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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.

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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

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., Broughton, 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 (E_i/h_i) per unit of handling time (PERR) where E_i represents the energetic value based on edible proportion of the resource and h_i 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

trade-offs in how to invest their time given the opportunity costs (or cost equivalent) of pursuing another resource. Accordingly prey rank only indicates whether or not a resource is included in the diet when encountered, but does not indicate how common it is in the diet. If a high ranked resource is infrequently encountered it will not be common in the diet because the opportunity costs to a forager who only searches for rare resources will be high. This is because pursuing one prey or resource can often preclude the ability to exploit other resources. The overall costs of acquisition are partitioned into two mutually exclusive curves: search and handling. Changes in the time allocated to either search or handling allow researchers to make powerful predictions concerning changes in diet breadth (Hawkes and O'Connell, 1992; Winterhalder, 1981).

Because resource rankings are based on the ratio of the energetic value of the resource to handling costs, significant variation in either of those variables can influence the order in which resources are added to and deleted from the diet and, by extension, the diet breadth. For example, variation in the amount and distribution of fat in some prey species as a result of seasonal fluctuations in forage and individual state (sexual reproduction, age, health) can determine the energetic value and macronutrient content of edible animal products. Using historic and prehistoric data, Speth (1983: 157–158; Speth and Spielmann, 1983) identified a range of strategies that hunters could use to counter the effects of consuming excessively lean meat from game, including targeting small prey such as beaver (*Castor canadensis*) and waterfowl that retain body fat during lean seasons. This strategy essentially involves reranking resources (or portions thereof) based on fat content whereby smaller-sized, but fat rich, resources are preferentially targeted over larger-sized but lean animals (also see Hill et al., 1987).

Traditionally, search time is viewed as the largest component of the costs of prey acquisition. Because of the known relationship between body size and animal density (Peters, 1986), larger-sized prey tend to be less abundant on the landscape and have higher search costs and take more time to locate than smaller-sized prey. Consequently, animal densities and abundances are assumed to be the most important factors determining the overall costs of prey procurement (e.g., Simms, 1984: 106). But high handling costs can also comprise a large component of prey acquisition, especially for resources that occur in patches or have other characteristics that make them difficult to capture, and these costs strongly influence prey choice (e.g., Nilsson and Brönmark, 1999). Pursuit costs are traditionally defined as those that accrue to a predator after prey are encountered (Smith, 1991: 232), but in many cases pursuit can include the time invested in tracking prey before it is encountered. This is especially true in ethnographic contexts, where hunters often track and pursue prey over great distances (see Hill et al., 1987: 17–18; Kuchikuri, 1988; Lee, 1979: 213–214; Liebenberg, 1990; Marshall, 1976; Wilmsen and Durham, 1988: 72). Tracking spoor and other physical signs can be considered part of the pursuit costs in many different contexts, including when animals are territorial, use runways or paths, or show high unpredictability in spatial behavior (see Marshall, 1976; Wilmsen and Durham, 1988). In these instances search and pursuit overlap and the tradeoffs in the opportunity costs associated with search and handling are not mutually exclusive (Hill et al., 1987: 17–18). Although the pursuit of prey by tracking does not preclude the ability of taking alternate resources, it can restrict the range of resources that a hunter might encounter. For example, Aché hunters captured alternate and lower-ranked prey while they tracked high-value white-lipped peccaries (*Tayassu pecari*) (Hill et al., 1987). But tracking peccaries involved traveling at higher than normal walking speeds and intensive attention to specific animal signs that effectively restricted the range of alternate resources that could be taken.

The costs of pursuit are traditionally understood to encompass the time spent stalking, chasing and dispatching prey. Excessive pursuit costs can appreciably influence a hunter's choice of whether or not to pursue the animal even after it is encountered (see Marks, 1976). In some cases, large-game are rarely pursued or ignored because of the high costs associated with pursuit (i.e., high failure rates, long or cumbersome pursuits, personal endangerment or requisite specialized skill set or technology). Existing ethnographic observations document many instances where the pursuit costs significantly depress the PERR's of large-sized animals, making them less efficiently exploited than smaller-sized prey (Bird et al., 2012; Smith, 1991; Winterhalder, 1977). For instance, Winterhalder (1977: Tables 42–44) reports pursuit costs incurred by the Boreal Cree hunting moose (*Alces alces*) (and caribou, *Rangifer tarandus*), the largest-sized traditional terrestrial animal in the region. Moose have the highest PERR's of all prey, but only during summer and spring hunts. Ironically, winter is the season with the highest encounter rates for moose but it is also associated with the highest pursuit costs per animal. During the winter, pursuit costs of moose greatly increase to 25 h of pursuit per animal unit acquired (Winterhalder, 1977). The low productivity of winter moose hunting (8220 kcal/h) is evident when compared to the PERR for beaver trapped during the same season (range: 5690–23,620 kcal/h, median 14,665 kcal/h). In another example, white-lipped peccaries (25–40 kg), the largest-sized peccary available to Aché hunters, have PERR's (5323 kcal/h) that are lower than that of the smaller-sized collared peccary (*Pecari tajacu*; 16–27 kg; 6120 kcal/h) largely because of requisite pursuit time (Hill et al., 1987). On average it takes Aché hunters 7.5 man-hours of pursuit for one successful white-lipped peccary kill (see also Hawkes et al., 1982; Murphy, 1960: 55).

Calculations of pursuit costs based on ethnographic observations usually include the time invested in unsuccessful hunts (i.e., failed hunts), which can comprise a large proportion of the overall costs of pursuit (Bird et al., 2012). Unsuccessful hunts are cases in which prey are stalked and/or pursued but the hunter either does not attempt to dispatch or fails to wound/hit/capture the animal. But hunting failure can also include a number of other scenarios that involve prey losses. These include circumstances where (1) a wounded animal escapes and is not captured because it is not mortally wounded, (2) a wounded animal flees and dies but the carcass is never found, and (3) the carcass is appropriated by another predator or the meat spoils before it is found by hunters. The impact of hunting failure on PERR's is clearly illustrated in the ethnographic record. Winterhalder (1977) found that hunting failures comprised 43% of the total amount of time devoted to the pursuit of moose/caribou after being encountered for all seasons combined. Broken down by season, these data show that the season (winter) with the highest encounter rates with moose/caribou also had the highest failure rate resulting in the lowest PERR. In another example, Smith (1991: Table 6.11) shows how high hunt failure rates and long pursuits of beluga whales (*Delphinapterus leucas*) by Inujjuamuit hunters make them one of the most unproductive prey items relative to other sea mammals, despite being the largest animal available.

