates, especially those found in USOs. Cooking plant foods is more worth the investment in time because the larger C_i , which is also frequently applied to a higher proportion of the material of the prey item, results in a greater increase in bioavailable calories (Figs. 5 and 6). *P. gairdneri* root benefits from cooking more than any game items examined. *Cymopterus bulbosus* and *Lewisia rediviva* also stand out as USOs that derive a larger benefit from cooking than many other game and plant prey items. Figure 6 shows how the mean postencounter return rate for each prey type decreases as the cost of cooking increases. The rate of decrease is high for game and low for plant foods. Notably, all plant items result in a higher benefit from cooking than game items at high cooking costs.

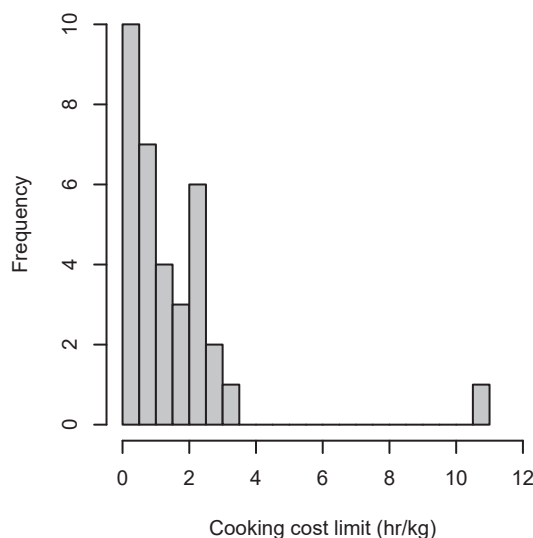


Figure 4. Histogram showing the distribution of the cooking cost limit for the sample of Great Basin prey items. This indicates that although all prey items benefit calorically from cooking, it is not worth cooking most of them beyond a little over 3 hours of time investment per kilogram.

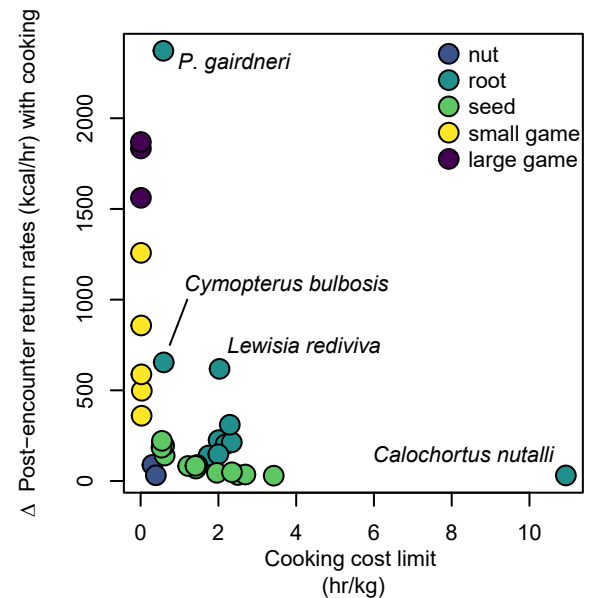


Figure 5. Plot showing the distribution of individual prey items, color-coded by prey type, against the cooking cost limit and the gain (delta) in postencounter return rates resulting from cooking. Game (in yellow and purple dots) tends to benefit most from cooking, but only when the cost of cooking is small. The benefit of cooking seeds (light green) is smaller, but it is still worth cooking them across a range of increased handling times. Nuts (dark blue) benefit only from short cooking times (although it should be noted that the removal of toxic properties, such as leaching tannins from acorns, is not accounted for here). Roots (teal) in the data set have the highest range in macronutrient variation and so also range widely in the outcomes of cooking. Four root prey items from this sample stand out. *Perideridia gairdneri*, *Cymopterus bulbosus* and *Lewisia rediviva* all obtain high benefits from cooking (see reported values in Table 4). For *C. bulbosus* and *L. rediviva*, the benefit persists even as cooking costs rise beyond that which is worth investing in many other prey items. *Calochortus nuttalli* does not obtain a high benefit from cooking, but the benefits decrease slowly as the costs of cooking rise. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

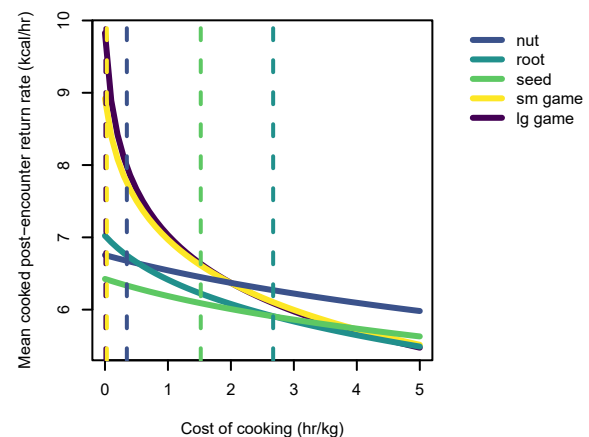


Figure 6. This figure shows how the mean postencounter return rate for each prey type decreases as the cost of cooking increases. Dashed vertical lines are the mean cooking cost limit for each prey type (note that the dashed line for large game is obscured by that for small game—both cooking cost limits are small). Cooking affects different prey items (both in benefit and cost) differentially, resulting in a shifting importance for different types of prey based on the amount of time required to invest in cooking. Thus, while small and large game items benefit greatly from cooking, the benefit is quickly lost as the cost of cooking increases. In contexts where the cost of cooking increases above ~4 hours/kg, seeds and roots become more valuable than game. In contexts where cooking requires large time investments, plant foods should dominate the diet. Even in these contexts, human foragers receive an energetic benefit by investing in cooking plants.

4. Discussion

The aforementioned analysis demonstrates how the benefit derived from cooking varies across different prey types. The cooking cost worth paying also varies across prey items. In particular, while meat tends to have a high energetic yield that is improved by cooking, the benefits of cooking meat, derived from the improved bioavailability of cooked protein and lipid calories, are lost at a rapid rate as the cost of cooking rises. In contrast, the value of cooking plants, which primarily derive a benefit from improved carbohydrate caloric bioavailability, drops at a slower rate as the cost of cooking increases. Notably, some species in particular, such as *P. gairdneri*, may experience an extreme increase in post-encounter return rates with cooking. It should be expected that additional geophyte species throughout the world might experience similarly high benefits to consumers via cooking. Theoretically, foragers will be most likely to cook prey items where and when they benefit the most from cooking. This study thus provides new insights into how we should think about the costs of making a living that include cooked foods. In the following section, I discuss the implications of how variable costs of cooking should factor into broader archaeological and evolutionary patterns, as well as contemporary applied contexts where people rely on biomass fuels.

