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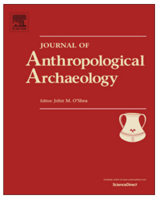

When bigger is not better: The economics of hunting megafauna and its implications for Plio-Pleistocene hunter-gatherers

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ABSTRACT

Big game acquisition is viewed as pivotal in the evolution of early hominins and is often associated with the emergence of features that are hallmarks of *Homo*. We explore the energetic justification for the preference for big game under the premise that larger-sized prey is always more efficiently exploited than smaller-sized game. Using quantitative cost/benefit data derived from ethnographic, ethnoarchaeological and historic sources, we show that certain large-sized game (megafauna) are often more expensive to acquire than smaller-sized prey. Comparative analysis shows that African elephants (*Loxodonta africana*), the largest-sized terrestrial animal, are lower ranked and less efficient to acquire than many smaller-sized animals irrespective of their encounter rates. These data challenge the idea that prey body size can be used as a proxy for profitability and rank in zooarchaeological analyses. Prey profitability, especially for large-sized and costly taxa, is strongly influenced by prey characteristics relative to existing dispatch technology and the range of nonconsumptive benefits associated with hunting certain megafauna. Nonconsumptive rewards associated with these opportunities can only be gained by certain individuals and are not broadly available to everyone. We suggest that the idea of 'big game' specialization needs to be reframed in archaeology.

1. Introduction

The idea that big game acquisition has a long-standing antiquity among humans and their ancestors is deeply ingrained in our intellectual history (e.g., Bunn, 2006; Isaac, 1978, 1984). Early researchers, arguing by analogy drawn from contemporary hunter-gatherers, viewed big game hunting as pivotal in the development of sharing, provisioning offspring, the use of central places and the sexual division of labor (Isaac, 1978, 1984). The current consensus is that meat-eating and the acquisition of animals by hominin ancestors underwrote a suite of adaptations such as an enlarged brain-size, modern gut proportions (Aiello and Wheeler, 1995) and microbiomic communities (Moeller et al., 2014), changes in life-history, alloparenting, and prolonged juvenile dependency (Finch and Stanford, 2004; Kaplan et al., 2000, 2001; Kennedy, 2003, 2005). Special importance is often attached to the acquisition and exploitation of very large-sized animals or megafauna in the paleoarchaeological record. The large quantities of meat associated with big carcasses could support and promote food sharing beyond the level of family provisioning and the acquisition of megafauna may reflect cooperative acquisition involving a number of individuals (Domínguez-Rodrigo et al., 2014; Rose and Marshall, 1996). The carcass acquisition strategies of hominin ancestors remain highly controversial, but there is evidence that early hominins were butchering animal carcasses by 2.6 mya (Domínguez-Rodrigo et al., 2005) and exploiting the meat and marrow of megafauna by 1.8 mya (Sahnouni et al., 2013; Domínguez-Rodrigo et al., 2014). But questions concerning the context and scale of prehistoric big game acquisition and specialization remain unanswered. These questions also have special relevance to arguments about what role, if any, prehistoric hunters played in the extirpation of Pleistocene megafauna,[1] especially proboscideans (e.g., Grayson and Meltzer, 2015; Grayson et al., 2001; Haynes, 2002; Martin, 1973; Meltzer, 2015).

Arguments about the preference for large game often appeal to rationale derived from the prey choice model (hereafter PreyCM) to support big game specialization among Pleistocene hunters

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[1] Megafauna can be defined in a variety of ways. In reference to Pleistocene extinctions, Paul Martin (1967a, 1967b) defined megafauna as prey over approximately 44 kg or 100 lbs body weight. However, megafauna is often used to refer to animals that weight over a metric ton 1000 kg. Here we use megafauna to refer to the largest African living animals in different categories (bovids, girafids and proboscids).

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(Domínguez-Rodrigo et al., 2014; Haynes, 2002; Surovell and Waguespack, 2009; Waguespack and Surovell, 2003). According to the PreyCM, high value prey (as measured by post-encounter return rates or PERR's) will always be pursued whenever encountered. This is the basis for the more general assumption used by zooarchaeologists that body size is a robust proxy measurement for prey rank (Broughton et al., 2011). This fundamental assumption is often used because experimental or actualistic quantitative data modeling potential PERR's for prehistoric prey are limited and unavailable for many animals. The link between prey body size and prey rank is especially relevant to interpretations of changes in the abundances of large and small-sized fauna in zooarchaeological assemblages. Increases in the abundances of large relative to small-sized prey are seen as reflecting changes in the encounter rates with high ranked game that are often attributed to the onset of favorable environmental conditions (e.g., Broughton and Bayham, 2003; Broughton et al., 2011; Wolverton, 2005; but see Hildebrandt and McGuire, 2002). Conversely, reductions in the relative abundances of large relative to small prey are viewed as signs of decreasing foraging efficiency arising from resource depression or reduced encounter rates with high ranked resources linked to anthropogenic effects such as overhunting (e.g., Brougton, 1994; Janetski, 1997).