Pursuit costs and the probability of unsuccessful or failed hunts vary as a function of a variety of factors including terrain, vegetation, season, human group-size and organization, and the density and range of regional carnivores and scavengers (e.g., Hitchcock et al., 1996). But the greatest general influences on pursuit costs are prey characteristics relative to available dispatch technology (especially see Frison, 2004). One well-recognized characteristic that influences pursuit costs is prey speed because fleet animals can be associated with prolonged chases. There are a number of well-known ethnographic observations where hunters avoid chasing certain animals because they are simply too fast (Table 1).

Table 1

Ethnographic examples of animals that have high pursuit costs due to prey characteristics and/or hunting technology constraints.

Animal/context taxon	Body-weight (kg)	Prey characteristic/constraint	Source
Walrus/Inujjuamuit <i>Odobenus rosmarus</i>	864–1227	Distant patches, requires expensive equipment	Smith (1980: 302–303)
Harp seal/Inujjuamuit <i>Pagophilus groenlandicus</i>	140–190	Too fast	Smith (1980: 302–303)
Giraffe/Dobe San <i>Giraffa camelopardis</i>	450–1930	Strong, hard to stalk	Lee (1979: 231)
Ostrich/Dobe San <i>Struthio camelus</i>	63–145	Swift, hard to kill	Lee (1979: 232)
Zebra/Dobe San <i>Equus quagga</i>	175–322	Distant patches	Lee (1979: 233)
African Buffalo/Dobe San <i>Syncerus caffer</i>	500–900	Dangerous and aggressive	Lee (1979: 233)
Elephant/Dobe San <i>Loxodonta africanus</i>	2200–6300	Requires coordinated effort	Lee (1979: 234)
Forest Buffalo/Mbuti <i>Syncerus caffermanus</i>	250–450	Dangerous and aggressive	Turnbull (1965)
Okapi/Mbuti <i>Okapia johnston</i>	210–250	Difficult to catch, cryptic	Turnbull (1965)
White-lipped peccary/Aché <i>Tayassu pecari</i>	25–40	Aggressive, requires coordinated effort	Hill and Hawkes (1983)
Barking deer/Semaq Beri <i>Muntiacus muntjak</i>	14–35	Hard to track, poisoned darts often lost	Kuchikuri (1988)
Mouse deer/Semaq Beri <i>Tragulid napu</i>	5–8	Hard to track, poisoned darts often lost	Kuchikuri (1988)
Elephants/Semaq Beri <i>Elaphas maximus</i>	2721–5443	Hard to kill with available technology	Kuchikuri (1988)
Wild Pigs/Semaq Beri <i>Sus scrofa</i>	50–90	Hard to kill with available technology	Kuchikuri (1988)
Tapir/Semaq Beri <i>Tapirus indicus</i>	250–320	Hard to kill with available technology	Kuchikuri (1988)
Collared peccary <i>Pecarita jacu</i> /Waorani	16–27	Hard to track and kill without dogs	Yost and Kelly (1983: 205–206)
Deer <i>Mazama spp.</i> /Waorani	11–48	Hard to track and kill without dogs	Yost and Kelly (1983: 205–206)
Tapir <i>Tapirus spp.</i> /Waorani	150–400	Hard to track and kill without dogs	Yost and Kelly (1983: 205–206)

Additionally, some prey hide, flee to inaccessible areas or use physical obstacles (thickets, high cliffs, etc.), rapidly and randomly change flight directions, and possess other physical and behavioral traits – notably aggression – that can influence human pursuit (see Frison, 2004; Lyman, 1989; Simmons and Ilany, 1977; Stiner et al., 2000).

The range of available dispatch technologies influence pursuit costs (especially failed pursuits) in a variety of different and sometimes non-intuitive ways. Some dispatch technologies have decreased failure rates when used in particular contexts. In open terrain with limited cover, projectiles launched at a distance often have higher failure rates than thrusting spears used at close quarters, such as from hunting blinds (Hitchcock and Bleed, 1997: 357–361). Limitations on the efficacy of different hunting tools can restrict the range of prey that can be efficiently dispatched. For example, Yost and Kelly (1983: 205–206) reported that Waorani hunters ignored or rarely pursued the three largest bodied animals in the Amazon – the collared peccary, deer (*Mazama sp.*) and tapir (*Tapirus terrestris*) – because these animals were difficult to track. The situation changed after they acquired dogs, which corner the animals and allow hunters to approach close enough to make a kill. Similarly, Kuchikuri (1988) reports that larger-sized terrestrial ungulates such as wild pig (*Sus scrofa*), tapir (*Tapirus indicus*), and elephant (*Elaphas maximus*) were rarely pursued by Malaysian Semaq Beri hunters because they usually carried blowguns and the poisoned darts were ineffectual on these rarely encountered animals. But even large horn-billed birds that were commonly encountered were not pursued because the birds would often escape after being hit but before the poison incapacitated it making the darts irretrievable (Kuchikuri, 1988). In this case, the

probability of hunting failure due to the prey characteristics and the value of the hunting dart exceeded the probability of making a kill.

The degree to which prey are processed for immediate or delayed consumption is often contingent on the transports costs of the prey. Extensive processing effort can greatly inflate the handling costs of specific prey (e.g., Bartram, 1993a: 121; Byers and Ugan, 2005; Smith, 1991) and depress the PERR. Smith (1991: 232–235, Table 6.11) showed how the inclusion of the post-acquisition processing costs of plucking feathers from Canadian geese (*Branta canadensis*) depresses PERR's of the highest ranked summer resource to a much lower ranked resource (from 51,020 to 4930 kcal/h) relative to alternative prey. Mass collection of certain kinds of resources that will quickly spoil if not processed can also result in high labor costs. Other kinds of processing techniques for long-term storage can greatly increase prey handling costs including smoking, pounding and grinding meat into a powder, the manufacture of bone grease and grease cakes, and the production of pemmican. For example, drying increases the shelf-life of meat and greatly reduces the transport costs (Lupo, 2006), but as reported by Bartram (1993a: 127) traditional biltong production by Kua hunters in the eastern Kalahari is associated with very high field processing costs.

Other considerations that influence handling costs include transport costs (see O'Connell et al., 1988, 1990). In the absence of transport equipment or animals, the transport costs of game acquired away from residential sites increases with prey body size, the number of carcasses, distance to camp, and other factors (Lupo, 2006). Some hunters, such as the Hadza, muster transport parties comprised of a large number of people to carry selected prey body

segments to residential camps (O'Connell et al., 1988, 1990). The Hadza also consume animal parts at the kill site (such as limb bone marrow), use specific butchering techniques, and assemble make-shift carrying devices to reduce the costs of transporting loads (see Lupo, 2006). In the case of extremely large-sized prey, such as elephants or whales, large numbers of butchers (sometimes entire villages) converge on the carcass and sometimes erect temporary villages near the body for processing to reduce transport costs (Ransom, 1946).

