



An experimental lion-to-hammerstone model and its relevance to understand hominin-carnivore interactions in the archeological record



Elia Organista ^{a, *}, Marta Pernas-Hernández ^a, Agness Gidna ^c, José Yravedra ^a, Manuel Domínguez-Rodrigo ^{a, b}

^a Department of Prehistory, Complutense University, Prof. Aranguren s/n, 28040 Madrid, Spain

^b IDEA (Instituto de Evolución en África), Museo de los Orígenes, Plaza de San Andrés 2, 28005 Madrid, Spain

^c Paleontology Unit, National Museum of Tanzania, Shaaban Robert Street, P.O. Box 511, Dar es Salaam, Tanzania

ARTICLE INFO

Article history:

Received 6 November 2015

Received in revised form

11 December 2015

Accepted 14 December 2015

Available online xxx

Keywords:

Referential framework

Lions

Tooth marks

Hammerstone breakage

ABSTRACT

Traditional scavenging models have emphasized that a secondary intervention of hominins to carcasses previously consumed by carnivores should yield high tooth mark frequencies on long bone shafts. It has also been shown that the most feasible scavenging scenario for early Pleistocene African hominins would have been acquiring carcasses from felid kills and prior to hyenid intervention. Oddly, most experiments conducted in the past 20 years have been mostly based on bone modification patterns created by durophagous carnivores. Previous works emphasized that a felid-hominin model would be reflected in low frequencies of tooth-marked shaft specimens. The present work intends to put this hypothesis fully to test by replicating the complete felid-hominin scenario. Hammerstone breakage of bones from wild lion kills was simulated and the resulting anatomical and bone portion distribution of tooth mark frequencies was documented. Here, it is shown that wild lions inflict moderate damage to long bone ends. In contrast, hammerstone-broken shaft specimens bear very few tooth marks (usually <10% of fragments). It is shown that most damage inflicted by lions on carcasses during consumption occur on upper limb bones. Distal portions of radius-ulnae and tibiae are the least affected areas. This referential framework can potentially be applied to the archaeological record to reassert primary access to carcasses in some early Pleistocene African sites and unravel hominin-carnivore contribution to middle and late Pleistocene Eurasian palimpsests.

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1. Introduction

Several referential frameworks have been built in order to infer site formation processes and bone assemblage properties (e.g., Brain, 1969, 1981; Bunn and Kroll, 1986, 1988; Cavallo, 1998; Domínguez-Rodrigo, 1993, 1994; Hill, 1979; O'Connell et al., 2002; Potts, 1982, 1988; Shipman, 1975; Tappen, 1995). Thus, a variety of biological agents have been identified as potential independent and interactive contributors to bone assemblage formation. Given that hominin roles in archaeofaunal formation are the main concern of Paleolithic archaeological research, taphonomists have through time developed several techniques with which hominin-carnivore interactions (or lack thereof) could be interpreted.

Until the early 1990s, researchers on African early Pleistocene focused on skeletal elements frequencies to determinate carcass-acquisition strategies by hominins (Brain, 1981; Binford, 1978, 1981; Bunn, 1982, 1983; Bunn et al., 1988, 1991; Cruz-Uribe, 1991; Hill, 1975; Klein, 1975; O'Connell et al., 1988, 1990, 1992; Potts, 1982, 1988; Pickering, 2001, 2002), but it was subsequently shown how different processes could potentially result in equifinality (see review in Lyman, 2004; Domínguez-Rodrigo et al., 2007). To overcome this equifinality, different behavioural models were proposed on the basis of bone surface modifications using tooth and percussion marks (e.g., Blumenschine, 1988, 1995; Blumenschine and Marean, 1993; Selvaggio, 1994; Capaldo, 1995) and cut marks (e.g., Bunn, 1981, 1982, 1986; Bunn and Kroll, 1986; Domínguez-Rodrigo, 1997a, b).

Blumenschine's study on the ecology of scavenging in Ngorongoro and Serengeti ecosystems (Blumenschine, 1986) suggested

* Corresponding author.

E-mail address: eliaorganista77@gmail.com (E. Organista).

that earlier access to carcasses by non-human carnivores could be detected by the identification of a sharp contrast in tooth mark frequencies on long limb bone mid-shaft sections (Blumenschine, 1988, 1995). His experiments were conducted mainly with durophagous carnivores (e.g., hyenids). Blumenschine's studies found that primary carnivore (i.e., hyenid) access to bone assemblages results in a high percentage of midshaft specimens bearing tooth marks (usually >70%). Secondary access by carnivores (i.e., hyenids) to defleshed and demarrowed bones by humans results in lower percentages of tooth-marked midshaft specimens (5–15%).

Domínguez-Rodrigo et al., (2007) built a referential framework in order to quantify tooth mark percentages made by leopards on long bones from small carcasses using Brain's (1981) experimental collection on carcasses consumed by leopards. This approach reproduced virtually the frequency of tooth-marked specimens from felid-consumed carcasses after breaking bones with hammerstones. This study assessed how mid-shaft portions reproducing a carnivore (felid)-first experimental scenario showed a substantially lower percentage of tooth marks on small and medium-sized carcasses (<15%) as well as on large-sized carcasses (<22.2%) when compared to the carnivore (i.e. hyenid)-first model reproduced by Blumenschine (1988, 1995) and Capaldo (1995). It was, thus, concluded that the same low-frequency of tooth marks occurs in models where felids intervene first or in models where hyenids intervene secondarily to hominin-processed bone assemblages (Domínguez-Rodrigo et al., 2007).

