Journal of Archaeological Method and Theory (2026) 33:47
https://doi.org/10.1007/s10816-026-09780-6

RESEARCH

Paleolithic Dietary Flexibility? Methodological Considerations in Analogy-Based Reconstructions of Paleolithic Energetic Returns

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Received: 20 July 2025 / Accepted: 25 March 2026

Abstract

Trophic level, which serves as a basic determinant of the evolutionary pathway of animals, including humans, emerges as, primarily, a product of relative energetic returns and food items availability. The concept of trophic level flexibility during the Paleolithic period for the highly adaptable human species represents a prevailing paradigm in the field of paleoanthropology. This paradigm largely relies on the observed variability of trophic levels among recent hunter-gatherer societies. We examine various methodological aspects involved in using ethnographic quantitative data as an analogical source for reconstructing the energetic returns of humans during the Paleolithic period and, consequently, their trophic level. By analyzing datasets from several studies, we highlight potential limitations that may arise when applying such analogies. In the past we argued that Paleolithic humans preferred to acquire the largest available prey. This assertion met with objection, based on ethnographic analogies. In addition to pointing out the limitations to the validity of such analogies, we propose that archaeofaunal records provide detectable reflection of prey ranking and thus their relative energetic returns without the need for detailed numerical reconstruction of energetic returns based on the ethnographic record. We introduce the Kakwani Concentration Index, originally developed in Economics to measure directionality and strength of inequality, as a measure of directionality and strength in the size ranking of prey in Archaeological assemblages to test preference for large prey. We propose that the paradigm of flexibility is based on adaptations that occurred following the Late Quaternary Megafaunal Extinctions during and after which prey size availability patterns have markedly changed. In contrast, as evidenced by the technological persistence of simple hunting tools and assemblages with large herbivores throughout the Lower and Middle Paleolithic, subsistence strategies likely centered on large prey, which can be deduced by the lack of composite projectile hunting tools for a substantial portion of human evolution. The paper re-emphasizes that ethnoarchaeological analogies should be treated as testable hypotheses, and they may hold potential validity for behaviors that exhibit

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cross-cultural correlates. Ultimately, it suggests that no such correlates are present in some influential hunting energetic returns and human trophic level reconstructions. We argue that the technological, ecological and cognitive non-analog features of ethnographic energetic returns datasets are too great to be predictive of the Paleolithic nutritional pattern.

Keywords Ethnoarchaeology · Subsistence · Trophic level · Energetic return · Paleolithic · Ecology · Technology

Introduction

Energetic returns (the energetic content of acquired food items net of search, pursuit and handling/preparation energetic costs) play a significant role in shaping animal subsistence behavior. The ranking of the energetic returns largely determines the animal's diet where items with higher return are preferred. Energetic returns thus also determine the "Trophic Level" of an animal, *i.e.*, the relative reliance on primary and secondary sources in the food chain, in the case of humans, the relative reliance on plants and animals. The efficiency with which organisms acquire and assimilate energy from food is a central driver of evolutionary adaptations. Relative levels of energetic returns are tightly linked to evolutionary pathways, as they represent adaptations to optimize energy gain from available food sources under varying environmental constraints (Parsons, 2005). Thus, exploring human evolution, "The first task of the prehistorian must be to decide which trophic level the population he is studying occupied" (Wilkinson, 2014:p. 544).

The paradigm of the dietarily flexible Paleolithic human may account for the preference in using descriptive subsistence modes rather than the term "trophic level" when discussing trends in human evolution (El Zaatari et al., 2016; Rendu et al., 2019). Due to the absence of direct archaeological quantitative evidence for energetic returns, researchers have often depended on ethnoarchaeology for insights. This reliance is also apparent, for example, in the intensive application of ethnoarchaeological analogies in research concerning Neandertal subsistence (French, 2018).

This paper explores methodological considerations associated with using ethnographic quantitative data as an analogical source for understanding Paleolithic energetic returns derived from human food acquisition activities. In a previous paper, several problems with using ethnographic analogies to reconstruct human trophic levels were discussed, including a detailed description of non-analogous ecological and technological contexts of groups like the Hadza and San (Ben-Dor & Barkai, 2020). Here, we augment that discussion by referring to ethnoarchaeological theory concerning the use of analogies.

One basic paradigm ingrained in paleoanthropology that we suggest warrants reexamination is that Paleolithic humans possessed significant flexibility in their trophic level, depending on their immediate environment. This notion has contributed to the development of the Variability Selection Hypothesis (Potts, 1998).

The notion of trophic level flexibility draws significant support from the observed wide variability in trophic levels among recent hunter-gatherers, which ranges from obligate carnivory in northern latitudes to predominantly plant-based diets in some equatorial groups such as the Hadza and San. Varied trophic levels have undisputedly existed among recent human groups, depending on the ecological regions they occupied and the technological solutions they adopted (Cordain et al., 2000; Marlowe, 2005).

However, it is worth reexamining whether recent flexibility in hunter-gatherers' subsistence can be reliably used to infer Paleolithic flexibility. We assert that the answer to both questions is negative, especially for the Early and Middle Paleolithic periods, although it becomes partially positive with the "Broad Spectrum Revolution" (Flannery, 1973; Stiner, 2001) during the terminal Paleolithic. The marked increase in shorter-lived, more localized human cultures during the terminal Paleolithic may reflect an increased ecological fragmentation and variability in technical adaptations, a process that is now defined as flexibility.

Similarly, the long duration and global presence of Lower and Middle Paleolithic cultures (Oldowan, Acheulean, and to a lesser extent Mousterian), with their persistent characteristic stone tool-kits, suggest a long duration of similar economic activity of acquiring and processing similar size composition of prey during each of these periods (Dembitzer et al., 2022; Finkel & Barkai, 2021; Litov et al., 2026; Thompson et al., 2019; Venditti et al., 2019). Based on an extensive review of human physiology, metabolism and genetics, as well as archaeological patterns and zoological analogs we suggested a more specialized adaptation of early humans during these periods to carnivory (Ben-Dor et al., 2021). This determination has led to our unifying Prey-Size Hypothesis of human evolution (Ben-Dor & Barkai, 2021a).

A detailed comparison of East African ecological conditions between the Early Paleolithic and the present day was presented in a study titled: "Early hominins evolved within non-analogue ecosystem" (Faith et al., 2019). In that work, Faith *et al.* identified a marked, continuous decline in megaherbivore and other large herbivore species richness in Africa during (and preceding) the Paleolithic. Megaherbivores, particularly proboscideans, function as "keystone" species that significantly influence ecosystem diversity and act as ecological engineers by altering vegetation succession (Sinclair et al., 2003; Søndergaard et al., 2025).

