



An ecological neo-taphonomic study of carcass consumption by lions in Tarangire National Park (Tanzania) and its relevance for human evolutionary biology



Agness O. Gidna^{a, b}, Bernard Kisui^c, Audax Mabulla^d, Charles Musiba^e, Manuel Domínguez-Rodrigo^{a, f, *}

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

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

^c African Wildlife Foundation, P.O. Box 2658, Arusha, Tanzania

^d Archaeology Unit, University of Dar es Salaam, Dar es Salaam, P.O. Box 35050, Tanzania

^e Department of Anthropology, University of Colorado Denver, 1201 5th Avenue, Suite 270, Denver, CO 80217, USA

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

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ABSTRACT

Actualistic observations on modern lions (*Panthera leo*) from Tarangire National Park (Tanzania) have expanded the reported range of carcass consumption behaviors by these felids. The present study confirms that lions efficiently deflesh small and medium-sized carcasses and they can even thoroughly deflesh carcasses heavier than 500 kg, such as those of buffaloes. Ecology plays a major role in the intensity with which lions deflesh their prey. The most intensive carcass consumption episodes in Tarangire were documented in alluvial environments near water. Bone damage is proportional to the intensity of carcass consumption and upper limb bones, usually the most defleshed elements, are also the most heavily damaged. Butchery experiments with stone tools modelling secondary access to lion kills yielded a low cut mark frequency with an anatomical distribution of cut marks occurring more frequently on intermediate than on upper limb bones and on ends and metadiaphyses than on mid-shafts. The combination of the damage inflicted by lions on bones and the occurrence of cut marks as the result of secondary-access butchery by humans provides a heuristic framework with which to understand similar patterns in the archaeological record.

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1. Introduction

Hill's (1975, 1980) and Brain's (1981) works on carcass modification patterns by various predators and scavengers and Binford's (1983) preliminary observations on bone deposition around ponds in Kruger National Park (South Africa) were some of the antecedents of Blumenschine's (1986) study on the ecology of scavenging in the Ngorongoro and Serengeti ecosystems. Blumenschine's study showed how scavenging opportunities enabled by strictly flesh-eating predators in specific habitats and times of the year could be determined by resource availability: after felids defleshed carcasses and prior to the intervention of bone-crunching hyenas a theoretical scavenging niche was open for

hominins in riverine settings at the end of the dry season. This was expanded by Tunnell's (1990) study of carcass availability in Maasai Mara (Kenya) and Tappen's (2001) study in Virunga National Park (Democratic Republic of Congo). The latter study challenged generalizations on the ecological variables determining the ecology of scavenging in Africa savannas as defined in a Serengeti-based model.

None of these studies showed how these scavenging opportunities could be detected in the archaeological record. Experiments with carnivores were subsequently carried out to diagnose diverse types of hominin and carnivore interactions based on bone surface modifications (namely, tooth marks) inflicted on bones by non-human carnivores (Blumenschine, 1988, 1995; Selvaggio, 1994; Capaldo, 1995). Results suggested that primary access to carcasses by non-human carnivores could be detected by a sharp contrast in tooth mark frequencies on long bone mid-shaft sections. These experiments, however, displayed some conceptual flaws because they were carried out with hyenids (Blumenschine, 1988) or with a

* Corresponding author. Department of Prehistory, Complutense University, c/ Prof. Aranguren s/n, Fac. Geography and History, 28040 Madrid, Spain.

E-mail address: m.dominguez.rodrigo@gmail.com (M. Domínguez-Rodrigo).



Fig. 1. Geographic distribution of the carcasses in the present study (GPS coordinates). Z, zebra; b, buffalo; w, wildebeest; wh, warthog. White colour for defleshed carcasses; yellow colour for carcasses with flesh with scraps; red colour for fleshed carcasses or carcasses with bulk flesh. Code for each carcass: taxon-year-carcass number. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

plethora of uncontrolled agents (Selvaggio, 1994) instead of felids under controlled circumstances (see Domínguez-Rodrigo, 2008, 2012). Observations on carcass scavenging opportunities in the Maasai Mara ecosystem made by Domínguez-Rodrigo (1999) contradicted previous assertions of carcass resource availability in the area (Tunnell, 1990) and showed for the first time how much flesh (in the form of scraps) survived felids' initial consumption of carcasses and how it was anatomically distributed. This was reflected on the frequency distribution of cut marks inflicted by the use of stone tools, which could potentially be used to determine primary or secondary access to carcass remains by early Pleistocene hominins (Bunn, 1981; Domínguez-Rodrigo, 1997a, 1997b). These studies and others expanding the behavioral variability of carcass consumption by felids provided information on the exact anatomical distribution of flesh scraps on long bones (by section and orientation), which could further reinforce analogically-based interpretations on the location of cut marks on fossil bones (Domínguez-Rodrigo et al., 2007a). These referential frameworks were recently questioned by Pobiner's (2007) study of felid behavior in a private ranch in Laikipia (Kenya). However, the selection of an environment highly-impacted by humans (by poisoning competing hyenas and shooting lions) and substantially different ecologically from any national park or reserve where previous studies had been carried out (which are more apt as proxies for Plio-Pleistocene savannas), received some criticism (Domínguez-Rodrigo, 2008, 2012; but see Pobiner, 2008).

