Seasonal resource categorisation and behavioral adaptation among chimpanzees: Implications for early hominin carnivory

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Abstract

Seasonality plays a critical role in determining the yearly dietary variability of many nonhuman primates living in tropical and subtropical environments. Much previous research has emphasised the seasonal importance of both preferred resources—eaten whenever available—and fallback foods—eaten during periods of scarcity to compensate for an insufficient availability of preferred resources. However, previous discussions of this dichotomy have often overlooked why different populations of the same taxon may exhibit a different level of engagement with identical resources, especially those that require additional technological investment by virtue of being embedded. Similarly, not enough attention has been given to diachronic trends in the incorporation of novel resources to seasonal consumption patterns among non-human primates. In this paper, we present a framework for understanding the spatio-temporal relationships between preferred and fallback resources in a more systematic way, explicitly through the lens of landscape knowledge and seasonal fluctuations in quality and availability among chimpanzee communities. We argue it is the interplay between resource quality and the available knowledge pertaining to its exploitation that will determine the categorisation of a resource. In this regard, the accumulation of further information through encounter, experimentation, and behavioural (including technological) innovation enables resources with high nutritional potential to attain preferred status. We end with an exploration of the gradual consolidation of the hominin carnivory niche in the Early Pleistocene of East Africa, to demonstrate the utility of our framework—specifically the interplay between seasonality and the concept of landscape knowledge—for understanding behavioural change in the archaeological record.

Keywords

Seasonality, Fallback Foods, Preferred Foods, Landscape Knowledge, Primate Models, Human Evolution

Short Heading

Seasonal resource categories in primates

Article Text

1. Introduction

Seasonal fluctuations in resource availability have profound effects on the diets of both extant nonhuman primates and modern human hunter-gatherer populations (e.g. Goodall, 1986; Hawkes et al., 1989, 1997; Kitanishi, 1995; Yamakoshi, 1998; Boesch and Boesch-Achermann, 2000; Matsumoto-Oda, 2002; Laden and Wrangham, 2005; Marlowe and Berbesque, 2009; Wrangham et al., 2009; Sato et al., 2012; Lee, 2013; Oelze et al., 2014; Nakamura et al., 2015; Boesch and Wittig, 2019; Kwiecien et al., 2021). It is thus highly likely that hominin diets were subject to similar intra-annual pressures (e.g. Potts, 1996, 1998; Foley, 1993; Sponheimer et al., 2006; Joannes-Bayou et al., 2019), given the indication from climatic data that rainfall seasonality reached levels comparable to the modern day by at least 2 Ma (Blumenthal et al., 2019). Recent research has emphasised the importance of seasonal fluctuations in resource availability to the behavioural strategies employed by early members of the genus *Homo* (Hosfield, 2020; Linares-Matás and Clark, 2022).

Much of the discussion surrounding such intra-annual changes in resource consumption among living populations draws a distinction between preferred foods and less-preferred fallback foods, with each making important seasonal dietary contributions (e.g. Lambert, 2007; Marshall and Wrangham, 2007; Marshall et al., 2009). Marshall and Wrangham (2007) have provided operational definitions for observing each of these categories in extant primate populations, suggesting that preferred foods are those disproportionately selected for consumption relative to their abundance in the environment (see also Leighton, 1993). In contrast, fallback foods are defined by consumption that is negatively associated with that of preferred foods (Marshall and Wrangham, 2007). Selection from a range of available foodstuffs relative to their abundance in the environment should depend on a number of variables that determine their attractiveness, and by extension their preferred and fallback categorisation.

Any attempt to draw a distinction between preferred and fallback foods is necessarily reliant, implicitly or explicitly, on concepts taken from Optimal Foraging Theory (OFT; Lambert, 2007; Lambert and Rothman, 2015). OFT suggests that, when faced with a choice between different foodstuffs, individuals should make foraging decisions which maximise nutritional return rates in the face of a set of costs and benefits, and the constraints involved in the exploitation of specific resources (e.g. MacArthur and Pianka, 1966; Charnov, 1976; Hawkes et al., 1982; Foley, 1985; Stephens and Krebs, 1986; Parker and Maynard-Smith, 1990; Winterhalder and Smith, 1992; Ferraro, 2007; Kelly, 2013). Within this overarching framework, Dietary Breadth Models (DBMs) provide a basis for ranking the resources available within the environment based on their specific search and handling costs, benefits, and constraints, with the highest-ranked resources considered to be those that provide the greatest return rates. Assuming the highest-ranked resource is actively sought-after and taken whenever available, any other encountered resource will only be incorporated into the diet only if its post-encounter return rate is greater than the overall return rate of exploiting the preferred resource alone (Bird and O'Connell, 2006; Kelly, 2013). Therefore, if an individual is assumed to follow an optimal diet, preferred foods are those with the highest rankings that are taken whenever encountered, whereas fallback foods are those with lower overall rankings that should only be taken when the overall return rates of preferred foods are low, especially during certain intra- or inter-annual periods of scarcity. These foods should be taken at rates independent of their own abundance (O'Connell and Hawkes, 1981, 1984).

While DBMs can provide a useful referential framework for modelling the feeding behaviour of certain populations, both in modern contexts and in the archaeological record (Bird and O'Connell, 2006), it must be acknowledged that its assumptions are rarely met. In particular, optimal foraging models assume that individuals are completely aware of the spatial and temporal distribution of each

resource available within their range (Plante et al., 2014). However, a plethora of studies have shown that specific primate populations do not exploit specific resources within their range because they lack the knowledge to do so (e.g. McGrew et al., 1997; Humle and Matsuzawa, 2004; Gruber et al., 2009). This does not necessarily take away from the utility of terms derived from these models, but does suggest that the consideration of additional variables may account for a greater number of observations (e.g. Jeschke et al., 2002; Nathan et al., 2008; Martin et al., 2013).

In this paper, we propose that landscape knowledge may be one such relevant additional variable that may help explain temporal changes in resource use, in both extant and extinct populations (see also Clark and Linares-Matás, 2020; Linares-Matás and Clark, 2022). Before we discuss this concept in detail, we first present a framework (in section 2) for an explicitly seasonal categorisation of resources according to their preferred or fallback nature, giving examples for each of these categories from observations of chimpanzee (*Pan troglodytes*) dietary behaviours. In section 3, we then define landscape knowledge and argue it is critical to our seasonal framework, as a way of explaining shifts in the importance of specific foodstuffs both between populations and within populations over time. We also examine the relationship between resource categorisation and technological investment (section 3.3.), arguing that any association between the two is likely to be incidental, with landscape knowledge independently facilitating the changes to each. We use our framework to examine the early consumption of terrestrial animal resources in the archaeological record, to explore changes in their dietary importance over time.

2. Seasonality and Resource Categorisation

2.1. Fallback Foods

In the context of Dietary Breadth Models (DBMs), nutritional density acts alongside a number of additional factors in determining net nutritional returns, and therefore resource ranking. These factors can include intrinsic variables such as the concentration of secondary metabolites or fiber and/or the presence of mechanical defences (Lambert, 2007: 327; Marshall and Wrangham, 2007). Furthermore, the nutritional quality of a given resource will also be dependent on the specific anatomical and/or behavioural adaptations of the populations consuming them, as this determines the energy that can be extracted from processing the resource (Lambert and Rothman, 2015). This means that certain resources considered a fallback in certain populations may represent a preferred foodstuff in populations adapted to respond to their constraints. An additional consideration for understanding the role and nature of fallback resources in primate diets is that of ecological interaction, as the requirement for an individual to access fallback foods in periods of preferred food scarcity may also be exacerbated by intra- and/or inter-specific competition with sympatric organisms for the remaining items of that resource. For example, western gorillas (*Gorilla gorilla*) and chimpanzees have a similar preference for fruit resources, but gorillas in the same environment are often forced to incorporate larger quantities of vegetative foods during periods of low fruit availability, as chimpanzees adapt to retain access to the remaining fruits. This may include directly forming large nesting groups on fruit trees to monopolise their limited resources (Basabose and Yamagiwa, 2002; Oelze et al., 2014; Tédonzong et al., 2019).

Different authors have disagreed as to how to subdivide foodstuffs within the overall framework of fallback foods. Lambert (2007) argued the category should be split based on the nutritional returns of specific resources consumed when preferred foods are scarce, into higher- and lower-quality fallback foods. In contrast, Marshall and Wrangham (2007) preferred to emphasise the frequency of consumption, drawing a distinction between “fillers” consumed only as supplements during periods of preferred food scarcity and “staples” consumed throughout the year, but with peaks during these

periods. While we integrate aspects of both in our discussion, we more closely follow Lambert's (2007) distinction between higher- and lower-quality fallbacks, because we feel quality is more closely tied to the spatial and temporal distribution of resources than the frequency of consumption, and thus quality may have clearer behavioural implications. While Marshall et al. (2009) suggest that fillers tend to be of higher quality than staples, categories defined based on the frequency of consumption will still incorporate a wide range of energetic returns that prevent a clear distinction between them. For example, chimpanzee consumption of terrestrial herbaceous vegetation (THV) at Kahuzi-Biega, Democratic Republic of Congo (Yamagiwa and Basabose, 2009), and Underground Storage Organs (USOs) at Ugalla, Tanzania (Hernandez-Aguilar et al., 2007), both fit Marshall and Wrangham's (2007) definition of a filler resource, and yet clearly have very different spatial distributions and accessibility requirements, as well as varying considerably in terms of nutritional composition and quality. These factors decisively impact their respective consumption patterns, to the extent that they ought to be considered in different resource categories.

The advantage of incorporating low-quality fallback foods in the diet is that they frequently have a widespread, predictable, and reliable distribution, both in time and space (Tab. 1), meaning they can be easily accessed (low search costs) at times of preferred food scarcity or nutritional stress (Lambert, 2007; Marshall and Wrangham, 2007; Marshall et al., 2009). For example, chimpanzees tend to consume more herbaceous vegetation and bark during periods of fruit scarcity (e.g. Nishida, 1976; Goodall, 1986; Conklin-Brittain et al., 1998; Pruetz, 2006; Yamagiwa and Basabose, 2009; Sanz and Morgan, 2013; Piel et al., 2017; Matthews et al., 2019; Abwe et al., 2020). These lower-quality foodstuffs may be particularly important during unexpected and/or particularly severe periods of resource scarcity, meaning they have important implications for the ability of many species to survive pronounced stress (e.g. Campbell-Smith et al., 2011).

Higher-quality fallback foods are those which can provide a substantial number of calories upon consumption, allowing the maintenance of a higher-quality diet throughout the year, but usually retain a relatively lower-ranking in the diet due to the existence of intrinsic or extrinsic constraints which limit the overall nutritional return rate (Lambert, 2007). These resources often have a much patchier spatial distribution than lower-quality fallback resources (Tab. 1), entailing higher search costs, and may frequently be embedded or mechanically protected, meaning they can also have higher handling costs (Lambert, 2007). No clear distinction can be made in temporal distribution between higher- and lower-quality fallbacks, as both must be available during periods of scarcity and thus are usually available year-round. Higher-quality fallbacks, such as USOs (Hernandez-Aguilar et al., 2007), may, however, experience some fluctuation in seasonal availability, as long as they are available during periods of preferred food scarcity.

One example of a higher-quality fallback resource may be USO consumption among certain primate populations. Their exploitation has been observed among the savanna chimpanzees from Issa, Ugalla with a clear focus on the wet season (Hernandez-Aguilar et al. 2007), likely when fruits are scarce (Yoshikawa and Ogawa, 2015: 205; Piel et al., 2017). Chimpanzees have also been observed to exploit USOs, in the form of human-cultivated cassava (*Manihot esculenta*), in the tropical forest of Bossou, Republic of Guinea, which are accessed when fruit availability is lowest (Hockings et al., 2010). Yellow baboons (*Papio cynocephalus*) in the Okavango Delta, Botswana, also obtain USOs, but from shallow aquatic contexts during reduced dry season preferred food availability (Wrangham et al., 2009).

2.2. Preferred Foods

As outlined in Table 1, we divide preferred foods into seasonal preferred resources and core preferred resources, to reflect differences in their temporal consumption signatures. Resources from each category are patchily distributed in space and among the highest ranked foodstuffs, but seasonal preferred resources are overwhelmingly exploited in particular seasons of high availability,

accessibility, and/or nutritional quality, when net returns are greatest. In contrast, core preferred resources are preferentially consumed for most of the year, even in the face of these seasonal fluctuations and consumption peaks. We illustrate the differences between seasonal and core preferred resources, as well as between fallback and preferred resources, through chimpanzee consumption of two resource categories: fruits and colonial invertebrates.

Chimpanzee Fruit Consumption

Chimpanzees are a heavily frugivorous taxon, but not all fruits are of equal nutritional quality. As such, seasonal consumption signatures of individual fruit resources are useful to illustrate the applicability of our framework for characterising dietary preferences. As frequently pointed out in discussions of chimpanzee subsistence (e.g. Marshall and Wrangham, 2007), many fruit resources are eagerly consumed by chimpanzees whenever they are available, often during tightly-constrained availability peaks, a pattern that matches our prediction for seasonal preferred resources. For example, the chimpanzees of Rubondo Island, Tanzania, show a particular preference for consumption of *Garcinia huillensis* during its main fruiting period between August and October (Moscovice et al., 2007). In addition, *Sacoglottis gabonensis* fruits are one of a number of species consumed in the Taï Forest during discrete periods of peak availability, in this case also from August–October (Goné Bi and Wittig, 2019).

Other fruiting plants may be considered core preferred resources if they maintain an extent of availability (and quality) throughout the year, as well as a high dietary ranking. Fig fruits (*Ficus* spp.) are clearly considered a preferred resource year-round at certain chimpanzee sites, such as the Ugandan sites of Budongo Forest Reserve (Newton-Fisher, 1999; Tweheyo and Lye, 2003), Bwindi Impenetrable National Park (Stanford and Nkurunungi, 2003) and Kalinzu Forest (Kagoro-Rugunda and Kayanja, 2011), Nyungwe National Park, Rwanda (Gross Camp et al., 2009; Moore et al., 2018; Matthews et al., 2019), and Kahuzi-Biega (Yamagiwa and Basabose, 2009), although its specific ranking depends on local ecological factors. Nonetheless, even figs exhibit fluctuations in their abundance, requiring behavioural adaptation to maximise consumption in periods of overall scarcity (Basabose, 2004).

At the same time, periods of reduced preferred fruit availability may also require the greater incorporation of lower-ranked fruits of lower nutritional quality to fulfill dietary requirements. For example, the Rubondo chimpanzees opportunistically consume the fruits of the liana *Saba comorensis* year-round, but with peak procurement in the late dry and the transitional month of September, coinciding with the main period of low tree fruit availability (Moscovice et al., 2007). Similarly, while Fongoli chimpanzees consume *Adansonia digitata* (baobab) fruit throughout the year, there are particular peaks during the early and late dry season (Pruetz, 2006). Pruetz (2006: 170) points out that the woody husk and chalky pulp allow the resource to remain on trees for months without rotting, and thus can be reliably sought and consumed when other resources are less available. These consumption patterns would be more consistent with the dietary role of a high-quality fallback.

Chimpanzee Colonial Invertebrate Consumption

Foraging from dense clusters of colonial invertebrates represents an important procurement strategy for chimpanzees at many sites during seasonal periods of greater aggregation and activity. For example, winged termite alates of the genera *Macrotermes* and *Pseudocanthotermes* represent a particularly attractive resource due to their high fat content relative to non-reproductive workers and soldiers (Hladik, 1977; Deblauwe and Janssens, 2008; Lesnik, 2014; O'Malley and Power, 2014). Chimpanzees at many sites are known to favour these alates whenever they are seasonally available. At Gombe, *Macrotermes* winged termite alates are eagerly captured by hand and consumed when they emerge from their mounds in the early wet season—a behaviour also observed at Comoé, Côte

d'Ivoire (Lapiente 2020)—while *Pseudocanthotermes* alates, which are smaller than their *Macrotermes* counterparts (Lesnik, 2014), are similarly exploited when they emerge during the early dry (Goodall, 1986; McGrew, 1992; O'Malley and Power, 2014). Within the K group of Mahale chimpanzees, Tanzania, *Pseudocanthotermes* alates consumption is maximised by destroying mounds when the reproductives are about to emerge from their towers, softened by the rains, in the late wet season (Uehara, 1982). This is not a period of low fruit availability at Mahale (Uehara, 1982; Takahata et al., 1984; Itoh and Muramatsu, 2015). A similar pattern is documented at La Belgique, Dja Biosphere Reserve, southeastern Cameroon, where consumption of *Macrotermes* alates occurs upon their emergence in the late wet season, coinciding with peak fruit availability (Deblauwe, 2009). This evidence suggests that chimpanzees are willing to forgo certain opportunities for fruit exploitation in order to make use of this attractive and time-limited resource. The well-defined intra-annual peaks in availability and procurement of termite alates by chimpanzees, when preferred fruits are often likely to be abundant, is suggestive of termite alates forming a seasonal preferred resource.