The debate on the relevance of recent hunter-gatherer conditions to Paleolithic circumstances is not new, with the Kalahari Debate, which began in the 1980s, serving as a notable example. Researchers working with the Kalahari San advocated for their "pristine" status as representatives of a hunter-gatherer lifestyle (Lee, 1968, 1979). In this debate, "pristine" was defined by isolation from outside contact (Wilmsen, 1983). Conversely, critics argued that the San had experienced significant historical interactions with neighboring pastoralists, which profoundly influenced their economic and social activities (Denbow & Wilmsen, 1986; Wilmsen, 1983). Wilmsen's (1983) paper, "The ecology of illusion," encapsulates a sense of skepticism towards uncritical ethnoarchaeological analogies. The debate has intensified over time, with some researchers using strong language to express their views, as seen in titles like "To hell with ethnoarchaeology" (Gosselain, 2016) and "The tyranny of ethnography" (Lieberman et al., 2007; Wobst, 1978), which reflect growing frustration, although this frustration has not achieved consensual status (Smith et al., 2019).

The use of analogies to predict past human behavior predates the Kalahari Debate. Researchers interested in post-Paleolithic societies considered conditions for the proper use of analogies in archaeology. Ascher (1961:p. 319), drawing on the works of Clark, Willey, and Childe, concluded that analogies should be sought from “cultures which manipulate similar environments in similar ways.”

The awareness that clear analogies with the deep archaeological past do not exist led to explorations of alternative methods of testing the validity of analogies.

For example, Gardin (1997) acknowledged that analogical inference is everyday practice in archaeology, but also that it depends on transferring known attributions from “more or less similar” cases. His main drive was to formalize the steps from the description of data to the inference. This approach was applied to ethnoarchaeology by emphasizing that the value of analogies does not lies in superficial similarity but in the identification of regularities in the data, grounded in explanatory mechanisms. Gallay (2011) and Roux (2007) have stressed that valid analogies depend on universals, laws of technology, economy, or cognition, that can be transferred across contexts when their conditions of application are explicitly defined. Albarella (2011), in his formulation of ethnozooarchaeology, highlights the need to integrate ecological, economic, and cultural dimensions, treating human–animal relationships as a domain where analogy can illuminate but not predetermine interpretation. In this sense, analogy is best conceived as a research strategy and part of actualistic studies, producing middle-range theories that link archaeological traces to both static correlates (*e.g.*, carcass processing constraints) and dynamic ones (*e.g.*, conditions of technological change). For Paleolithic archaeozoology, this framework makes analogies most relevant when they are testable, transparent, and constrained by universal mechanisms such as bioenergetics, thereby avoiding rhetorical appeals to “sameness” while still providing essential bridges between present observations and deep prehistory.

Recent minimal recommendations tend towards cautiously examining each case individually (Currie, 2016; French, 2018) and discussing both commonalities and differences between ethnographic data and Paleolithic conditions (Kelly, 2013: p. 273–4). See Hayden and Guy (2024) as an excellent example of such discussion.

Methodological Considerations in Ethnoarchaeological Energetic Return Analogies

Most papers that claim analogical validity could benefit from including an analysis or at least a basic discussion of the comparability of ecological conditions. Regarding technological solutions, while the investigation of technological change across Paleolithic cultures forms a cornerstone of archaeology, the implications for energetic returns arising from substantial technological differences between ethnographic contexts and supposedly analogous Paleolithic contexts are seldom discussed in detail. We have identified four potential causes for mismatches in energetic returns between recent hunter-gatherer groups and Paleolithic humans: disparate

Table 1 Energetic returns of segments from Morin et al. (2021)'s dataset

Biome	Weapon	*N*	Mean recalculated return cal/hr	Median recalculated return
All	All	129	14,897	6772
Rainforest	Bow/spear	26	4062	2310
Woodland/Savanna	Bow/spear	12	6495	3089
Tundra	All (*N* = 14 guns)	15	28,633	16,259

ecology and technology that are not bridged by identifying regularities and universals sensu Roux (2007), the necessity of isolating hunter-gatherer activities from non-hunter-gatherer contexts, internal contradictions within the ethnographic record, and the application of static models to dynamic situations.

Different Ecology and Technology

Morin et al. (2021) have done outstanding work in compiling and standardizing comprehensive dataset on energetic returns, which includes 129 cases of recent hunter-gatherers hunting various prey using multiple techniques. This dataset categorizes information by biomes, taxonomic levels, and technologies, thereby enabling an analysis of its relevance to Paleolithic contexts. Since many extant hunter-gatherers inhabit rainforests, 53% (69 of 129) of the dataset points come from rainforest-dwelling groups. To control for technology, we calculated the average energetic return for rainforest groups using bows or spears ($N = 26$) as 4062 cal per hour (cal/hr) (Table 1). The average return from bow or spear hunting in Woodland/Savanna/Desert environments ($N = 12$), which are supposedly closer to Paleolithic conditions, stands at 6495 cal, which is 60% higher than the rainforest return. This suggests that ecology serves as a key determinant of energetic return for a given hunting technology.

For example, Tundra ($N = 15$), with a double than the total mean return of 28,633 cal/hr, containing mostly colonial birds hunted with guns provide the highest return per biome. Regarding technology, the higher-than-average returns cluster with mass hunting ($N = 13$, 26,084 cal/hr), trap ($N = 7$, 24,380 cal/hr), and guns ($N = 35$, 17,811 cal/hr). Regarding taxa, only amphibians\reptiles ($N = 15$) with an average of 20,152 cal/hr, and to a lesser extent arboreal mammals\birds ($N = 37$) at 15,608 cal/hr bring higher return than average.

Does the Morin et al. (2021) dataset meet the "regularities/universals" condition sensu Roux (2007)? Morin *et al.* did not use these terms to justify their claim for inference to the Paleolithic behaviors but we examine it here to comply with recent standards of using analogies in ethnoarchaeology. Firstly, can irregularity of returns per prey size be considered an inferential pattern? Even if it is, can a "Universal" mechanism be identified to explain the irregularity in energetic returns?

One mechanism that could cause irregularity is the multiplication of combinations of biomes, taxa, and technologies. However, here we have to return to the historical context and must ask, is the universal mechanism applicable to the target period? It may be universal in a geographic sense but is it universal in a historic sense?

For most of the Paleolithic period, spears were the primary hunting tool, becoming archaeologically visible towards the end of the Lower Paleolithic (LP) (*e.g.*, Ashton et al., 2016), and during the Middle Paleolithic (*e.g.*, Hutson et al., 2025). In these periods, spears allowed flexible use via stone tip hafting and adaptation to thrusting or throwing and persistence hunting and some forms of trapping may have been available as well as throwing sticks for hunting smaller prey and birds. However, it is quite likely that hunters achieved lower energetic returns, relative to hunting large prey, when hunting small, evasive prey with spears compared to the UP with a choice of weapons that included composite projectile weapons. One of the advantages of a composite projectile system like bow and arrow is that it is easier to aim and more efficient in targeting small evasive prey at a distance (Tomka, 2013). It is worth mentioning that the LP and Middle Paleolithic (MP) spear use comprised approximately 97% of the Paleolithic era, or, 88%, if we accept early MP composite weapon (Lombard et al., 2024; Yaroshevich et al., 2016) rather than late MSA (Backwell et al., 2018). So analogies with source groups that use bow and arrow may be relevant to 3–12% of human evolution only.