The present study builds upon previous research and tries to address the following issues:

1. It expands the knowledge on the variability of carcass consumption behavior by lions and the resulting resource availability for a potential scavenger having secondary access to carcass remains.
2. It analyzes bone modification patterns inflicted by these felids during carcass consumption.

3. It analyzes for the first time variability in resource availability and bone modification according to a set of ecological variables.
4. It enlarges substantially the sample of stone-tool-processed carcasses scavenged at lion kills, by enlarging the number of small- and medium-sized carcasses already reported and by providing for the first time a similar experimental scenario for animals more than 500 kg.

The latter point was developed in the present work because for some early Pleistocene sites, taphonomic evidence of hominins manipulating megafaunal remains has been increasing over the past few years. Hominin modification patterns for buffalo-sized animals and even bigger carcasses have recently been reported at BK (Upper Bed II, Olduvai Gorge) (Domínguez-Rodrigo et al., 2009). The lack of adequate analogical frameworks prevents the understanding on how access to these carcasses occurred. Several prides of modern lions targeting buffaloes were closely monitored in modern savanna habitats and access to the consumed carcasses was carried out with the aid of stone implements. The place selected to carry out this study was Tarangire National Park (Tanzania), where predation on buffaloes can be commonly documented (Fig. 1).

2. Description of the Tarangire ecosystem

Tarangire has often been defined as a woodland ecosystem. However, "woodland" does not properly apply to most of the landscape but to the habitats extending on both sides of the river. Grasslands to the east, both in the park boundaries and outside into the Simanjiro plains from where a great part of the fauna migrate into Tarangire during the dry season, show a mixed ecosystem. Therefore, it is better defined as an *Acacia* savanna (Lamprey, 1964). Nine distinct plant associations have been identified, of which the *Acacia tortilis* parkland appears the most attractive to both fauna and visitors. Other zones are riverine grassland, *Acacia-Commiphora*

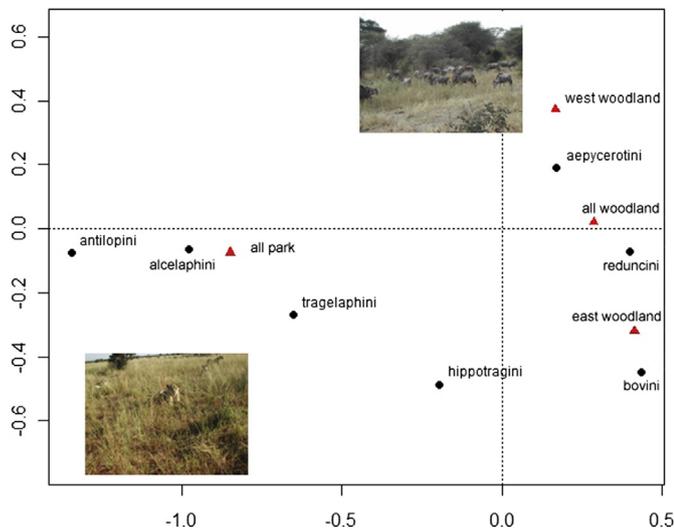


Fig. 2. Correspondence analysis of the variables shown in Table 2 for Tarangire ecosystem and habitat-specific bovid frequencies, comparing bovid tribe distribution and biotope type (all Tarangire, west woodland, east woodland and all alluvial woodland). Dimension 1 account for 80% of variance and Dimension 2 for 11%. Data for Tarangire National Park was obtained from Snelson and Scott (1992). Data for habitat-specific woodland was obtained from Lamprey (1962). See Domínguez-Rodrigo and Musiba (2010) for further data and explanation.

woodland, *Combretum-Dalbergia* woodland, sparse gallery forest and woodland along drainage lines, whistling-thorn *Acacia drepanolobium*, and black cotton soil pans with a thin grass cover. *Euphorbia* spp. and succulents are found in the deeper gullies and on rocky ridges. Baobab trees *Adansonia digitata* commonly occur in association with several of these communities.

Lamprey's (1962, 1963, 1964) count of animals in Tarangire involved continuous monitoring every month in several transects during four consecutive years. Ground transect count was confirmed with aerial counting. Transects were monitored on a daily basis, which renders the resulting estimates some of the most accurate produced for any census carried out in bushy environments.