In addition to consumption of their alates, chimpanzees across Africa have been observed using tools to fish for non-reproductive *Macrotermes* and *Pseudocanthotermes* termite soldiers which bite down on the sticks and can thus be subsequently extracted from the mound (e.g. Hladik, 1977; Goodall, 1986; Deblauwe et al., 2006; Bogart and Pruetz, 2011; O'Malley and Power, 2014; Stewart and Piel, 2014). Less commonly, chimpanzees may use percussive tools to gain access to the mounds of other termite genera, namely *Cubitermes* and *Thoracotermes*, such as at Bili-Uéré during the wet season (Hicks et al., 2019). Termite fishing peaks in the early wet season at a number of chimpanzee localities, including the Tanzanian sites of Gombe, Mahale, and Ugalla, as well as Mt. Assirik, Senegal (Hladik, 1977; McGrew et al., 1979; Uehara, 1982; McGrew, 1992; O'Malley and Power, 2014; Stewart and Piel, 2014). At Bai Hokou, Central African Republic, termite probing and fishing followed the onset of the first rains of the wet season, and also took place during rainstorms in the late wet (Fay and Carroll, 1994: 312). Peak termite consumption is greatest around the middle of the wet season at the site of La Belgique, southeastern Cameroon (Deblauwe, 2009). At Fongoli, another savanna chimpanzee study site in Senegal, termite fishing occurs year-round but peaks slightly earlier than elsewhere, across the transition from the late dry to the early wet season (Bogart and Pruetz, 2008; Bogart and Pruetz, 2011).

Various ant genera, such as arboreal ants (*Crematogaster* spp. and *Camponotus* spp.), army/driver ants (*Dorylus* spp.), and/or weaver ants (*Oecophylla longinoda*), are also a nutritious resource available to chimpanzees (Deblauwe and Janssens, 2008). While weaver ants are often consumed by hand (Tutin and Fernandez, 1992; Deblauwe, 2009), army ant procurement frequently involves technological investment by selecting and dipping a stick into the nest (e.g. McGrew, 1974; Sanz and Morgan, 2013; Koops et al., 2015; Sommer et al., 2017; Hicks et al., 2019). Army ants tend to live in extremely large colonies, thus providing a dense and predictable resource (Hölldobler and Wilson, 1990). Consumption of army ants tends to show a seasonal signature, with greatest consumption occurring at the beginning of the rainy season at Goualougo, Republic of Congo (Sanz et al., 2010), and in the wet season more broadly at Bossou, Guinea (Humle et al., 2009). The former site also preserves evidence of recurrent use of wooden tools for nest perforation (Sanz et al., 2010; Sanz and Morgan, 2013). In contrast, however, chimpanzees at Comoé tend to dip for *Dorylus* ants to a much greater extent in the dry season (Lapiente, 2020).

Peaks in termite fishing and ant dipping may coincide with periods of lower fruit availability at some sites, such as Ugalla (Yoshikawa and Ogawa, 2015; Piel et al., 2017) and La Belgique (Deblauwe, 2009), where they could be said to play a higher-quality fallback role. However, it is unclear whether the temporal decoupling of termite fishing and/or army ant dipping with fruit consumption at these sites is truly due to fallback consumption, or simply an attempt by the chimpanzees to exploit distinct attractive resources at non-overlapping seasonal availability peaks. The relatively consistent emphasis on termite fishing in the wet season is likely at-least partially a function of intra-annual changes in

termite behaviour, as they often retreat deeper into mounds during the dry season and are thus less accessible (Wood et al., 1982). Indeed, there appears to be an association between peak termite consumption and peak fruit availability at both Mahale (Uehara, 1982; Takahata et al., 1984; Matsumoto-Oda, 2002; Itoh and Muramatsu, 2015) and Fongoli (Bogart and Pruetz, 2008). At Goualougo, ant dipping was correlated with rainfall but not the abundance of any specific foodstuffs (Sanz and Morgan, 2013), underlining the suggestion that acquisition is primarily related to the behaviour of the ants within their nests and their accessibility. Indeed, army ants are more active on the surface—when they form marching columns, rather than staying within their nests—during periods of lower ant-food availability. This falls during the rainy season at Comoé (Lapiente, 2020: 81), making chimpanzee dipping and army ant consumption in general less likely at this time of year. Therefore, while it is possible that these resources could play a fallback role in some populations, the consistent seasonal responses to termite soldier and army ant behaviour may be more reflective of periods of peak attractiveness, rather than the availability (or lack thereof) of other resources. This pattern is consistent with these colonial invertebrates being exploited as a preferred resource, with an at-least seasonal signature.

Further still, sustained, year-round insect consumption—unrelated to variation in fruit availability—occurs at Fongoli, Gashaka (Nigeria), Goualougo, Ndoki (northern Republic of the Congo), and Seringbara (Guinea), often at greater levels than would be expected from encounter rates alone (Suzuki et al., 1995; Bogart and Pruetz, 2008; Sanz and Morgan, 2013; Koops et al., 2015; Sommer et al., 2017). These data may imply that army ants and non-reproductive termites can approach a core preferred resource in certain contexts. Specifically, with regards to year-round army ant consumption at Gashaka and Seringbara, this suggests an ability to overcome seasonal variability in ant behaviour, either due to ecological differences that allow the ants to stay in their nests for longer, or a tendency for chimpanzees to continue fishing when nest occupancy is lower. Sustained termite consumption may similarly suggest ecological differences that prevent retreat into the deepest part of the mounds during the dry season or, as is perhaps more likely, a sustained effort by chimpanzees to continue to extract termites. Bogart and Pruetz (2011) suggest that the motivation for continued termite consumption at Fongoli may be that it helps mediate resource fluctuations characteristic of an open and seasonal savanna environment, perhaps also indicating that seasonality represents an important selective pressure for tool-mediated colonial invertebrate consumption among chimpanzees (see also Kalan et al., 2020).

3. Landscape Knowledge

3.1. Definition

Into this discussion of resource categorisation, we wish to add the concept of landscape knowledge as a way of understanding changes in the importance of specific resources in a population over time. The notion of landscape knowledge is not a new one, and indeed was developed extensively through theoretical, archaeological, and modelling studies of human (and indeed hominin) dispersal in an edited volume by Rockman and Steele (2003). However, it is clear that many of the concepts discussed in this volume are applicable to other contexts and additional taxa, as is made explicit by Golledge (2003: 28) with reference to the ability of other animals to update their spatial location relative to a “home base” as a journey proceeds. Clark and Linares-Matás (2020) define landscape knowledge as the extent to which a population is aware of the distribution and predictability of individual resources within their unique range. This includes information regarding the spatial and temporal distributions of specific resources and, if applicable, their nutritional returns, harvesting requirements, and external processing requirements. The definition also reflects a more generalised integration of Rockman’s (2003) concepts of both “locational” (referring to the spatial distribution and physical characteristics

of resources) and “limitational” (referring to the constraints of specific resources, including seasonal variation) landscape knowledge.

We would also suggest that landscape knowledge is necessarily cumulative, frequently incorporating information gained from individual interaction with a resource that adds to existing information learnt previously. This may include building on a former episode of individual learning or, as is more likely, upon learning by another individual that has spread to the remainder of the population. Indeed, a key assumption of the model is that new individual innovations can eventually spread to the rest of the population to become incorporated into the individual knowledge of others. A discussion of the nature of social learning in chimpanzee populations is beyond the scope of this paper (see Moore, 2013 for a review), but it is clear that such innovations can appear on top of existing cultural practices in chimpanzees, and spread through the population (e.g. Biro et al., 2003). Nonetheless, a greater reliance on individual or lower-fidelity forms of social learning may place constraints on the extent of knowledge that can be accumulated, or the speed of its accumulation, in non-human primates (cf. Tomasello, 1999). For Rockman (2003), a key part of human landscape knowledge is that of “social” knowledge, reflecting the integration of social behaviour into the landscapes a population inhabits. This may be a culmination of more developed forms of social learning.

3.2. Landscape Knowledge and Resource Categorisation

It is important to emphasise that individual resources should each have their own knowledge requirements, with some resources requiring much greater levels of knowledge to exploit fully. For example, consistent consumption of terrestrial animal tissue requires a greater knowledge base than does the consumption of THV, given animals are much more patchily distributed in time and space, are more difficult to acquire, and require more external processing. We argue that such resource-specific knowledge should correlate with the dietary role of that resource within a given population, with progression of high potential resources along the continuum associated with additional knowledge requirements. In this way, landscape knowledge can be measured by its effect on the use of individual resources over time, particularly for those resources with greater knowledge requirements.

As pointed out in Table 1, lower-quality fallback resources tend to have quite widespread distributions across both space and time, and therefore the knowledge of the landscape required for their consumption should be relatively low. There may be some need to understand harvesting requirements, such as plucking leaves or stripping bark, but this is still relatively minimal. In contrast, higher-quality fallback foods (such as USOs) tend to be much patchier within the landscape (Tab. 1), and therefore add a requirement for the spatial mapping of the environment, and the distribution of these resources within it. This is something that chimpanzees display an expert ability for (Ban and Normand, 2019; Green et al., 2020), and this allows them to repeatedly revisit specific points in the landscape in pursuit of specific resources (Normand et al., 2009). Furthermore, these resources may also present more intensive harvesting and/or external processing requirements, due to a need for extractive foraging and/or more intensive mechanical protection of the resource (cf. Lambert, 2007; Lambert and Rothman, 2015). This further increases the knowledge required for their regular consumption.

As we have discussed, higher-ranked, preferred resources tend to have greater fluctuations in their availability, accessibility, and/or nutritional quality across time when compared to fallback foods. Therefore, in order to fully and successfully exploit them, an individual must also be able to integrate time as a critical variable in their resource mapping. This should facilitate exploitation of resources with distinct periods of attraction, such as when termite alates emerge from their mounds, or when their mounds are vulnerable to breakage. Year-round exploitation of these temporally-patchy resources is subsequently dependent on a) some continued availability of the resource at other times

of the year (which is not the case for termite alates), and b) knowledge of how to exploit the resource during these periods. This may be a requirement to turn seasonal fishing for termite soldiers into a year-round behaviour.

Assuming landscape knowledge is cumulative, it follows that limitations in the extent of knowledge about a resource should constrain its role within the diet of a specific population. This principle is clearly demonstrated among chimpanzees, where there is huge variability in the extent to which different resources are exploited, even between neighbouring populations with similar resource availability and when these resources should be considered extremely attractive. For example, McGrew et al. (1997) note that the chimpanzees of Lopé Reserve, Gabon, show a complete absence of nut-cracking behaviour. This is in spite of an abundance of nuts, their high return potential, the widespread availability of potential hammerstones and anvils, and the ubiquitous presence of the behaviour among other West African chimpanzee groups (e.g. Boesch and Boesch, 1983; Boesch et al., 1994). McGrew et al. (1997) argue that the absence of this behaviour can, therefore, only be due to the lack of knowledge required to exploit this resource, demonstrating how knowledge requirements can underpin resource exploitation. Similarly, Koops et al. (2022) recently demonstrated that nut cracking is not a behaviour that can be spontaneously innovated when no individuals have any prior familiarity with the resource, as at Seringbara, even when presented with all the possible elements to do so (palm or *Coula edulis* nuts, with or without shells, and possible hammers and anvils). This pattern of resource avoidance due to a knowledge deficit may even extend to the aforementioned termite alates so eagerly consumed by numerous chimpanzee populations, as chimpanzees of Bili-Uéré do not seem to recognise winged *Macrotermes* reproductives as a potential resource when they emerge from their mounds. That these alates represent an attractive resource is demonstrated by the fact that local Zande people working as field assistants frequently scoop them from the reproductive swarms and eat them directly (Hicks et al., 2019).

In this context, we introduce the term “experimental resources” (see Table 1) to account for the acquisition of new subsistence behaviours in a given population. This category is intended to allow for occasional and innovative interactions with resources that are not part of the usual dietary repertoire, regardless of their initial dietary quality, and subsequent increases in the frequency of their consumption. Observations of chimpanzees from the Tai Forest show that chimpanzees innovate new behaviours frequently (perhaps two per year), and these are often directed towards foodstuffs that were available previously (Boesch, 1995, 2003). Furthermore, providing captive chimpanzees with novel foodstuffs is particularly stimulating (Fulk et al., 1992), perhaps hinting at a desire to interact with new resources. In the wild when presented with the completely novel palm and *Coula* nut resources, Seringbara chimpanzees explored the potential foodstuffs through close observation, sniffing, and touching (Koops et al., 2022). We might also tentatively expect experimentation with resources in the wild to be more common when known resources are more abundant, as a risk-reduction strategy. This is consistent with results of the same study, whereby chimpanzees at Seringbara interacted with the experimentally-presented palm and *Coula* nuts at a much greater rate during a period of higher-fruit abundance (Koops et al., 2022).

Initial episodes of interaction should serve to provide information regarding the nutritional quality of a resource, as well as its spatial distribution of a resource and how to exploit it, before it can be exploited more consistently. Assuming these initial interactions with a novel resource are not lost in the population (due to stochastic processes or a ubiquity of habitual resources), landscape knowledge regarding these variables should accumulate through repeated encounter. We suggest that the seasonal consumption signature of this resource should also develop alongside the buildup of this resource-specific knowledge. If a resource is abundant in time and space, the likelihood of encounter and therefore experimentation will be much greater, while much less knowledge will need to be accrued regarding their distribution and how best to consume them. However, these resources will tend to be of lower nutritional quality, and are therefore unlikely to possess the potential to obtain

preferred dietary status. In contrast, random encounters with more patchily-distributed resources that allow for experimentation will be less frequent, and more interactions with them may be needed to understand their spatial distribution and seasonality. The patchiness of distribution may have limited past interaction with these resources, explaining why consumption of particularly attractive resources can be so infrequent in particular populations. This is particularly true if the resource is embedded, such as for underground storage organs or termites, as the chances of random encounter are further reduced when the resource is hidden from sight. In this context, while it is harder to acquire knowledge about resources with a patchy distribution, we argue that those exhibiting a high degree of nutritional quality have a greater potential to eventually become incorporated into the diet as preferred resources.

To illustrate the relevance of experimentation to higher-quality resources, we can use observations of how individuals of a population interact with a novel or unfamiliar resource. For example, Gruber et al. (2009) presented chimpanzees from the Kanyawara and Sonso communities of Uganda with a task in which honey had to be extracted from holes drilled into horizontal logs. In response, the Kanyawara chimpanzees frequently produced sticks that could extract the honey, and revisited the apparatus when in the area. In contrast, the Sonso chimpanzees used their fingers, or attempted to use leaf sponges (that they use to obtain water from hollows in trees), while also engaging with the holes for less time, and feeding only opportunistically when foraging at a nearby tree (Gruber et al., 2009). This is at-least part likely to be due to the fact that the Kanyawara chimpanzees consume *Apis mellifera* honey at least once a month, and occasionally use probing sticks to obtain the waxy honey of carpenter bees (*Xylocopa* spp.), whereas the Sonso chimpanzees only rarely and opportunistically exploit honey as a resource. As such, the Sonso chimpanzees had only very limited landscape knowledge pertaining to honey that they could deploy in the task, and experimented with information they had learnt in other contexts. In contrast, the responses of the Kanyawara chimpanzees could only be related to prior interaction with honey as a resource, and accumulation of landscape knowledge regarding effective strategies for its consumption.

