

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

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**Summary** - 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 systematic framework for understanding the spatio-temporal relationships between preferred and fallback resources, 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.

## 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; Kwicien 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 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.

### Seasonality and resource categorisation

#### *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, p. 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; Pruett 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, Uganda with a clear focus on the wet season (Hernandez-Aguilar et al. 2007), likely when fruits are scarce (Yoshikawa and Ogawa 2015, p. 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).

#### *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

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

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

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 Tã 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, p. 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, p.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 Goulougo Republic of Congo (Sanz et al. 2010), and in the wet season more broadly at Bossou, Guinea (Humble 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 Goulougo, 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, p.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), Goulougo, 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).

## Landscape knowledge

### 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, p.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 suggest that landscape knowledge is necessarily cumulative, frequently incorporating information garnered 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 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.

#### *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 Taï 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 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.

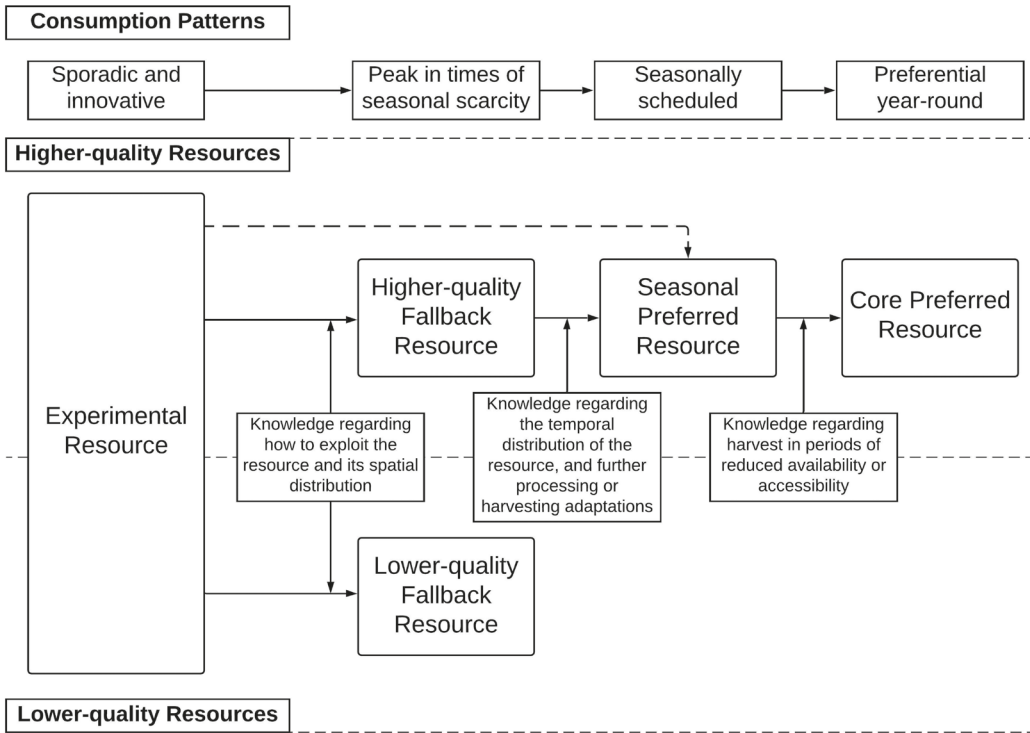
At the same time, if the temporal distribution of a resource does not allow its consumption during periods of preferred food scarcity and other constraints against exploitation are weak or absent, an experimental resource need not become a higher-quality fallback food before it transitions towards a 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 (*Ptilocolobus rufomitratu*s) 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.

## 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



**Fig. 1 - Flowchart describing movement of foodstuffs through the continuum of possible dietary categories.**

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, p.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 Kyanja 2011).

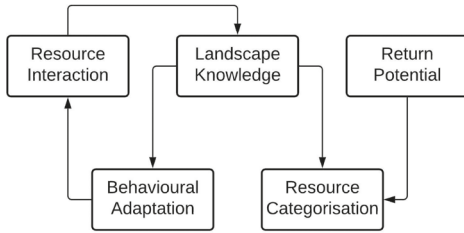
However, the hypotheses that, a) higher-quality fallback foods are one of the main drivers of general behavioural adaptation and b) preferred foods should largely be associated with harvesting adaptations, do not seem to hold for all responses to preferred resources. First of all, we emphasise that examples of tool use in the context of fallback food consumption are relatively rare in the chimpanzee literature (Sanz and Morgan 2013, Tab. 1). This suggests that technological investment may be particularly biased towards the domain of preferred foods. Indeed, *Coula* nut processing by chimpanzees of the Tai 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





**Fig. 2 - Proposed relationship between landscape knowledge, behavioural adaptation, and resource categorisation.**

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 Goulougo 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 Goulougo 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 Tai Forest, and Yealé (e.g. Anderson et al. 1983; Boesch and Boesch 1983, 1984; 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 Tai 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 Tai 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, p. 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 Tai 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 Tai 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.

### 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; Pruett 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 Tai Forest (Boesch and Boesch-Achermann 2000) and Fongoli (Pruett 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, p. 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 2022). These patterns are reflected in the greater dry season emphasis on duikers (*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 pan-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, Tab. 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; Diez-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,b).

## 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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