4.1. Cooking and archaeological patterning in the prehistoric Numic Great Basin

Building on the example drawn from the Great Basin, I will illustrate some ways in which the results allow for some predictions to be made about archaeological patterning for prehistoric Numic foragers. Similar interpretations could be applied to any time or region. As mentioned earlier, historic ethnographic evidence suggests that Numic foragers tended to occupy the valleys in the warmer months and the wooded hillsides in the cooler months. Numic ethnographers suggested that this patterning was driven by seasonal prey availability (Steward, 1938; Couture et al., 1986). However, the cost of cooking any of the acquired resources would also have been heavily impacted by moving between different vegetation regimes. The relative cost of cooking at an encampment in the woodlands, where firewood is abundant, would have been low compared than in the valleys. Therefore, prey items that derive a benefit from cooking when cooking costs are low, such as game, are predicted to be captured, cooked and consumed more in wooded contexts. Prey items that benefit from cooking despite higher cooking costs, such as seeds and roots, should be taken (and cooked) more in the valleys.

The apparent intensification on seeds among prehistoric Numic foragers in the Great Basin has been a topic of debate among archaeologists for some time (Bettinger and Baumhoff, 1982; Aikens, 1994; Eerkens, 2004; Rhode et al., 2006). Seeds are frequently considered low-ranked resources, and indeed in their raw form they tend to provide fewer calories per hour of handling time than most other prey items (following the logic of the prey-choice model articulated by Charnov, 1976a). Why would Numic foragers spend time collecting low-ranked grass seeds in the valleys when the cost of cooking them where they are abundant is high? Consider a scenario where all prey items in the diet are to be cooked. In contexts where the cost of cooking is relatively high, the relative ranking of available prey items is rearranged and some seeds may be higher ranked than other available prey items. This increase in the ranking of seeds in a high-cost cooked diet supports arguments about why a broad-spectrum revolution involved intensification on low-ranked resources for the Numa and others (Stiner, 2001).

Such examination raises the question about when something needs to be cooked at all, or when it can simply be consumed raw.

The analysis offered here only considers when the benefits of cooking would outweigh the costs when the currency of that trade-off is calories. Such is the case for *Perideridia* spp., which can be eaten raw, but for which cooking should occur frequently given the large benefit derived. There are, however, a number of additional issues to consider. Some portion of raw calories may not be bioavailable (discussed further in section 4.3). Some prey items might be dangerous to consume uncooked owing to parasites or toxins. Although animal prey have high caloric value, the risk of parasites may necessitate cooking, but the benefit of cooking meat, measured in terms of caloric bioavailability, is lost quickly as the cost of cooking increases. The result for subsistence choices could have been that meat was eaten raw, rare or not at all if the cost of cooking decreased the rank of animal prey sufficiently. At times when cooking meat was necessary to reduce parasite loads and the cost of cooking was high, animal prey should be frequently bypassed. *Camassia quamash*, or camas, is a Great Basin plant whose roots are known ethnographically to have been consumed by Numic foragers, yet this material is quite toxic raw. Cooking is required to neutralize the toxicity. Therefore, camas should not be chosen as part of a diet when the cost of cooking is prohibitively large. Whether a prey item needs to be cooked before it is edible is another dimension to consider along with the cooking trade-off. In the Numic Great Basin, predictions about when and where such prey items were taken can be generated by considering in what vegetative contexts the costs of cooking would be low enough so the benefit of cooking outweighs the costs. The prehistoric Great Basin is only one example of where consideration of the trade-off inherent in cooking should influence archaeological interpretations about past human-environment interactions. Considering the costs of cooking should be especially important in environmental contexts where the costs were likely high, such as arid or arctic environments with little available fuel, or any context where ecological circumstances are prone to deforestation. Deforestation would increase the cost of cooking over time and could have been a large factor in radical social change, such as that observed at Chaco Canyon in northwestern New Mexico (Lekson, 2006; Heitman and Plog, 2015), the Mayan Lowlands (Shaw, 2003; McNeil et al., 2010; McNeil, 2012) or the Roman deforestation of the Mediterranean woodlands (Hughes, 2011).

4.2. Cooking and human evolution

Although the importance of cooking in the human career is indisputable, details about the location, chronology and the relationship between cooking and other important characteristics of hominin evolution over the last few million years are yet to be untangled in a way that allows us to understand causal relationships. Fundamentally, the timing and location of the first possible cooking fires is under dispute and rightly so given the difficulties posed by interpreting such ancient archaeological sites. Archaeological evidence is proposed for dates as early as 1.5 Ma (Gowlett et al., 1981; Hlubik et al., 2019), and arguments based on the role of cooking in the acquisition of biological traits (such as reduction in dentition and digestive tract as well as increased brain size) push the adoption of cooking beyond 2 Ma (see discussions in the studies by Hardy et al., 2015; Parker et al., 2016). Other researchers take a more conservative approach, arguing for the earliest evidence of hearths based on archaeological evidence (Goren-Inbar et al., 2004; Roebroeks and Villa, 2011; Berna et al., 2012). Not only is the time and location of the first intentionally cooked meal in question but also which of our hominin ancestors was the chef.

My intention here is not to comment specifically on the many pros and cons of accepting or rejecting the proposed archaeological and fossil evidence for the first hearth fires across this huge range of

proposed dates, as many authors have already done (e.g., Wrangham et al., 1999; Wrangham and Conklin-Brittain, 2003; Klein, 2009; Wrangham and Carmody, 2010; Organ et al., 2011; Hardy et al., 2015; Parker et al., 2016). Rather, considering where and when the ecological conditions would have promoted a low cost of cooking could be used as an indicator of when the likelihood of adopting cooking would have been most energetically advantageous. The context of adoption is important because cooking is most beneficial in areas where the cost of cooking is low and the available prey items are those where a consumer would benefit greatly from investing in cooking. The important characteristic of such an environment is likely to be that it contained an abundance of fuel because fuel harvest and transport is a fundamental aspect of cooking. Future work aimed at identifying such potential environments will be important for informing debates about the time and location of the first controlled fires used for cooking.

The cooking trade-off also touches upon many other debates about the relative importance and order of acquisition of characteristics of the genus *Homo*. For example, much discussion has been spent on the importance of meat in foraging contexts. The appearance of stone tools is often interpreted as evidence for the importance of meat (Washburn and Lancaster, 1968; Leakey, 1971; Isaac, 1978). However, the analysis presented here suggests that cooked meat would rank higher than cooked plant foods only when the cost of cooking is low. Therefore, plant resources would have been expected to dominate the diet in scenarios where cooking added significant costs in time to prepare an item for consumption. This prediction supports arguments made about the importance of plant resources to human foragers, particularly the underground storage organs of geophytes, which also happen to be the most likely resource to derive a high benefit from cooking, on average (Hawkes et al., 1989; although this is not necessarily true for all USOs, as noted by Schnorr et al., 2015). Locations where the presence of early foragers coincides with abundant geophytes and fuel, such as the South African cape, are highly suggestive of places where the adoption of cooking would have been most advantageous (Singels et al., 2016; De Vynck et al., 2016b). One does not obtain a caloric benefit from eating cooked meat as the cost of cooking increases, affirming the idea that men's investment in hunting is a fitness signal rather than an effort toward provisioning (Bliege Bird et al., 2001; O'Connell et al., 2002).