Once experimentation with higher-quality resources allows for the initial buildup of landscape knowledge, particularly regarding resource distribution and how to exploit them, the resources may then attain a more consistent role within the diet. If higher-quality resources that are the subject of experimentation are available during times of preferred food scarcity, they may then become integrated into the diet as a higher-quality fallback. Subsequent accumulation of knowledge regarding the temporal distribution of the resource, alongside further adaptations to processing and/or harvesting, may allow the resource to progress towards a seasonal preferred resource. However, if there are constraints against achieving a higher ranking in the diet (e.g. limited nutritional density, high harvesting costs, and/or high processing costs), the resource may never progress past a higher-quality fallback.

At the same time, if the temporal distribution of a resource does not allow its consumption during periods of preferred food scarcity and other constraints against exploitation are weak or absent, an experimental resource need not become a higher-quality fallback food before it transitions towards a seasonal preferred food. However, this would require further experimental interactions with the resource to develop a sufficient understanding of its spatial and temporal distributions. The development and consolidation of landscape knowledge would be the final step in turning a seasonal preferred resource into a core preferred resource, assuming its temporal constraints can be overcome. This should involve identifying ways the resource can be exploited when it is less available or accessible.

This process of resource movement along the continuum of resource categories as landscape knowledge develops highlights a key part of our model (summarised in Figure 1), as it allows for differences between populations of the same species in similar environments, and changes within a

given population over time. This principle is highlighted by the recent publication of the discovery (or rediscovery) of a Red Colobus (*Piliocolobus rufomitratus*) hunting habit by the M group of chimpanzees from Mahale (Hosaka et al., 2020). Over 46 years of observation, the chimpanzees transitioned from mainly hunting animals other than Red Colobus by seizure, particularly ungulates, towards red colobus (captured by chase) becoming the primary prey species, and finally towards an overwhelming bias for consumption of this primate. This transition progressed through four distinct stages of behavioural change: intermittent individual kills by mature or adolescent males, sporadic multiple kills by mature or adolescent males, gradual incorporation of mature females into hunting parties, and a greater frequency of multiple kills, involving females more often (Hosaka et al., 2020). From our perspective, these changes reflect a gradual accumulation of knowledge by the chimpanzees about how best to hunt Red Colobus and maximise returns, incorporating information about their distribution, predator avoidance strategies, and successful hunting strategies.

3.3. Landscape Knowledge and Behavioural Adaptation

The relationship between resource categorisation and adaptation, both anatomical and behavioural, for both fallback and preferred foods has been discussed extensively through their respective procurement and handling costs (e.g. Lambert, 2007; Marshall and Wrangham, 2007; Constantino et al., 2009; Marshall et al., 2009; McGraw et al., 2011; Lambert and Rothman, 2015). In seasonal periods of preferred food scarcity, Foley (1987, 1993) suggests that chimpanzees may employ two distinct behavioural strategies: 1) decrease energetic investment and focus on lower-ranked but more abundant resources (i.e. lower-quality fallbacks), or 2) increase energetic investment to successfully procure the remaining desirable resources (i.e. higher-quality fallbacks or preferred foods). In this context, Lambert (2007) argues that behavioural adaptation lies largely in the domain of higher-quality fallback resources, as populations aim to maintain high dietary quality throughout the year. Given the first stages of landscape knowledge accumulation should include a focus on how to exploit a particular resource (Fig. 1), incipient stages of behavioural adaptation would be expected to be associated with higher-quality fallback foods.

Taking tool use as one example of behavioural adaptation, Fox et al. (1999) proposed three non-mutually-exclusive hypotheses for understanding the selective pressure behind great ape (in this instance, orangutan) tool use, and to account for observed differences in tool presence between sites. Two of these are especially relevant for understanding chimpanzee tool use, and are frequently discussed in the literature: the 'necessity hypothesis' (that tool use is critical to access resources available when preferred resources are less available) and the 'opportunity hypothesis' (that tool use is explained by frequent encounter with specific resources and tool materials). We may also consider the 'relative profitability hypothesis' of Rutz and St Clair (2012), developed through the study of New Caledonian Crow tool use, which emphasises that extractive tool use should be expressed when its net returns are greater than non-tool-using strategies in a given context. The necessity hypothesis is the only prediction with an explicit link to resource categorisation, and corresponds to the proposed association between fallback foods and behavioural adaptation. The relative profitability hypothesis, however, can theoretically integrate the arguments of the necessity and opportunity models into the net returns of a resource in relation to their search and handling costs.

Evidence for an association between fallback food consumption and technological investment can be found in the form of chimpanzee consumption of USOs at Ugalla, where exploitation is aided by the manufacture of wooden digging sticks, and heavily biased towards the early wet season (Hernandez-Aguilar et al., 2007; Yoshikawa and Ogawa, 2015: 205). This is a period of lower fruit availability (Yoshikawa and Ogawa, 2015; Piel et al., 2017). Oil palm (*Elaeis guineensis*) consumption at Bossou is another resource often cited in support of necessity, where the tool-using behaviours of nut-cracking and pestle pounding of pith are frequently deployed and both negatively associated with fruit availability (Yamakoshi, 1998; Humle and Matsuzawa, 2004).

Marshall and Wrangham (2007; see also Marshall et al., 2009) have argued that preferred foodstuffs should overwhelmingly result in adaptations to harvesting, rather than processing. This suggestion may indeed hold for chimpanzee fruit consumption, as chimpanzees demonstrate complex responses to fluctuations in fruit availability. For example, the complex fission-fusion dynamics of many chimpanzee groups involve splitting into smaller foraging groups when fruits are scarce (e.g. Janson and van Schaik, 1988; Tsukahara, 1993; Chapman et al., 1994, 1995; Doran, 1997; Basabose, 2004; Itoh and Nishida, 2007). This is likely to be a function of reduced preferred fruit abundance at individual resource patches, which can only support the nutritional needs of smaller feeding parties when fruits are scarce. At a broader level, fluctuations in fruit abundance may also influence habitat selection by chimpanzees. In the mixed mature forest areas of the Kalinzu Forest of Uganda, chimpanzee presence and fruit availability were positively correlated, with chimpanzee numbers in *Musanga*-dominated secondary forest greater during the low-fruited season as they exploited the fruit *Musanga leo-errerae* when other preferred fruits were less available (Furuichi et al. 2001; Kagoro-Rugunda and Kayanja, 2011).

However, the hypotheses that, a) higher-quality fallback foods are one of the main drivers of general behavioural adaptation and b) preferred foods should largely be associated with harvesting adaptations, do not seem to hold for all responses to preferred resources. First of all, we emphasise that examples of tool use in the context of fallback food consumption are relatively rare in the chimpanzee literature (Sanz and Morgan, 2013: Table 1). This suggests that technological investment may be particularly biased towards the domain of preferred foods. Indeed, *Coula* nut processing by chimpanzees of the Taï forest is not associated with periods of fruit scarcity and takes place in tightly-constrained periods of availability during the dry season (Boesch and Boesch, 1983, 1984; Doran, 1997). As such, these nuts are likely to be a preferred resource targeted when seasonally available. The fact that nut-cracking is a processing adaptation in this population, rather than a harvesting one, also demonstrates that highly-ranked resources can result in processing as well as harvesting adaptations.

We would suggest that the nature and complexity of behavioural adaptation should be more closely related to the extent of landscape knowledge accumulation for specific resources of higher quality, rather than simply their categorisation in the diet. In this context, behavioural adaptation may occur in response to higher-quality fallbacks, seasonal preferred resources, or core preferred resources, with the predictability of returns on investment a more direct driver of investment than resource ranking itself. These predictions are underpinned by the following process: as landscape knowledge about an attractive resource increases, this should reduce the cost of investment in more complex exploitation strategies, as the return on investment should be greater (in terms of increased nutritional return rate) and, in particular, more predictable (lower variance). This opens up a positive feedback loop in which behavioural adaptation allows for more complete interaction with a resource, and therefore the accumulation of greater landscape knowledge and further investment in adaptation. In this context, landscape knowledge is related to both the nature of behavioural adaptation and resource categorisation, but in separate pathways. This is illustrated in Figure 2.

It is important to emphasise that behavioural adaptations to a specific resource should be associated with the specific challenges presented by that resource, with some resources clearly requiring a greater complexity of adaptation to incorporate into the diet. Nonetheless, broadly speaking, the closer a resource progresses along the continuum of resource categorisation towards its maximal consumption signature, the more landscape knowledge that would have been acquired about the resource, and the more complex the corresponding adaptation(s) to overcome its constraints. If a resource has nutritional limitations that prevent it from reaching preferred status, then greatest technological investment will clearly remain in the domain of higher-quality fallback consumption, as landscape knowledge about the resource will continue to be accumulated, despite its lack of preferred status. However, if resource quality is high enough to become preferred, behavioural adaptation in a

fallback context should reduce the cost of resource acquisition, and allow the further accumulation of knowledge, allowing it to move along the resource preference continuum. This may explain why most tool-using behaviours in chimpanzees are not associated with fallback food consumption. Further still, resources with the potential to reach core preferred status in some populations should stimulate a greater complexity of behavioural adaptation in these groups than in those where the resource remains a seasonal preferred resource.

We also suggest that harvesting adaptations, specifically, are more important in mediating the transition between seasonal preferred resources and core preferred resources, rather than the transition from fallback to preferred foodstuffs. Such (additional) harvesting adaptations are likely to be particularly important in maintaining year-round access to a preferred resource in the face of seasonal fluctuations in availability or accessibility. These hypotheses can be tested against behavioural variability in extant primate populations, and here we evaluate them through the use of two key case studies of tool-assisted resource consumption in chimpanzees: termite fishing and nut-cracking behaviours.

Termite Fishing

As discussed above, chimpanzee investment in tool manufacture and use for termite fishing occurs alongside in the context of a preferred nature of termite consumption. These tool-using behaviours can be ubiquitous among certain populations (e.g. Sanz et al., 2010; Sanz and Morgan, 2013). In addition, there is substantial diversity in termite fishing technology. For example, chimpanzees at Issa, Ugalla, tend to exploit individual plants for tools more intensively than at Gombe or Mahale, with the number of removals from a given plant positively associated with distance from termite mounds. This suggests the Ugalla chimpanzees have learnt to adapt to the constraints of their drier and more open environment (Pascual-Garrido and Almeida-Warren, 2021). Furthermore, these groups also tend to use different materials for production of sticks for fishing: the Ugalla and Mahale chimpanzees exclusively use bark despite an abundance of twigs and grasses, while all three materials (alongside vines) are utilised at Gombe. This may indicate the existence of different cultural preferences (Pascual-Garrido and Almeida-Warren, 2021), suggesting that the accumulation of population-specific landscape knowledge influences cultural behaviour.

As part of this cultural diversity in chimpanzee termite fishing, sites showing year-round preferential consumption frequently display unique harvesting adaptations that hint at consolidated landscape knowledge. For example, chimpanzees at Okorobikó-Matama, Rio Muni, Equatorial Guinea, are able to consume termites year-round because the heavy rainfall consistently makes nests easy to perforate with sticks, while the frequent repair of nests by the termites makes this a sustainable resource for exploitation (Jones and Sabater Pi, 1969; McGrew et al., 1979). Knowledge of the predictable characteristics of termite consumption at the site also facilitate increased investment and standardisation in the tools used, which are selected to be longer and thicker than those often used for termite fishing at Gombe and Mt. Assirik (Jones and Sabater Pi, 1969; Sabater Pi, 1974; McGrew et al., 1979). Chimpanzees at Goualougo utilise short puncturing tools to open subterranean *Macrotermes lilljeborgi* nests before fishing for the termites (Sanz et al., 2014). However, while these puncturing tools would also be effective at opening the overground towers of *Macrotermes muelleri*, the chimpanzees instead choose to make use of thinner perforating twigs to pierce the thinner crust of these mounds before fishing for termites (a behaviour also observed at Goualougo for accessing army ant nests; Sanz et al., 2010). Sanz et al. (2010, 2014) suggest this behaviour for both termites and ants may be an attempt to extend the viability of the mounds/nests for more predictable future foraging bouts, or, in the case of termite exploitation, to produce a tool with reduced costs compared to the puncturing tools, which requires greater material selectivity and increased manufacture time. In either case, the selection and manufacture of different tools for these tasks by chimpanzees appears

to reflect an attempt to enhance the returns of colonial invertebrate exploitation, keeping resource ranking high.

An association between landscape knowledge and both year-round resource consumption and tool complexity in termite fishing behaviours is perhaps clearest among chimpanzees of the Ndoki forest, where *Macrotermes muelleri* soldiers are harvested through the sequential use of different artefacts in a “tool-set” (Suzuki et al., 1995; Kuroda et al., 1996). Perforating sticks are first selected from the young saplings of *Thomandersia laurifolia* (500mm long, 10mm in diameter) and then prepared by removing small leaves and twigs, while fishing probes are produced from Marantaceae stems (500mm long, 5mm in diameter), with the lower 15cm peeled to form a brush (Suzuki et al., 1995). The perforating sticks are used to make small holes in the wall of the mound, before the fishing probes are inserted into the mound, where the soldiers bite the brush and are extracted (Suzuki et al., 1995). This inferred complex sequence of tool use allows for recurrent termite consumption, even in the face of relatively high mound hardness throughout the year and the known seasonal variability in the behaviour of the termites. As mentioned previously, termites retreat further underground during the dry season and were less active at the surface, but the chimpanzees were able to continue to access this resource through use of both tool forms (Suzuki et al., 1995). Taken together, these results demonstrate that the accumulation of landscape knowledge is important for increasing the complexity of technological investment, and that there may appear to be a relationship between movement along the continuum of resource categorisation and technological complexity when resource returns are high enough to facilitate a preferred status. These sites with year-round termite consumption also appear to underline the importance of harvesting adaptations in turning a seasonal preferred resource into a core preferred resource.

Nut-cracking

Nuts and seeds are rich in proteins and particularly fats, and thus frequently present an attractive resource for both nonhuman primates and modern human hunter-gatherers (e.g. Eaton et al., 1997; Lombard and Kyriacou, 2018). Nut and seed availability is often a seasonal phenomenon, linked to the ripening and rotting of fruits and grasses at particular points in the year, although the longevity of these resources can make them a viable foodstuff for much of the year (e.g. Testart, 1982; Kitanishi, 1994; Goren-Inbar et al., 2002; Lee, 2013). Chimpanzee nut-cracking has been observed at a number of (West African) sites, including Bossou, Diéké, (Côte d’Ivoire), Djouroutou (Côte d’Ivoire), Sapo (Liberia), Tiwai (Sierra Leone), the Taï Forest, and Yealé (e.g. Boesch and Boesch, 1983; 1984; Anderson et al., 1983; Whitesides, 1985; Yamakoshi, 1998; Humle and Matsuzawa, 2001, 2004; Carvalho, 2007, 2011; Carvalho et al., 2008, 2009). Nut-cracking behaviour displays a marked diversity, united by forceful blows with a wooden or stone hammer, while the nut rests on a wooden or stone anvil, sometimes with an added wedge stone to stabilise the anvil (Boesch, 2003; Hirata et al., 2009; Luncz et al., 2018, 2019). It is also one of the most complicated tool-using behaviours observed in chimpanzees, taking at least a few years to learn (Matsuzawa, 1994; Inoue-Nakamura and Matsuzawa, 1997; Boesch and Boesch-Achermann, 2000; Boesch, 2003; Hirata et al., 2009; Biro et al., 2010).

As we have mentioned above, cracking of oil palm nuts at Bossou may represent a fallback strategy for these chimpanzees, linked to low fruit availability (Yamakoshi, 1998; Humle and Matsuzawa, 2004). However, consumption of numerous other nut species, particularly *Coula edulis*, by another West African chimpanzee population, the South Group of the Taï Forest, does not appear to relate to low fruit availability (Boesch and Boesch, 1983, 1984). Instead, consumption follows a clear seasonal schedule, in which individuals collect nuts from the tree to crack open from the very beginning of one of the two yearly dry seasons, and continue to exploit them throughout the season, collecting many off the ground as the season progresses and they drop from the trees (Boesch and Boesch, 1983, 1984).