Search costs are often the primary cost associated with acquiring prey and encounter rates determine whether a resource is in or out of the diet, but ethnographic data show that handling costs can also strongly influence PERR's and prey ranking's. Excessive handling costs influence the profitability of exploiting certain large-sized game, making them less efficient choices relative to smaller-sized resources and, in some cases, can actually deter hunters from pursuing certain prey given the constraints of hunting technology. Examples cited here show that even when certain large-sized animals are encountered, hunters may actively choose to pursue smaller-sized, but more efficiently procured and lower risk game. There are also a range of nonconsumptive costs that influence the procurement of big game and these include the social and organizing costs associated with distributing the meat (Bird et al., 2013; also see Lee, 1972). Recently, Bird et al. (2013) report that Martu hunters often avoid pursuing feral camels (*Camelus dromedaries*) to avoid the social and organizational problems associated with the acquisition and distribution of these large-sized animals.

3. Handling costs and prey-size

If handling costs influence prey ranking and profitability, one might next question whether handling costs vary in a predictable fashion with prey body size—a common proxy measure of profitability. To answer this question we assembled quantitative data from ethnographic, ethnohistoric and ethnoarchaeological studies that reported measures of the different components of handling costs. These data are derived from studies where hunters pursued prey on foot and used a variety of dispatch weapons and techniques including rifles, muzzle-loaders, spears, blow pipes and poisoned darts, bows and poisoned arrows, and hand capture. Prey-size is measured by the median live-weight for adult male and female animals combined.

Fig. 1 shows the relationship between prey body size and pursuit costs (as measured by time after prey are encountered) from a sample of 40 animals is positive and significant ($R = 0.405$, $p < 0.05$). However the coefficient of determination ($R^2 = 0.163$) indicates body size accounts for only a small part of the variation in pursuit costs (time). Hunting failure rates are often (but not always) subsumed as part of the total costs of pursuit, and here we present hunting success rates separately to explore how failure relates to carcass size. Hunting success here is a ratio of the number of animals killed to the total number of animals pursued. Fig. 2 shows an inverse relationship between hunting success rates and body size for a sample of 62 cases. Larger-sized prey are generally associated with lower hunting success rates than smaller-bodied prey, but the relationship is weak ($R = -0.213$, $R^2 = 0.045$, $p = 0.09$). Because the sample used in these analyses combines different dispatch technologies and prey captured in different ecological contexts, the correlations are not robust but only suggestive of general trends. We expect that in samples where hunting technology and ecology can be held constant these relationships would be robust.

Pursuit costs and success rates are also strongly linked to prey characteristics. While speed is an important characteristic that

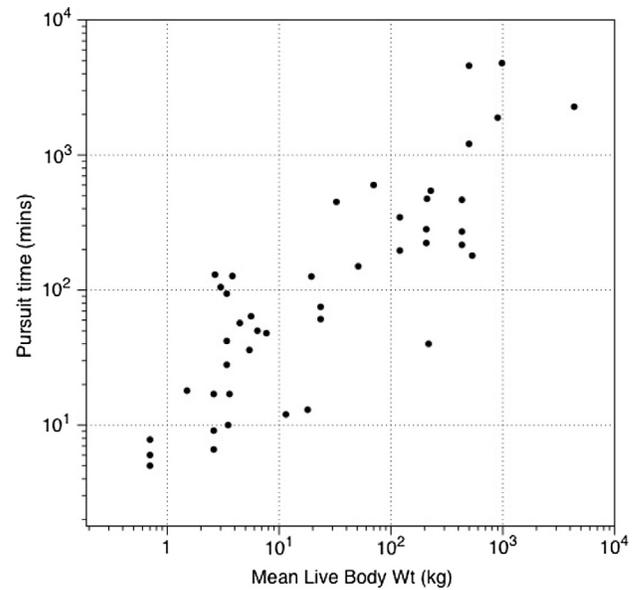


Fig. 1. Relationship of pursuit time to prey body size. Data compiled from Foa (1899), Hill et al. (1987: 9), Kuchikuri (1988: Table VIII), Lupo and Schmitt (unpublished Bofi/Aka field notes), Smith (1991: Tables 53 and 611), Winterhalder (1977: 334, 336, 338), and Appendix A (this publication).

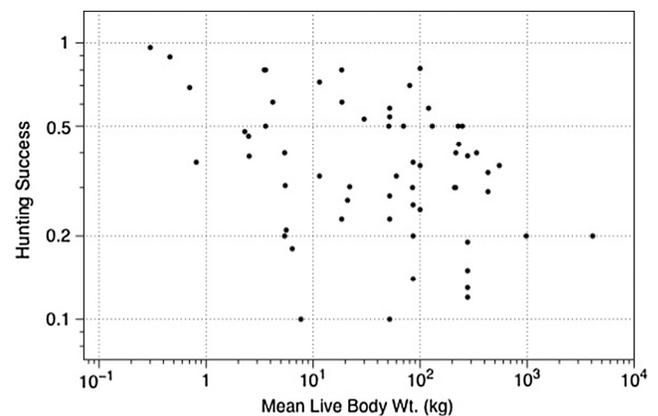


Fig. 2. Relationship of hunting success to prey body size. Data compiled from Anderson (1888), Bartram (1993b), Bird et al. (2009), Crowell and Hitchcock (1978), Hitchcock and Bleed (1997), Kuchikuri (1988: Table III), Lupo and Schmitt (2005), Marks (1976), and Winterhalder (1977).

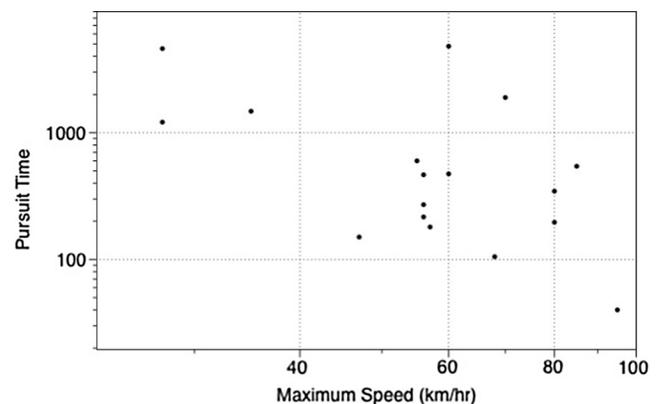


Fig. 3. Relationship of pursuit times to maximum ground speed of prey.