However, applications of the PreyCM to ethnographic populations show that prey or resource package-size does not always predict profitability or resource ranking (Smith, 1991; Winterhalder, 1981). While meat, as a resource, is higher ranked than most plant foods, some larger-sized prey have very high acquisition costs making them inefficient choices relative to smaller-sized prey (e.g., Smith, 1991). Recently, Bird et al. (2009, 2012) examined the different components of prey handling costs and nominate pursuit costs, especially failed hunts, as having a significant influence on the ranking of large-sized and highly mobile prey. Quantitative data from Australian Martu foragers show that the hunting of large-bodied and highly mobile prey are often characterized by long pursuits, high opportunity costs and an increased likelihood of pursuit failure (i.e., failure to kill an animal after pursuit is engaged). In their sample the largest-sized prey, the hill kangaroo (*Macropus robustus*) and Bustard (*Ardeotis australis*), are highly mobile and associated with low success rates that rendered them inefficient choices relative to smaller-bodied game. Bird et al. (2009, 2012) suggest that Martu hunters pursue inefficient big game as part of a political strategy. These observations support other ethnographic studies that show a high probability of failure associated with certain kinds of big game (Hawkes et al., 1991; Hitchcock et al., 1996; Hitchcock and Bleed, 1997; Lee, 1979). Data collected nearly two decades ago from Hadza hunter-gatherers, for example, show that men who target big game have high failure rates (approximately 97% per individual on any given day) and often return empty-handed (Hawkes et al., 1991). Smaller-sized prey provide smaller caloric returns but these animals have a lower risk of failure and are less variable in energetic return than larger-sized game. Furthermore, prohibitions and customs governing meat consumption and redistribution often limit the caloric rewards that hunters and their families can garner from these opportunities. These customs take several forms, from prohibiting hunters from eating the meat of their own kill (Bahuchet, 1990; Endicott, 1988:117; Kaplan et al., 1990:129; Testart, 1987) to societal norms that support the generous and widespread meat sharing with nonfamily members (e.g., Hawkes, 1993; Weissner, 2002). Cumulatively, these studies invite a re-examination of the idea that large-sized game are always the most efficient prey target (as measured by energetic return) and that prey body size can be used as a proxy for prey rank in zooarchaeological applications of the PreyCM (see Lupo, 2007).

In this paper we use empirical quantitative and qualitative data from an array of sources to examine the relationship between PERR's and prey body size. We begin by exploring the different components of handling costs (pursuit and hunting failure, processing and transport) and then analyze these components in relation to carcass-size. Quantitative data presented here show that most components of handling costs (pursuit, processing and transport) are generally positively correlated with body size. The success rates for hunting game are highly variable depending on dispatch technology, but are inversely correlated with prey size suggesting that larger-sized game are more difficult to acquire than smaller-sized prey. Using data derived from ethnographic and historical sources, we then reconstruct the different components of the handling costs to calculate the potential PERR for African elephants - the largest sized terrestrial mammal - as an example. Comparison of the PERR's among common African game species show that elephants are not the highest ranked prey. These data show that current prey ranking systems based solely on body size do not match rankings based on PERR's. We argue that while big game are quite often the highest ranked resource, prey handling costs and resulting return rates are strongly influenced by prey characteristics and the available hunting technology of hunting large prey. Sociopolitical currencies can provide additional incentives for the procurement of costly big game and under some circumstances these benefits can lead to the emergence of specializations or social niches. This is especially true if procurement of costly prey is limited not only by skill but by access to knowledge or affiliations. Under these circumstances, the nonconsumptive rewards associated with these opportunities can only be gained by certain individuals and are not broadly available to everyone in the society. This means that the idea of a "big game hunting" should be qualified relative to the pay-offs associated with procuring large-animals in different contexts. Although there may be some ecological contexts where many in the hunting population pursue large-game, in many contexts only a few specialists pursue costly prey.

2. Prey choice models and the components of handling costs

Models derived from Human Behavioral Ecology (HBE) are described in great detail elsewhere (e.g., Smith, 1983; Winterhalder and Smith, 2000) and here we only provide details as related to the costs of prey acquisition for the PreyCM (e.g., MacArthur and Pianka, 1966; Pianka, 1983; Pyke, 1984). As originally proposed, the model addresses, which resources foragers exploit from the available array of resources. The model generally assumes that a forager's goal is aimed at maximizing energetic efficiency, but the predictive value of alternative currencies, including those that are not based on energy is now widely recognized and utilized by many researchers (see Houston and McNamara, 2014). In most applications of the PreyCM, resources (or resource types) are ranked by a single dimension of profitability: energetic returns (Ei/hi) per unit of handling time (PERR) where *Ei* represents the energetic value based on edible proportion of the resource and *hi* is the handling time. Handling includes the time it takes to pursue, dispatch, process and consume a resource after it is encountered. The model assumes that foragers randomly encounter prey and add resources into the diet in rank order (from highest to lowest) until the overall mean return rate declines. Three general predictions follow from the PreyCM (after Pyke et al., 1977:141): (1) high-ranked resources are pursued whenever encountered; (2) lower-ranked resources are included in the diet as a function of the encounter rates with high-ranked resources; and (3) resources are incorporated into the diet in rank order from highest to lowest. The model assumes that time is limited and foragers make

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