To highlight the relevance of landscape knowledge in nut-cracking behaviour, we can investigate the cultural differences observed between neighbouring populations with similar nut, hammer, and anvil availability, such as the North, South, and East Groups of the Taï Forest. While all three groups have been observed to crack *Coula* nuts on a wooden anvil, and all follow the same seasonal signatures originally observed in the South Group (Boesch and Boesch, 1983, 1984), they significantly differ in the types of hammers used, the number of blows deployed to break open nuts, and in the number of nuts consumed per minute (Luncz et al., 2018). The South Group preferentially utilise stone tools—shown to be the most efficient hammer in each population—while the other two groups show a greater use of wooden tools. Furthermore, the East Group employs fewer blows per nut, implying greater force in each blow and a greater likelihood of shattering the inner kernel, resulting in reduced caloric return. Indeed, the behavioural inefficiency of the East Group results in an average loss of 5400 nuts per season and 74,000 fewer kilocalories per year, when compared to the South Group (Luncz et al., 2018). The similar number of nuts cracked per minute between the North and South populations, despite use of different stones and a similar number of hits per nut, may suggest that the North Group physiologically compensate for the use of a less efficient material (wood), but that this is not reflected in the simple nut return rate (Luncz et al., 2018).

These observations clearly suggest that further adaptations can develop alongside frequent use of a particular behaviour in a given population, facilitating increasing nutritional returns. There appears to be a sequence to the development of these adaptations, each time increasing processing efficiency: 1) using a wooden hammer to smash the nut, 2) reducing the force deployed to each blow and increasing the number of blows, and 3) switching to a stone hammer. The authors of this paper suggest that the costs of suboptimal behavioural variants, such as in the East Group, may be offset by other behaviours that increase energy intake or reduce output in that population (Luncz et al., 2018: 69). This may be supported by the conformity of chimpanzee females to the new group standard when migrating to one of the less-efficient nut-cracking populations, despite knowledge of the more efficient techniques, although this may also be related to the benefits of group belonging (Luncz et al., 2018). Taken together, we would suggest that the observations of nut-cracking from the three Taï populations supports the existence of our proposed relationship between landscape knowledge regarding how nuts can be best exploited, and corresponding behavioural adaptation.

Returning to Bossou, these chimpanzees may be considered to have developed additional nut-cracking innovations compared to those of even the Taï South Group, including the use of loose stones as anvils, and occasionally the addition of another stabilising stone (Matsuzawa and Yamakoshi, 1996; Boesch, 2003; Carvalho, 2007; Biro et al., 2010). This further investment may reflect a need to overcome the specific constraints of this nut, such as a potential lack of suitable natural rock outcrops or tree roots for use as anvils (Biro et al., 2010). This technological investment in a potential fallback context highlights that that complexity is more directly associated with landscape knowledge, which will continue to accumulate even when a resource is constrained from reaching a preferred ranking. This may be related to the reduced caloric returns of oil palm, for which Matsuzawa (2003) reports that the kernel (~2g) provides a caloric return of 663 kcal/100g, making the energetic value of the entire nut (~7.2g) around 184 kcal/100g (assuming only the kernel is eaten). This contrasts with 356 kcal/100g for *Coula* nuts (Boesch and Boesch, 1983). Alternatively, it may be that oil palm nuts are actually a preferred food rather than a fallback, with seasonal periods of peak availability simply coinciding with when fruits are scarce, and that chimpanzee consumption is responding to these patterns.

Summary

Taken together, we would suggest that the combined evidence of termite fishing and nut-cracking support our proposed relationship between landscape knowledge and behavioural (in these cases technological) adaptation. We emphasise that tool use may develop regardless of resource

categorisation, and that the predictability of returns—underpinned by accumulation of knowledge regarding the spatial and temporal distribution of a resource, as well as how to harvest and process it—are a more direct indicator of investment. Nonetheless, the complexity of behavioural adaptation may appear to show a relationship with movement along the continuum of resource categorisation, from higher-quality fallback to preferred foods, if the quality of the resource allows it to take on a preferred status. In this instance, accumulation of landscape knowledge will allow technological complexity and resource categorisation to shift in parallel. In contrast, if nutritional constraints prevent a resource becoming more than a higher-quality fallback, there will be no apparent relationship between resource categorisation and technological complexity. In such instances, landscape knowledge will continue to accumulate, and technological complexity may continue to increase (assuming there is a corresponding dietary return), but there will be no change to resource ranking.

4. Seasonal Approaches to Hominin Carnivory

To illustrate the utility of our model in exploring changes in seasonal resource categorisation over time in the archaeological record, we present a case study regarding early hominin carnivory. We wish to emphasise that this is a preliminary application of the role of landscape knowledge in the archaeological record, and are aware that this is not a straightforward task. In particular, most of the sites that we are presented with in the earlier archaeological record represent palimpsests that are likely to reflect an amalgamation of behaviour over large swathes of time (e.g. Domínguez-Rodrigo, 2009), and this makes it more difficult to identify a) the signatures of seasonality required to assess resource categorisation, and b) trends of landscape knowledge accumulation (e.g. Roebrooks, 2003; Meltzer, 2003). Nonetheless, we would contend that it is still possible to identify markers of seasonality in early archaeological sites (e.g. Linares-Matás and Clark, 2022), and trends in behaviour over time, both within and across sites, and that these changes can be explored through the lens of landscape knowledge (Clark and Linares-Matás, 2020). It is important as a first discussion, therefore, to demonstrate the concept has some explanatory power for observations in the archaeological record.

Before we assess trends over time in the archaeological record, we wish to briefly outline some prevailing findings regarding animal consumption in chimpanzees and modern human hunter-gatherers. Some extent of animal consumption is relatively common among primates, particularly among chimpanzees, although this still never approaches the level of modern human hunter-gatherer populations (Watts, 2020). Chimpanzee hunting is frequently directed towards Red Colobus monkeys (*Piliocolobus spp.*), although it can also involve other animals, including small ungulates, rodents, and smaller primates (Stanford et al., 1994; Pruetz et al., 2015; Moore et al., 2017). There is much evidence for a seasonal signature in chimpanzee hunting behaviours, but they vary between localities (Mitani and Watts, 2005). For example, chimpanzee hunting is most common during the wet season at both the Taï Forest (Boesch and Boesch-Achermann, 2000) and Fongoli (Pruetz et al., 2015). On the other hand, the greatest emphasis on meat consumption at Gombe (Stanford et al., 1994), Loango National Park, Gabon (Klein et al., 2021), and Ugalla (Moore et al., 2017) occurs during the dry season.

While preliminary data suggest peak meat consumption at Fongoli does not seem to map onto peak fruit availability (Pruetz 2006; Bogart and Pruetz, 2008, 2011; Pruetz et al. 2015), a more consistent finding is that most sites seem to show peak consumption when fruit is relatively abundant. In the case of Ugalla, hunting may not directly map onto the peak abundance of fruit (Moore et al., 2017), but fruit is nonetheless still available throughout the dry season before its low point in the early wet (Yoshikawa and Ogawa, 2015; Piel et al., 2017). Further still, Watts and Mitani (2002) document that hunting success at Ngogo (Kibale National Park, Uganda) is positively correlated with fruit availability, perhaps suggesting that the energetically-costly behaviour of hunting is not a response to low food

availability, instead facilitated by the safety net provided by seasonal food abundance. A similar pattern may be documented at Kahuzi-Biega, where the (rare) consumption of mammalian tissue is associated with greater periods of fruit availability (Basabose and Yamagiwa, 1997; Yamagiwa and Basabose, 2009), and perhaps at Loango, where fruit is abundant during the dry season (Head et al., 2011). At the Tai Forest, there is fruit available throughout the year due to distinct seasons of fruiting by the different available species (Goné Bi and Wittig, 2018) and it is certainly available when meat consumption is greatest in the wet (Alexandre, 1980; Doran, 1997). Peak meat consumption at Mahale also appears to be a period of particularly high fruit availability (Uehara, 1982; Takahata et al., 1984; Matsumoto-Oda, 2002). Mitani and Watts (2005) argue that findings such as these question the extent to which meat can be considered a predictable nutritional safety net (i.e. a high-quality fallback) during periods of seasonal scarcity. Instead, chimpanzee carnivory is likely to represent the acquisition of a preferred resource during periods of increased success or reduced cost, while hunting itself may also act as an arena through which social capital can be accrued (e.g. Watts and Mitani, 2002).

Carnivory is more prominent among modern human hunter-gatherers in tropical and subtropical latitudes, focused on a greater variety of prey, and exhibiting a more consistent seasonal signature. These patterns are the function of a preference for ungulate prey, and the distinctly seasonal nature of their feeding behaviour and attractiveness. The reduction of plant availability and the evaporation of seasonal watercourses during the dry season in Africa often leads to the spatial concentration of herbivores around permanent water sources, leading to greater hunting and scavenging opportunities (Hurtado and Hill, 1990: 298; Foley, 1993; O'Connell et al., 2002; Lee, 2013; Hawkes, 2016). The dry season also represents a period of relatively high fat concentration for ungulate individuals, as fat accumulates as a result of high dietary quality in the wet season, and then subsequent depletion lags behind the reduction in dietary quality seen in the dry (Sinclair, 1975; Speth, 1987; Linares-Matás and Clark, 2021). These patterns are reflected in the greater dry season emphasis on ducks (*Cephalophus* spp.) and water chevrotain (*Hyemoschus aquaticus*) among the Baka of southeastern Cameroon and for the Mbuti of the Ituri Forest, northeastern Congo (Ichikawa, 1983; Hart and Hart, 1986; Sato et al., 2012). Similarly, seasonal changes to ungulate behaviour allow for animal tissue to reach ~40% of food brought back to camp by weight in the late dry season, compared to only ~10% during the early wet (O'Connell et al., 1988; Hawkes et al., 1991; Marlowe and Berbesque, 2009). Nonetheless, this also highlights that animal resources frequently play an important dietary role year-round in modern human hunter-gatherer populations (e.g. Ichikawa, 1983; Hart and Hart, 1986; O'Connell et al., 1988, 2002; Hurtado and Hill, 1990; Hawkes et al., 1991; Sato et al., 2012; Lee, 2013), and will usually be considered a core preferred resource.

While chimpanzee hunting strategies are unlikely to be wholly representative of the panin-hominin last common ancestor, they share with bonobos an emphasis on smaller prey classes, which include rodents, small ungulates, and occasionally arboreal primates (Hohmann and Fruth, 2008; Surbeck and Hohmann, 2008). As such, it is most likely that ancestral animal consumption also focused initially on smaller prey species, with the prominent role played by larger ungulates in modern hunter-gatherer populations indicating the existence of major shifts towards a focus on this prey category in the hominin lineage (Foley, 2001; Bunn, 2007; Thompson et al., 2019; Pobiner, 2020; Linares-Matás and Yravedra, 2021). This may have been particularly important in the context of the more open and seasonal environments (e.g. Cerling et al., 2011), and may have required an almost complete reset of landscape knowledge pertaining to animal tissue. Alongside this, we would expect increasing investment in behavioural adaptation towards animal consumption as landscape knowledge of the resource increases. This accumulation of landscape knowledge would also have changed the resource categorisation of animal products over time, likely resulting in an apparent association between the greatest complexity of behavioural responses and animal tissue becoming a core preferred resource. Chimpanzees themselves show clear evidence of landscape knowledge regarding how to capture their prey (particularly red colobus; e.g. Hosaka et al., 2020), even using wooden spears to hunt galagos at

Fongoli (Pruetz and Bertolani, 2007; Pruetz et al., 2015), and how best to consume the carcass upon acquisition (Gilby and Wawrzyniak, 2018).

While carcasses can be obtained through a number of different strategies, each involve very different landscape knowledge requirements (Linares-Matás and Clark, 2022: Table 2), and thus we would expect the greater knowledge thresholds to initially make more complex strategies prohibitive. This would suggest passive scavenging strategies should emerge first in a novel carnivorous niche, followed by those of intermediate knowledge requirements (such as confrontational scavenging or compensatory hunting), and finally turning to those with the greatest requirements (particularly additive hunting of peak prime individuals). In order to accrue this knowledge for large ungulate consumption, hominins would have first had to interact with ungulate remains as an experimental resource, in order to recognise new prey species and size classes as a potential source of nutrition. This is something that chimpanzees may lack the knowledge for, as individuals at Ngogo almost always ignore perfectly edible tissue from carcasses dispatched by obligate carnivores (Watts, 2008). Given their limited landscape knowledge requirements, abandoned carcasses are, nonetheless, the most likely context for hominins to have begun to accumulate information about these species, perhaps by attempting to scavenge from the remains (e.g. Blumenschine, 1987; Thompson et al., 2019; Pobiner, 2020). Chimpanzees in the forested environment of Ngogo only encounter edible carcasses once every 100 days or so (Watts, 2008), but hominins are likely to have encountered potential scavenging opportunities much more frequently than this in more open environments, especially when attracted to permanent water sources during the dry season. Sporadic interactions with these remains would serve to show hominins that these larger creatures could function as a viable resource, and that they could have high nutritional potential, despite associated risks (Pobiner, 2020).

The earliest secure evidence for animal consumption in the archaeological record dates to around 2.6-2.5 Ma from the sites of Gona and Bouri, Ethiopia (de Heinzelin et al., 1999; Domínguez-Rodrigo et al., 2005), but may stretch back as far as 3.4 Ma at the site of Dikika, also Ethiopia (McPherron et al., 2010; but see e.g. Domínguez-Rodrigo and Alcalá, 2016). All of the remains with purported cut-marks at each of these sites belong to ungulate species, showing that hominins had begun (and perhaps completed) the shift in preferred prey by the beginning of the Early Pleistocene. Thompson et al. (2019) argue that the origins of the “hominin predatory pattern” lie in scavenging in the Pliocene, a plausible timing for when hominins began to interact with larger ungulate carcasses. This may match the gradual increase in the importance of C4 foods to hominins after 4 Ma (Sponheimer et al., 2013). These early interactions with ungulate remains may have involved use of tools (e.g. possibly in the case of Dikika), but we would emphasise the evidence for tool-assisted consumption of animal tissue is vanishingly rare before the onset of the Early Pleistocene, and early interactions with ungulate remains need not have required tools at all (McCall, 2005). Instead, we may predict that any early tool use in the context of ungulate carcasses as an experimental resource would represent an attempt to deploy knowledge learned in a different context (such as an attempt to break open a bone with a stone used for nut-cracking, or use of a flake accidentally detached during pounding behaviours; cf. Harmand et al., 2015; Proffitt et al., 2016; Gürbüz and Lycett, 2021). A potential way of testing this hypothesis is through the expansion of analyses currently used to investigate carnivore tooth marks (e.g. Courtenay et al., 2021) to include an experimental reference sample derived from models of australopithecine jaws and the interaction of their teeth with fresh bone, against which the Pliocene palaeontological record could be analysed.

Furthermore, while we agree with Thompson et al. (2019) in the need to distinguish within-bone nutrients and meat as different attractive resources from animal carcasses, we emphasise that meat is much more likely to be visible on any given carcass that has been encountered. This may bias early interactions with carcasses towards the meat with bone marrow lagging behind, as greater landscape knowledge would have been required to identify and target within-bone tissue such as marrow and head contents. Therefore, while both types of mark have been reported for the Dikika specimens

(McPherron et al., 2010), we may predict that future evidence of Pliocene animal consumption is more likely to be represented by cut-marks than percussion marks. The continuation of this lag may explain why ungulate bones with evidence for hominin exploitation before 2 Ma are overwhelmingly biased towards cut-marks, rather than percussion marks (Pobiner, 2020), albeit there are taphonomic caveats in the ease of percussion mark identification (see Thompson et al., 2019; Pobiner, 2020).

It is unclear as to the dietary role of animal tissue in the first part of the early Pleistocene, from 2.6–2.1 Ma. Pobiner (2020) has pointed out that there is relatively limited evidence for hominin exploitation of animals from this period, with a total of just 31 potential bone fragments bearing evidence for hominin engagement from just 4 site complexes. We do note, however, the conclusion of Domínguez-Rodrigo et al. (2005) that the cutmarked remains from Gona 2.6–2.5 Ma (OGS-6, EG-13, and WG-9) include evidence of disarticulation of an equid calcaneus, defleshing of an upper limb bone, and evisceration of a medium-sized bovid, identified by marks on the ventral surface of a rib. According to the authors, these marks are suggestive of early access to the animal remains from the very beginning of this time period. Nonetheless, the evidence is not yet sufficient to determine the contribution of animal resources to Oldowan diets, and whether they constituted a higher-quality fallback or a seasonal preferred food in the period between 2.6 and 2.1 Ma.