Several lessons for palaeoecologists can be grasped from Lamprey's (1964) data. First, some purported taxa interpreted in the fossil record as resident can be migratory (such as buffalo [*Syncerus caffer*]) or highly seasonally-fluctuating in certain years (waterbuck [*Kobus ellipsiprymnus*]). The immigrant species (zebra [*Equus buchelli*], buffalo, wildebeest [*Connochaetes taurinus*], elephant [*Loxodonta africana*], and eland [*Taurotragus oryx*]) show significant variation from year to year in each area sampled. For resident species (lesser kudu [*Tragelaphus imberbis*], impala [*Aepyceros melampus*], warthog [*Phacochoerus africanus*], giraffe [*Giraffa camelopardalis*], and dik dik [*Madoqua kirkii*]), there is a closer correspondence when comparing their density year after year.

Lamprey (1964) showed the distribution of fauna per habitat on one random day of the end of the wet season during a drought year. Although one day is a non-valid sample, it is a good start to observe that waterbucks hardly move away more than 2 km from the river. Lamprey (1963) showed that the highest density peaks for most taxa occur in ecotones, that is in areas that mark the transition from one habitat type to the other (from open to moderately dense), probably because of the diversity of food in a short range. He also showed that open-country animals such as zebras are very tolerant of bush habitats. Both observations cast some doubts on rigid habitat interpretations from observing taxa alone.

Lamprey (1963, 1964) carried out his study in an area of the Tarangire Park sampling about 4 km on each side of the alluvial plain

of the Tarangire River, which is mostly covered by woodland. This habitat shows several biotope forms under the woodland habitat: *Acacia* woodland to the west of the river and *Acacia-Commiphora* woodland to the east of the river. The former is moderately dense to more open close to the river and the latter is very dense to more open also close to the river. The sampled area makes a perfect proxy for alluvial woodland in the vicinity of the river. The data derived from this restricted woodland habitat are different when compared to the census of the park spanning a higher diversity of habitats (Domínguez-Rodrigo and Musiba, 2010). A Pearson's Chi-square test ($X^2 = 125.73$, $p = 0.000$) proving that the null hypothesis of independent variables is wrong shows that bovid tribe distribution and habitat type are clearly related and that the bovid representation documented in the alluvial woodland differs significantly from that of the whole assemblage of habitats in the park (Domínguez-Rodrigo and Musiba, 2010). A correspondence analysis shows this graphically (Fig. 2; data from Domínguez-Rodrigo and Musiba, 2010). A two dimension solution provides a clear picture of the separation between the park census and the targeted woodland census. In the latter, the distribution of the *Acacia* woodland to the west of the river is marked by a higher presence of *Aepycerotini* and lower frequency of *Bovini* compared to the east side of the river where the denser *Acacia-Commiphora* woodland occurs. The woodland habitat (characterized by a high percentage of *Aepycerotini*, *Bovini* and *Reduncini*) is markedly different from the park faunal composition in which *Alcelaphini* are the dominant tribe.

Local taxa may move out when immigrants move in to avoid competition. For example, impalas constitute 80% of the fauna in the wet season and only 10% in the dry season because of competition with zebras (Lamprey, 1963, 1964). Most predation takes place in the dry season and therefore, most of the carcasses accumulated are dominated by equids, where most of the local fauna are impalas. This has important repercussions not only for ecological interpretations (see Domínguez-Rodrigo and Musiba, 2010), but also for the study of lion predation and resource availability for scavengers (this work).

3. Sample and method

The study was carried out consecutively for three years, during the middle of the dry season (September–October 2008), the end of the dry season and first part of the rainy season (November–December 2009), and the beginning and middle of dry season (July–August 2010). Six prides of lions were continuously monitored with the aid of radio-collars. A minimum of one lion in each pride wore a radio-collar during the time of this study. This was enabled by the on-going Tarangire lion Project based at the park and under the directorship of one of us (B.K.). These prides were thus monitored year-round, including when they leave the park towards the Simanjiro plains in the wet season and their return to Tarangire during the dry season. The radio-collar transmitters enabled the simultaneous monitoring of more than one pride at the time and there were times when prolonged carcass consumption episodes by lions were documented in more than one pride of lions at the same time.

In contrast to the few-hour carcass consumption process commonly documented in open habitats of the Serengeti (Blumenschine, 1986) or Maasai Mara (Domínguez-Rodrigo, 1999), carcass consumption in Tarangire was most frequently more prolonged, and it involved a full day and commonly more than one day (irrespective of carcass size). This type of delayed consumption was similar to that documented in Galana and Kulalu (Kenya) (Domínguez-Rodrigo, 1999). A common feature between the latter and Tarangire is that lions, at least during the time of the study, lived in small numbers instead of large prides (Table 1).

Table 1
Composition of the Tarangire lion-hunted carcass sample.