In fact, Morin et al. (2021) findings of no association between prey size and energetic returns may unintentionally support an important aspect of our unifying theory (Ben-Dor & Barkai, 2021a). We hypothesized that declining prey size and resultant bioenergetic pressure served as a unifying driver in human evolution and argued that the evolution of composite projectile weapons allowed for hunting smaller evasive prey with reduced loss in energy returns, compared to hunting large prey (Ben-Dor & Barkai, 2023). Morin et al. (2021) findings present the end of this process—hunting smaller prey with new tools while maintaining acceptable energy returns.

Statistical Power of Morin et al. (2021) Dataset

We assigned individual weights to the animals in the dataset (Supplementary Data) and divided them into five bins—< 10 kg, 11–50 kg, 51–150 kg, 151–1000 kg, and > 1000 kg. Figure 1 shows the distribution of individual prey to the bins and the distribution of biomes within these bins.

The dataset is heavily imbalanced toward small prey and, secondarily, rainforest taxa. We accept that these data show no detectable association between prey size and recalculated returns. However, the large-animal strata are tiny ($N = 15$ for 151–1000 kg; $N = 2$ for > 1000 kg). A non-significant p-value does not constitute evidence of "no association." Given the small N in the large-prey strata, the correct standard is evidence for the null (Cohen, 2013). With $N = 2$, inference regarding very large prey is impossible. Thus, the non-significant tests primarily reflect low power and wide confidence intervals, not affirmative evidence of absence (Button et al., 2013; Gelman & Carlin, 2014). A more accurate conclusion would have been that current evidence is inconclusive due to low power in the large-prey domain. In

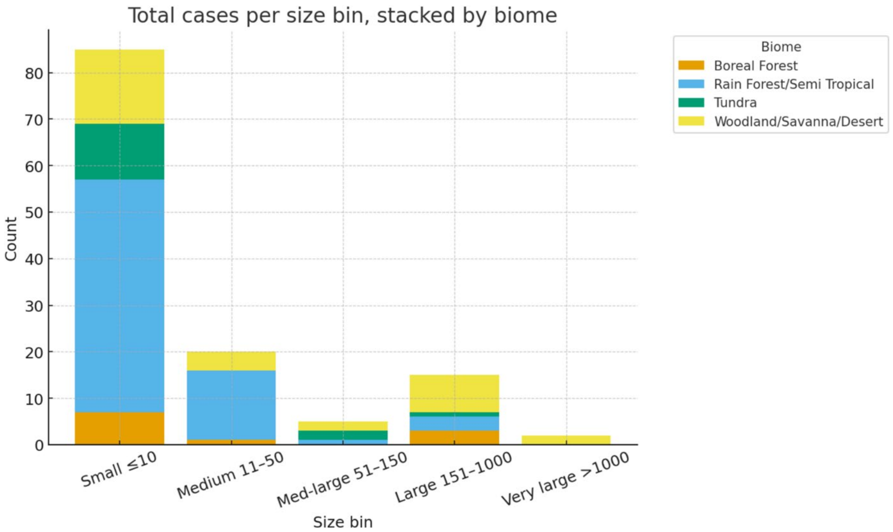

Fig. 1 Number of cases in Morin et al. (2021)' dataset by size bins. Small: 0–10 kg, medium: 11–50 kg, medium large: 51–150 kg, large: 151–1000 kg, very large: > 1000 kg

summary, the statement "no association" is not statistically secured, especially for large prey where theoretical effects are expected.

In this light, the relatively low returns attributed to the two > 1000 kg animals in the set, giraffe and elephant, that do not test against actualistic and archaeological tests (see Testing Analogical Hypotheses), stand to increase further the biased results. The bias must be in the original data (relying on rainforests instead of savanna elephant hunting for example) as the distance between the original and calculated returns in Morin *et al.* is not far.

The dataset of Lupo and Schmitt (2016: Appendix A) mainly includes data from rainforest dwellers such as the Efe and Aka in Congo, and the Hadza and San in Tanzania and Botswana, whose ecology has changed significantly since European contact (Ben-Dor & Barkai, 2020; Lee & Yellen, 1976; Marlowe, 2010). Additionally, the weapons used include poisoned arrows and muzzle-loaders. It does present a regularity; energetic returns are inversely associated with prey size in their dataset. Lupo and Schmitt (2016) do consider the applicability of their finding to specific ecological and technological context so the question remains if their findings are applicable to the Paleolithic context. As discussed above, we suggest they are limited, given the ecological and technological differences between their ecological and technological circumstances and Paleolithic circumstances. No attempt at identifying a universal was done.

The "Grandmother Hypothesis" (Hawkes & Coxworth, 2013; Hawkes et al., 2018) provides another instance where the use of ethnography-based analogy to predict early human behavior, based on trophic level, could benefit from an investigation into its validity. The hypothesis is based on the significant economic contribution of Hadza females and states that the economic support, beyond self needs, provided by grandmothers, was the selective agent for the extended lifespan of human females.

The analogy relies on data from one group, the Hadza, which is presented as suitable due to its geographic proximity to early African human archaeological sites (Hawkes, 2016). In terms of regularities and universals, in most of the ethnographic examples, males bring most of the calories (Kaplan et al., 2000) so no claim can be made for regularity. The claim for analogy, based on geographic proximity, lose value when the ecological and technological changes to that area during the last two million years are considered (Ben-Dor & Barkai, 2020; Faith et al., 2019).

Carving Out Non-pristine Activity

Researchers sometimes artificially separate or “carve out” hunting-gathering activities from other, often more recent, economic activities, such as when studying contemporary horticultural groups. This practice limits the comparability of the carved-out data to Paleolithic reality. The subsistence segment studied may be influenced by the carved-out activity. Thus, any claim of analogy must be accompanied by an analysis, or at least a discussion, of this potential influence.

In other words, the level of “pristineness,” in its traditional sense, should be considered. Many horticultural-hunter-gatherer groups live in dense forests of South America and Southeast Asia. As seen in one dataset (Morin et al., 2021), these groups significantly contribute to the hunting energy return data, and they also provide most of the data points in another study (Kraft et al., 2021). However, human occupation of dense forests is relatively recent, primarily within the last 40,000 years (Roberts et al., 2017), although recent findings suggest much earlier ages, up to 150,000 years ago (Ben Arous et al., 2025). While experts debate whether hunter-gatherers could survive in dense forests without trade or horticulture (Bahuchet et al., 1991; Bailey et al., 1989), all recently known dense-forest groups either practice horticulture or trade with non-hunter-gatherer neighbors (Bailey et al., 1989). The Ache of Paraguay exemplify this issue. They are among the most studied hunter-gatherer groups, providing 41% of the rainforest datapoints in one dataset (Morin et al., 2021). To quote from a study(Hawkes et al., 1982: p.381): “More than 130 Ache now live at a Catholic mission established in 1978 as an agricultural colony…they grow manioc, sugarcane, corn, and sweet potatoes, and they keep a few pigs, goats, chickens, and burros. The mission provides additional resources…Some Ache members reside full time at the mission, but others spend more than half their time in the jungle on long-range foraging trips…”. Researchers measured the Ache’s hunting energy returns, finding that they obtain 78% of their food from meat and rank food preferences by energy returns, ranging from 936 cal/hr to 22,411 cal/hr. They found that the Ache preference complied with Optimal Foraging models (OFM) (Hawkes et al., 1982; Hill et al., 1987). However, the crucial question is whether these specific energy returns can be quantitatively compared to those of hunter-gatherer groups foraging in open African Paleolithic landscapes. The differences extend beyond technology (such as bows, arrows, and dogs) and environment. Support from a