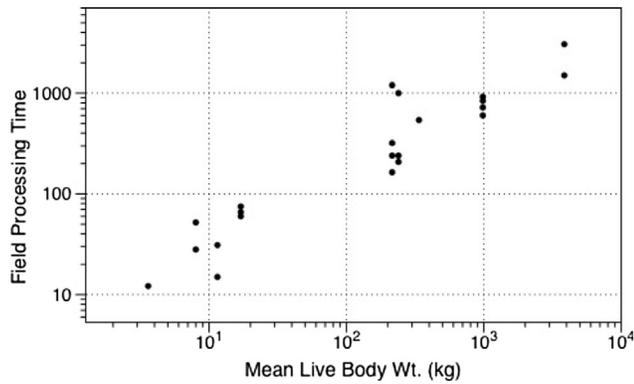


Fig. 4. Relationship of field processing time to prey body size. Data compiled from Bartram (1993a: Table 7–3) and O’Connell (unpublished Hadza field notes).

makes some prey difficult to capture, larger-bodied animals are generally slower than smaller-bodied prey (Garland, 1983). Fig. 3 shows that there is a significant inverse relationship ($R = -0.411$, $R^2 = 0.168$, $p < 0.05$) between pursuit time for prey and maximum achievable speeds for the largest-sized prey (>120 kg) (e.g., Garland, 1983). These data underscore our earlier point that a range of different prey characteristics (predator defense mechanisms, physical characteristics, and ground speed of animal) can influence handling costs.

Megafauna can take days to process and carry which adds to the risk of meat spoilage if the carcass is not processed in a timely fashion. Field butchering costs generally correlate to prey body size; bigger animals take longer to process (O’Connell et al., 1988, 1990; Lupo, 2006). Fig. 4 shows field processing costs closely track carcass-size ($R = 0.740$) and that body size accounts for approximately 54% of the variation in processing costs ($R^2 = 0.548$, $p < 0.05$, $n = 52$). Large-sized game also present significant transport problems for hunters who can either selectively transport or process body-parts as described above, or move the entire encampment to the kill site (Lupo, 2006). As Fig. 5 shows, the correlation between body size and transport costs (as measured by the number of carriers) is very strong ($R = 0.888$, $R^2 = 0.788$, $p < 0.05$, $n = 31$).

An examination of the different components of handling costs derived from empirical data shows that large-sized game often are very costly to procure relative to smaller-sized prey. Pursuit costs and especially failure rates show general trends indicating that large-sized game are more costly to pursue and more risky to procure than smaller-sized game. Processing and transport costs are also strongly positively linked to body size. Despite this trend, large game yields huge quantities of meat and fat and other products that can make them attractive targets to subsistence hunters. The question that researchers face is determining when the costs of procurement exceed the value of the target relative to other possible targets.

4. When is bigger not better? African elephants as prey

To further explore how elevated handling costs influence PERR’s and prey rankings, we assembled quantitative and qualitative data for African elephants, the largest-sized extant terrestrial mammal. These data were derived from ethnographic, ethnoarchaeological sources and historic accounts of elephant hunting written by professional big-game hunters (Bahuchet, 1985; Byers and Ugan, 2005; du Chaillu, 1861; Foa, 1899; Le Vallaint, 1790; Letcher, 1911; Marks, 1976; Putnam, 1948). Data were also derived from an interview with one of the last living Aka *tūma*’s (elephant

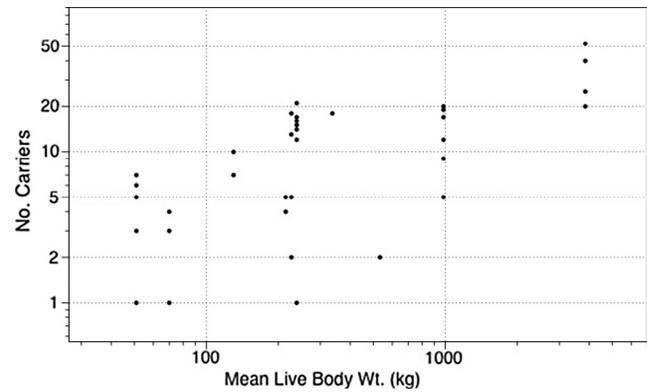


Fig. 5. Relationship of transport party size (number of carriers) to prey body size. Data compiled from Bartram (1993a: Table 7–3), Foa (1899), Lee (1979: 224), and O’Connell et al. (1988, 1990).

hunter) in the Central African Republic conducted by one of us (KDL) in 2005 (see Appendix A). Given their size and slow ground speed, elephants would seemingly represent an energetically efficient and high-ranked resource. In fact, Asian and African elephants were hunted wherever the animals naturally occurred, but more ethnographic and historical information is available on African elephants than their Asian counterparts.

Many tribes in Africa hunted elephants, but quite a lot of the ethnographic and historical hunting of these animals was driven by commercial demand for ivory, especially during the mid 18th–20th century. There are only a handful of detailed ethnographic descriptions of hunter-gatherers pursuing elephants using traditional technology. Elephants were apparently hunted by the San with spears in cooperative hunts involving large numbers of people (see Lebzelter, 1934), but at the time of Lee’s (1979) study the !Kung were unable to organize enough people to execute a collaborative hunt. The Hadza did not hunt elephant because the poison on their arrows was insufficient to kill animals in this size-range (Woodburn, 1968). The richest ethnographic record of traditional elephant hunters come from ethnographic descriptions of foragers (i.e., pygmies) who occupy forested areas in Central Africa. In this context, forest foragers used iron or metal spears that were sometimes tipped with poison (Bahuchet, 1985; Harrison, 1905; Turnbull, 1965); albeit historically poisoned wooden spears were used for this purpose (Turnbull, 1965).

Although many different techniques were used to acquire elephants in the sources consulted here, we only consider the costs for hunting elephants in pedestrian, on-encounter hunts with hand-held, dispatch technologies (i.e., poisoned and un-poisoned spears, bows and poisoned arrows, muzzle-loaders and 19th–early 20th century rifles). Table 2 shows the handling costs of elephants (and other species) broken down into different components. Although transport costs are part of the handling costs, these are not normally included because of the difficulty of measuring all the dimensions that influence transport such as the number of people in carrying parties and known and unknown physiological costs of carrying loads (e.g., terrain, temperature, vegetation). Even so, the costs of transporting an elephant carcass could be considerable; Foa (1899), for example, reported that on average it took 40–52 men to carry the flesh and bone or 20–25 men to carry the dried meat (filleted) of an elephant from the field to his hunting camps.