Year	Habitat	Taxon	Consumption time	Number of lions	Adult	Juvenile
2008	Bush	Warthog	2 h	3	2	1
2008	Bush	Buffalo	12 h	6	3	3
2008	Plain	Wildebeest	70 h	4	2	2
2008	Forest	Giraffe	8 h	2	2	0
2008	Plain	Buffalo	12 h	10	4	6
2008	Bush	Buffalo	9 h	2	2	0
2008	Bush	Buffalo	23 h	1	1	0
2008	Bush	Zebra	49 h	3	1	2
2008	Plain	Zebra	12 h	1	1	0
2008	Bush	Zebra	8 h	16	12	4
2008	Bush	Zebra	24 h	3	3	0
2008	Plain	Zebra	9 h	13	10	3
2008	Forest	Zebra	72 h	3	1	2
2008	Plain	Zebra	12 h	6	4	2
2008	Bush	Zebra	12 h	2	2	0
2008	Forest	Wildebeest	6 h	4	2	2
2009	Plain	Buffalo	16 h	5	2	3
2009	Forest	Buffalo	5 h	1	1	0
2009	Forest	Warthog	12 h	2	2	0
2009	Plain	Zebra	92 h	1	1	0
2009	Bush	Wildebeest	6 h	2	2	0
2009	Bush	Buffalo	19 h	5	2	3
2009	Bush	Buffalo	15 h	2	2	0
2009	Forest	Zebra	9 h	1	1	0
2009	Forest	Zebra	3 h	5	5	0
2009	Forest	Zebra	44 h	1	1	0
2009	Bush	Buffalo	3 h	5	5	0
2009	Bush	Wildebeest	2 h	13	13	0
2009	Bush	Zebra	9 h	5	5	0
2009	Forest	Wildebeest	1 h	4	4	0
2010	Plain	Warthog	3 h	7	2	5
2010	Bush	Wildebeest	17 h	7	2	5
2010	Plain	Buffalo	24 h	4	4	0
2010	Bush	Zebra	24 h	7	2	5
2010	Bush	Zebra	9 h	4	3	1
2010	Forest	Zebra	21 h	4	4	0
2010	Forest	Zebra	24 h	4	4	0
2010	Plain	Wildebeest	24 h	7	2	5
2010	Forest	Wildebeest	24 h	2	2	0
2010	Forest	Wildebeest	24 h	2	2	0
2010	Forest	Zebra	22 h	2	0	2
2010	Forest	Wildebeest	3 h	7	2	5

A total of 42 carcasses were studied (Table 1) out of several more that were monitored, but which were not included in this study because either observational control was lost at some point of the monitoring of carcass consumption (if consumption lasted more than one day and other prides consuming carcasses were being monitored at the same time) or remains were lost to hyenas during nocturnal observation or consumption was interrupted by non-natural agencies (e.g., tourists stressing lions at a kill). Carcass monitoring for the study documenting the distribution of flesh was frequently continuous. In those cases where monitoring had to be interrupted and later resumed (provided lions were still with the carcass), the appendicular anatomical sections already consumed by lions were examined when lions were resting a short distance away from the carcass and sometimes collected if they were already dismembered. When observations were resumed after a temporary absence from the kill, carcass state was compared to that documented upon abandonment by lions and if no evidence was documented of further consumption or modification by other agents (which were never observed to intervene until lions completely gave up control of the carcass), then the consumption process was continued and remains were collected afterwards. This involved only a small number of carcasses and most were monitored uninterruptedly from initial consumption until abandonment by lions, especially those involving one day and/or night.

Monitoring took place both during daylight as well as during night time with special permission from TANAPA (Tanzanian National Parks). Kills were assigned GPS coordinates and then plotted via Google Earth (Fig. 1).

Prior to the collection of carcass remains, detailed note was taken on the exact location of surviving flesh (in the form of bulk muscle [partial or complete] or as scraps) on each element (Table 2). Then, aging of the individuals was made by documenting dental eruption and wear patterns. In some cases several mandibles were collected. Although detailed information was taken on flesh survival on each anatomical element and conspicuous damage to bones at the kill site, only limb bones were collected for a more detailed analysis of bone surface modification and manipulation with stone tools. The transported carcass parts were cleaned at the camp by boiling them with a solution of neutral detergent until the scraps were detached. In few cases, hyenas visiting the camp at night took some of the bones exposed for drying, which made us move the bones above the ground to a tin roof of the store building of the lion research home base, where they were not accessible by hyenas or other carnivores. After drying, bones were stored in metal boxes to prevent rodents or other animals from having access to them. Only those carcasses where control was complete (e.g., observation started early in the consumption process and finished upon abandonment by lions) were used to analyze the distribution of bone damage patterns (Table 3).

Table 2
Survival of flesh on the Tarangire lion-hunted carcass sample.