The acquisition and processing of plant resources, as well as the acquisition of firewood, is commonly conducted primarily by women across ethnographic contexts (Sen and Sen, 1985; Gurven et al., 2009; Patrick, 2011). Female lifetime fertility and interbirth intervals in foraging societies are constrained by the ability to both carry needed resources along with a child as well as provision children who are unable to sufficiently forage for themselves (Blurton Jones, 1986; Coddling et al., 2011). Because of this constraint on women's mobility, the location of camps and other central places of occupation should preferentially be located near or among women's resources (Zeanah, 2004), including resources that reduce the cost of cooking, such as firewood.

The method presented here for articulating the costs of cooking serves to highlight the impact of access to firewood on women's ability to allocate time to other activities, including child care. The needs of children, including increased sensitivity to parasites and lack of ability to digest raw foods, only increase the need for cooking in child-rearing situations. Understanding the specific costs associated with cooking in any given ecological or social context may also predict situations where men and/or children become more invested in cooking activities. For example, prehistoric foragers in landscapes where mobility is high and fuels are unevenly distributed would benefit most from locating themselves

near access to firewood. In situations where mobility is low, overall foraging return rates would benefit by the participation of more people in firewood collection activities. Such variation should inform on our understanding of land use patterns, time allocation and the sexual division of labor.

4.3. Future work on the relationship between bioavailability and the characteristics of prey and consumers

Modeling diet breadth presents a challenge, in part, because the caloric value of edible materials is measured using proxies whose relationship to absorption in vivo likely varies and is not well understood.

Using the caloric value of prey items as a proxy for bioavailability is problematic in numerous ways. Often, only a single value is reported. Here, I treat this value as representative of the maximum possible caloric value of the edible material, which I argue is sufficient to support the main points presented here, but remains insufficient for more fine-grained actualistic studies because the caloric value actually absorbed by a consumer is not well determined (Carmody et al., 2011). Frequently, if caloric values are reported for cooked foods, they often only account for material loss during the process of cooking, such as the fat loss from meats (Kretser et al., 2017), and do not account for the chemical and physical changes produced by the application of heat. Although some research suggests that combustion might be sufficient to approximate caloric absorption in some cases, based on comparisons between methods for measuring energy content of pre-digested food and that of resulting feces (Henken et al., 1986; Murtagh-Mark et al., 1995), this research does not capture the difference in absorption rates between different types of macronutrients, nor does it capture variation in how processing methods impact bioavailability. Because of the unknown relationship between the caloric value of materials measured by the Atwater system and the rate of absorption of those calories in vivo, absolute measures of the caloric value of prey items are currently not possible. However, assuming the caloric value for a type of macronutrient is consistent across prey species, a relative measure of caloric value is possible, as well as the relative caloric value of different types of processing as examined in this study.

Another issue noted by some is the omission of considering the importance of micronutrients and ratios of macronutrients in understanding prey choice (e.g., Hill, 1988; Hockett and Haws, 2003). Indeed, most research that applies behavioral ecology relies on the convention of calories as the most important currency in creating hypotheses about foraging and consider calories a sufficient proxy for successful nutritional outcomes (Hawkes and O'Connell, 1985). This convention assumes that, on average, a diet that meets caloric needs in foraging contexts also includes sufficient variation in prey types to also meet micronutrient needs (Eaton et al., 1996); an assumption that extends to the analysis presented here. However, future work focused on how cooking impacts micronutrient absorption, especially in wild prey items, would further clarify the importance of micronutrients on prey choice in foraging contexts. Such shifts in micronutrient absorption have been measured (Gharibzadeh and Jafari, 2017).

It should also be noted that the studies used to derive the cooking transform applied here (Boback et al., 2007; Carmody and Wrangham, 2009; Carmody et al., 2011; Groopman et al., 2015) are limited in two ways. The first way is that they conduct their analyses using modern commercially available domesticated foods, which differ in many important ways from the wild foods in foraging contexts. I derive and apply a generalized cooking transform here and apply it to the gross macronutrient composition of a

sample of prey items. In reality, there are many types of proteins, lipids and carbohydrates, and not only do those types vary between edible species but they also may experience shifts in caloric bioavailability in nuanced ways not captured here. The second issue not captured by these studies, or the current analysis, is how macronutrient and micronutrient absorption is affected by numerous characteristics of both the prey items and the consumer, such as the gut biome. Another aspect in need of more exploration is the relationship between cooking and parasite loads in prey items. Reducing parasite exposure by killing parasites through cooking may be measured in the energetic terms presented here but may also result in a number of improved health outcomes.

A need for additional experimental and ethnographic data is also demonstrated here. To fully apply this model to archaeological or modern contexts, a more complete set of information for relevant prey items, especially the extent of variation across conditions and standardized approaches to recording costs such as handling time, is needed (De Vynck et al., 2016a). Additionally, it remains unclear how much and how long heat needs to be applied for a prey item to achieve a cooked state. Future work at the intersection of food science, nutrition and ecology is needed to elaborate the costs and benefits of cooking. Ethnographic and experimental work to further examine the trade-offs inherent in cooking, as well as in the acquisition of firewood more broadly, is underway by the author.

4.4. Applications of the cooking trade-off

I argue that prey choice models that do not consider the costs and benefits of cooking are underdetermined and require some account of how cooking impacts these values to accurately estimate diets. Models focused on articulating transitions in human behavior should target the most important links between human behavior and local environments to better understand the types of ecological feedback loops that create future constraints on human behavior. In other words, when considering both the effects of a behavior on the surrounding resource base and future behaviors, models should give up some generality in favor of a more realistic approximation of the system in question (Levins, 1966). Necessary and potentially scarce resources, such as biomass fuels, offer one example of a resource that must be considered in our understanding of human behavior.

Further elaborations that explore variation in the costs of cooking would be useful in many specific contexts. For example, firewood collection in modern contexts does not consist of merely picking sticks up off the ground but rather involves substantial field processing, such as chopping down a tree or removing branches (Orians and Pearson, 1979; Metcalfe and Barlow, 1992). The adoption of specific technologies, such as the use of chainsaws and trucks, may allow modern firewood collectors to decrease cooking costs and the opportunity costs of gathering firewood (O'Connell and Hawkes, 1984). Field processing of the wood itself should also factor into measures of cooking costs and will vary depending on the distribution and condition of the wood. The marginal value of firewood patches may also be an important variable influencing settlement patterns (Charnov, 1976b). Examples of how this link between the cost of cooking and settlement patterns has already been applied include the work of Dering (1999) and Varien et al. (2007) for pre-historic Western North America and by Venkataraman et al. (2017) for historic Batek hunter-gatherers in Malaysia.