Pursuit costs listed here do not include the time spent tracking elephants, which could be considerable. Most sources that discuss elephant hunting in any detail describe how hunters made use of elephant trails, noting the presence of fresh dung, broken and/or saliva coated vegetation, and sounds as important indicators of the imminent presence of elephants well before the animals were

Table 2Comparison of body and edible fraction weights, post-encounter returns, and hunting success rates of common African prey.^a

Species	Body wt (kg) ^b	Edible wt (kg) ^c	Handling costs (mins)			Pursuit + butchering time	Total time	Success species rate
			Pursuit time	Butchering time	Dry/smoke time			
Elephant	4104	1724	2282	5157	37,740	7439	40,022	0.20
<i>Loxodonta africanus</i>								
Giraffe	983	590	4800	770	6284 ^d	5570	11,084	0.20
<i>Giraffa camelopardis</i>								
Buffalo	533	320	180	481	3408 ^d	661	3588	0.50
<i>Syncerus scaffer</i>								
Eland	337	219	1893	540	2332 ^d	2433	4225	0.40
<i>Tauritragus oryx</i>								
Zebra	239	132	60	302	1406 ^d	362	1466	0.50
<i>Equus quagga</i>								
Wildebeest	227	114	544	44	1214 ^d	588	1758	0.50
<i>Connochaetes taurinus</i>								
Kudu	215	108	40	481	1151 ^d	521	1190	0.40
<i>Tragelaphus strepisceros</i>								
Gemsbok	215	108	474	481	1151	955	1625	0.30
<i>Oryx gazella</i>								
Hartebeest	130	65	544	44	–	588	588	0.50
<i>Alcelaphus buselaphus</i>								
Warthog	70	46	600	30	–	630	630	0.50
<i>Phacochoerus africanus</i>								
Impala	51	33	150	26	–	176	176	0.50
<i>Aepyceros melampus</i>								
Bush duiker	18.5	15	13	49	–	62	62	0.80
<i>Sylvicapra grimmia</i>								
Steenbok	11.5	9.2	18	23	–	41	41	0.72
<i>Raphicerus campestris</i>								
Bat-eared Fox	3.6	3	16	12	–	28	28	0.80
<i>Otocyon megalotis</i>								
Springhare	3.5	3	10	12	–	22	22	0.80
<i>Pedetes capensis</i>								

^a Raw data used to determine handling costs and success rates are listed in [Appendix A](#).

^b Body weights are the median value of adult males and females. For most animals these values were derived from [Kingdon \(1997\)](#). Median weights for elephants, buffalo, eland, zebra, warthog, and impala are from [Robinette \(1963\)](#), and giraffe mean weights are from [Hall-Martin et al. \(1977\)](#).

^c Edible proportion of elephant carcasses (0.42) are derived from [Byers and Ugan \(2005\)](#); buffalo (0.60), eland (0.65), zebra (0.55), warthog (0.65), and impala (0.65) are from [Marks \(1976\)](#); wildebeest (0.50), kudu (0.50), gemsbok (0.50), and hartebeest (0.50) are derived from [Lee \(1979:230\)](#); bush duiker, steenbok, bat-eared fox, and springhare are assumed to be 0.80 edible based on experimental butchering conducted by [Lupo et al. \(2013\)](#).

^d Meat drying times for giraffe, eland, kudu, buffalo, zebra and wildebeest are not known. We used the average value (mins per kg) derived from known cases involving gemsbok (approximately 10.65 min per kg) as reported by [Bartram \(1993b\)](#).

actually seen. Pursuit costs listed in [Table 2](#) are calculated from the time invested after the animal was encountered until the carcass was recovered, multiplied by the number of people involved in the hunt. Ethnographic sources of indigenous African hunters specify that elephants were usually pursued by small groups of hunters that attempted to target an isolated animal during the heat of the afternoon when it was less alert or sleeping ([Baker, 1867](#); [Holder, 1886](#); [Lundeberg and Seamour, 1910](#)). After the animal was hit and if it was not killed outright, a second chase often ensued which could take several days with hunters covering dozens of kilometers until they found the animal dead or dying (e.g., [Bahuchet, 1985](#); [Turnbull, 1965](#)).

Elephant processing costs (evisceration, dismemberment and filleting) are described by several historical descriptions written by European or American big-game hunters sources. These endeavors usually involved a large number of people who stripped off all edible materials at the kill location or carcass find site and only highly valued parts, such as the meat and tusks, were transported. In Africa, elephant meat was often smoked or dried and many descriptions include this as part of the processing time ([du Chaillu, 1861](#); [Foa, 1899](#); [Letcher, 1911](#)). [Byers and Ugan \(2005\)](#) estimated that it could take between 100 and 300 person hours to butcher an elephant, depending on the carcass size, and up to 745 person hours if drying/smoking time is included. Here we separate the time it takes to butcher and fillet meat from meat drying and smoking time because the latter effort significantly increases handling times and may not be applicable to all ecological contexts.

The pursuit times listed in [Table 2](#) do not include unsuccessful hunts (or failure rates). Hunt failure rates using traditional weaponry such as spears and arrows are difficult to estimate. But [Marks \(1976\)](#) reported that Bisa hunters using muzzle-loaders had success rates of only 20%. In this case only 20% of the elephants that were shot were killed and the carcasses recovered. The high rates of failure are directly linked to the physical characteristics of elephants. Elephants are large, have remarkably tough skin, and can withstand multiple assaults and often escape. [Harako \(1976\)](#), for example, describes one Mbuti elephant hunt in which the animal was hit but the metal spear tip bent on impact and the animal escaped. High rates of hunting failure are repeatedly reported by 19th and 20th century big game hunters who describe large numbers of pre-existing bullet wounds and sometimes spears (and other weaponry) embedded in the bodies of elephants they dispatched ([Foa, 1899](#); [Gudger, 1932](#); [Wood, 1876: 121](#)). In the most striking example, [Foa \(1899: Appendix I\)](#) reported 30 pre-existing bullets imbedded in the body of one female elephant that he finally dispatched. Similarly, [Gudger \(1932\)](#) reports that it was very common for European ivory workers of the 19th and early 20th century to encounter bullets and iron spear-tips embedded in ivory imported from Africa. These metal objects were overgrown by ivory indicating that these were the results of pre-existing assaults prior to the death of the animal.

To determine the average edible fraction of an elephant carcass, we use 0.42 of the average live weight (after [Byers and Ugan, 2005](#)). The caloric value of elephant meat is unknown and while the meat was generally prized, the fat content is reputedly highly

Table 3

Comparison of edible fractions (kcal) and post-encounter return rates for common African prey.

(Ei/hi) Prey	Total kcal Edible fraction ^a	Post-encounter (Ei/hi) Pursuit + butchering	Post-encounter (Ei/hi) Total time
Elephant	2,241,200 ^b	3615.3	672.0
Giraffe	725,700 ^c	1563.4	785.7
Buffalo	416,000 ^{c,d}	18880.5	3478.3
Eland	273,750 ^c	2700.4	1555.0
Zebra	178,200 ^{d,e}	14767.9	3646.6
Wildebeest	147,060 ^d	7503.1	2509.5
Kudu	142,560 ^f	6567.1	2875.1
Gemsbok	142,560 ^f	2687.0	1579.1
Hartebeest	76,050 ^{c,d}	3880.1	3880.1
Warthog	60,720 ^c	2891.4	2891.4
Impala	33,660 ^d	5737.5	5737.5
Bush duiker	19,800 ^f	15329.0	15329.0
Steenbok	9660 ^g	10178.3	10178.4
Bat-eared fox	4770 ^h	8177.1	8177.1
Springhare	4770 ^h	10407.3	10407.3

^a Whenever possible kcal values for each specific animal were used. If two or more sources reported kcal values that differed, we used the average value of those sources. Although the distribution of fat within the body can inflate the caloric value of specific parts (i.e., limb marrow comprised largely of fat), here we do not accommodate differences in fat content among body segments.