Year	Carcass n.	Taxon	Bulk flesh	Scraps on ULB ^a	Scraps on ILB ^b
2008	1	Warthog	None	1 Fem, 1 hum	2 rad, 1 tib
2008	2	Buffalo	None	None	None
2008	3	Wildebeest	All	All	All
2008	4	Giraffe	2 Rad, 2 tib	2 Hum, 2 fem	All
2008	5	Buffalo	2 Rad, 2 tib	2 Hum, 2 fem	All
2008	6	Buffalo	2 Rad, 2 tib	2 Hum, 2 fem	All
2008	7	Buffalo	2 Rad, 2 tib, 1 fem, 1 hum	1 Hum, 1 fem	All
2008	8	Zebra	None	None	None
2008	9	Zebra	2 Rad, 2 tib	2 Hum, 2 fem	All
2008	10	Zebra	None	None	None
2008	11	Zebra	None	None	None
2008	12	Zebra	None	None	None
2008	13	Zebra	None	None	None
2008	14	Zebra	2 Tib	2 Hum, 2 fem	2 Rad
2008	15	Zebra	None	None	None
2008	16	Wildebeest	2 Hum, 2 rad, 2 tib	2 Fem	All
2009	1	Buffalo	2 Rad, 2 tib	1 Hum	All
2009	2	Buffalo	All	1 Hum, 2 fem	All
2009	3	Warthog	None	1 Fem	1 Tib, 1 rad
2009	4	Zebra	2 Tib, 2 rad	None	None
2009	5	Wildebeest	None	None	2 Rad, 2 tib
2009	6	Buffalo	2 Tib, 1 hum, 2 rad	1 Hum, 2 fem	All
2009	7	Buffalo	2 Rad, 2 tib, 1 fem	2 Hum, 1 fem	All
2009	8	Zebra	2 Hum, 2 rad, 2 tib	2 Fem	All
2009	9	Zebra	None	2 Hum, 2 fem	2 rad, 2 tib
2009	10	Zebra	2 Rad, 2 tib	2 Hum, 2 fem	All
2009	11	Buffalo	2 Tib, 2 rad	2 Hum, 2 fem	All
2009	12	Wildebeest	None	All	All
2009	13	Zebra	2 Tib, 2 rad	2 Hum, 1 fem	All
2009	14	Wildebeest	None	1 Fem, 1 hu,	2 Tib, 2 rad
2010	1	Warthog	None	1 Fem	None
2010	2	Wildebeest	None	1 Fem, 1 hum	1 Tib
2010	3	Buffalo	2 Rad	2 Fem, 1 hum	1 Tib
2010	4	Zebra	2 Tib, 2 rad	2 Hum, 2 fem	All
2010	5	Zebra	1 Tib, 2 rad	2 Fem, 1 hum	1 Tib
2010	6	Zebra	1 Rad	None	2 Tib, 1 rad

Table 2 (continued)

Year	Carcass n.	Taxon	Bulk flesh	Scraps on ULB ^a	Scraps on ILB ^b
2010	7	Zebra	None	1 Fem	1 Tib
2010	8	Wildebeest	None	2 Hum	1 Tib
2010	9	Wildebeest	2 Rad	2 Hum	2 Tib
2010	10	Wildebeest	1 Hum, 1 rad	2 Hum, 1 fem	2 Tib, 1 rad
2010	11	Zebra	None	None	None
2010	12	Wildebeest	None	1 Hum, 2 fem	None

^a ULB, Upper limb bones (humerus and femur).

^b ILB, Intermediate limb bones (Radius–ulna and tibia).

Table 3

Frequency of tooth marked specimens per element type and according to carcass size.

	Proximal	Shaft	Distal	Total with damage	Total collected
Small/medium sized					
Humerus	54 (79.4)	27 (39.7)	17 (25)	56 (82.3)	68
Radius–ulna	42 (72.4)	13 (22.4)	7 (12)	40 (68.9)	58
Femur	53 (82.8)	30 (46.8)	48 (75)	60 (93.7)	64
Tibia	27 (49)	8 (14.5)	7 (12.7)	28 (50.9)	55
					245
Large					
Humerus	14 (87.5)	5 (31.2)	5 (31.2)	14 (87.5)	16
Radius–ulna	5 (25)	2 (10)	1 (5)	5 (25)	20
Femur	13 (65)	9 (45)	8 (40)	15 (75)	20
Tibia	2 (11.1)	0 (0)	0 (0)	28 (11.1)	18
					74
Total					
Humerus	68 (80.9)	32 (38)	22 (26.1)	70 (83.3)	84
Radius–ulna	47 (60.2)	15 (19.2)	8 (10.2)	45 (57.6)	78
Femur	66 (78.5)	39 (46.4)	56 (66.6)	75 (89.2)	84
Tibia	29 (39.7)	8 (10.9)	7 (9.5)	30 (41)	73