Numerous authors (e.g. Bunn, 2007; Antón et al., 2014; Domínguez-Rodrigo and Pickering, 2017; Pobiner 2020; O’Connell and Hawkes, in prep.) have argued that the dearth of sites and hominin engagement with animal remains from 2.6–2.1 Ma is a reflection of a change in the importance of animal remains after 2 Ma, and not merely an outcome of taphonomic or research bias (although see Barr et al., 2022). Assuming, for now, that the increased amount of evidence for engagement with faunal remains after 2 Ma is a true reflection of hominin behaviour, it may be consistent with the suggestion that the importance of animal exploitation would have covaried with the available landscape knowledge pertaining to it. Such a change could also be accounted for by higher animal encounter rates at this time in the context of increasingly open environments (e.g. Cerling et al., 2011), or novel/intensified hominin food procurement strategies, but as far as a relationship between environmental factors and behaviour exists, both would require a role for landscape knowledge in understanding the seasonal costs and benefits associated with animal exploitation. Indeed, more consolidated landscape knowledge networks at this time may be evidenced in a potential increase in raw material transport, and in the greater diversity and complexity of reduction schemes in lithic assemblages (e.g. Gallotti, 2018; Clark and Linares-Matás, 2020).

Of particular importance to the accumulation of knowledge facilitating increased animal consumption is information regarding the spatial (and likely temporal) distribution of carcasses, alongside how to obtain carcasses more predictably and/or with greater frequency. In the period 2.0–1.84 Ma, we focus on two particular sites to suggest there is clear evidence that hominins had been able to ensure the use of animal resources as a preferred resource: Kanjera South, Homa Peninsula, Kenya, and FLK-Zinj, Olduvai Gorge, Tanzania (Bunn, 1981; Bunn and Kroll, 1986; Bunn and Ezzo, 1993; Domínguez-Rodrigo et al., 2007; Domínguez-Rodrigo, 2009; Ferraro et al., 2013; Parkinson, 2013, 2018; Oliver et al., 2019). As we have summarised and argued elsewhere (Linares-Matás and Clark, 2022), these sites are likely to display evidence of hominin hunting in distinct seasonal contexts. For Kanjera South, we have argued that the site represents a strategy of repeated wet season capture of juvenile bovids, combined with scavenging particular body parts (especially heads) of larger animals. For FLK-Zinj, we argued that the site represents a strategy of dry season hunting, biased towards vulnerable elderly individuals for small bovids and towards pregnant females and lone late prime adult males for larger bovids (i.e. waterbuck). We would suggest that these case studies demonstrate that hominins had accumulated substantial information about the ecology of the respective prey classes they were targeting at each site, as well as specific points in space and time that would allow them relatively predictable success in resource acquisition. This may have been accompanied with organic tool production (perhaps wooden thrusting spears) for dispatch of prey (e.g. Bunn and Pickering, 2010;

Lemorini et al., 2014, 2019), as well as the clear evidence for deployment of lithic technologies for carcass processing at both sites (Leakey, 1971; de la Torre and Mora, 2005; Braun et al., 2009; Lemorini et al., 2014, 2019; Gallotti, 2018).

It is perhaps likely that most archaeological sites prior to 1.5Ma with evidence for animal exploitation represent dry season occupations, characterised by multi-individual accumulations near perennial water sources, matching those left by the Hadza in the second half of the dry season (O'Connell and Hawkes, in prep.). We would argue that this pattern is at-least partially a reflection of hominin meat acquisition being constrained by the current state of landscape knowledge pertaining to carcass acquisition. In particular, it is much easier to learn how to exploit animal resources in the dry season, when they cluster in specific locations on the landscape, making it possible to incorporate animal products as a seasonal preferred resource when populations learned how to maintain predictable access to carcasses. In this way, Kanjera South represents a peculiar outlier in the overall trends just described. It is likely that the particular affordances of the well-watered grasslands of the Kanjera palaeolandscape allowed the population(s) inhabiting the site an opportunity to more consistently access animal resources in the wet season, perhaps allowing animal tissue to take on a core preferred role which may have been rare in the wider Oldowan context.

Furthermore, in addition to the aforementioned seasonal constraints, Oldowan hunting strategies appear to have also been limited in their ability to consistently dispatch peak prime individuals (but see Bunn and Gurtov, 2014), while acquisition was also tethered to specific points in the landscape, at specific points in the year. In the case of these two sites, the grassland of Kanjera South would have provided a specific opportunity to acquire juveniles cached in long grasses in the wet season (cf. Oliver et al., 2019), while wooded habitats nearby to perennial water sources would have provided potential ambush sites and mitigated carnivore risks during the dry season, as documented at Olduvai FLK-Zinj and DS (cf. Ashley et al., 2010; Bunn and Pickering, 2010; Bunn and Gurtov, 2014; Arraíz et al., 2017; Cobo-Sánchez, 2020; Díez-Martín et al., 2021). However, , further social and technological adaptations may have been required to obtain and process carcasses from a broader range of encounters at unfamiliar or less predictable points in the landscape. Indeed, while hominins at sites such as FLK-Zinj may have been able to curate stone material for reduction after carcasses had been obtained at specific ambush points of high return (cf. Potts, 1984, 1991), this caching behaviour would have been more difficult when the number of potential prey encounter spots increased. As such, the later introduction of more mobile processing technologies, through the adoption of core reduction sequences that allow for a greater portability of flakes—perhaps during the Acheulean—may have been crucial in facilitating this shift. Developments in harvesting behaviour and technology would have been particularly important in obtaining access to prime-aged individuals and/or larger prey sizes (cf. Linares-Matás and Yravedra, 2021) and therefore in maintaining access to animal resources throughout the year (e.g. O'Connell et al., 1988; Hawkes et al., 1991). In later periods, these changes may have manifested in more complex hunting equipment, such as the use of wooden throwing spears/javelins (e.g. Thieme, 1997; Milks et al., 2019), stone-tipped thrusting spears/javelins (e.g. Wilkins et al., 2012; Sahle et al., 2013; Wilkins et al., 2014; Lombard, 2021), and/or bone/stone-tipped bow-and-arrow technologies (e.g. Lombard and Phillipson, 2010; Lombard, 2011, 2020a, 2020b).

5. Conclusion

In this paper, we have attempted to explore the seasonal basis of resource categorisation and technological investment in chimpanzees and other nonhuman primate taxa to develop a framework through which to examine variability within Early Pleistocene subsistence strategies. In particular, we integrate work on the distinction between fallback and preferred foodstuffs into a single continuum of resource quality and seasonal consumption signature, allowing for resources to move along the

continuum over time in a population-specific process. This process is underpinned by the accumulation of landscape knowledge about specific resources in the population, with differences in the extent of this knowledge between populations of the same primate taxon allowing for resources to have quite distinct dietary roles despite a similar resource availability. We emphasise the importance of resource experimentation in incorporating new foodstuffs into the dietary repertoire of a population, with repeated encounters allowing for a better understanding of the spatial and temporal distributions of these resources facilitating a more important dietary role later on. We also believe that these concepts can be developed much further through quantitative studies which model the accumulation of landscape knowledge over time. It should be feasible to explore these concepts through the lens of agent-based modelling, but incorporating elements of complex systems theory (particularly Complex Adaptive Systems) may offer additional promising insights into how the interaction of different variables impacts the way that landscape knowledge manifests (see Holland, 2014). We are particularly interested in how such dynamics may create an emergent body of knowledge that collectively transcends that which any one individual possesses or would be able to acquire. Understanding the nature of these relationships between landscape knowledge and foraging behaviour may be particularly important, for example, in the exploitation of embedded resources (such as USOs, nuts, or bone marrow), which require a specific awareness that the edible component of the resource exists and an understanding of its potential returns, as well as familiarity with suitable extraction methods.

Through the lens of chimpanzee extractive foraging behaviours, such as nut-cracking among West African populations or more widespread cultural innovations involving fishing and dipping for colonial invertebrates, we suggest that behavioural adaptation is more directly determined by the accumulation of landscape knowledge, rather than simply resource categorisation. Repeated consumption will lead to the accumulation of knowledge pertaining to its location, harvest, and processing, allowing the development of additional return-maximising behaviours, even if the resource is primarily exploited as a fallback. Nonetheless, when the specific properties of a resource enable it to reach preferred status, the population-specific process of incorporation along the continuum of resource categorisation will occur in parallel with increases in spatio-temporal activity planning and technological investment. This co-evolution, facilitated and instigated by the consolidation and expansion of landscape knowledge networks, would result in more predictable resource exploitation patterns throughout the year.

In the context of the Early Pleistocene, we argue that the relationships between landscape knowledge and resource categorisation on one hand and technological investment on the other are extremely useful for understanding the nature of hominin behavioural change. In particular, we argue that the expansion of more open and seasonal environments in the late Pliocene and at the beginning of the Early Pleistocene set the context for initial experimentation with animal tissue from larger ungulates. Repeated interaction with this resource, perhaps initially through scavenging and subsequently through hunting of vulnerable demographics—with the consequent accumulation of landscape knowledge—would have facilitated an increased importance of these resources to hominin diets over time. This would have included information on the distribution of animals across time and space, how to dispatch an animal or to obtain the carcass, and how to process the available tissue. The gradual accumulation of knowledge will also have facilitated investment in processing and harvesting technologies that would have allowed for dietary niche expansions, including within-bone resources. Drastic shifts in environmental context, due to intense climatic transformation or through processes of longer-distance dispersal into different continental regions may have led to a dramatic disruption of landscape knowledge and a need to learn the information pertaining to resource use from scratch. These settings offer exciting high-visibility opportunities for testing the dynamics of landscape knowledge development and their influence on behavioural adaptation in the archaeological record.

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References

- Abwe EE, Morgan BJ, Doudja R, et al (2020) Dietary Ecology of the Nigeria–Cameroon Chimpanzee (*Pan troglodytes ellioti*). *Int J Primatol* 41:81–104. <https://doi.org/10.1007/s10764-020-00138-7>
- Alexandre DY (1980) Caractère saisonnier de la fructification dans une forêt hygrophile de Côte d'Ivoire. *Revue d'Ecologie (Terre Vie)* 34:335–357
- Anderson JR, Williamson EA, Carter J (1983) Chimpanzees of Sapo Forest, Liberia: Density, nests, tools and meat-eating. *Primates* 24:594–601. <https://doi.org/10.1007/BF02381692>
- Antón SC, Potts R, Aiello LC (2014) Evolution of early *Homo*: An integrated biological perspective. *Science* 345:1236828. <https://doi.org/10.1126/science.1236828>
- Arráiz H, Barboni D, Ashley GM, et al (2017) The FLK Zinj paleolandscape: Reconstruction of a 1.84Ma wooded habitat in the FLK Zinj-AMK-PTK-DS archaeological complex, Middle Bed I (Olduvai Gorge, Tanzania). *Palaeogeography, Palaeoclimatology, Palaeoecology* 488:9–20. <https://doi.org/10.1016/j.palaeo.2017.04.025>
- Ashley GM, Barboni D, Dominguez-Rodrigo M, et al (2010) A spring and wooded habitat at FLK Zinj and their relevance to origins of human behavior. *Quaternary Research* 74:304–314. <https://doi.org/10.1016/j.yqres.2010.07.015>
- Ban SD, Normand E (2019) Spatial cognitive abilities in foraging chimpanzees. In: Boesch C, Wittig R, Crockford C, et al. (eds) *The Chimpanzees of the Taï Forest*, 1st edn. Cambridge University Press, pp 440–450
- Barr WA, Pobiner B, Rowan J, et al (2022) No sustained increase in zooarchaeological evidence for carnivory after the appearance of *Homo erectus*. *Proceedings of the National Academy of Sciences* 119:e2115540119. <https://doi.org/10.1073/pnas.2115540119>
- Basabose AK (2004) Fruit availability and chimpanzee party size at Kahuzi montane forest, Democratic Republic of Congo. *Primates* 45:211–219. <https://doi.org/10.1007/s10329-004-0087-7>
- Basabose AK, Yamagiwa J (2002) Fruit availability and chimpanzee party size at Kahuzi montane forest, Democratic Republic of Congo. *International Journal of Primatology* 23:263–282. <https://doi.org/10.1023/A:1013879427335>
- Basabose K, Yamagiwa J (1997) Predation on mammals by chimpanzees in the Montane Forest of Kahuzi, Zaire. *Primates* 38:45–56
- Bird DW, O'Connell JF (2006) Behavioral Ecology and Archaeology. *J Archaeol Res* 14:143–188. <https://doi.org/10.1007/s10814-006-9003-6>

Biro D, Carvalho S, Matsuzawa T (2010) Tools, Traditions, and Technologies: Interdisciplinary Approaches to Chimpanzee Nut Cracking. In: Lonsdorf EV, Ross SR, Matsuzawa T (eds) *The Mind of the Chimpanzee*. University of Chicago Press, Chicago, IL, pp 140–155

Biro D, Inoue-Nakamura N, Tonooka R, et al (2003) Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Anim Cogn* 6:213–223. <https://doi.org/10.1007/s10071-003-0183-x>

Blumenshine RJ (1987) Characteristics of an Early Hominid Scavenging Niche. *Current Anthropology* 28:383–407

Blumenthal SA, Cerling TE, Smiley TM, et al (2019) Isotopic records of climate seasonality in equid teeth. *Geochimica et Cosmochimica Acta* 260:329–348. <https://doi.org/10.1016/j.gca.2019.06.037>

Boesch C (2003) Is culture a golden barrier between human and chimpanzee? *Evolutionary Anthropology: Issues, News, and Reviews* 12:82–91. <https://doi.org/10.1002/evan.10106>

Boesch C, Boesch H (1983) Optimisation of Nut-Cracking With Natural Hammers By Wild Chimpanzees. *Behaviour* 83:265–286. <https://doi.org/10.1163/156853983X00192>

Boesch C, Boesch H (1984) Possible causes of sex differences in the use of natural hammers by wild chimpanzees. *Journal of Human Evolution* 13:415–440. [https://doi.org/10.1016/S0047-2484\(84\)80055-X](https://doi.org/10.1016/S0047-2484(84)80055-X)

Boesch C, Boesch-Achermann H (2000) *The Chimpanzees of the Taï Forest*. Oxford University Press, Oxford

Boesch C, Marchesi P, Marchesi N, et al (1994) Is nut cracking in wild chimpanzees a cultural behaviour? *Journal of Human Evolution* 26:325–338. <https://doi.org/10.1006/jhev.1994.1020>

Boesch C, Wittig R (eds) (2019) *The Chimpanzees of the Taï Forest: 40 Years of Research*. Cambridge University Press, Cambridge

Bogart SL, Pruett JD (2008) Ecological context of savanna chimpanzee (*Pan troglodytes verus*) termite fishing at Fongoli, Senegal. *American Journal of Primatology* 70:605–612. <https://doi.org/10.1002/ajp.20530>

Bogart SL, Pruett JD (2011) Insectivory of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. *American Journal of Physical Anthropology* 145:11–20. <https://doi.org/10.1002/ajpa.21452>

Braun DR, Plummer TW, Ditchfield PW, et al (2009) Oldowan Technology and Raw Material Variability at Kanjera South. In: Hovers E, Braun DR (eds) *Interdisciplinary Approaches to the Oldowan*. Springer Netherlands, Dordrecht, pp 99–110

Bunn HT (1981) Archaeological evidence for meat-eating by Plio-Pleistocene hominids from Koobi Fora and Olduvai Gorge. *Nature* 291:574–577. <https://doi.org/10.1038/291574a0>

Bunn HT (2007) Meat made us human. In: Ungar PS (ed) *Evolution of the Human Diet: The Known, the Unknown, and the Unknowable*. Oxford University Press, Oxford, pp 191–211