^b Byers and Ugan (2005) calculate energetic values of elephant meat using three different values: 100, 125 and 167 kcal/100 g. We use the average of these values (130 kcal/100 g).

^c Bender (1992) reports: giraffe = 123 kcal/100 g; eland 125 kcal/100 g; buffalo = 120 kcal/100 g; hartebeest = 130 kcal/100 g; warthog = 132 kcal/100 g.

^d Ledger (1968) reports: buffalo = 140 kcal/100 g; zebra 127 kcal/100 g; wildebeest 129 kcal/100 g; hartebeest 104 kcal/100 g; impala = 102 kcal/100 g.

^e www.fatsecret.uk report zebra steaks at 175 kcal/100 g; oslink.co.uk reports zebra meat at 103 kcal/100 g.

^f Gemsbok, kudu, and bush duiker meat nutritional values are averages (132 kcal/100 g) based on 150 kcal/100 g (Leung, 1968) and 114 kcal/100 g for antelope (http://www.nutritionvalue.org/Game_meat%2C_raw%2C_antelope_nutritional_value.html).

^g We assume steenbok meat has the same nutritional value as springbok (105 kcal/100 g [oslink.co.uk]).

^h Bat-eared fox and spring hare are assumed to have nutritional values (159 kcal/100 g) that are the average of twelve African rodents reported by Malaisse and Parent (1982).

Table 4

Ranking of the top four (1–4; 1 is highest) and lowest four (5–8; 8 is the lowest) prey based on different economic measures.

Prey body size	Post encounter return rate (Ei/hi) pursuit + butchering	Post encounter return rate (Ei/hi) total time
1. Elephant	1. Buffalo	1. Bush duiker
2. Giraffe	2. Bush duiker	2. Springhare
3. Buffalo	3. Zebra	3. Steenbok
4. Eland	4. Springhare	4. Bat-eared fox
5. Bush duiker	5. Warthog	5. Gemsbok
6. Steenbok	6. Eland	6. Eland
7. Bat-eared fox	7. Gemsbok	7. Giraffe
8. Springhare	8. Giraffe	8. Elephant

unpredictable (Baker, 1867), but varies largely with age, reproductive status, and season (Albi, 1971). Fat, however, is predictably concentrated in the masseter and zygomatic arch of the skull and internally around the kidney (Albi, 1971). The foot is also a well-known repository for fat and was highly desired by indigenous populations and foreign hunters (e.g., Baker, 1867; Foa, 1899). The foot is largely comprised of fat and one foot could possibly yield as much as a 3.9 L of storable fat (Christy, 1924). Elephant feet and the trunk were among the mostly highly prized body parts for consumption (Foa, 1899). Bone marrow is limited in elephants because the internal construction of the bone and medullary cavities are reduced in size and contain little free marrow in comparison to bovids. While different parts of the elephant carcass varied in fat content and may have enhanced the value of certain segments, here we use one caloric value for the entire carcass derived from estimates provided by Byers and Ugan (2005).

For comparative purposes, Table 2 shows the components of the handling costs for 15 common African game animals that geographically overlap with elephants and are alternate prey targets. Raw data on handling costs and success rates are shown in Appendix A. Estimates of meat smoking and drying times are derived

from Bartram (1993a, 1993b) and are only shown for larger-sized game (>200 kg) because smaller-bodied animals are not commonly processed in this manner.

PERR's are found by dividing the energetic value of the prey (based on the edible fraction) by the handling time (Table 3). To accommodate failure rates we follow Ugan and Simms (2012: 182) suggestion and discount the PERR's by hunting failure rates (i.e., multiplying the PERR by the success rate). Here we list two values for PERR's for elephants and other common prey. One value uses handling costs that include pursuit and butchery, and the other is based on total processing costs (pursuit, butchery and meat drying/smoking); both values are discounted for hunting failure.

Although the sample size reported here is admittedly modest, the total handling costs parallels body size ($R = 0.998$). This correlation agrees with the previous piecemeal analysis of different components of handling costs which showed that larger-sized prey have higher handling costs than smaller-sized animals (see Table 2). Table 3 shows how higher handling costs influence the PERR's used to rank prey. Elephants, the largest animal in this sample, are not the highest ranked prey based on PERR's. Note that this also true of giraffe. In fact, there are no statistically significant relationships between prey-size and the PERR's (pursuit/butchery only and total processing costs) for this sample of animals ($R = -0.351$, $R^2 = 0.123$, and $R = -0.410$, $R^2 = 0.167$, respectively). This is further demonstrated in Table 4, which compares the 4 highest and 4 lowest ranked animals in the sample using different economic measures. The rankings by PERR's do not match those arranged by body size (Column 1, Table 4). The ranking of prey by PERR using only pursuit and butchering times shows that buffalo, one of the largest-bodied animals in the sample, is the highest ranked prey followed by animals that are considerably smaller in size such as bush duiker and springhare (Column 2, Table 4). Note that the lowest ranked prey is the giraffe; elephants are ranked in the middle of the suite of prey examined here and are not shown. If total processing time is considered, the 4 highest-ranked prey are the smallest-

sized animals in the sample and elephant and giraffe are the lowest ranking animal resources (Column 3, Table 4). Small game are high ranked because in comparison to larger-sized game they have: (1) a high ratio of edible meat to body-weight (Stahl, 1982), (2) lower variance in hunting success rates, (3) low handling costs, and (4) most can be taken by a single hunter.

Examination of how the different components of handling costs influence prey rank offers insights into the strategies that hunters would have to use to reduce acquisition costs through the adoption of new hunting technologies and/or carcass processing techniques. In the examples discussed here, the high failure rate associated with elephant hunting makes them particularly inefficient hunt with traditional technology and historic firearms. For example, the probability of hunting success rates for elephants would have to be an unrealistic 100% for the PERR (18,076.6 kcal/h) to be high enough to make it the second highest ranked prey below buffalo. If pursuit costs were reduced by 30% and the success rate for hunting elephants is 1.00, the PERR would be high enough (19,909 kcal/h) to make it the highest ranking prey of the group considered here.