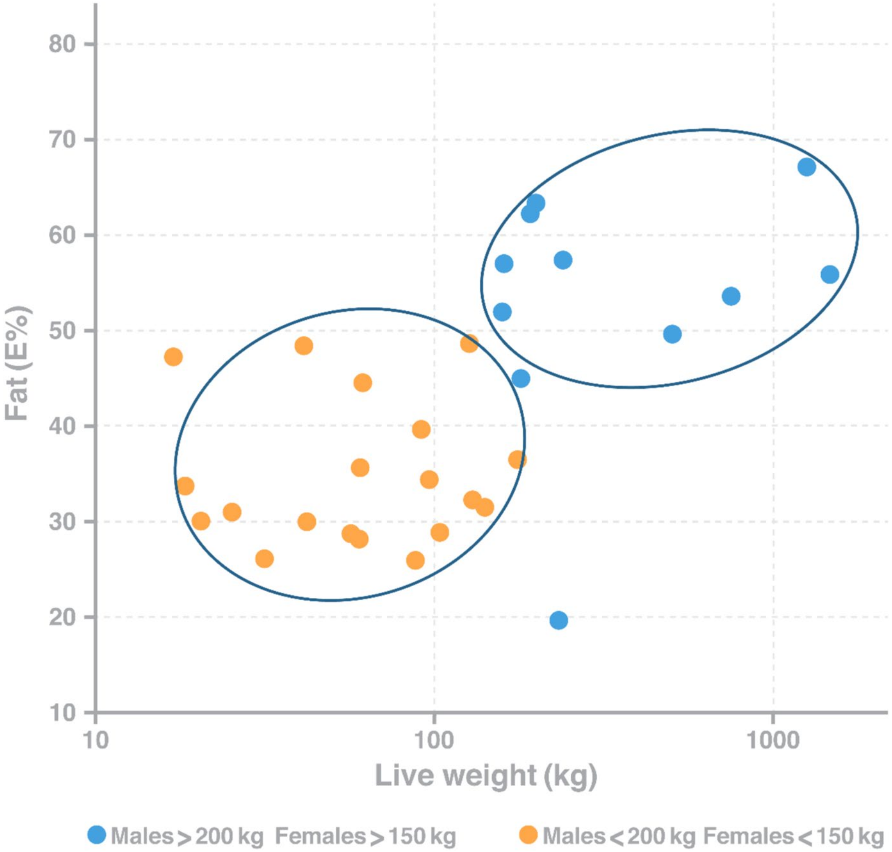

Fig. 2 Caloric fat content as a function of live weight in East African herbivores, based on data in Ledger (1968)

modern economy may have enabled survival with lower energy returns on hunting than would otherwise be feasible. Paleolithic hunter-gatherers lacked horticulture as a fallback if returns were as low as those observed among the Ache.

Another application of “carving out” is found in a paper titled: “Reframing Prehistoric Human-Proboscidean Interactions: on the Use and Implications of Ethnohistoric Records for Understanding the Productivity of Hunting Megaherbivores” (Lupo & Schmitt, 2023). The data used come from an African period when the primary goal of elephant hunting was ivory. The calculations of hunting and handling costs lead to the conclusion, by analogy, that elephant hunting was a low-return activity in the Paleolithic. However, the calculations exclude the return from ivory, whereas the hunters’ decisions on costs must have incorporated it. They “carve out” the main goal of the hunt, considering only the caloric return from elephant meat and fat. We argue that drawing a direct analogy between return rates derived from ivory-driven hunts and those motivated solely by nutritional objectives involves conceptual error. When ivory carries substantial market value, the total return per successful kill increases well beyond its consumptive value (meat and fat). This expanded return structure justifies the pursuit of higher-cost and lower-probability opportunities than would be rational under strictly nutritional valuation.

In economic terms, once ivory becomes a high-value commodity, the pursuit threshold shifts. Hunters can afford to invest greater effort and accept higher failure rates because expected returns remain positive. Conversely, under purely nutritional conditions—such as those prevailing in the Paleolithic—the acceptable cost and risk structure would be narrower.

Framed differently, intensive ivory demand can generate a pattern consistent with diminishing marginal returns: as more elephants are pursued to meet market demand, increasingly costly individuals are targeted, lowering average net returns relative to a subsistence-only baseline (Fig. 2).

Additionally, the paper discusses the attractiveness of elephant hunting methods but does not consider disparate ecological conditions. For example, pitfall trapping is dismissed by citing hunter-gatherers' ridicule of farmers' attempts at pitfalls. However, pitfalls are a known method for hunting elephants (Agam & Barkai, 2018; Hall, 1977), and its efficiency, by eliminating pursuit costs, depends on the regional density of elephants. Since the paper documents intensive elephant hunting targeted at ivory, which caused catastrophic population declines (Spinage, 1973), the elephant density during the studied period was likely not typical of the Paleolithic. Precontact African elephants are estimated to have constituted over 50% of herbivore biomass density in many areas (Hempson et al., 2015).

When control over certain hunting methods was employed, prey size emerged as a factor in determining energetic returns. A recent analysis of energetic returns from endurance hunting, community drives, and encounter hunting was carried by Morin et al., (2024: Fig. 3b). The analysis emphasizes the ecological variability of successful hunts. There is little technology involved in endurance hunting (though good memory retention is needed for tracking). The same applies to community drives. Morin et al. (2024) found that energetic return increases with prey size. This makes sense because part of the energetic expense in hunting is fixed. Running down very large prey may not take double the time as pursuing prey half its size. The same holds for community drives.

Fat Content Preference and the Protein Constraint—A Crucial Universal in Reconstructing Hunting Returns

Even with proper source data, simple hunting energetic returns could not provide an exact prediction of prey ranking.

Human protein metabolism faces well-documented physiological constraints that create specific dietary requirements with profound implications for subsistence strategies. Research indicates that protein intake is limited to approximately 35% of daily caloric intake due to the liver's limited capacity for processing protein waste products (Bilsborough & Mann, 2006; Speth, 2010). This constraint necessitates that the remaining 65% of caloric needs be met through non-protein sources, either plant carbohydrates and oils or animal fat.

The partitioning between fat and carbohydrates/oils for meeting non-protein caloric requirements depends heavily on the relative availability and energetic returns of hunting versus plant gathering. During periods of limited plant availability, particularly common during dry seasons and glacial periods in Europe and other northern regions, fat requirements from animal sources could approach 65% of total caloric intake.

The first potentially valid regularity is where the same behavior is observed irrespective of ecological conditions.

Speth (2010) provides ample evidence for the importance of fat in prey targeting across varied ecological conditions among recent hunter-gatherers and historic travelers. Earlier, a review of ethnographic sources noted the same pattern, leading to "The Fat Hypothesis," which posits that humans target prey based on fat content (Jochim, 1981). Archaeological evidence also supports the prominence of fat in prey targeting and body parts transportation (Ben-Dor & Barkai, 2024; Morin & Ready, 2013; Speth, 1983). Morin et al., (2021:P. 616–617) point out that "Fat preempt energy as a relevant currency" and cite Morin (2012) and other references in support.