Bunn HT, Ezzo JA (1993) Hunting and Scavenging by Plio-Pleistocene Hominids: Nutritional Constraints, Archaeological Patterns, and Behavioural Implications. *Journal of Archaeological Science* 20:365–398. <https://doi.org/10.1006/jasc.1993.1023>

Bunn HT, Gurtov AN (2014) Prey mortality profiles indicate that Early Pleistocene *Homo* at Olduvai was an ambush predator. *Quaternary International* 322–323:44–53. <https://doi.org/10.1016/j.quaint.2013.11.002>

Bunn HT, Kroll EM (1986) Systematic Butchery by Plio/Pleistocene Hominids at Olduvai Gorge, Tanzania. *Current Anthropology* 27:431–452. <https://doi.org/10.1086/203467>

Bunn HT, Pickering TR (2010) Bovid mortality profiles in paleoecological context falsify hypotheses of endurance running–hunting and passive scavenging by early Pleistocene hominins. *Quaternary Research* 74:395–404. <https://doi.org/10.1016/j.yqres.2010.07.012>

Campbell-Smith G, Campbell-Smith M, Singleton I, Linkie M (2011) Raiders of the Lost Bark: Orangutan Foraging Strategies in a Degraded Landscape. *PLOS ONE* 6:e20962. <https://doi.org/10.1371/journal.pone.0020962>

Carvalho S (2007) Applying the Concept of Chaîne Opératoire to Nut-Cracking: An Approach Based on Studying Communities of Chimpanzees (*Pan troglodytes verus*) in Bossou and Diecké (Guinea). Master's dissertation, University of Coimbra

Carvalho S (2011) Diécké Forest, Guinea: Delving into Chimpanzee Behavior Using Stone Tool Surveys. In: Matsuzawa T, Humle T, Sugiyama Y (eds) *The Chimpanzees of Bossou and Nimba*. Springer Japan, Tokyo, pp 301–312

Carvalho S, Biro D, McGrew WC, Matsuzawa T (2009) Tool-composite reuse in wild chimpanzees (*Pan troglodytes*): archaeologically invisible steps in the technological evolution of early hominins? *Anim Cogn* 12:103–114. <https://doi.org/10.1007/s10071-009-0271-7>

Carvalho S, Cunha E, Sousa C, Matsuzawa T (2008) Chaînes opératoires and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. *Journal of Human Evolution* 55:148–163. <https://doi.org/10.1016/j.jhevol.2008.02.005>

Cerling TE, Wynn JG, Andanje SA, et al (2011) Woody cover and hominin environments in the past 6 million years. *Nature* 476:51–56. <https://doi.org/10.1038/nature10306>

Chapman CA, Chapman LJ, Wrangham RW (1995) Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behav Ecol Sociobiol* 36:59–70. <https://doi.org/10.1007/BF00175729>

Chapman CA, White FJ, Wrangham RW (1994) Party size in chimpanzees and bonobos: A reevaluation of theory based on two similarly forested sites. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG (eds) *Chimpanzee Cultures*. Harvard University Press, Cambridge, M.A., pp 41–58

Charnov EL (1976) Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9:129–136. [https://doi.org/10.1016/0040-5809\(76\)90040-X](https://doi.org/10.1016/0040-5809(76)90040-X)

Clark J, Linares-Matás G (2020) The Role of Landscape Knowledge Networks in the Early Pleistocene Technological Variability of East Africa. *Archaeological Review from Cambridge* 35:25–44. <https://doi.org/10.17863/CAM.71847>

Cobo-Sánchez L (2020) Taphonomic and Spatial Study of the archaeological Site DS from Bed I in Olduvai Gorge (Tanzania). PhD Dissertation, Universidad Complutense de Madrid

Conklin-Brittain NL, Wrangham RW, Hunt KD (1998) Dietary Response of Chimpanzees and Cercopithecines to Seasonal Variation in Fruit Abundance. II. Macronutrients. *International Journal of Primatology* 19:971–998. <https://doi.org/10.1023/A:1020370119096>

Constantino PJ, Lucas PW, Lee JJ-W, Lawn BR (2009) The influence of fallback foods on great ape tooth enamel. *American Journal of Physical Anthropology* 140:653–660. <https://doi.org/10.1002/ajpa.21096>

Courtenay LA, Herranz-Rodrigo D, González-Aguilera D, Yravedra J (2021) Developments in data science solutions for carnivore tooth pit classification. *Sci Rep* 11:10209. <https://doi.org/10.1038/s41598-021-89518-4>

de Heinzelin J, Clark JD, White T, et al (1999) Environment and Behavior of 2.5-Million-Year-Old Bouri Hominids. *Science* 284:625–629. <https://doi.org/10.1126/science.284.5414.625>

de la Torre I, Mora R (2005) Technological Strategies in the Lower Pleistocene at Olduvai Beds I & II. *Universite de Liège, Service de Préhistoire, Liège*

Deblauwe I (2009) Temporal Variation in Insect-eating by Chimpanzees and Gorillas in Southeast Cameroon: Extension of Niche Differentiation. *Int J Primatol* 30:229–252. <https://doi.org/10.1007/s10764-009-9337-2>

Deblauwe I, Guislain P, Dupain J, Van Elsacker L (2006) Use of a tool-set by *Pan troglodytes troglodytes* to obtain termites (*Macrotermes*) in the periphery of the Dja Biosphere Reserve, southeast Cameroon. *Am J Primatol* 68:1191–1196. <https://doi.org/10.1002/ajp.20318>

Deblauwe I, Janssens GPJ (2008) New insights in insect prey choice by chimpanzees and gorillas in Southeast Cameroon: The role of nutritional value. *American Journal of Physical Anthropology* 135:42–55. <https://doi.org/10.1002/ajpa.20703>

Diez-Martín F, Cobo-Sánchez L, Baddeley A, et al (2021) Tracing the spatial imprint of Oldowan technological behaviors: A view from DS (Bed I, Olduvai Gorge, Tanzania). *PLoS ONE* 16:e0254603. <https://doi.org/10.1371/journal.pone.0254603>

Dominguez-Rodrigo M, Alcalá L (2016) 3.3-Million-Year-Old Stone Tools and Butchery Traces? More Evidence Needed. *PaleoAnthropology* 2016:46–53. <https://doi.org/10.4207/PA.2016.ART99>

Domínguez-Rodrigo M (2009) Are all Oldowan Sites Palimpsests? If so, what can they tell us about Hominid Carnivory? In: Hovers E, Braun DR (eds) *Interdisciplinary Approaches to the Oldowan*. Springer Netherlands, Dordrecht, pp 129–147

Domínguez-Rodrigo M, Egido RB, Egeland CP (2007) Deconstructing Olduvai: A Taphonomic Study of the Bed I Sites. Springer Netherlands, Dordrecht

Domínguez-Rodrigo M, Pickering TR (2017) The meat of the matter: an evolutionary perspective on human carnivory. *Azania* 52:4–32. <https://doi.org/10.1080/0067270X.2016.1252066>

Domínguez-Rodrigo M, Rayne Pickering T, Semaw S, Rogers MJ (2005) Cutmarked bones from Pliocene archaeological sites at Gona, Afar, Ethiopia: implications for the function of the world's oldest stone tools. *Journal of Human Evolution* 48:109–121. <https://doi.org/10.1016/j.jhevol.2004.09.004>

Doran D (1997) Influence of Seasonality on Activity Patterns, Feeding Behavior, Ranging, and Grouping Patterns in Tai Chimpanzees. *International Journal of Primatology* 18:183–206. <https://doi.org/10.1023/A:1026368518431>

Eaton S, Eaton III S, Konner M (1997) Paleolithic nutrition revisited: A twelve-year retrospective on its nature and implications. *Eur J Clin Nutr* 51:207–216. <https://doi.org/10.1038/sj.ejcn.1600389>

Fay JM, Carroll RW (1994) Chimpanzee tool use for honey and termite extraction in Central Africa. *Am J Primatol* 34:309–317. <https://doi.org/10.1002/ajp.1350340403>

Ferraro JV (2007) Broken Bones and Shattered Stones: On the Foraging Ecology of Oldowan Hominins. PhD Dissertation, University of California

Ferraro JV, Plummer TW, Pobiner BL, et al (2013) Earliest Archaeological Evidence of Persistent Hominin Carnivory. *PLOS ONE* 8:e62174. <https://doi.org/10.1371/journal.pone.0062174>

Foley R (1985) Optimality Theory in Anthropology. *Man* 20:222. <https://doi.org/10.2307/2802382>

Foley R (2001) The evolutionary consequences of increased carnivory in hominids. In: Stanford CB, Bunn HT (eds) *Meat-eating and human evolution*. Oxford University Press, New York, NY, pp 305–331

Foley RA (1993) The influence of seasonality on hominid evolution. In: Ulijaszek SJ, Strickland SS (eds) *Seasonality and Human Ecology*, 1st edn. Cambridge University Press, pp 17–37

Foley RA (1987) *Another Unique Species: Patterns in Human Evolutionary Ecology*. Longman, Harlow

Fox EA, Sitompul A, van Schaik CP (1999) Intelligent tool use in wild Sumatran orangutans. In: Parker ST, Mitchell RW, Miles HL (eds) *The mentalities of gorillas and orangutans*. Cambridge University Press, Cambridge, pp 99–116

Fulk R, Loomis M, Garland C (1992) Nutrition of captive chimpanzees. In: Fulk R, Garland C (eds) *The care and management of chimpanzees (Pan troglodytes) in captive environments: a husbandry manual developed for the chimpanzee species survival plan*. North Carolina Zoological Society, Asheboro, NC

Furuichi T, Hashimoto C, Tashiro Y (2001) Fruit Availability and Habitat Use by Chimpanzees in the Kalinzu Forest, Uganda: Examination of Fallback Foods. *International Journal of Primatology* 22:929–945. <https://doi.org/10.1023/A:1012009520350>

Gallotti R (2018) Before the Acheulean in East Africa: An Overview of the Oldowan Lithic Assemblages. In: Gallotti R, Mussi M (eds) *The Emergence of the Acheulean in East Africa and Beyond: Contributions in Honor of Jean Chavaillon*. Springer International Publishing, Cham, pp 13–32

Gilby IC, Wawrzyniak D (2018) Meat Eating by Wild Chimpanzees (*Pan troglodytes schweinfurthii*): Effects of Prey Age on Carcass Consumption Sequence. *Int J Primatol* 39:127–140. <https://doi.org/10.1007/s10764-018-0019-9>

Golledge RG (2003) Human wayfinding and cognitive maps. In: Rockman M, Steele J (eds) *Colonization of unfamiliar landscapes: The archaeology of adaptation*. Routledge, London, pp 25–43

Goné Bi ZB, Wittig R (2019) Long-term diet of the chimpanzees (*Pan troglodytes verus*) in Tai National Park: interannual variations in consumption. In: Boesch C, Wittig R (eds) *The Chimpanzees of the Tai Forest: 40 Years of Research*. Cambridge University Press, Cambridge, pp 242–260

Goodall J (1986) The Chimpanzees of Gombe: Patterns of Behavior. Harvard University Press, Cambridge, M.A.

Goren-Inbar N, Sharon G, Melamed Y, Kislev M (2002) Nuts, nut cracking, and pitted stones at Gesher Benot Ya'aqov, Israel. PNAS 99:2455–2460. <https://doi.org/10.1073/pnas.032570499>

Green SJ, Boruff BJ, Grueter CC (2020) From ridge tops to ravines: landscape drivers of chimpanzee ranging patterns. Animal Behaviour 163:51–60. <https://doi.org/10.1016/j.anbehav.2020.02.016>

Gross-Camp ND, Masozera M, Kaplin BA (2009) Chimpanzee seed dispersal quantity in a tropical montane forest of Rwanda. Am J Primatol 71:901–911. <https://doi.org/10.1002/ajp.20727>

Gruber T, Muller MN, Strimling P, et al (2009) Wild Chimpanzees Rely on Cultural Knowledge to Solve an Experimental Honey Acquisition Task. Current Biology 19:1806–1810. <https://doi.org/10.1016/j.cub.2009.08.060>

Gürbüz RB, Lycett SJ (2021) Did the use of bone flakes precede the use of knapped stone flakes in hominin meat processing and could this be detectable archaeologically? Journal of Anthropological Archaeology 62:101305. <https://doi.org/10.1016/j.jaa.2021.101305>

Harmand S, Lewis JE, Feibel CS, et al (2015) 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. Nature 521:310–315. <https://doi.org/10.1038/nature14464>

Hart TB, Hart JA (1986) The ecological basis of hunter-gatherer subsistence in African Rain Forests: The Mbuti of Eastern Zaire. Hum Ecol 14:29–55. <https://doi.org/10.1007/BF00889209>

Hawkes K (2016) Ethnoarchaeology and Plio-Pleistocene sites: Some lessons from the Hadza. Journal of Anthropological Archaeology 44:158–165. <https://doi.org/10.1016/j.jaa.2016.07.005>

Hawkes K, Hill K, O'Connell JF (1982) Why hunters gather: Optimal foraging and the Ache of Eastern Paraguay. American Ethnologist 9:379–398

Hawkes K, O'Connell JF, Blurton Jones NG, et al (1991) Hunting income patterns among the Hadza: big game, common goods, foraging goals and the evolution of the human diet. Philosophical Transactions of the Royal Society of London Series B: Biological Sciences 334:243–251. <https://doi.org/10.1098/rstb.1991.0113>

Hawkes K, O'Connell JF, Blurton Jones NG (1997) Hadza Women's Time Allocation, Offspring Provisioning, and the Evolution of Long Postmenopausal Life Spans. Current Anthropology 38:551–577. <https://doi.org/10.1086/204646>

Hawkes K, O'Connell JF, Blurton-Jones NG (1989) Hardworking Hadza grandmothers. In: Standen V, Foley RA (eds) Comparative Socioecology: The Behavioural Ecology of Humans and Other Mammals. Blackwell Scientific, Oxford, pp 341–366

Head JS, Boesch C, Makaga L, Robbins MM (2011) Sympatric Chimpanzees (*Pan troglodytes troglodytes*) and Gorillas (*Gorilla gorilla gorilla*) in Loango National Park, Gabon: Dietary Composition, Seasonality, and Intersite Comparisons. Int J Primatol 32:755–775. <https://doi.org/10.1007/s10764-011-9499-6>

Hernandez-Aguilar RA, Moore J, Pickering TR (2007) Savanna chimpanzees use tools to harvest the underground storage organs of plants. Proceedings of the National Academy of Sciences 104:19210–19213. <https://doi.org/10.1073/pnas.0707929104>

Hicks TC, Kühl HS, Boesch C, et al (2019) Bili-Uéré: A Chimpanzee Behavioural Realm in Northern Democratic Republic of Congo. *Folia Primatol* 90:3–64. <https://doi.org/10.1159/000492998>

Hirata S, Morimura N, Houki C (2009) How to crack nuts: acquisition process in captive chimpanzees (*Pan troglodytes*) observing a model. *Anim Cogn* 12:87–101. <https://doi.org/10.1007/s10071-009-0275-3>

Hladik CM (1977) Chimpanzees of Gabon and chimpanzees of Gombe: Some comparative data on the diet. In: Clutton-Brock TH (ed) *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes*. Academic Press, London, pp 481–501

Hockings KJ, Anderson JR, Matsuzawa T (2010) Flexible feeding on cultivated underground storage organs by rainforest-dwelling chimpanzees at Bossou, West Africa. *Journal of Human Evolution* 58:227–233. <https://doi.org/10.1016/j.jhevol.2009.11.004>

Hohmann G, Fruth B (2008) New Records on Prey Capture and Meat Eating by Bonobos at Lui Kotale, Salonga National Park, Democratic Republic of Congo. *FPR* 79:103–110. <https://doi.org/10.1159/000110679>

Holland JH (2014) *Complexity: A Very Short Introduction*. Oxford University Press

Hölldobler B, Wilson EO *The ants*. The Belknap Press of Harvard University Press, Cambridge, M.A.