Lower pursuit costs and higher success rates might be achieved through the use of alternative dispatch technologies not considered here, but quantitative data are unavailable for some of these techniques. For example, historical reports describe the widespread use of pit traps for large game including elephants (Weeks, 1909). But these devices were labor intensive to construct and did not catch many adult animals because elephants quickly became trap wary (Lydekker, 1908; Sparrman, 1785; Wood, 1876). In the ethnographic record cooperative hunts using natural or artificial barriers and involving large numbers of hunters may have had higher success rates than the dispatch techniques discussed here (du Chaillu, 1861; Cooper and Johnston, 1914; Foa, 1899; Wood, 1876:533). Cooperative hunts reduced the risk of elephant escape (via barriers), incorporated multiple hunter assaults conducted over a short time span, and sometimes resulted in the synchronous dispatch of one or more elephants. But while cooperative hunts might decrease hunting failure rates, these do not necessarily decrease handling time because larger labor forces increase pursuit effort as measured by person hours. du Chaillu (1861), for example, describes 500 Fan spear hunters using natural vegetation barriers to dispatch 4 elephants in one day. In this case the animals were killed by a volley of hundreds of spears and these kinds of hunts were usually under the direction of a chief or local leader (du Chaillu, 1861). On a smaller scale, Harako (1976) describes spear-hunting groups with 16 people led by a *tûma*, but even these smaller-sized groups greatly increase the cost of pursuit. It is also not clear if these smaller-sized cooperative endeavors actually increased success because all of the elephant hunts described by Harako (1976) were failures. While cooperative endeavors may increase hunting success but the labor costs (person hours) increase accordingly and do not necessarily reduce handling costs.

Processing time comprises a large proportion of elephant handling costs, especially if meat drying and smoking are included as part of the costs. Butchering and filleting meat account for 0.69 of the total handling costs and if meat drying and/or smoking are included comprise 0.94 of the total cost of processing. High processing costs not only result from the large amounts of edible soft tissue, but carcasses in this size-range can require a great deal of effort to dismember (see also see Byers and Ugan, 2005 on flipping carcasses). Clearly, different ecological circumstances may present a different range of options for meat preservation or even immediate consumption that might reduce the labor force required to process a large animal carcass. However, in the cultural contexts discussed here that lack access to sophisticated technology (i.e., automatic weapons, mechanized systems of search and transport),

offer few alternatives that hunters can adopt to significantly reduce handling costs, especially processing.

5. Costly signals and social niche specialization

Elephant hunting is inefficient in comparison to other smaller sized prey when measured by conventional currencies (energy/time), but nonconsumptive benefits can often enhance the value of pursuing certain high-cost prey. Several ethnographic studies identify different contexts in which hunters pursue inefficient or expensive prey as a costly signaling strategy aimed at advertising special skills abilities. These individuals can benefit from nonconsumptive rewards such as access to mates, larger networks of allies and/or trading partners, increased popularity and political deference (e.g., Bliege Bird and Smith, 2005; Hawkes, 2000; Sosis, 2000; Weissner, 2002). Some of these benefits can positively influence an individual's reproductive success (Henrich and White, 2001; Smith, 2004). Elephant hunting may be such a case, but it is complicated because from the mid-16th century until the present, the high demand for ivory inflated the value of procuring these animals. Prior to the global commoditization of ivory it is not clear how often elephants were actually targeted by subsistence hunters in Africa. Several historical sources report that traditionally elephants were largely killed to reduce domesticated crop losses. The meat, skin and other soft tissues were utilized, but the indigenous demands for ivory were limited and historical sources note that stockpiles of unused ivory were only depleted after the market demand increased in Europe and America (Knight, 1848; Sparrman, 1785). Consequently, prior to the emergence of the historic large-scale market for ivory, the economic incentives for hunting elephants would have been diminished.

Yet there is substantive evidence that forest foragers targeted elephants prior to the Atlantic era and the commoditization of ivory. Linguistic analysis of the proto-language of forest foragers identifies common words for elephants (i.e., the composition of groups) and elephant hunters, suggesting a great antiquity of elephant hunting prior to commercial ivory exploitation and the advent of iron (Bahuchet, 1993: 42; Lupo, 2011). The fact that elephant hunter or *tûma* was an ancient and specific designation among forest foragers who otherwise have few social categories suggests that the importance of this position transcends the ivory trade.

Among forest foragers in the Congo Basin, elephants were only pursued by specialists or 'super specialists' (Putnam, 1948). *Tûma* reputedly possessed supernatural powers and knowledge of magical herbs (Bahuchet, 1985) that allowed them to become invisible and kill the animals. Traditionally, the skill-set and honorary title of *tûma* was passed from father to son after the latter served a period of apprenticeship (Bahuchet, 1985; Harako, 1976). The title conferred great prestige and men who were *tûma*'s were especially highly regarded by settled village farmers with whom the foragers had a multidimensional relationship (Bahuchet and Guillaume, 1982; Lupo et al., 2014). The *tûma*'s ability to kill elephants was directly tied to farmers who provided access to the special iron and metal spears used to kill the animals. Bahuchet (1985) described the *tûma* as specialists who planned and led elephant hunts and usually delivered the first spear into the animal. The number of men who were *tûma*'s was small. Turnbull (1965) estimated that only four out of every 12–15 hunters were elephant hunters, and Harako (1976) reported that there was only one per every few villages. Despite the high value attached to ivory in the historic and ethnographic period, *tûma*'s did not target elephants often. Elephants were killed infrequently and Turnbull (1965) reported that one per year was normal and the most he ever

heard of was three, which was considered exceptionally high (see also Bahuchet, 1985; Harako, 1976).

Ethnographically, *tûma*'s derived prestige value from hunting elephants qualifies as a costly signal because elephants are expensive to hunt, associated with a high degree of failure and have a high variance in returns, and the hunts were executed to broadcast the signal to many. The carcasses had value to many people, but the ability to acquire the animals was directly linked to the hunter's skills, special knowledge, and affiliations (see Bliege Bird et al., 2001). By hunting elephants, the *tûma* displays information to others in his immediate group. However, elephant-hunting and role of *tûma* in this context might be better understood as a social niche or specialization. Being a *tûma* has a clearly defined social role in forest forager society and strongly influences the responses of others, in this case neighboring ethnically distinct farmers (see Montiglio et al., 2013). According to Harako (1976:89) "The *tûma* is not necessarily a political authority in the band, but he keeps his social standing in relations with the village. The band can, thanks to the existence of '*tûma*', receive economic and social benefit from relationships with the village and with other bands." In this case hunting very costly prey not only confers advantages on the individual *tûma*, but also has extended benefits for the entire group and the position has clearly defined institutionalized prestige value that defines a *tûma*'s social role within both forager and farmer society. Social niches, such as this, may be very common in small-scale societies where different ethnic groups have an on-going and established relationship that can generate benefits for individuals, but clearly defined sociopolitical boundaries limit the range of benefits that are available. In these cases, certain individuals with highly desirable skills may become specialists.

Irrespective of whether or not hunting expensive prey is a costly signal or associated with defined social roles, the number of people who engage in these activities in any society is limited. As discussed here only a handful of people had the abilities, skills and affiliations to pursue elephants and reap the nonconsumptive benefits. This suggests that the idea of 'big game specialization' as commonly envisioned by archaeologists should be reframed to account for specializations such as these. In the ethnographic record, big game specialization often only applies to a few people - not the entire group (also see Dwyer and Minnegal, 1993; Neitschmann, 1973; Stearman, 1989). In the case of forest foragers, most hunters engage in other types of hunting activities on a daily basis and most of these activities (but not all) are associated with a lower risk of hunting failure (Lupo and Schmitt, 2005).