The study focused on two research questions: how the degree of carcass defleshing was related to ecological variables and how this was reflected on damage patterns inflicted on carcasses during consumption by lions. For the first question, the following variables were defined:

1. Carcass size. This was applied inter-specifically (different-sized taxa) and intra-specifically (different ages of the same taxon) (Table 1). Carcasses were divided into three sizes: small (Bunn's (1982) sizes 1 and 2), medium-sized (Bunn's (1982) size 3) and large (Bunn's (1982) size 4).
2. Number of lions at kill. This included differentiating adults from juveniles and infants (Table 1).
3. Carcass state upon recovery. This involved differentiating if the carcass was fleshed (when evisceration had taken place and flesh was intact on limbs and most of the axial skeleton), moderately fleshed (when bulk flesh was documented in more than one element) and defleshed (when flesh was either non-existent or documented in the form of scraps). The definition of "scrap" refers to any bone that retained less than 10% of its original flesh mass (Domínguez-Rodrigo, 1999).
4. Habitat type. Although Lamprey (1964) had differentiated several types of habitats, using different types of botanical taxa and the combination of topography, bush and grasses (see above), here we will initially adhere to a more physiognomic scheme using different degrees of cover by differentiating among gallery forest-woodland, bushy plain and open grassland.
5. Season. We differentiated among early-middle dry season (July–September), middle-late dry season (September–November) and beginning of rainy season (late November–December).

6. Distance from the Tarangire River, which is the main source of water during the dry season, measured in lineal kilometers.

For the study of different bone damage patterns, the following variables were documented:

1. Presence of tooth mark damage. Bone alterations were recorded according to the portion eaten, gnawed or modified, following descriptions provided by Binford (1981): scores (defined as deep furrows or shallow indentations shaped as longitudinal scratches on bone surfaces), punctures (deep holes produced by the crushing of the bone), pits (small, shallow depressions, often appearing in multiple sets) and furrowing (defined as the removal of cancellous tissue from bone). Tooth marks on limb bones were microscopically identified following the methodological criteria specified by Blumenschine (1988, 1995) and Blumenschine and Selvaggio (1988, 1991), with the aid of hand lenses and binocular lenses (when necessary) mostly under 20×.
2. Tooth mark size. Marks were measured with the aid of a digital calliper. Length (maximum axis of pits or major axis of scores) and breadth of each mark were measured. Due to the large investment of time required by carefully measuring tooth marks, only the carcasses obtained during 2008 were used for this analysis.
3. Tooth mark distribution. Marks were tallied according to bone section (epiphysis [both, proximally and distally] and mid-shaft).
4. Bone breakage.

Bone damage patterns were documented first by quantifying the presence of tooth-marked elements on the complete bone sample. However, this frequency is unrealistic as an analog modeling lion-inflicted bone damage on carcasses that are fragmented and/or modeling secondary access to lion-consumed carcasses by hominins. For this reason, damage patterns were also tallied per fragmented long bone. Given that the collected carcasses constitute the largest taphonomic collection of lion-modified bones available to date, fragmenting the bones would have affected the usefulness of this collection for other taphonomists. For this reason, we proceeded to employ the same approach as Domínguez-Rodrigo et al.'s (2007b) when analyzing tooth mark frequency and distribution in Brain's experimental collection of complete felid modified bones available in the Traansval Museum (South Africa). This approach consisted of creating virtual fragmentation of each element by procuring a bone of each type from an equid, a suid, a deer (as a proxy for a middle-sized antelope) and a buffalo and fragmenting them with a hammerstone after butchery. The fragments of each element thus obtained were overlaid to templates of each long bone on its four orientations (cranial, caudal, medial and lateral) where each tooth mark identified had been carefully drawn. Then, tallying of tooth-marked specimens of each virtual element was carried out. For the analysis of long bone damage patterns metapodials were excluded because they are abandoned unmodified most of the time.

A sample of carcasses was further processed with the aid of stone tools to replicate scenarios of hominins having secondary access to felid-defleshed carcasses. Due to logistic problems, this could only be done at the end of 2009 and more extensively during 2010. For this study, the carcasses (appendicular skeleton) that were completely collected and processed with stone tools were carcass 9 from 2009 and all carcasses from 2010. The resulting cut marks were also drawn on templates of each bone. These bones were subsequently virtually fragmented following the same procedure as for the analysis of tooth mark frequencies per broken