Hosaka K, Nakamura M, Takahata Y (2020) Longitudinal changes in the targets of chimpanzee (*Pan troglodytes*) hunts at Mahale Mountains National Park: how and why did they begin to intensively hunt red colobus (*Piliocolobus rufomitratus*) in the 1980s? *Primates* 61:391–401. <https://doi.org/10.1007/s10329-020-00803-8>

Hosfield R (2020) *The earliest Europeans – a year in the life: seasonal survival strategies in the Lower Palaeolithic*. Oxbow Books, Oxford

Humle T, Matsuzawa T (2001) Behavioural Diversity among the Wild Chimpanzee Populations of Bossou and Neighbouring Areas, Guinea and Côte d'Ivoire, West Africa. *Folia Primatol* 72:57–68. <https://doi.org/10.1159/000049924>

Humle T, Matsuzawa T (2004) Oil Palm Use by Adjacent Communities of Chimpanzees at Bossou and Nimba Mountains, West Africa. *International Journal of Primatology* 25:551–581. <https://doi.org/10.1023/B:IJOP.0000023575.93644.f4>

Humle T, Snowdon CT, Matsuzawa T (2009) Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Anim Cogn* 12:37–48. <https://doi.org/10.1007/s10071-009-0272-6>

Hurtado AM, Hill KR (1990) Seasonality in a Foraging Society: Variation in Diet, Work Effort, Fertility, and Sexual Division of Labor among the Hiwi of Venezuela. *Journal of Anthropological Research* 46:293–346. <https://doi.org/10.1086/jar.46.3.3630428>

Ichikawa M (1983) An Examination of the Hunting-Dependent Life of the Mbuti Pygmies, Eastern Zaire. *African Study Monographs* 4:55–76. <https://doi.org/10.14989/68001>

Inoue-Nakamura N, Matsuzawa T (1997) Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 111:159–173. <https://doi.org/10.1037/0735-7036.111.2.159>

Itoh N, Muramatsu D (2015) Patterns and trends in fruiting phenology: some important implications for chimpanzee diet. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds) Mahale Chimpanzees: 50 Years of Research. Cambridge University Press, Cambridge, pp 174–194

Itoh N, Nishida T (2007) Chimpanzee grouping patterns and food availability in Mahale Mountains National Park, Tanzania. *Primates* 48:87–96. <https://doi.org/10.1007/s10329-006-0031-0>

Janson CH, van Schaik CP (1988) Recognizing the many faces of primate food competition: methods. *Behaviour* 105:165–186

Jeschke JM, Kopp M, Tollrian R (2002) Predator Functional Responses: Discriminating Between Handling and Digesting Prey. *Ecological Monographs* 72:95–112. [https://doi.org/10.1890/0012-9615\(2002\)072\[0095:PFRDBH\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2002)072[0095:PFRDBH]2.0.CO;2)

Joannes-Boyau R, Adams JW, Austin C, et al (2019) Elemental signatures of *Australopithecus africanus* teeth reveal seasonal dietary stress. *Nature* 572:112–115. <https://doi.org/10.1038/s41586-019-1370-5>

Jones C, Sabater Pi J (1969) Sticks used by Chimpanzees in Rio Muni, West Africa. *Nature* 223:100–101. <https://doi.org/10.1038/223100a0>

Kagoro-Rugunda G, Kayanja FIB (2011) *Ficus* sp. and *Musanga leo-errerae*: coexistent keystone fruits for chimpanzees in Kalinzu forest. *African Journal of Ecology* 49:389–396. <https://doi.org/10.1111/j.1365-2028.2011.01292.x>

Kalan AK, Kulik L, Arandjelovic M, et al (2020) Environmental variability supports chimpanzee behavioural diversity. *Nat Commun* 11:4451. <https://doi.org/10.1038/s41467-020-18176-3>

Kelly RL (2013) The Lifeways of Hunter-Gatherers: The Foraging Spectrum, 2nd Revised ed. edition. Cambridge University Press, Cambridge

Kitanishi K (1994) The Exchange of Forest Products (*Irvingia* nuts) between the Aka Hunter-gatherers and the Cultivators in Northeastern Congo. *Tropics* 4:79–92. <https://doi.org/10.3759/tropics.4.79>

Kitanishi K (1995) Seasonal Changes in the Subsistence Activities and Food Intake of the Aka Hunter-Gatherers in Northeastern Congo. *African Study Monographs* 16:73–118. <https://doi.org/10.14989/68133>

Klein H, Bocksberger G, Baas P, et al (2021) Hunting of mammals by central chimpanzees (*Pan troglodytes troglodytes*) in the Loango National Park, Gabon. *Primates* 62:267–278. <https://doi.org/10.1007/s10329-020-00885-4>

Koops K, Schöning C, McGrew WC, Matsuzawa T (2015) Chimpanzees prey on army ants at Seringbara, Nimba Mountains, Guinea: Predation patterns and tool use characteristics. *American Journal of Primatology* 77:319–329. <https://doi.org/10.1002/ajp.22347>

Koops K, Soumah AG, van Leeuwen KL, et al (2022) Field experiments find no evidence that chimpanzee nut cracking can be independently innovated. *Nat Hum Behav* 1–8. <https://doi.org/10.1038/s41562-021-01272-9>

Kuroda S, Nishihara T, Suzuki S, Oko RA (1996) Sympatric chimpanzees and gorillas in the Ndoki Forest, Congo. In: McGrew WC, Marchant LF, Nishida T (eds) Great Ape Societies. Cambridge University Press, Cambridge, pp 71–81

Kwiecien O, Braun T, Brunello CF, et al (2021) What we talk about when we talk about seasonality – A transdisciplinary review. *Earth-Science Reviews* 103843. <https://doi.org/10.1016/j.earscirev.2021.103843>

Laden G, Wrangham R (2005) The rise of the hominids as an adaptive shift in fallback foods: Plant underground storage organs (USOs) and australopith origins. *Journal of Human Evolution* 49:482–498. <https://doi.org/10.1016/j.jhevol.2005.05.007>

Lambert JE (2007) Seasonality, fallback strategies, and natural selection: a chimpanzee versus cercopithecoid model for interpreting the evolution of hominin diet. In: Ungar P (ed) *Evolution of Human Diet: The Known, the Unknown, and the Unknowable*. University of Oxford Press, Oxford, pp 324–343

Lambert JE, Rothman JM (2015) Fallback Foods, Optimal Diets, and Nutritional Targets: Primate Responses to Varying Food Availability and Quality. *Annual Review of Anthropology* 44:493–512. <https://doi.org/10.1146/annurev-anthro-102313-025928>

Lapiente JM (2021) The Chimpanzees of the Comoé National Park, Ivory Coast. Status, distribution, ecology and behavior. Universität Würzburg

Leakey MD (1971) *Olduvai Gorge: Volume 3, Excavations in Beds I and II, 1960-1963*. Cambridge University Press, Cambridge

Lee RB (2003) *The Dobe Ju/'hoansi*. Wadsworth Thomson Learning, Belmont, CA

Leighton M (1993) Modeling dietary selectivity by Bornean orangutans: Evidence for integration of multiple criteria in fruit selection. *International Journal of Primatology* 14:257–313. <https://doi.org/10.1007/BF02192635>

Lemorini C, Bishop LC, Plummer TW, et al (2019) Old stones' song—second verse: use-wear analysis of rhyolite and fenitized andesite artifacts from the Oldowan lithic industry of Kanjera South, Kenya. *Archaeol Anthropol Sci* 11:4729–4754. <https://doi.org/10.1007/s12520-019-00800-z>

Lemorini C, Plummer TW, Braun DR, et al (2014) Old stones' song: Use-wear experiments and analysis of the Oldowan quartz and quartzite assemblage from Kanjera South (Kenya). *Journal of Human Evolution* 72:10–25. <https://doi.org/10.1016/j.jhevol.2014.03.002>

Lesnik JJ (2014) Termites in the hominin diet: A meta-analysis of termite genera, species and castes as a dietary supplement for South African robust australopithecines. *Journal of Human Evolution* 71:94–104. <https://doi.org/10.1016/j.jhevol.2013.07.015>

Linares-Matás GJ, Clark J (2021) Seasonality and Oldowan behavioral variability in East Africa. *Journal of Human Evolution* 103070. <https://doi.org/10.1016/j.jhevol.2021.103070>

Linares-Matás GJ, Yravedra J (in press) “We hunt to share”: Subsistence strategies and social dynamics in the Early Pleistocene of East Africa. *World Archaeology*

Lombard M (2011) Quartz-tipped arrows older than 60 ka: further use-trace evidence from Sibudu, KwaZulu-Natal, South Africa. *Journal of Archaeological Science* 38:1918–1930. <https://doi.org/10.1016/j.jas.2011.04.001>

Lombard M (2021) Variation in hunting weaponry for more than 300,000 years: A tip cross-sectional area study of Middle Stone Age points from southern Africa. *Quaternary Science Reviews* 264:107021. <https://doi.org/10.1016/j.quascirev.2021.107021>

Lombard M (2020b) Testing for poisoned arrows in the Middle Stone Age: A tip cross-sectional analysis of backed microliths from southern Africa. *Journal of Archaeological Science: Reports* 34:102630. <https://doi.org/10.1016/j.jasrep.2020.102630>

Lombard M (2020a) The tip cross-sectional areas of poisoned bone arrowheads from southern Africa. *Journal of Archaeological Science: Reports* 33:102477. <https://doi.org/10.1016/j.jasrep.2020.102477>

Lombard M, Kyriacou K (2020) Hunter-Gatherer Women. In: *Oxford Research Encyclopedia of Anthropology*. Oxford University Press

Lombard M, Phillipson L (2010) Indications of bow and stone-tipped arrow use 64 000 years ago in KwaZulu-Natal, South Africa. *Antiquity* 84:635–648. <https://doi.org/10.1017/S0003598X00100134>

Luncz LV, Mundry R, Soiret S, Boesch C (2019) Cultural diversity of nut-cracking behaviour between two populations of wild chimpanzees (*Pan troglodytes verus*) in the Côte d'Ivoire. In: Boesch C, Wittig R (eds) *The Chimpanzees of the Taï Forest: 40 Years of Research*. Cambridge University Press, Cambridge, pp 194–220

Luncz LV, Sirianni G, Mundry R, Boesch C (2018) Costly culture: differences in nut-cracking efficiency between wild chimpanzee groups. *Animal Behaviour* 137:63–73. <https://doi.org/10.1016/j.anbehav.2017.12.017>

MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. *American Naturalist* 100:603–609

Marlowe FW, Berbesque JC (2009) Tubers as fallback foods and their impact on Hadza hunter-gatherers. *American Journal of Physical Anthropology* 140:751–758. <https://doi.org/10.1002/ajpa.21040>

Marshall AJ, Boyko CM, Feilen KL, et al (2009) Defining fallback foods and assessing their importance in primate ecology and evolution. *Am J Phys Anthropol* 140:603–614. <https://doi.org/10.1002/ajpa.21082>

Marshall AJ, Wrangham RW (2007) Evolutionary Consequences of Fallback Foods. *Int J Primatol* 28:1219–1235. <https://doi.org/10.1007/s10764-007-9218-5>

Martin J, Moorter B van, Revilla E, et al (2013) Reciprocal modulation of internal and external factors determines individual movements. *Journal of Animal Ecology* 82:290–300. <https://doi.org/10.1111/j.1365-2656.2012.02038.x>

Matsumoto-Oda A (2002) Behavioral seasonality in mahale chimpanzees. *Primates* 43:103–117. <https://doi.org/10.1007/BF02629670>

Matsuzawa T (1994) Field experiments on use of stone tools in the wild. In: Wrangham RW, McGrew WC, de Waal FBM, Heltone PG (eds) *Chimpanzee Cultures*. Harvard University Press, Cambridge, M.A., pp 351–370

Matsuzawa T (2003) Koshima Monkeys and Bossou Chimpanzees: Long-Term Research on Culture in Nonhuman Primates. In: de Waal FBM, Tyack PL (eds) *Animal Social Complexity*. Harvard University Press, pp 374–387

Matsuzawa T, Yamakoshi G (1996) Comparison of chimpanzee material culture between Bossou and Nimba, West Africa. In: Russon AE, Bard K, Parkers S (eds) *Reaching into thought*. Cambridge University Press, Cambridge, pp 211–232

Matthews JK, Ridley A, Niyigaba P, et al (2019) Chimpanzee feeding ecology and fallback food use in the montane forest of Nyungwe National Park, Rwanda. *Am J Primatol* 81:. <https://doi.org/10.1002/ajp.22971>

McCall GS (2005) An Experimental Examination of the Potential Function of Early Stone Age Tool Technology and Implications for Subsistence Behavior. *Lithic Technology* 30:29–43. <https://doi.org/10.1080/01977261.2005.11721023>

McGrew WC (1974) Tool use by wild chimpanzees in feeding upon driver ants. *Journal of Human Evolution* 3:501–508. [https://doi.org/10.1016/0047-2484\(74\)90010-4](https://doi.org/10.1016/0047-2484(74)90010-4)

McGrew WC (1992) *Chimpanzee Material Culture: Implications for Human Evolution*. Cambridge University Press, Cambridge

McGrew WC, Ham RM, White LJ, et al (1997) Why Don't Chimpanzees in Gabon Crack Nuts? *International Journal of Primatology* 18:353–374. <https://doi.org/10.1023/A:1026382316131>

McGrew WC, Tutin CEG, Baldwin PJ (1979) Chimpanzees, Tools, and Termites: Cross-Cultural Comparisons of Senegal, Tanzania, and Rio Muni. *Man* 14:185. <https://doi.org/10.2307/2801563>

McPherron SP, Alemseged Z, Marean CW, et al (2010) Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature* 466:857–860. <https://doi.org/10.1038/nature09248>

Meltzer DJ (2003) Lessons in landscape learning. In: Rockman M, Steele J (eds) *Colonization of unfamiliar landscapes: The archaeology of adaptation*. Routledge, London

Milks A, Parker D, Pope M (2019) External ballistics of Pleistocene hand-thrown spears: experimental performance data and implications for human evolution. *Scientific Reports* 9:. <https://doi.org/10.1038/s41598-018-37904-w>

Mitani JC, Watts DP (2005) Seasonality in hunting by non-human primates. In: Brockman DK, van Schaik CP (eds) *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates*. Cambridge University Press, Cambridge, pp 215–241

Moore J, Black J, Hernandez-Aguilar RA, et al (2017) Chimpanzee vertebrate consumption: Savanna and forest chimpanzees compared. *Journal of Human Evolution* 112:30–40. <https://doi.org/10.1016/j.jhevol.2017.09.004>

Moore JF, Mulindahabi F, Gatorano G, et al (2018) Shifting through the forest: home range, movement patterns, and diet of the eastern chimpanzee (*Pan troglodytes schweinfurthii*) in Nyungwe National Park, Rwanda. *Am J Primatol* 80:e22897. <https://doi.org/10.1002/ajp.22897>

Moore R (2013) Social learning and teaching in chimpanzees. *Biol Philos* 28:879–901. <https://doi.org/10.1007/s10539-013-9394-y>

Moscovice LR, Issa MH, Petrzelkova KJ, et al (2007) Fruit availability, chimpanzee diet, and grouping patterns on Rubondo Island, Tanzania. *American Journal of Primatology* 69:487–502. <https://doi.org/10.1002/ajp.20350>

Nakamura M, Hosaka K, Itoh N, Zamma K (eds) (2015) *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge

Nathan R, Getz WM, Revilla E, et al (2008) A movement ecology paradigm for unifying organismal movement research. *PNAS* 105:19052–19059. <https://doi.org/10.1073/pnas.0800375105>

Newton-Fisher NE (1999) The diet of chimpanzees in the Budongo Forest Reserve, Uganda: Diet of Budongo chimpanzees. *African Journal of Ecology* 37:344–354. <https://doi.org/10.1046/j.1365-2028.1999.00186.x>

Nishida T (1976) The Bark-Eating Habits in Primates, with Special Reference to Their Status in the Diet of Wild Chimpanzees. *Folia Primatol* 25:277–287. <https://doi.org/10.1159/000155720>

Normand E, Ban SD, Boesch C (2009) Forest chimpanzees (*Pan troglodytes verus*) remember the location of numerous fruit trees. *Anim Cogn* 12:797–807. <https://doi.org/10.1007/s10071-009-0239-7>