The value of articulating the cooking trade-off is not limited to illuminating details of the human past. Accessing fuel remains a common problem for many people today (Cline-Cole et al., 1990; World Bank, 2003; Biran et al., 2004; Dovie et al., 2004; Chambwera and Folmer, 2007; Baland et al., 2010; Gelabert et al., 2011; Twine and Holdo, 2016). About half of all wood harvested from the

world's forests is used for fuel, accounting for 9% of global energy (Bailis et al., 2015). Modern deforestation of vast areas in India and sub-Saharan Africa and resulting soil loss and decrease in land productivity has caused large regional ecological and humanitarian crises (Eckholm et al., 1984; Agarwal, 1986; Soussan, 1988; Mercer and Soussan, 1992; Dovie et al., 2004; Wessels et al., 2013; Sulaiman et al., 2017), and echo historic deforestation events caused by a demand for firewood in Europe and North America (Nef, 1977). Efforts to address this issue will benefit greatly from models that link specific elements of household economics, such as variability in the cooking requirements for available foods, to levels of firewood consumption. Understanding how household economic decisions aggregate to community and regional scales, and how those aggregated decisions create collective action problems, is a key step in addressing these issues. Explicit knowledge of the costs of cooking may also bring needed understanding to current humanitarian crises, such as where women suffer increasing costs of maintaining cook fires as access to fuels decreases in refugee camps (Patrick, 2011; Kuroiwa, 2014).

5. Conclusions

Incorporating the costs and benefits of cooking should inform our predictions about subsistence behaviors and should include a consideration of how the trade-offs between resources (i.e., firewood, prey items, and other raw materials) interact. Integrating the costs and benefits of cooking a prey item will add an important dimension to future analyses. Generally, cooking plant foods increases the postencounter return rate for many prey items that would otherwise be valued too low (if edible at all) to include in a diet. Some plant foods, such as starch-rich geophytes, are especially worth cooking, which supports their importance at the onset of the adoption of cooking in the human lineage.

Conflict of interest

The author reports no conflicts of interest.

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Supplementary Online Material

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References

- Agarwal, B., 1986. Cold hearths and barren slopes: The woodfuel crisis in the third world. Riverdale Company, Riverdale.
- Aikens, C.M., 1994. Adaptive strategies and environmental change in the Great Basin and its peripheries as determinants in the migrations of Numic-speaking peoples. In: Madsen, D.B., Rhode, D. (Eds.), Across the West: Human Population Movement and the Expansion of the Numa. University of Utah Press, Salt Lake City, pp. 35–43.
- Atwater, W.O., Snell, J.F., 1897. Report of preliminary investigations on the metabolism of nitrogen and carbon in the human organism with a respiration calorimeter of special construction. USDA Office of Experiment Stations. Government Printing Office, Washington D.C.
- Atwater, W.O., Snell, J.F., 1903. Description of a bomb-calorimeter and method of its use. J. Am. Chem. Soc. 25, 659–699. <https://doi.org/10.1021/ja02009a001>.