element (see supra). This has expanded significantly the number of available carcasses defleshed by felids and subsequently processed with lithic artifacts (see Domínguez-Rodrigo, 1997a, 1997b, 1999). However, previous experiments were carried out only with medium-sized carcasses. The current study includes for the first time size-4 carcasses (buffaloes). To create an analogue representing primary access to carcasses of this size, two completely defleshed appendicular skeletons of a buffalo and a cow were also butchered with stone tools. The buffalo skeleton was obtained at a lion kill that had been disturbed by humans and the carcass was abandoned with fleshed limbs. In all these butchery experiments, defleshing and not dismembering was targeted, following the same protocol as in Domínguez-Rodrigo (1997a, 1997b). However, it differs from the latter study in targeting bulk meat removal and not every single small scrap of flesh that exists after filleting has taken place. This probably conditions the result displayed in this study. Once bones were completely defleshed, special care was used in disarticulating the bones on the same points with a metal knife, so that the possible resulting cut marks were easily differentiated from those inflicted while using stone tools. Only upper (humerus and femur) and intermediate (radius–ulna and tibia) long bones were used because lower limb bones (metapodials) are non-discriminatory of the order of access to carcasses (Domínguez-Rodrigo, 1997a, 1997b). Marks were tallied according to element type and element section (epiphysis or shaft). The stone artefacts used were flakes made of chert, quartz, and basalt. Butchery was performed by the first author of this work (A.G.).

4. Results

4.1. Carcass consumption and flesh availability upon abandonment

Carcasses were consumed during longer periods than reported in Serengeti (Blumenschine, 1986), irrespective of their size. Small carcasses were consumed between 6 h (median) and 8 h (mean). Mean and median values for large and medium-sized carcasses are very similar, with only slightly higher values for the latter, which

suggests that at Tarangire, carcass size (other than for small animals) does not determine the amount of time lions spend at any given kill (Fig. 3). Large carcasses were consumed on average about 13.8 h (median = 12 h). Medium-sized carcasses were abandoned most commonly after 14 h (median), although the average is 23.6 h due to a few outliers. Despite this difference in consumption time, a Kruskal–Wallis test shows that carcass size alone does not produce significant differences in the amount of time carcasses lasted before complete consumption (chi-squared = 3.0266, $df = 2$, p -value = 0.2202). This documented time is longer than reported for carcass persistence (time of exposure prior to complete consumption) in Serengeti (4 h for small animals and more than 20 for medium-sized carcasses) (Blumenschine, 1986). However, the concept of carcass persistence is different from the concept of time spent at the kill by lions. The latter was frequently reported for one or 2 h at Serengeti (Blumenschine, 1986) and up to 3 h on average in Maasai Mara (Domínguez-Rodrigo, 1999). Stay at kills lasted substantially longer at Tarangire, probably because prides were smaller and also because the presence of bush near kills enabled access to shade. Furthermore, most kills occurred not far from the Tarangire river (Fig. 1), which was also a very influential factor on the time spent at kills because lions need frequent access to water, especially after they eat.

No significant difference was found between carcass size and habitat (chi-squared = 1.5368, p -value = 0.4637). Most carcasses consumed by lions in open plains (90%; $n = 10$) were abandoned defleshed (Fig. 4; Table 2). The proportion of carcasses with bulk flesh abandoned in bushier habitats is higher since defleshed carcasses in bushy plain (48%; $n = 17$) and in gallery forest (73%; $n = 15$) occur in a lower frequency. When tallied according to carcass size, small carcasses were abandoned completely defleshed (except one carcass with some bulk flesh), irrespective of the number of lions feeding on it (Fig. 5). Seventeen out of twenty two medium-sized carcasses (77%) were also abandoned completely defleshed (Fig. 6), whereas some bulk flesh was documented in the remaining 23%. Defleshed large carcasses constitute a smaller portion compared to smaller animals: five out of thirteen (38%)