O’Connell JF, Hawkes K (1981) Alyawara plant use and optimal foraging theory. In: Winterhalder B, Smith EA (eds) *Hunter-gatherer foraging strategies: Ethnographic and archaeological analysis*. University of Chicago Press, Chicago, IL, pp 99–125

O’Connell JF, Hawkes K (1984) Food Choice and Foraging Sites among the Alyawara. *Journal of Anthropological Research* 40:504–535. <https://doi.org/10.1086/jar.40.4.3629795>

O’Connell JF, Hawkes K (in prep) Evolution of human life history: subsistence, mating sex ratios, carnivore competition

O’Connell JF, Hawkes K, Jones NB (1988) Hadza Hunting, Butchering, and Bone Transport and Their Archaeological Implications. *Journal of Anthropological Research* 44:113–161. <https://doi.org/10.1086/jar.44.2.3630053>

O’Connell JF, Hawkes K, Lupo KD, Blurton Jones NG (2002) Male strategies and Plio-Pleistocene archaeology. *Journal of Human Evolution* 43:831–872. <https://doi.org/10.1006/jhev.2002.0604>

Oelze VM, Head JS, Robbins MM, et al (2014) Niche differentiation and dietary seasonality among sympatric gorillas and chimpanzees in Loango National Park (Gabon) revealed by stable isotope analysis. *Journal of Human Evolution* 66:95–106. <https://doi.org/10.1016/j.jhevol.2013.10.003>

Oliver JS, Plummer TW, Hertel F, Bishop LC (2019) Bovid mortality patterns from Kanjera South, Homa Peninsula, Kenya and FLK-Zinj, Olduvai Gorge, Tanzania: Evidence for habitat mediated variability in Oldowan hominin hunting and scavenging behavior. *Journal of Human Evolution* 131:61–75. <https://doi.org/10.1016/j.jhevol.2019.03.009>

O’Malley RC, Power ML (2014) The energetic and nutritional yields from insectivory for Kasekela chimpanzees. *Journal of Human Evolution* 71:46–58. <https://doi.org/10.1016/j.jhevol.2013.09.014>

Parker GA, Maynard Smith J (1990) Optimality theory in evolutionary biology. *Nature* 348:27–33. <https://doi.org/10.1038/348027a0>

Parkinson JA (2013) A GIS Image Analysis Approach to Documenting Oldowan Hominin Carcass Acquisition: Evidence from Kanjera South, FLK Zinj, and Neotaphonomic Models of Carnivore Bone Destruction. PhD Dissertation, City University of New York

Parkinson JA (2018) Revisiting the hunting-versus-scavenging debate at FLK Zinj: A GIS spatial analysis of bone surface modifications produced by hominins and carnivores in the FLK 22 assemblage, Olduvai Gorge, Tanzania. *Palaeogeography, Palaeoclimatology, Palaeoecology* 511:29–51. <https://doi.org/10.1016/j.palaeo.2018.06.044>

Pascual-Garrido A, Almeida-Warren K (2021) Archaeology of the Perishable: Ecological Constraints and Cultural Variants in Chimpanzee Termite Fishing. *Current Anthropology* 62:333–362. <https://doi.org/10.1086/713766>

Piel AK, Strampelli P, Greathead E, et al (2017) The diet of open-habitat chimpanzees (*Pan troglodytes schweinfurthii*) in the Issa valley, western Tanzania. *Journal of Human Evolution* 112:57–69. <https://doi.org/10.1016/j.jhevol.2017.08.016>

Plante S, Colchero F, Calmé S (2014) Foraging strategy of a neotropical primate: how intrinsic and extrinsic factors influence destination and residence time. *Journal of Animal Ecology* 83:116–125. <https://doi.org/10.1111/1365-2656.12119>

Pobiner BL (2020) The zooarchaeology and paleoecology of early hominin scavenging. *Evolutionary Anthropology* 51:21824. <https://doi.org/10.1002/evan.21824>

Potts R (1984) Home Bases and Early Hominids: Reevaluation of the fossil record at Olduvai Gorge suggests that the concentrations of bones and stone tools do not represent fully formed campsites but an antecedent to them. *American Scientist* 72:338–347

Potts R (1991) Why the Oldowan? Plio-Pleistocene Toolmaking and the Transport of Resources. *Journal of Anthropological Research* 47:153–176. <https://doi.org/10.1086/jar.47.2.3630323>

Potts R (1996) Evolution and Climate Variability. *Science* 273:922–923. <https://doi.org/10.1126/science.273.5277.922>

Potts R (1998) Variability selection in hominid evolution. *Evolutionary Anthropology: Issues, News, and Reviews* 7:81–96. [https://doi.org/10.1002/\(SICI\)1520-6505\(1998\)7:3<81::AID-EVAN3>3.0.CO;2-A](https://doi.org/10.1002/(SICI)1520-6505(1998)7:3<81::AID-EVAN3>3.0.CO;2-A)

Proffitt T, Luncz LV, Falótico T, et al (2016) Wild monkeys flake stone tools. *Nature* 539:85–88. <https://doi.org/10.1038/nature20112>

Pruetz JD (2006) Feeding ecology of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. In: Hohmann G, Robbins MM, Boesch C (eds) *Feeding Ecology in Apes and Other Primates*. Cambridge University Press, Cambridge, pp 161–182

Pruetz JD, Bertolani P (2007) Savanna Chimpanzees, *Pan troglodytes verus*, Hunt with Tools. *Current Biology* 17:412–417. <https://doi.org/10.1016/j.cub.2006.12.042>

Pruetz JD, Bertolani P, Ontl KB, et al (2015) New evidence on the tool-assisted hunting exhibited by chimpanzees (*Pan troglodytes verus*) in a savannah habitat at Fongoli, Sénégal. *Royal Society Open Science* 2:140507. <https://doi.org/10.1098/rsos.140507>

Rockman M (2003) Knowledge and learning in the archaeology of colonization. In: Rockman M, Steele J (eds) *Colonization of unfamiliar landscapes: The archaeology of adaptation*. Routledge, London, pp 3–24

Rockman M, Steele J (eds) (2003) *Colonization of unfamiliar landscapes: The archaeology of adaptation*. Routledge, London

Roebrooks W (2003) Landscape learning and the earliest peopling of Europe. In: Rockman M, Steele J (eds) *Colonization of unfamiliar landscapes: The archaeology of adaptation*. Routledge, London, pp 99–115

Rutz C, St Clair JJH (2012) The evolutionary origins and ecological context of tool use in New Caledonian crows. *Behavioural Processes* 89:153–165. <https://doi.org/10.1016/j.beproc.2011.11.005>

Sabater Pí J (1974) An elementary industry of the chimpanzees in the Okorobikó mountains, Rio Muni (Republic of Equatorial Guinea), West Africa. *Primates* 15:351–364. <https://doi.org/10.1007/BF01791672>

Sahle Y, Hutchings WK, Braun DR, et al (2013) Earliest Stone-Tipped Projectiles from the Ethiopian Rift Date to >279,000 Years Ago. *PLoS ONE* 8:e78092. <https://doi.org/10.1371/journal.pone.0078092>

Sanz CM, Deblauwe I, Tagg N, Morgan DB (2014) Insect prey characteristics affecting regional variation in chimpanzee tool use. *Journal of Human Evolution* 71:28–37. <https://doi.org/10.1016/j.jhevol.2013.07.017>

Sanz CM, Morgan DB (2013) Ecological and social correlates of chimpanzee tool use. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368:20120416. <https://doi.org/10.1098/rstb.2012.0416>

Sanz CM, Schöning C, Morgan DB (2010) Chimpanzees prey on army ants with specialized tool set. *Am J Primatol* 72:17–24. <https://doi.org/10.1002/ajp.20744>

Sato H, Kawamura K, Hayashi K, et al (2012) Addressing the wild yam question: how Baka hunter-gatherers acted and lived during two controlled foraging trips in the tropical rainforest of southeastern Cameroon. *AS* 120:129–149. <https://doi.org/10.1537/ase.110913>

Sinclair ARE (1975) The Resource Limitation of Trophic Levels in Tropical Grassland Ecosystems. *The Journal of Animal Ecology* 44:497. <https://doi.org/10.2307/3608>

Sommer V, Buba U, Jesus G, Pascual-Garrido A (2017) Sustained myrmecophagy in Nigerian chimpanzees: Preferred or fallback food? *American Journal of Physical Anthropology* 162:328–336. <https://doi.org/10.1002/ajpa.23122>

Speth JD (1987) Early hominid subsistence strategies in seasonal habitats. *Journal of Archaeological Science* 14:13–29. [https://doi.org/10.1016/S0305-4403\(87\)80003-1](https://doi.org/10.1016/S0305-4403(87)80003-1)

Sponheimer M, Alemseged Z, Cerling TE, et al (2013) Isotopic evidence of early hominin diets. *PNAS* 110:10513–10518. <https://doi.org/10.1073/pnas.1222579110>

Sponheimer M, Passey BH, de Ruiter DJ, et al (2006) Isotopic Evidence for Dietary Variability in the Early Hominin *Paranthropus robustus*. *Science* 314:980–982. <https://doi.org/10.1126/science.1133827>

Stanford CB, Nkurunungi JB (2003) Behavioral Ecology of Sympatric Chimpanzees and Gorillas in Bwindi Impenetrable National Park, Uganda: Diet. *International Journal of Primatology* 24:901–918. <https://doi.org/10.1023/A:1024689008159>

Stanford CB, Wallis J, Mpongo E, Goodall J (1994) Hunting Decisions in Wild Chimpanzees. *Behaviour* 131:1–18

Stephens DW, Krebs JR (1986) *Foraging Theory*. Princeton University Press, Princeton, N.J.

Stewart FA, Piel AK (2014) Termite fishing by wild chimpanzees: new data from Ugalla, western Tanzania. *Primates* 55:35–40. <https://doi.org/10.1007/s10329-013-0362-6>

Surbeck M, Hohmann G (2008) Primate hunting by bonobos at LuiKotale, Salonga National Park. *Current Biology* 18:R906–R907. <https://doi.org/10.1016/j.cub.2008.08.040>

Suzuki S, Kuroda S, Nishihara T (1995) Tool-Set for Termite-Fishing By Chimpanzees in the Ndoki Forest, Congo. *Behav* 132:219–235. <https://doi.org/10.1163/156853995X00711>

Takahata Y, Hasegawa T, Nishida T (1984) Chimpanzee predation in the Mahale mountains from August 1979 to May 1982. *Int J Primatol* 5:213–233. <https://doi.org/10.1007/BF02735758>

Tédonzong LRD, Willie J, Tagg N, et al (2019) The distribution of plant consumption traits across habitat types and the patterns of fruit availability suggest a mechanism of coexistence of two sympatric frugivorous mammals. *Ecol Evol* 9:4473–4494. <https://doi.org/10.1002/ece3.5017>

Testart A (1982) The Significance of Food Storage Among Hunter-Gatherers: Residence Patterns, Population Densities, and Social Inequalities. *Current Anthropology* 23:523–537

Thieme H (1997) Lower Palaeolithic hunting spears from Germany. *Nature* 385:807. <https://doi.org/10.1038/385807a0>

Thompson JC, Carvalho S, Marean CW, Alemseged Z (2019) Origins of the Human Predatory Pattern: The Transition to Large-Animal Exploitation by Early Hominins. *Current Anthropology* 60:1–23. <https://doi.org/10.1086/701477>

Tomasello M (1999) *The Cultural Origins of Human Cognition*. Harvard University Press, Cambridge, M.A.

Tsukahara T (1993) Lions eat chimpanzees: The first evidence of predation by lions on wild chimpanzees. *American Journal of Primatology* 29:1–11. <https://doi.org/10.1002/ajp.1350290102>

Tutin CEG, Fernandez M (1992) Insect-eating by sympatric Lowland gorillas (*Gorilla g. gorilla*) and chimpanzees (*Pan t. troglodytes*) in the Lopé Reserve, Gabon. *American Journal of Primatology* 28:29–40. <https://doi.org/10.1002/ajp.1350280103>

Tweheyo M, Lye KA (2003) Phenology of figs in Budongo Forest Uganda and its importance for the chimpanzee diet. *African Journal of Ecology* 41:306–316. <https://doi.org/10.1111/j.1365-2028.2003.00475.x>

Uehara S (1982) Seasonal Changes in the Techniques Employed by Wild Chimpanzees in the Mahale Mountains, Tanzania, to Feed on Termites (*Pseudacanthotermes spiniger*). *FPR* 37:44–76. <https://doi.org/10.1159/000156020>

Watts DP (2008) Scavenging by chimpanzees at Ngogo and the relevance of chimpanzee scavenging to early hominin behavioral ecology. *Journal of Human Evolution* 54:125–133. <https://doi.org/10.1016/j.jhevol.2007.07.008>

Watts DP (2020) Meat eating by nonhuman primates: A review and synthesis. *Journal of Human Evolution* 149:102882. <https://doi.org/10.1016/j.jhevol.2020.102882>

Watts DP, Mitani JC (2002) Hunting Behavior of Chimpanzees at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology* 23:1–28. <https://doi.org/10.1023/A:1013270606320>

Whitesides GH (1985) Nut cracking by wild chimpanzees in Sierra Leone, West Africa. *Primates* 26:91–94. <https://doi.org/10.1007/BF02389050>

Wilkins J, Schoville BJ, Brown KS (2014) An Experimental Investigation of the Functional Hypothesis and Evolutionary Advantage of Stone-Tipped Spears. *PLOS ONE* 9:e104514. <https://doi.org/10.1371/journal.pone.0104514>

Wilkins J, Schoville BJ, Brown KS, Chazan M (2012) Evidence for Early Hafted Hunting Technology. *Science* 338:942–946. <https://doi.org/10.1126/science.1227608>

Winterhaider B, Smith EA (eds) (1992) *Evolutionary Ecology and Human Behavior*. Aldine de Gruyter, New York, NY

Wood TG, Johnson RA, Bacchus S, et al (1982) Abundance and Distribution of Termites (Isoptera) in a Riparian Forest in the Southern Guinea Savanna Vegetation Zone of Nigeria. *Biotropica* 14:25–39. <https://doi.org/10.2307/2387757>

Wrangham R, Cheney D, Seyfarth R, Sarmiento E (2009) Shallow-water habitats as sources of fallback foods for hominins. *American Journal of Physical Anthropology* 140:630–642. <https://doi.org/10.1002/ajpa.21122>

Yamagiwa J, Basabose AK (2009) Fallback foods and dietary partitioning among *Pan* and gorilla. *American Journal of Physical Anthropology* 140:739–750. <https://doi.org/10.1002/ajpa.21102>

Yamakoshi G (1998) Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: Possible implications for ecological importance of tool use. *American Journal of Physical Anthropology* 106:283–295. [https://doi.org/10.1002/\(SICI\)1096-8644\(199807\)106:3<283::AID-AJPA2>3.0.CO;2-O](https://doi.org/10.1002/(SICI)1096-8644(199807)106:3<283::AID-AJPA2>3.0.CO;2-O)

Yoshikawa M, Ogawa H (2015) Diet of Savanna Chimpanzees in the Ugalla Area, Tanzania. *African Study Monographs* 36:189–209. <https://doi.org/10.14989/200275>

Tables

Resource Category	Nutritional Density	Spatial Resource Distribution	Temporal Resource Distribution	Resource Exploitation Patterns	Landscape Knowledge Requirements
Core Preferred Resources	High	Usually Patchy	Year-round with seasonal peaks	Year-round	Consolidated
Seasonal Preferred Resources	High	Patchy	Fluctuating availability or quality	Seasonally scheduled	Moderate to High
Higher-quality Fallback Foods	Medium to High	Patchy	Usually year-round	Peak in times of seasonal scarcity	Moderate
Lower-quality Fallback Foods	Low to Medium	Usually abundant	Year-round	Peak in times of seasonal scarcity	Low
Experimental Resources	Medium to High	Patchy	Variable	Sporadic, Innovative	Incipient

Table 1. Resource categorisation in relation to their ranking, seasonal signatures, and landscape knowledge requirements.

Figures

Figure 1. Flowchart describing movement of foodstuffs through the continuum of possible dietary categories.

Figure 2. Proposed relationship between landscape knowledge, behavioural adaptation, and resource categorisation.