- Bailis, R., Drigo, R., Ghilardi, A., Masera, O., 2015. The carbon footprint of traditional woodfuels. *Nat. Clim. Change* 5, 266. <https://doi.org/10.1038/nclimate2491>.
- Baland, J.-M., Bardhan, P., Das, S., Mookherjee, D., Sarkar, R., 2010. The environmental impact of poverty: Evidence from firewood collection in rural Nepal. *Econ. Dev. Cult. Change* 59, 23–61. <https://doi.org/10.1086/655455>.
- Barkai, R., Rosell, J., Blasco, R., Gopher, A., 2017. Fire for a reason: Barbecue at middle Pleistocene Qesem Cave, Israel. *Curr. Anthropol.* 58, S314–S328. <https://doi.org/10.1086/691211>.
- Barlow, R.K., Metcalfe, D., 1996. Plant utility indices: Two Great Basin examples. *J. Archaeol. Sci.* 23, 351–371. <https://doi.org/10.1006/jasc.1996.0033>.
- Berna, F., Goldberg, P., Horwitz, L.K., Brink, J., Holt, S., Bamford, M., Chazan, M., 2012. Microstratigraphic evidence of in situ fire in the Acheulean strata of Wonderwerk Cave, Northern Cape province, South Africa. *Proc. Natl. Acad. Sci. USA* 109, E1215–E1220. <https://doi.org/10.1073/pnas.1117620109>.
- Bettinger, R.L., Baumhoff, M.A., 1982. The Numic spread: Great Basin cultures in competition. *Am. Antiq.* 47, 485–503. <https://doi.org/10.2307/280231>.
- Binford, L.R., 1980. Willow smoke and dogs' tails: Hunter-gatherer settlement systems and archaeological site formation. *Am. Anthropol.* 45, 4–20. <https://doi.org/10.2307/279653>.
- Biran, A., Abbot, J., Mace, R., 2004. Families and firewood: A comparative analysis of the costs and benefits of children in firewood collection and use in two rural communities in sub-Saharan Africa. *Hum. Ecol.* 32, 1–25. <https://doi.org/10.1023/b:huec.0000015210.89170.4e>.
- Bliege Bird, R., Smith, E.A., Bird, D.W., 2001. The hunting handicap: Costly signaling in male foraging strategies. *Behav. Ecol. Sociobiol.* 50, 9–19. <https://doi.org/10.1007/s002650100338>.
- Blurton Jones, N.G., 1986. Bushman birth spacing: A test for optimal interbirth intervals. *Ethol. Sociobiol.* 7, 91–105. [https://doi.org/10.1016/0162-3095\(86\)90002-6](https://doi.org/10.1016/0162-3095(86)90002-6).
- Boback, S.M., Cox, C.L., Ott, B.D., Carmody, R., Wrangham, R.W., Secor, S.M., 2007. Cooking and grinding reduces the cost of meat digestion. *Comp. Biochem. Physiol. A. Mol. Integr. Physiol.* 148, 651–656. <https://doi.org/10.1016/j.cbpa.2007.08.014>.
- Botha, M.S., Cowling, R.M., Esler, K.J., de Vynck, J.C., Cleghorn, N.E., Potts, A.J., 2020. Return rates from plant foraging on the Cape south coast: Understanding early human economies. *Quat. Sci. Rev.* 106129. <https://doi.org/10.1016/j.quascirev.2019.106129>.
- Burrows, M.T., Hughes, R.N., 1991. Optimal foraging decisions by Dogwhelks, *Nucella lapillus* (L.): Influences of mortality risk and rate-constrained digestion. *Funct. Ecol.* 5, 461–475. <https://doi.org/10.2307/2389628>.
- Byers, D.A., Ugan, A., 2005. Should we expect large game specialization in the late Pleistocene? An optimal foraging perspective on early Paleoindian prey choice. *J. Archaeol. Sci.* 32, 1624–1640. <https://doi.org/10.1016/j.jas.2005.05.003>.
- Carmody, R.N., Wrangham, R.W., 2009. The energetic significance of cooking. *J. Hum. Evol.* 57, 379–391. <https://doi.org/10.1016/j.jhevol.2009.02.011>.
- Carmody, R.N., Weintraub, G.S., Wrangham, R.W., 2011. Energetic consequences of thermal and nonthermal food processing. *Proc. Natl. Acad. Sci. USA* 108, 19199–19203. <https://doi.org/10.1073/pnas.1112128108>.
- Chambwera, M., Folmer, H., 2007. Fuel switching in Harare: An almost ideal demand system approach. *Energy Pol.* 35, 2538–2548. <https://doi.org/10.1016/j.enpol.2006.09.010>.
- Charnov, E.L., 1976a. Optimal foraging: Attack strategy of a mantid. *Am. Nat.* 110, 141–151. <https://doi.org/10.1086/283054>.
- Charnov, E.L., 1976b. Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* 9, 129–136. [https://doi.org/10.1016/0040-5809\(76\)90040-X](https://doi.org/10.1016/0040-5809(76)90040-X).
- Cline-Cole, R.A., Main, H.A.C., Nichol, J.E., 1990. On fuelwood consumption, population dynamics and deforestation in Africa. *World Dev.* 18, 513–527. [https://doi.org/10.1016/0305-750x\(90\)90068-9](https://doi.org/10.1016/0305-750x(90)90068-9).
- Codding, B.F., Bliege Bird, R., Bird, D.W., 2011. Provisioning offspring and others: Risk-energy trade-offs and gender differences in hunter-gatherer foraging strategies. *Proc. Roy. Soc. Lond.* 278, 2502–2509. <https://doi.org/10.1098/rspb.2010.2403>.
- Couture, M.D., Ricks, M.F., Housley, L., 1986. Foraging behavior of a contemporary northern Great Basin population. *J. Calif. Great Basin Anthropol.* 8, 150–160. <https://www.jstor.org/stable/27825269>.
- De Vynck, J.C., Anderson, R., Atwater, C., Cowling, R.M., Fisher, E.C., Marean, C.W., Walker, R.S., Hill, K., 2016a. Return rates from intertidal foraging from Blombos Cave to Pinnacle Point: Understanding early human economies. *J. Hum. Evol.* 92, 101–115. <https://doi.org/10.1016/j.jhevol.2016.01.008>.
- De Vynck, J.C., Cowling, R.M., Potts, A.J., Marean, C.W., 2016b. Seasonal availability of edible underground and aboveground carbohydrate resources to human foragers on the Cape south coast, South Africa. *PeerJ* 4, e1679. <https://doi.org/10.7717/peerj.1679>.
- Dering, P., 1999. Earth-oven plant processing in Archaic period economies: An example from a semi-arid savannah in south-central North America. *Am. Antiq.* 64, 659–674. <https://doi.org/10.2307/2694211>.
- Dominy, N.J., Vogel, E.R., Yeakel, J.D., Constantino, P., Lucas, P.W., 2008. Mechanical properties of plant underground storage organs and implications for dietary models of early hominins. *Evol. Biol.* 35, 159–175. <https://doi.org/10.1007/s11692-008-9026-7>.
- Dovie, D.B.K., Witkowski, E.T.F., Shackleton, C.M., 2004. The fuelwood crisis in southern Africa—relating fuelwood use to livelihoods in a rural village. *GeoJournal* 60, 123–133. <https://doi.org/10.1023/b:gejo.0000033597.34013.9f>.