Some researchers using tooth marks suggested what could be considered a Felid-Hominid-Hyenid multiple-pattern interpretation for the FLK Zinj faunal assemblage at Olduvai Gorge (Blumenschine, 1988, 1995; Marean et al., 1992; Blumenschine and Marean, 1993; Selvaggio, 1994; Capaldo, 1995). This multiple-pattern interpretation for FLK Zinj has been strongly challenged in recent years by Domínguez-Rodrigo and Barba (2007), based on the frequency and distribution of cut marks, which reflect bulk defleshing of small and medium-sized animals and, thus, early hominin access to carcasses at FLK Zinj. More recent arguments against these models have been summarized by Gidna et al. (2014) and Domínguez-Rodrigo et al. (2012). The frequency and anatomical distribution of cut marks can inform us on the order of hominin access to carcass resources (Domínguez-Rodrigo, 1997a, 1997b). Tooth mark frequency and distribution also have the potential of informing about hominin-carnivore interactions as well as the carnivore type (felid or hyenid) involved in the modification of any given bone assemblage (Domínguez-Rodrigo et al., 2015, 2007).

However, compared to hyenas, little attention has been paid to neo-taphonomic experimentation with lions in their natural habitat in order to build a proper referential framework for understanding tooth marks in archaeofaunas. Recently, several studies have been published on the consumption behavior of wild felids and the resulting carcass damage patterns (Domínguez-Rodrigo et al., 2007; 2012; Gidna et al., 2014, 2015; Pobiner, 2015, Domínguez-Rodrigo, 2015). Experiments with wild and captive felids have yielded important differences of tooth mark percentages, emphasizing the use of wild carnivores as the basis for referential frameworks to be inferentially applied to the past (Gidna et al., 2013, 2015).

Depending on the type of access to animal carcasses, different frequency associations of cut, tooth and percussion marks will be observed (Domínguez-Rodrigo et al., 2014a). This association can be used as a diagnostic criterion in the type of access of hominins and carnivores to carcasses when analyzed simultaneously through multivariate statistical tests (Domínguez-Rodrigo et al., 2014a), instead of being analyzed as separate variables. This methodology was first suggested by Domínguez-Rodrigo et al. (2014a) and applied to the bone assemblages of FLK Zinj and BK (Domínguez-Rodrigo et al., 2009, 2014b; Organista et al., 2015) at Olduvai

Gorge (Tanzania). Domínguez-Rodrigo (2012) identified the partial use of bone surface modifications and the independent analysis of each mark frequency as major causes of the biased interpretations made by some authors (Pante et al., 2012; Blumenschine, 1988, 1995; Selvaggio, 1994 and Capaldo, 1997), where more emphasis has been laid on the use of tooth marks than cut marks for interpreting past hominin behaviours.

The present paper builds upon previous research of tooth mark frequency and anatomical distribution (Domínguez-Rodrigo et al., 2007, 2012; Gidna et al., 2014; Gidna et al., 2015) and aims to create a referential framework for lion-to-hammerstone models, which can be applied to hammerstone-broken archaeofaunas. Although initially applied to a limited number of carcasses consumed by medium-sized felids (Domínguez-Rodrigo et al., 2007), this study builds on such a preliminary study and on Gidna et al.'s (2014) study of tooth mark distribution on lion-consumed carcasses. It confirms the results obtained in both studies.

In addition, the modelling of bone assemblages initially created and/or modified by felids is not only useful for African archaeology. Felids have been a conspicuous agent in Eurasian Pleistocene cave archaeological and paleontological sites. Middle Pleistocene sites such as Ardenac Ib & Ila-b (France) (Tournepiche, 1996; Fourvel, 2012) or Arago levels M-N-O (Rivals et al., 2006) have also been interpreted as felid lairs where carcass consumption took place. Other Late Pleistocene sites, such as Los Rincones (Spain) (Sauqué et al., 2014) or Amalda VII (Yravedra, 2004, 2007, 2010, 2011) have also been interpreted as assemblages where leopards contributed with most (Los Rincones) or some (Amalda) carcasses. In the case of Amalda VII, palimpsests were created by the combined action of humans and medium-sized felids such as leopards, each preying on different taxa (Yravedra, 2007, 2010, 2011). Leopards abound in European Late Pleistocene caves (Diedrich, 2013). Lions have also been interpreted as bear hunters in several Pleistocene sites such as Urşilor Cave (Romania), or Zoolithen Cave (Germany) (Diedrich, 2012). Felids like jaguars were also commonly accumulating and modifying carcasses in South American Late Pleistocene and Holocene sites (Martín, 2012). Our current understanding of felid bone modification in these assemblages is hampered by a poor understanding on how modern felids modify carcasses. This work will contribute to widening our referential framework on how felids, and more specifically lions, modify long bones.

2. Materials and methods

Previously, carnivore bone damage has been quantified using the bone portion method (i.e., epiphyseal, near-epiphyseal and mid-shaft portions) (Blumenschine, 1988, 1995). Studies of cut marks claiming to overcome equifinality were based on a method combining bone section and element type (Domínguez-Rodrigo and Barba, 2007). Here, both methods will be used in combination to determine how carnivore types can also be differentiated according to the differential anatomical distribution of bone damage that they inflict on carcasses.

The analytical sample used in this study includes the faunal assemblage obtained by Gidna et al. (2014) on modern lion (*Panthera leo*) kills from Tarangire National Park (Tanzania). The sample is composed of 13 small size carcasses, corresponding to warthog, juvenile zebra and wildebeest, 16 medium-sized carcasses, composed of adult zebras and wildebeests, as well as 10 large sized carcasses corresponding to 9 buffaloes and 1 giraffe. Gidna et al.'s (2014) sample was collected consecutively for three years. It included data on the number of lions, time of consumption, habitat where kill was spotted, taxon and age of preys. Only complete-monitored carcasses (e.g., observation started early in the

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