6. Pleistocene megafauna and handling costs

Understanding the high acquisition costs associated with some large game has implications for current controversies surrounding Pleistocene megafauna. The analyses conducted here expands Byers and Ugan's (2005) previous examination of the economics of elephant procurement, which they used to model hypothetical PERR's for mammoths (*Mammuthus columbi*). In their analysis handling costs are based only on carcass processing times and do not include pursuit costs or failure rates. Byers and Ugan (2005) argue that although mammoths had high handling costs, they were characterized by relatively high post-encounter return rates on the order of 21,028–52,500 kcal/h (with a midpoint 30,029 kcal/h). They argue that mammoths might have been the highest ranking prey available to North American Paleoindian hunters if their PERR estimates were correct, and if mammoths were encountered frequently enough on the landscape. Using the allometric relationship between body size and prey density to approximate the encounter rate with mammoths and other prey, Byers and Ugan (2005)

conclude that proboscideans would never be encountered frequently enough to exclude other prey species from the diet and a big game specialization would not be supportable (but see Haynes, 2002; Surovell and Waguespack, 2009). Clearly understanding prey encounter rates is critical for determining diet breadth, but it is very difficult to estimate Pleistocene prey densities with accuracy especially when the results are projected over large areas. Our data suggest that elephants were low-ranked relative to other medium and large African prey and might have been infrequently targeted irrespective of their encounter rates on the landscape. Clearly, African elephants are not direct analogues for Pleistocene proboscideans, but our data show a more general trend of higher handling costs associated with larger-sized prey. If mammoths had handling costs similar to elephants, the PERR's would be considerably lower than previously reported. As discussed earlier, the high costs associated with megafauna hunting could only be reduced in a limited number of ways. Pleistocene hunters in certain ecological contexts such as central and northern Europe might have been able to reduce processing costs through minimal field processing and freezing meat at or near the site of dispatch. This strategy could plausibly reduce the high processing and transport costs associated with megafauna hunting, but high hunting failure rates would always make mammoths an expensive option if the only benefits associated with dispatching these animals are consumptive. Nonconsumptive benefits, as described above, could have enhanced the value of hunting megafauna. But if the value of hunting megafauna hinged on nonconsumptive benefits, then only a handful of individuals would be able to pursue and benefit from this activity.

7. Zooarchaeology and applications of foraging theory

A larger issue raised by this analysis concerns the general applicability of using body size as a proxy for prey rank in zooarchaeological assemblages. As discussed elsewhere (Lupo, 2007), large-sized animals are often the highest-ranked prey resource, but this is not always the case. The low ranking of extremely large-sized prey relative to alternative smaller-sized animals may be more widespread than previously expected, especially given the excessive handling costs associated with large-bodied prey. Clearly, these circumstances do not apply to all large prey in all instances. There are, for example, certain fleet and large-sized prey that have predictable social behavior patterns and use natural corridors or game trails, that can reduce pursuit costs. Winterhalder (1977: 324) explains how the hierarchical structure of caribou herds and the pattern of only following a lead animal even if that individual is slow, can expose the rest of the group to high predation. Prey profitability and rank needs to be based on the acquisition costs given the prevailing technology and prey ecology rather than body size (see Stiner et al., 2000).

A corollary issue concerns what prey abundances in zooarchaeological assemblages actually reflect and this is a question that has been and continues to be much debated among specialists (see Lupo and Schmitt, 2005; Speth, 2012, 2013). More specifically, is there a direct relationship between the relative abundances of large mammal remains in archaeological assemblages and their prehistoric encounter rates? Biases in zooarchaeological assemblages including taphonomic impacts, inadequate sampling, and limited identification practices and chronological controls are all well known (e.g., Lyman, 1994, 2003). Similarly, the actions of human hunters such as differential transport of skeletal remains are known (Lupo, 2006), but researchers often expend little effort developing estimates of prey abundances and densities (encounter rates) from sources independent of archaeological samples. Prey abundances established through paleontological and/or natural

evidence can often yield a different picture than those derived solely from archaeological assemblages (see Speth, 2012, 2013). Even without paleontological sources, independent measures of prey abundances are possible through biomolecular analyses to evaluate the relative size of different animal populations (e.g., Drummond et al., 2005; Stiller et al., 2010). These kinds of analyses, especially if paired with archaeological samples, could provide more revealing evidence of prey abundances and possible encounter rates across time and space. These analyses are crucial to any application of the PreyCM especially where the rarity of large and costly game might be linked to low encounter rates or high acquisition costs.

8. Conclusions

Applications of the PreyCM to anthropological and archaeological contexts have a long and successful history spanning several decades (e.g., Bird and O'Connell, 2006; Codding and Bird, 2015; Hawkes et al., 1982; Smith, 1991; Winterhalder, 1981; Winterhalder and Smith, 2000). The traditional PreyCM is a demonstrably robust model in some, but not all, contexts (e.g., Hill et al., 1987). Known modifications to this model based on empirical research in anthropology and allied fields have failed to be incorporated into archaeological applications. These modifications include but are not limited to considering alternate currencies such as social and political gains (see Lupo, 2007). Recent ethnographic observations demonstrate that excessive pursuit costs can depress the energetic profitability of large game relative to small game (Bird et al., 2009, 2012, 2013). Sociopolitical gains, however, can enhance the value of pursuing expensive and costly prey.

In this paper we employ some of the recent modifications to the PreyCM and examine one of the central assumptions of zooarchaeological applications of the PreyCM—body size equates to prey profitability. Although big game are often the most profitable prey target, quantitative and qualitative data presented here show that large-sized prey are generally more costly to acquire than smaller sized game. While encounter rates and search costs often determine whether or not a resource is in the diet, the value and the ranking of some large-sized prey can be markedly depressed due to excessive handling costs. Although social rewards such as prestige are often cited by researchers as one of the common benefits associated with big game hunting (e.g., Surovell and Waguespack, 2009), very few individuals are able to realize these rewards. Thus, social benefits associated with hunting large and dangerous prey were not necessarily generalized across the entire hunting populations, but accrued by only a few select individuals. This means that big game specialization cannot be universally viewed as a strategy practiced by all, especially if acquisition of costly prey hinged on possessing special skills. In the case example presented here, we further suggest that when the acquisition of costly prey is dependent not only on skill but also special knowledge and affiliations with external populations, social niches or specializations may emerge. Data presented here also speak to the larger zooarchaeological assumption that prey body size can be used as a proxy for prey rank (the bigger the prey, the higher the rank). We suggest that this assumption cannot be sustained and that analysts must consider prey characteristics relative to dispatch technology, including hunting failure rates, to evaluate profitability.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.jaa.2016.07.012>.

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