- Eaton, S., Boyd, Eaton, Stanley B., Konner, M.J., Shostak, M., 1996. An evolutionary perspective enhances understanding of human nutritional requirements. *J. Nutr.* 126, 1732–1740. <https://doi.org/10.1093/jn/126.6.1732>.
- Eckholm, E., Foley, G., Barnard, G., Timberlake, L., 1984. *Fuelwood: The Energy Crisis That Won't Go Away*. Earthscan, London.
- Eerkens, J.W., 2004. Privatization, small-seed intensification, and the origins of pottery in the western Great Basin. *Am. Antiq.* 69, 653–670. <https://doi.org/10.2307/4128442>.
- Englyst, H.N., Cummings, J.H., 1987. Digestion of polysaccharides of potato in the small intestine of man. *Am. J. Clin. Nutr.* 45, 423–431. <https://doi.org/10.1093/ajcn/45.2.423>.
- Fowler, C.S., 1989. *Willard Z. Park's Ethnographic Notes on the Northern Paiute of Western Nevada, 1933–1940*. University of Utah Anthropological Papers 114. University of Utah Press, Salt Lake City.
- Gelabert, L.P., Asouti, E., Martí, E.A., 2011. The ethnoarchaeology of firewood management in the Fang villages of Equatorial Guinea, Central Africa: Implications for the interpretation of wood fuel remains from archaeological sites. *J. Anthropol. Archaeol.* 30, 375–384. <https://doi.org/10.1016/j.jaa.2011.05.002>.
- Gharibzadeh, S.M.T., Jafari, S.M., 2017. The importance of minerals in human nutrition: Bioavailability, food fortification, processing effects and nano-encapsulation. *Trends Food Sci. Technol.* 62, 119–132. <https://doi.org/10.1016/j.tifs.2017.02.017>.
- Goren-Inbar, N., Alpers, N., Kislev, M.E., Simchoni, O., Melamed, Y., Ben-Nun, A., Werker, E., 2004. Evidence of hominin control of fire at Gesher Benot Ya'akov, Israel. *Science* 304, 725–727. <https://doi.org/10.1126/science.1095443>.
- Gowlett, J.A.J., Harris, J.W.K., Walton, D., Wood, B.A., 1981. Early archaeological sites, hominid remains and traces of fire from Chesowanja, Kenya. *Nature* 294, 125–129. <https://doi.org/10.1038/294125a0>.
- Grayson, D., 2011. *The Great Basin: A Natural Prehistory*. University of California Press, Berkeley.
- Groopman, E.E., Carmody, R.N., Wrangham, R.W., 2015. Cooking increases net energy gain from a lipid-rich food. *Am. J. Phys. Anthropol.* 156, 11–18. <https://doi.org/10.1002/ajpa.22622>.
- Curven, M., Winking, J., Kaplan, H., Rueden, C. von, McAllister, L., 2009. A bioeconomic approach to marriage and the sexual division of labor. *Hum. Nat.* 20, 151–183. <https://doi.org/10.1007/s12110-009-9062-8>.
- Hardy, K., Brand-Miller, J., Brown, K.D., Thomas, M.G., Copeland, L., 2015. The importance of dietary carbohydrate in human evolution. *Q. Rev. Biol.* 90, 251–268. <https://doi.org/10.1086/682587>.
- Hawkes, K., O'Connell, J.F., 1985. Optimal foraging models and the case of the !Kung. *Am. Anthropol.* 87, 401–405. <https://www.jstor.org/stable/678580>.
- Hawkes, K., O'Connell, J.F., Blurton Jones, N., 1989. *Hardworking Hadza grandmothers*. In: Standen, V., Foley, R.A. (Eds.), *Comparative Socio-Ecology of Humans and Other Mammals*. Basil Blackwell, London, pp. 341–366.
- Heitman, C.C., Plog, S., 2015. *Chaco revisited: New research on the prehistory of Chaco Canyon, New Mexico*. University of Arizona Press, Tucson.
- Heizer, R.F., 1963. Domestic fuel in primitive society. *J. Roy. Anthropol. Inst. G. B. Ireland* 93, 186–194. <https://doi.org/10.2307/2844241>.
- Henken, A.M., Lucas, H., Tijssen, P.A.T., Machiels, M.A.M., 1986. A comparison between methods used to determine the energy content of feed, fish and faeces samples. *Aquaculture* 58, 195–201. [https://doi.org/10.1016/0044-8486\(86\)90085-2](https://doi.org/10.1016/0044-8486(86)90085-2).
- Henry, A.G., 2017. Neanderthal cooking and the costs of fire. *Curr. Anthropol.* 58, S329–S336. <https://doi.org/10.1086/692095>.
- Henry, A.G., Büdel, T., Bazin, P.-L., 2018. Towards an understanding of the costs of fire. *Quat. Int.* 493, 96–105. <https://doi.org/10.1016/j.quaint.2018.06.037>.
- Herzog, N.M., 2014. Starch grain analysis in California and the Great Basin. *Calif. Archaeol.* 6, 171–189. <https://doi.org/10.1179/1947461x14z.00000000039>.
- Hill, K., 1988. Macronutrient modifications of optimal foraging theory: An approach using indifference curves applied to some modern foragers. *Hum. Ecol.* 16, 157–197. <https://doi.org/10.1007/BF00888091>.
- Hirakawa, H., 1997. Digestion-constrained optimal foraging in generalist mammalian herbivores. *Oikos* 78, 37–47. <https://doi.org/10.2307/3545798>.
- Hlubik, S., Cutts, R., Braun, D.R., Berna, F., Feibel, C.S., Harris, J.W.K., 2019. Hominin fire use in the Okote member at Koobi Fora, Kenya: New evidence for the old debate. *J. Hum. Evol.* 133, 214–229. <https://doi.org/10.1016/j.jhevol.2019.01.010>.
- Hockett, B., Haws, J., 2003. Nutritional ecology and diachronic trends in Paleolithic diet and health. *Evol. Anthropol.* 12, 211–216. <https://doi.org/10.1002/evan.10116>.
- Hughes, J.D., 2011. Ancient deforestation revisited. *J. Hist. Biol.* 44, 43–57. <https://doi.org/10.1007/s10739-010-9247-3>.
- Isaac, G., 1978. The food-sharing behavior of proto-human hominids. *Sci. Am.* 238, 90–108. <https://www.jstor.org/stable/24955711>.
- Jeschke, J.M., Kopp, M., Tollrian, R., 2002. Predator functional responses: Discriminating between handling and digesting prey. *Ecol. Monogr.* 72, 95–112. [https://doi.org/10.1890/0012-9615\(2002\)072\[0095:PFDRBH\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2002)072[0095:PFDRBH]2.0.CO;2).
- Kaldy, M.S., Johnston, A., Wilson, D.B., 1980. Nutritive value of Indian bread-root, squaw-root, and Jerusalem artichoke. *Econ. Bot.* 34, 352–357. <https://doi.org/10.1007/BF02858309>.
- Kelly, I.T., 1932. *Ethnography of the Surprise Valley Paiute*. University of California Press, Berkeley.
- Klein, R.G., 2009. *The Human Career: Human Biological and Cultural Origins*, 3rd ed. University of Chicago Press, Chicago.