To sum up, the ethnographically and historically widespread evidence that hunter–gatherers consistently target fat-rich prey represents a regularity sensu Roux (2007): it is observable across contexts and times. The physiological limit on human protein intake is a universal, deriving from human metabolism rather than culture. In this case, the universal explains the regularity: because humans cannot subsist on protein alone, they develop strategies that privileged access to fat, whether through selective carcass transport, marrow extraction, or prey choice.

The fat targeting prey-choice and prey size choice converge when prey size and fat content are correlated. The first to report that larger animals contain a higher relative content of fat were Pitts and Bullard (1967). Calder (1984) verified this correlation in terrestrial mammals. We analyzed Ledger (1968)'s dataset of 254 wild East African herbivores representing 19 species systematically dissected from the same environment (Fig. 2, Supplementary Data). Large-bodied herbivores (females $\geq$ 150 kg, males $\geq$ 200 kg) contained on average 52.7% calories from fat, compared with 34.4% in smaller species, a difference of 18.3 percentage points (a 53% relative increase). This difference is statistically strong: a Welch t-test (one-sided) gave $t = 4.33$, $p = 0.00035$, indicating the probability of observing so large a difference by chance is less than one in two thousand. The effect size is Cohen's $d = 1.88$, considered very large by conventional criteria. Bootstrapped 95% confidence limits for the absolute difference were 9.6–25.4 percentage points, showing the result is stable across resampling. In other words, In East African herbivores, large prey rich in fat provides higher useable energy per handling unit than lean prey. To summarize, Ignoring the protein constraint or the fat–mass relationship biases reconstructions toward smaller prey and underestimates the energetic rationale behind Pleistocene megafaunal specialization. It should be mentioned that Morin et al. (2021) gathered data on fat content from diverse sources and environments and did not find an association between prey size and fat content.

Applying the Kakwani Concentration Index to Test Prey Size-Based Energetic Returns

Theoretical Framework

To evaluate relative preferences for large-bodied prey, we propose that an ethnographically based, detailed estimation of specific energetic returns for individual prey species is an insufficient predictor of Paleolithic human behavior due to ecological and technological considerations. Furthermore, such estimations are not strictly necessary to ascertain the degree of specialization in large-prey hunting. Energetic returns must be integrated with relative ecological prey biomass density to accurately predict foraging behavior. Because ecological prey species density fluctuates across temporal and geographic scales and is not easily reconstructed for past periods, the relative energetic return, even if measurement problems are ignored, possesses limited power to predict behavior in a specific location and period.

Given the inherent inaccuracies of the archaeological record as a reflection of past reality, the interaction between relative energetic returns, relative fat content, and local biomass density is better reflected in the relative biomass contribution of the various species within a specific site or layer. Common abundance indices, such as the Simpson Index or Shannon Evenness, are not useful in this context because their measurement of faunal assemblage composition was designed to identify species dominance in terms of the number of individuals, regardless of expected energetic ranking (Faith & Du, 2018). The most numerically abundant species may not be the highest contributors of calories to the diet, as demonstrated by Owen-Smith and Mills (2008), who found that the most abundant lion prey species in Kruger Park, the impala, was a minor contributor to their subsistence.

To explicitly test the preference for large prey acquisition, and thus its implicit higher energetic return, higher relative fat content, or both (Pyke et al., 1977), we propose the use of the Kakwani Size-Ordered Concentration Index.

Quantification of Biomass Specialization

To quantify prey-size specialization, we adopted the Kakwani Concentration Index (KCI) from econometric inequality analysis (Kakwani, 1977; Wagstaff et al., 1989). By ranking taxa according to body weight, this index measures the extent to which biomass is concentrated in larger prey classes. This approach indicates both the directionality and strength of specialization, providing a size-sensitive alternative to standard taxonomic evenness measures which are blind to the ecological traits of the species involved.

The KCI addresses the relative subsistence importance of large prey by ranking all taxa in the assemblage by body weight from smallest to largest before calculating the cumulative distribution of biomass percentages. The index ranges from −1.0 (biomass concentrated in the smallest species) to + 1.0 (biomass concentrated in the largest species).

Table 2 Calibration of positive Kakwani Concentration Index, based on a sample of 184 archaeological Southern African layers with NISP > 30

Kakwani C	Expected top – 3 biomass	Large prey specialization
0.00	71%	Low
0.10	76%	Low
0.20	82%	Medium
0.25	85%	Medium high
0.30	88%	High
0.40	94%	Very high
0.50	95%	Very high
0.60	96%	Very high

Table 3 Results of KCI and mean biomass share of the top 3 groups of 184 archaeological faunal assemblages from Pleistocene southern Africa

Period	Layers (*n*)	Mean biomass share of top 3 size groups	One-sample p	Mean KCI	Large prey specialization
ESA	15	92%	0.005	0.33	High–very high
MSA	113	86%	$< 10^{-8}$	0.29	High
LSA	56	78%	0.003	0.24	Medium high

We applied the test to two archaeological faunal datasets, 184 layers from Pleistocene southern Africa and 43 MP and Aurignacian layers from southwestern Europe. We used the southern African dataset to calibrate the KCI to Paleoanthropological circumstances.

The Southern African Dataset

We tested the method on a dataset of NISPs from 184 archaeological layers with NISP > 30 from Pleistocene Sothern Africa. Large part of the region's faunal record is reported using size groups, so we turned all data, including data on specific taxa, to size groups (size 1: 5 kg to 23 kg, size 2: 24 to 84, size 3: 85 to 295, size 4: 296 to 950, size 5: 951 to 5000).

Calibration of Kakwani Concentration Index (KCI)

We calibrated the KCI index, based on the association with the cumulative top 3 size group biomass. The Spearman' p is 0.863 and the p-value is 6.7×10^{-56}. Kakwani C is therefore not an abstract inequality index here, it is tightly anchored to a biologically intuitive measure of large-prey dominance. In this data, the KCI can be described as indicated in Table 2. To avoid impossible linear extrapolation at high values, we fitted a saturating logistic model linking the Kakwani concentration index to the cumulative biomass share of the three largest prey classes. The relationship saturates near 96–97% biomass, with diminishing returns beyond $C \approx 0.3$. Under

Table 4 Large prey targeting in Middle and Upper Paleolithic assemblages across 9 sites plus two ethnographic examples: KCI and percentage of biomass from animals weighing over 150 kg

		KCI	*p*	KCI	*p*	> 150 kg	> 150 kg
Site	Location	MP	MP	UP	UP	MP	UP
Grotte XVI	France	0.568	0.01	0.334	0.13	92%	52%
Tournal	France	0.325	0.15	0.187	0.31	91%	72%
Saint-Césaire	France	0.347	0.06	0.073	0.36	93%	66%
Les Cottes	France	0.653	0.01	0.308	0.06	97%	100%
Regional (MP 7 layers, UP 14 layers)	France	0.421	0.01	0.266	0	93%	72%
Covalejos	Spain	0.431	0.01	0.363	0.01	94%	95%
Hornos	Spain	0.421	0.04	0.275	0.21	91%	96%
Morin	Spain	0.666	0	0.624	0	100%	99%
El Pendo	Spain	0.123	0.34	0.057	0.5	99%	100%
Ruso	Spain	0.097	0.38	0.253	0.25	100%	97%
Regional (MP 12 layers, UP 10 layers	Spain	0.322	0.02	0.375	0	97%	96%
Hadza	Tanzania	0.584	0.01			91%	
Ache	Paraguay	0.18	0.13			0%	

this model, values of $C = 0.4 to 0.6$ all correspond to > 94% large-prey biomass, indicating near-exclusive reliance on large prey.