- Knutsen, I., Salvanes, A.G.V., 1999. Temperature-dependent digestion handling time in juvenile cod and possible consequences for prey choice. *Mar. Ecol. Prog. Ser.* 181, 61–79. <https://doi.org/10.3354/meps181061>.
- Kretser, A., Murphy, D., Starke-Reed, P., 2017. A partnership for public health: USDA branded food products database. *J. Food Compos. Anal.* 64, 10–12. <https://doi.org/10.1016/j.jfca.2017.07.019>.
- Kuroiwa, Y., 2014. Curbing time-consuming, dangerous searches for firewood. UN Refugee Agency. <https://www.unhcr.org/en-us/news/makingdifference/2014/7/53c5bb26/curbing-time-consuming-dangerous-searches-firewood.html>.
- Larbey, C., Mentzer, S.M., Ligouis, B., Wurz, S., Jones, M.K., 2019. Cooked starchy food in hearths ca. 120 kya and 65 kya (MIS 5e and MIS 4) from Klasies River Cave, South Africa. *J. Hum. Evol.* 131, 210–227. <https://doi.org/10.1016/j.jhevol.2019.03.015>.
- Leakey, M.D., 1971. *Olduvai Gorge, Vol. 3: Excavations in Beds I and II, 1960–1963*. Cambridge University Press, Cambridge.
- Lekson, S.H. (Ed.), 2006. *The Archaeology of Chaco Canyon: An Eleventh-Century Pueblo Regional Center*. School of American Research Press, Santa Fe. <https://doi.org/10.5860/choice.44-5126>.
- Levins, R., 1966. The strategy of model building in population biology. *Am. Sci.* 54, 421–431. <https://doi.org/10.1007/s10539-006-9049-3>.
- Marean, C.W., 2010. Pinnacle Point Cave 13B (Western Cape Province, South Africa) in context: The Cape floral kingdom, shellfish, and modern human origins. *J. Hum. Evol.* 59, 425–443. <https://doi.org/10.1016/j.jhevol.2010.07.011>.
- McCarthy, H., 1993. *A political economy of Western Mono acorn production*. Ph.D. Dissertation, University of California at Davis.
- McNeil, C.L., 2012. Deforestation, agroforestry, and sustainable land management practices among the classic period Maya. *Quat. Int.* 249, 19–30. <https://doi.org/10.1016/j.quaint.2011.06.055>.
- McNeil, C.L., Burney, D.A., Burney, L.P., 2010. Evidence disputing deforestation as the cause for the collapse of the ancient Maya polity of Copan, Honduras. *Proc. Natl. Acad. Sci. USA* 107, 1017–1022. <https://doi.org/10.1073/pnas.0904760107>.
- Mercer, D.E., Soussan, J., 1992. Fuelwood problems and solutions. In: Sharma, N.P. (Ed.), *Managing the World's Forests: Looking for Balance between Conservation and Development*. Kendall/Hunt Publishing Company, Dubuque, pp. 177–213.
- Metcalfe, D., Barlow, K.R., 1992. A model for exploring the optimal trade-off between field processing and transport. *Am. Anthropol.* 94, 340–356. <https://doi.org/10.1525/aa.1992.94.2.02a00040>.
- Murtagh-Mark, C.M., Reiser, K.M., Harris Jr., R., McDonald, R.B., 1995. Source of dietary carbohydrate affects life span of Fischer 344 rats independent of caloric restriction. *J. Gerontol. A. Biol. Sci. Med. Sci.* 50, B148–B154. <https://doi.org/10.1093/gerona/50a.3.b148>.
- Nef, J.U., 1977. An early energy crisis and its consequences. *Sci. Am.* 237, 140–151. <https://doi.org/10.1038/scientificamerican1177-140>.
- Nichols, B.L., 1994. Atwater and USDA nutrition research and service: A prologue of the past century. *J. Nutr.* 124, 1718S–1727S. https://doi.org/10.1093/jn/124.suppl_9.1718S.
- Norton, H.H., Hunn, E.S., Martinsen, C.S., Keely, P.B., 1984. Vegetable food products of the foraging economies of the Pacific Northwest. *Ecol. Food Nutr.* 14, 219–228. <https://doi.org/10.1080/03670244.1984.9990789>.
- O'Connell, J.F., Hawkes, K., 1984. Food choice and foraging sites among the Alyawara. *J. Anthropol. Res.* 40, 504–535. <https://doi.org/10.1086/jar.40.4.3629795>.
- O'Connell, J.F., Hawkes, K., Blurton Jones, N.G., 1999. Grandmothering and the evolution of *Homo erectus*. *J. Hum. Evol.* 36, 461–485. <https://doi.org/10.1006/jhevol.1998.0285>.
- O'Connell, J.F., Hawkes, K., Lupo, K.D., Blurton Jones, N.G., 2002. Male strategies and Plio-Pleistocene archaeology. *J. Hum. Evol.* 43, 831–872. <https://doi.org/10.1006/jhevol.2002.0604>.
- Oku, T., Nakamura, S., 2014. Evaluation of the relative available energy of several dietary fiber preparations using breath hydrogen evolution in healthy humans. *J. Nutr. Sci. Vitaminol. (Tokyo)* 60, 246–254. <https://doi.org/10.3177/jnsv.60.246>.
- Organ, C., Nunn, C.L., Machanda, Z., Wrangham, R.W., 2011. Phylogenetic rate shifts in feeding time during the evolution of *Homo*. *Proc. Natl. Acad. Sci. USA* 108, 14555–14559. <https://doi.org/10.1073/pnas.1107806108>.
- Orians, G.H., Pearson, N.E., 1979. On the theory of Central place foraging. In: Horn, D.J., Stairs, G.R., Mitchell, R.D. (Eds.), *Analysis of Ecological Systems*. Ohio State University Press, Columbus, pp. 155–177.
- Papanikolaou, N.E., Milonas, P.G., Demiris, N., Papachristos, D.P., Matsinos, Y.G., 2014. Digestion limits the functional response of an Aphidophagous Coccinellid (Coleoptera: Coccinellidae). *Ann. Entomol. Soc. Am.* 107, 468–474. <https://doi.org/10.1603/AN13088>.
- Parker, A.K., Parker, C.H., Coddling, B.F., 2018. When to defend? Optimal territoriality across the Numic homeland. *Quat. Int.* <https://doi.org/10.1016/j.quaint.2018.05.034>.
- Parker, C.H., Keefe, E.R., Herzog, N.M., O'Connell, J.F., Hawkes, K., 2016. The pyrophilic primate hypothesis. *Evol. Anthropol.* 25, 54–63. <https://doi.org/10.1002/evan.21475>.
- Patrick, E., 2011. "We have no choice." Safe access to firewood & alternative energy in Eastern Democratic Republic of Congo (techreport). Women's Refugee Commission, NY. <https://reliefweb.int/report/democratic-republic-congo/we-have-no-choice-safe-access-firewood-alternative-energy-eastern>.
- R Core Team, 2019. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.
- Rhode, D., Madsen, D.B., Jones, K.T., 2006. Antiquity of early Holocene small-seed consumption and processing at Danger Cave. *Antiquity* 80, 328–339. <https://doi.org/10.1017/S0003598X00093650>.
- Roebroeks, W., Villa, P., 2011. On the earliest evidence for habitual use of fire in Europe. *Proc. Natl. Acad. Sci. USA* 108, 5209–5214. <https://doi.org/10.1073/pnas.1018116108>.
- Schnorr, S.L., Crittenden, A.N., Venema, K., Marlowe, F.W., Henry, A.G., 2015. Assessing digestibility of Hadza tubers using a dynamic in-vitro model. *Am. J. Phys. Anthropol.* 158, 371–385. <https://doi.org/10.1002/ajpa.22805>.
- Schoeninger, M.J., Bunn, H.T., Murray, S.S., Marlett, J.A., 2001. Composition of tubers used by Hadza foragers of Tanzania. *J. Food Compos. Anal.* 14, 15–25. <https://doi.org/10.1006/jfca.2000.0961>.