Running KCI on the combined data for each period, Early Middle and Late Stone Age (ESA, MSA, LSA) we received statistically significant values that confirm a systematic directional bias toward larger prey (Table 3). In addition, we performed one-sample test, comparing observed mean top three groups' biomass shares (NISP percentages multiplied by average group weight) to the 60% null expectation (3 groups out of 5). The test shows that while declining with time as is evident in the C index, large prey dominate assemblages far beyond random expectation in all periods.

These results demonstrate a persistent, statistically significant concentration of biomass toward larger prey, with a clear temporal attenuation through the Stone Age sequence.

MP and Aurignacian—Southwestern Europe Dataset

To determine if the observed concentration values were statistically non-random, we performed a Permutation Test (10,000 iterations) for each assemblage (Table 4). This test compares the observed KCI against a null distribution generated by randomly shuffling the observed biomass percentages across the available size classes.

Given the low species richness (5–12 taxa) in our dataset, common in zooarchaeological assemblages, individual sites often lack the statistical power to reach the standard significance threshold ($p < 0.05$). To address this for regional indices, we extended the species list to include zero values for all ecologically present herbivores based on the combined species list of all sites in the region. This step assumes that absence from the assemblage represents a deliberate prey-choice decision.

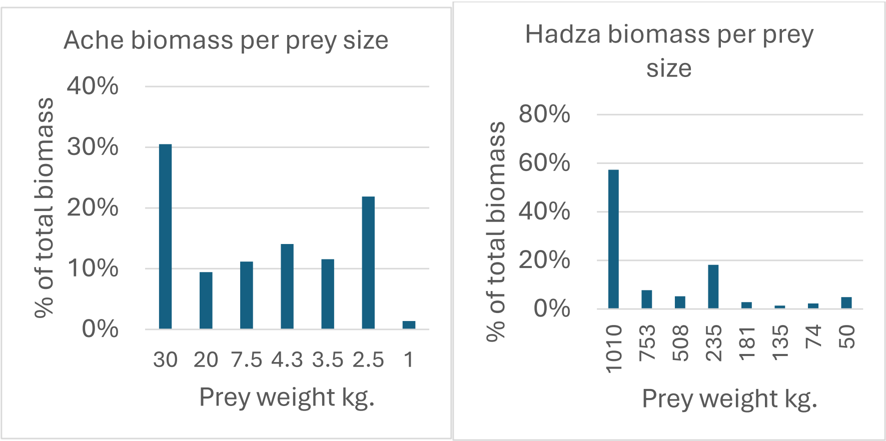

Fig. 3 Total biomass of hunted prey by prey weight. Ache of Paraguay (Hawkes et al., 1982:Table 1) and Hadza of Tanzania (Ben-Dor & Barkai, 2021b:Table 12.2) (Data in Supplementary Material)

All sites in Table 4 indicate a skew toward large prey when the index is calculated based on the species present at each site. The regional combined Concentration Index for the seven Middle Paleolithic (MP) layers in France is 0.421, indicating a strong concentration in the largest prey with a combined p-value of 0.01 using Fisher's Method. Combined KCI decline in the Aurignacian to a medium positive concentration, which remains statistically significant at $p < 0.003$. This decline is likely explained by the Late Quaternary Megafaunal Extinction during the transition from the MP to the Upper Paleolithic (UP), which caused the extinction and population decline of megafauna, particularly large (> 500 kg) and very large (> 1000 kg) prey species.

The Cantabrian assemblages also show a fairly strong, statistically significant concentration on large prey, with three sites exhibiting highly significant concentration and two showing lower, non-significant concentration. At a regional level, combining all layers produces a statistically significant high concentration on large prey in both the MP and the Aurignacian.

As discussed, fat content may have driven the targeting of large prey; African prey weighing over 150 kg has higher fat content than smaller prey (Fig. 3). Our results confirm that the vast majority of biomass (mostly over 90%) of this sample came from this fat-rich group. If reindeer (130 kg), a specialization in the Aurignacian (Grayson & Delpech, 2006), were included, the results of the Aurignacian would exceed 90% of the biomass, similar to the MP.

Advantages and Limitations

The KCI relies on data resulting from the interplay between relative return rates and the ecological density of various species. At the individual site level, it is possible for ecological density, and thus encounter rates, to be heavily skewed toward a single size class; this may potentially obscure the influence of relative energetic returns on assemblage composition.

However, across a broader regional scale, the probability of encountering such an atypical prey-size distribution is significantly lower, meaning the observed ranking more accurately reflects relative energetic returns. The extensive number of tested layers, combined with their broad temporal and geographical distribution, further reduces the likelihood that these patterns result from localized ecological anomalies. This reinforces the conclusion that the data reflects the higher energetic returns associated with large-prey hunting.

Furthermore, as faunal assemblages frequently contain a mixture of human and carnivore prey, data should ideally be adjusted to isolate the anthropogenic contribution. This is particularly important where significant carnivore impact is evident and statistically verifiable data are available.

In summary, both the Southern African and Southwestern European datasets confirm that small animals did not play a significant role in human subsistence within the tested periods and locations. Instead, these results provide a robust indication of a systemic focus on the higher energetic returns provided by the hunting of large prey.

Other Indications for Preference for Large Prey

Although a more comprehensive study applying KCI is called for, a pattern of preference for large prey, described by other methods, appears consistently in archaeological sites from diverse Paleolithic periods and locations which we sampled in previous studies (East and South Africa, the Levant, Southern Europe) (Ben-Dor & Barkai, 2021a, 2023; Dembitzer et al., 2022). A review of all Levantine Paleolithic sites with faunal record found that biomass contribution was dominated by proboscideans during the LP and large bovids (Bos) during the MP, when proboscideans disappear from the record (Dembitzer et al., 2022). By biomass we mean mass, mostly in terms of weight, of a biological nature. Preference for large prey and specifically proboscideans was also found in all stable isotope studies from Europe and North America when prey size was analyzed (Bocherens & Drucker, 2021; Chatters et al., 2024; Wissing et al., 2019). Recalculated return in Morin et al. (2021)'s dataset on elephants is 7467 cal/hr, half of the average for the dataset and lower than impala, yet they were the dominant species in the Levant during the LP in terms of caloric contribution. A comparison of 13 sites with both MP and UP faunal record in the Levant and Europe found that prey larger than 200 kg composed on average 69% and 49% of the biomass respectively (Ben-Dor & Barkai, 2025: Table 2). This is further corroborated by archaeological assemblages which consistently highlight a human inclination towards hunting large prey worldwide from the Pleistocene (*e.g.*, Bar-Yosef & Belmaker, 2011; Broughton et al., 2011; Bunn, 2006; Bunn & Ezzo, 1993; Dominguez-Rodrigo et al., 2014). As Stiner (2013:p. s288) writes, " … hominins were big-game hunters, and they were rather specialized in their focus on ungulate prey. Low-cost gatherable small prey were a perennial if minor contribution to MP diets at lower latitudes, but the overall breadth of the meat diet remained narrow throughout the period." Growing evidence of anthropogenic contribution to the Late Quaternary Megafauna Extinction (*e.g.*, Lemoine et al., 2025; Prates et al., 2025; Svenning et al., 2024), and explanation of the mechanism that drove the extinction of large prey (Ben-Dor & Barkai, 2024) also points towards preferential acquisition of large prey, which accelerated their demise.