- Sen, G., Sen, C., 1985. Women's domestic work and economic activity: Results from National Sample Survey. *Econ. Polit. Wkly.* WS49–WS56. <https://www.jstor.org/stable/4374341>.
- Shaw, J.M., 2003. Climate change and deforestation: Implications for the Maya collapse. *Anc. Mesoam.* 14, 157–167. <https://doi.org/10.1017/S0956536103132063>.
- Simms, S.R., 1987. Behavioral ecology and hunter-gatherer foraging: An example from the Great Basin. *Br. Archaeol. Rep. Int. Ser.* 381.
- Singels, E., Potts, A.J., Cowling, R.M., Marean, C.W., De Vynck, J., Esler, K.J., 2016. Foraging potential of underground storage organ plants in the southern Cape, South Africa. *J. Hum. Evol.* 101, 79–89. <https://doi.org/10.1016/j.jhevol.2016.09.008>.
- Smith, C.S., Martin, W., Johansen, K.A., 2001. Sego lilies and prehistoric foragers: Return rates, pit ovens, and carbohydrates. *J. Archaeol. Sci.* 28, 169–183. <https://doi.org/10.1006/jasc.2000.0554>.
- Smith, C.S., McNees, L.M., 2005. *Cymopterus bulbosus* and prehistoric foragers: Patch size, plant density, and return rates. *J. Ethnobiol.* 25, 1–23. [https://doi.org/10.2993/0278-0771\(2005\)25\[1:CBAPFP\]2.0.CO;2](https://doi.org/10.2993/0278-0771(2005)25[1:CBAPFP]2.0.CO;2).
- Soussan, J., 1988. *Primary Resources and Energy in the Third World*. Taylor & Francis, London.
- Steward, J.H., 1938. *Basin-Plateau Aboriginal Sociopolitical Groups*. Bureau of American Ethnology, Washington D.C.
- Stiner, M., 2001. Thirty years on the "Broad Spectrum Revolution" and Paleolithic demography. *Proc. Natl. Acad. Sci. USA* 98, 6993–6996. <https://doi.org/10.1073/pnas.121176198>.
- Sulaiman, C., Abdul-Rahim, A.S., Mohd-Shahwahid, H.O., Chin, L., 2017. Wood fuel consumption, institutional quality, and forest degradation in sub-Saharan Africa: Evidence from a dynamic panel framework. *Ecol. Indic.* 74, 414–419. <https://doi.org/10.1016/j.ecolind.2016.11.045>.
- Sun, T., Lærke, H.N., Jørgensen, H., Knudsen, K.E.B., 2006. The effect of extrusion cooking of different starch sources on the in vitro and in vivo digestibility in growing pigs. *Anim. Feed Sci. Technol.* 131, 67–86. <https://doi.org/10.1016/j.anifeeds.2006.02.009>.
- Thomas, D.H., 1973. An empirical test for Steward's model of Great Basin settlement patterns. *Am. Antiq.* 38, 155–176. <https://doi.org/10.2307/279362>.
- Twine, W.C., Holdo, R.M., 2016. Fuelwood sustainability revisited: Integrating size structure and resprouting into a spatially realistic fuelshed model. *J. Appl. Ecol.* 53, 1766–1776. <https://doi.org/10.1111/1365-2664.12713>.
- U.S. Department of Agriculture, Agricultural Research Service, 2019. FoodData Central [WWW Document]. URL: <https://fdc.nal.usda.gov>.
- Van Gils, J.A., Dekinga, A., Spaans, B., Vahl, W.K., Piersma, T., 2005. Digestive bottleneck affects foraging decisions in red knots *Calidris canutus*. II. Patch choice and length of working day. *J. Anim. Ecol.* 74, 120–130. <https://doi.org/10.1111/j.1365-2656.2004.00904.x>.
- Varien, M.D., Ortman, S.G., Kohler, T.A., Glowacki, D.M., Johnson, C.D., 2007. Historical ecology in the Mesa Verde region: Results from the Village Ecodynamics project. *Am. Antiq.* 72, 273–299. <https://doi.org/10.2307/40035814>.
- Venkataraman, V.V., Kraft, T.S., Dominy, N.J., Endicott, K.M., 2017. Hunter-gatherer residential mobility and the marginal value of rainforest patches. *Proc. Natl. Acad. Sci. USA* 114, 3097–3102. <https://doi.org/10.1073/pnas.1617542114>.
- Vincent, A.S., 1985. Plant foods in savanna environments: A preliminary report of tubers eaten by the Hadza of northern Tanzania. *World Archaeol.* 17, 131–148. <https://doi.org/10.1080/00438243.1985.9979958>.
- Wadley, L., Backwell, L., d'Errico, F., Sievers, C., 2020. Cooked starchy rhizomes in Africa 170 thousand years ago. *Science* 367, 87–91. <https://doi.org/10.1126/science.aaz5926>.
- Wandsnider, L., 1997. The roasted and the boiled: Food composition and heat treatment with special emphasis on pit-hearth cooking. *J. Anthropol. Archaeol.* 16, 1–48. <https://doi.org/10.1006/jaar.1997.0303>.
- Washburn, S.L., Lancaster, C., 1968. The evolution of hunting. In: Lee, R., DeVore, I. (Eds.), *Man the Hunter*. Aldine, Chicago, pp. 293–303. <https://doi.org/10.4324/9780203786567-39>.
- Wessels, K.J., Colgan, M.S., Erasmus, B.F.N., Asner, G.P., Twine, W.C., Mathieu, R., Van Aardt, J.A.N., Fisher, J.T., Smit, I.P.J., 2013. Unsustainable fuelwood extraction from South African savannas. *Environ. Res. Lett.* 8, 014007. <https://doi.org/10.1088/1748-9326/8/1/014007>.
- World Bank, 2003. *Household Energy Use in Developing Countries: A Multicountry Study*. Energy Sector Management Assistance Programme (ESMAP) technical paper series; no. 42. Washington, DC. <https://openknowledge.worldbank.org/handle/10986/19647>.
- Wrangham, R.W., Carmody, R., 2010. Human adaptation to the control of fire. *Evol. Anthropol.* 19, 187–199. <https://doi.org/10.1002/evan.20275>.
- Wrangham, R.W., Conklin-Brittain, N., 2003. Cooking as a biological trait. *Comp. Biochem. Physiol. A. Mol. Integr. Physiol.* 136, 35–46. [https://doi.org/10.1016/S1095-6433\(03\)00020-5](https://doi.org/10.1016/S1095-6433(03)00020-5).
- Wrangham, R.W., Jones, J.H., Laden, G., Pilbeam, D., Conklin-Brittain, N., 1999. The raw and the stolen: Cooking and the ecology of human origins. *Curr. Anthropol.* 40, 567–594. <https://doi.org/10.1086/300083>.

- Zeanah, D.W., 2002. Central place foraging and prehistoric pinyon utilization in the Great Basin. In: Fitzhugh, B., Habu, J. (Eds.), *Beyond Foraging and Collecting*. Springer, New York, NY, pp. 231–256.
- Zeanah, D.W., 2004. Sexual division of labor and central place foraging: A model for the Carson Desert of Western Nevada. *J. Anthropol. Archaeol.* 23, 1–32. [https://doi.org/10.1016/S0278-4165\(03\)00061-8](https://doi.org/10.1016/S0278-4165(03)00061-8).
- Zia-ur-Rehman, Z., Islam, M., Shah, W.H., 2003. Effect of microwave and conventional cooking on insoluble dietary fibre components of vegetables. *Food Chem.* 80, 237–240. [https://doi.org/10.1016/S0308-8146\(02\)00259-5](https://doi.org/10.1016/S0308-8146(02)00259-5).
- Zink, K.D., Lieberman, D.E., Lucas, P.W., 2014. Food material properties and early hominin processing techniques. *J. Hum. Evol.* 77, 155–166. <https://doi.org/10.1016/j.jhevol.2014.06.012>.