Another ecological factor that affects energetic return is prey density. The Late Quaternary Megafaunal Extinction caused a significant decline in large prey density during the end of the Pleistocene, especially in megaherbivores. Globally, 40 out of 48 species went extinct at the end of the Quaternary and other large size groups declined by more than 50%. Also, large species that did survive experienced substantial population declines (Svenning et al., 2024). Pursuit time generally increases as prey density decreases. When prey is sparse, hunters spend longer searching before encounter, which lengthens total pursuit and reduces energetic efficiency. In dense prey environments, encounters occur quickly, shortening pursuit time per successful hunt. This relationship is predicted by optimal foraging theory.

In summary, testing of the returns in the dataset of the > 1000 kg animals fail to confirm their low returns. We propose that testing the relative contribution of different size prey to Paleolithic faunal assemblages be used as an indication of relative ranking.

Testing Analogical Hypotheses with Actualistic Data

In addition to archaeological data, it is worth testing analogies also against actualistic data if available. This doesn't qualify the actualistic data to be used to analogically infer Paleolithic behavior. The conclusion that there is no association between prey size and energetic returns)Morin et al. (2021) and the conclusion that smaller prey brings higher energy returns (Lupo & Schmitt, 2016) fail when tested even against actual ethnographic data. If the two predictions were correct, the Optimal Foraging Model (which predicts that prey is added to the diet in order of declining energetic returns) would predict no association, or a reverse association, between prey size and relative biomass contribution of prey by size. Figure 3 describes the biomass contribution versus prey weight from hunting records of the Ache in Paraguay (Hawkes et al., 1982) and the Hadza in Tanzania (Ben-Dor & Barkai, 2021b:Table 12.2). The Ache case is closer to Morin et al. (2021)'s prediction; however, the largest prey still makes the largest biomass contribution. The relative support for Morin et al. (2021)'s prediction is unsurprising, as 53% of their dataset is from a rainforest biome, similar to the Ache's environment. However, an actual study of the Hadza showed that the largest prey contributes the most biomass. Of 60 recorded hunts, the giraffe, ranked second-lowest by Lupo and Schmitt (2016) and among the lowest return taxa (2710 cal/hr) in Morin et al. (2021), contributed 57% of the total biomass. Ninety percent of the biomass came from the four largest prey animals. The smallest prey (impala) with a much higher return in Morin et al. (2021)' s dataset (10,589 cal/hr) contributed the smallest biomass share despite having the highest number of individuals. Notably, the smallest animal in the Hadza assemblage is larger than the largest in the Ache assemblage, and the Hadza assemblage weight range more closely resembles typical Paleolithic assemblages though still missing the large megaherbivores like hippos and elephants.

Using the Kakwani C index, a comparison between the Hadza (KCI = 0.584) and Ache (KCI = 0.180) indices demonstrates that the Hadza assemblage closely mirrors the concentration on top-tier prey sizes observed in the Paleolithic samples. Conversely, the Ache assemblage differs markedly, displaying a relatively weak and non-significant concentration.

When Ethnographic Data Contradicts Itself

Sometimes, the problematic nature of ethnographic data becomes apparent through disagreements between datasets. One such case is the mismatch between two datasets, Morin et al. (2021) and Kraft et al. (2021). The first dataset excludes search costs, including only handling costs (pursuit and processing). The exclusion of search costs is common practice in the application of optimal foraging models, partly due to the difficulty in allocating search costs to specific food sources. The second dataset addressed this by applying average costs of search activities to the mean energetic return of all food sources, determining that hunting yields a net of 982 cal per hour. However, reconciling their average with the first dataset's average, which excludes search costs and stands at 6402 cal per hour (Woodland – Bow and arrows), reveals incompatible results. The implied search costs of 5420 cal per hour (6402 minus 982) are simply challenging to accept. The inclusion of search costs may render the net returns in the second dataset even less comparable to Paleolithic circumstances. The returns per hour in Kraft et al. (2021) was calculated by dividing the total caloric content of prey by the total hours spent searching, pursuing, and preparing it. Because the total caloric content of prey is critical and varies enormously between recent and Paleolithic prey, an average value may be meaningless for analogies. Is searching for a 500-g bat in a Papuan jungle treetop comparable to searching for a 6,000-kg elephant on the savannah? For the returns to be comparable, the search time for an elephant would need to be 12,000 times that for the bat. This seems highly unlikely given the high visibility of large animals in open landscapes and their predictable use of paths to water sources. A well-known method for hunting elephants—digging pit traps—relies on these predictable daily paths (Agam & Barkai, 2018).

For example, consider a common Paleolithic prey like the Zebra, which provides approximately 210,000 cal (Ben-Dor et al., 2011 for Wildbeest). Using figures from the Morin et al. (2021), the total handling hours (excluding search costs) would be 210,000 cal divided by 6495 cal)Table 1), equaling 32 h. Dividing 210,000 cal by the Kraft et al. (2021) 982 cal return equals 213 h (this time including searching and handling). This implies 182 h for search time (214 minus 32 handling hours per Morin et al. (2021)). O'Connell et al. (2025) reports 4 animals taken by the Hadza in 27 h, including search and pursuit time of 36 animals, meaning 7 h search and pursuit time per taken animal compared to the 213 h predicted by Kraft et al. (2021) although it is important to point out that these are dry season figures and wet season search times are longer.

These calculations illustrate how data from rainforest small-prey hunting may not be applicable to Paleolithic conditions. Citing the supplementary material from

Kraft et al., (2021:Unumbered) about their Papua New Guinea tribal data: "Original data were from 3000 h of Etolo adult men hunting small mammals (monotremes, marsupials, rodents, and fruit bats) in the highlands of Papua New Guinea." None of these animals were significant human prey during the Paleolithic, and rainforests were not a typical human habitat.

Applying Static Models to Dynamic Situations

Morin et al. (2021) and Lupo and Schmitt (2016) present another aspect of potential analogy misuse. They use a "snapshot" of present-day hunter-gatherer energy returns to represent analogical relevance for the entire Paleolithic period. Conclusions regarding the association between prey size and energy returns disregard the dynamics and changes in hunting gear introduction, assimilation and replacement during the Paleolithic period. Contemporary hunters select the most efficient weapon from a repertoire that has been developed throughout the existence of the genus Homo.

For most of human evolution, until approximately 300,000 years ago, it appears that humans had used mostly wooden spears and throwing sticks (Milks, 2020). Evidence for wooden tip spears and throwing sticks exists only from about 400 thousand years ago and 200 thousand years ago (Ashton et al., 2016; Hutson et al., 2025), though the absence of evidence is not evidence of absence for earlier periods. Wood preservation is so rare that even after 200 thousand years ago (when spears were undoubtedly used), no further archaeological evidence for them or for bows has been found. We assume that Acheulean humans, who produced hand axes and wooden implements (Barham et al., 2023; Domínguez-Solera et al., 2022; Goren-Inbar et al., 2002; Gürbüz & Lycett, 2021), could also produce spears. In support, a 500 thousand year old spear's stone tip with impact damage was identified in Africa (Wilkins & Schoville, 2016). Recently, wooden-tipped spears were primarily used as thrusting spears (Lombard & Moncel, 2023) to dispatch trapped large prey (such as elephants) at close range (Agam & Barkai, 2018; Churchill, 1993), while metal-tipped spears were used by groups whose ancestors effectively used wooden spears in elephant hunting (Ichikawa, 2021; Lewis, 2021).

Most of the prey in the ethnographic datasets could not have been hunted effectively with wooden-tipped spears. Imagine attempting to hunt birds, squirrels, or rodents (which compose significant part of the datasets) with wooden-tipped spears. This prey likely would have been hard to capture even with later common stone-tipped spears (Shea, 2012). Thus, it is reasonable to conclude that when humans only had wooden-tipped spears and throwing sticks, hunting large prey not only yielded higher returns than small prey, but capturing significant amounts of small prey with significant energy returns would have been almost impossible. Put differently, the persistent use of wooden spears by Paleolithic hunters for hundreds of thousands of years across the Old World perfectly fitted the available large game; the transition to distance killing with bows and arrows could have been a result of the disappearance of large game and the need to hunt elusive small prey, rather than a spontaneous overcoming of cognitive or technological limitations of successful Paleolithic ancestors (Ben-Dor & Barkai, 2023).

Conclusion

Theoretical Foundations of Ethnographic Analogy

Two primary claims were tested. First, "ethnographic pristineness" in energetic-return analogies must require ecological and technological equivalence with Paleolithic conditions, rather than mere insulation from modern contact. Alternatively, the regularities of the ethnographic record must be demonstrated, and their underlying universals made explicit, before quantitative transfers are attempted. Second, any inferential leap from ethnographic data to the Paleolithic must be treated as a hypothesis to be tested against archaeological, physiological, and bioenergetic evidence, rather than as an assertion based on convenience or proximity.

Critique of Extant Datasets

The body of evidence supports our claims. The Morin dataset, for instance, is heavily weighted toward rainforest contexts and small prey, with a negligible sample size for large and very large taxa. The non-significant results in the large-prey bins primarily reflect low statistical power and wide confidence intervals rather than secure evidence of no association. This lack of robustness cautions against drawing strong inferences regarding size -return relationships for Paleolithic settings, which were typically dominated by large ungulates.

The Kakwani Index and Empirical Testing

We propose utilizing the Kakwani Concentration Index (KCI) to quantify the hunting bias toward large prey in archaeological assemblages. In accordance with Optimal Foraging Models, this bias translates to higher energetic returns for large-bodied taxa, provided that ecological densities are not skewed. Testing this against datasets from Southern Africa and Southwestern Europe confirms the dominance of large prey. Furthermore, research involving direct empirical tests contradicts the low rankings previously assigned to large prey.

In the actualistic Hadza record, the largest taxa supplied over 50% of the total biomass. The giraffe, which was ranked among the lowest return-rate taxa by Morin *et al.* and Lupo and Schmidt, and thus predicted to contribute only marginally, actually contributed the bulk of the biomass. Similarly, archaeological sequences across Africa, the Levant, and Europe consistently demonstrate the dominance of large herbivores wherever they were available. Stable isotope studies further corroborate this pattern of significant large-prey concentration in Europe.

Mechanisms of Mismatch: Density and Technology

Several mechanisms explain the discrepancy between ethnographic and Paleolithic energetic returns. Pursuit time and failure costs are density-dependent; when prey densities are high, encounter rates rise and average pursuit times fall, thereby increasing net returns. Furthermore, strategies such as pitfall trapping can eliminate pursuit costs almost entirely. Historical ivory hunting demonstrates that technological choices and prey density can invert traditional rankings; even Morin et al. (2021) acknowledge that shifts in prey abundance can upend expected outcomes.

Another source of mismatch is the static nature of the ethnographical record vis. The dynamic nature, both ecologically and technologically, of the Paleolithic. Consequently, static rankings abstracted from low-density rainforest cases must be applied with extreme caution to high-density Pleistocene savannas where animals are hunted with evolving weapons.

Technological Evolution and Physiological Constraints

Technological change became increasingly dynamic toward the end of the Pleistocene. For approximately 97% of the Paleolithic, spears were the primary hunting tool, a system highly efficient for large prey but poorly suited to the small, evasive taxa that dominate many Holocene datasets. Later complex projectile innovations allowed for viable returns on smaller prey. Thus, the dietary flexibility observed in modern hunter-gatherers reflects technological adaptation and altered prey communities rather than inherent Paleolithic omnivory.

A universal physiological constraint further dictates prey ranking. Humans cannot sustain more than ~ 35% of their caloric intake from protein; diets must therefore supply substantial non-protein energy. Ethnographic, historical, and archaeological data show a consistent targeting of fat and fat-rich tissues. Large herbivores contain higher average proportions of fat, increasing the usable energy per handling unit. Ignoring this protein constraint and the positive relationship between fat and body mass biases reconstructions toward small-prey analogies.

Conclusion: A Parsimonious Reconstruction

Methodological contradictions reinforce the need for caution. Incorporating average search costs from small-prey rainforest contexts yields net returns that are incompatible with handling-only figures from savanna cases and actualistic observations of large ungulates. Therefore, claims of broad Paleolithic trophic flexibility require evidence of analogous prey communities, densities, and weapon systems.

In the absence of such equivalence, the most parsimonious interpretation is a high, relatively stable trophic level throughout most of the Paleolithic, with significant flexibility emerging only during the terminal Paleolithic and thereafter. Future analogies should be framed as explicit hypotheses built on stated universals and tested against physiological proxies, stable isotopes, and faunal biomass distributions. Centering physiology, ecology, and archaeology clarifies the energetic pressures and prey declines that fundamentally shaped human evolution.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10816-026-09780-6.

Acknowledgements We would like to acknowledge the significant contribution of the editor and four reviewers to the improvement of this paper.

Author Contribution Miki Ben-Dor: conceptualization, investigation and all conducted analyses, writing—original draft preparation. Ran Barkai: conceptualization, supervision, writing—review & editing.

Funding Open access funding provided by Tel Aviv University.

Data Availability Data for all figures is available at the Supplementary Material.

Declarations

Competing interests The authors declare no competing interests.

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