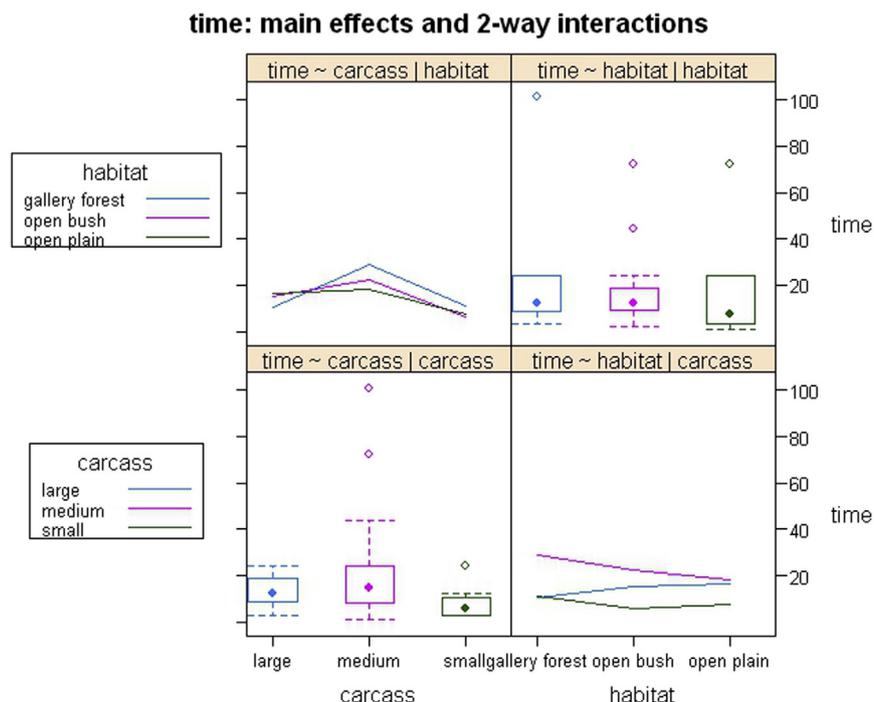


Fig. 3. Ecological analysis of two-way interactions of carcass size, habitat type and time of consumption of carcasses by lions. Time is expressed in hours.

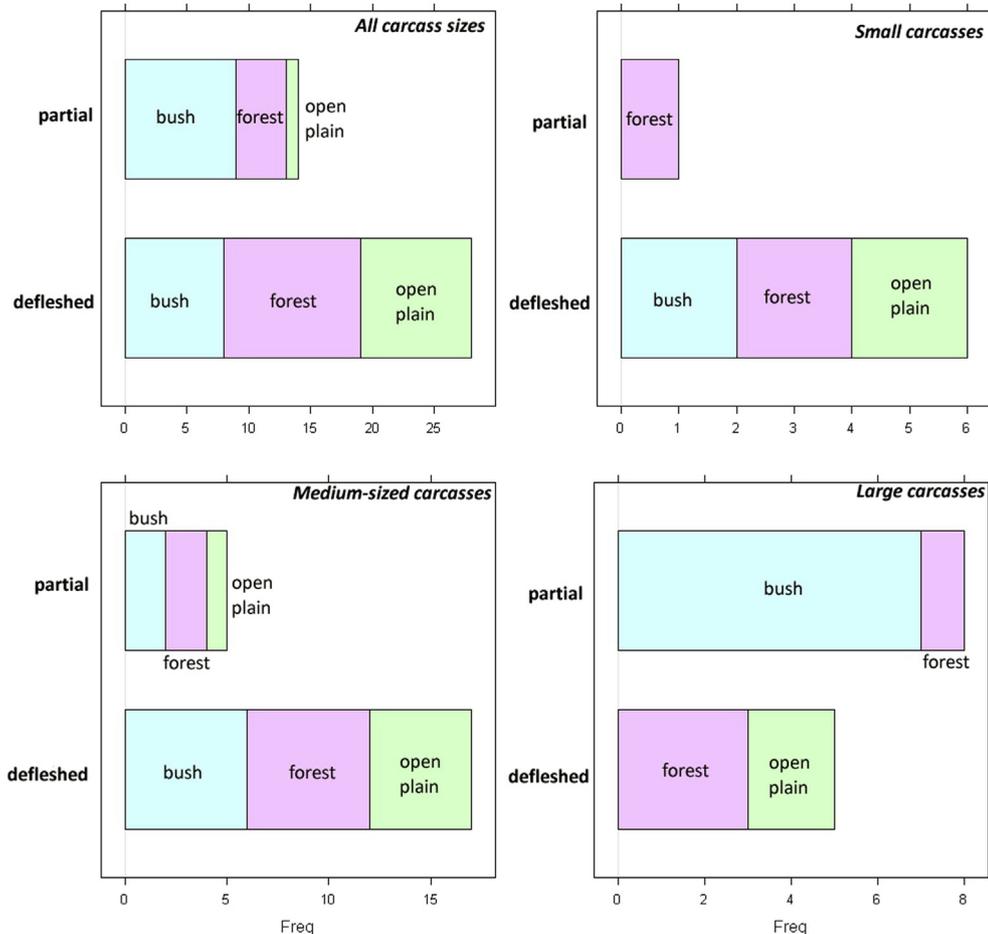


Fig. 4. Intensity of carcass consumption by lions (partially fleshed and defleshed carcasses) according to carcass size and habitat type. Frequencies are expressed in absolute numbers.

buffaloes were defleshed upon abandonment with only flesh scraps surviving (Fig. 7), whereas the remaining 62% showed bulk flesh in various degrees (Fig. 8). It could be argued that the number of lions also determines the amount of flesh available, but a χ^2 test suggests otherwise ($\chi^2 = 2.68$, $p = 0.61$). As can be seen in Fig. 1, the more

fleshed buffalo carcasses were documented in the south of the Tarangire river during the 2009 field season, coinciding with the end of the dry season and the beginning of the rains. At the end of the dry season, water was scarce (that part of Tarangire river was dry) and lions had to travel longer distances to have access to water. Under such circumstances, carcasses were occasionally abandoned partially fleshed after an initial consumption by the pride. This was more commonly documented in larger carcasses than medium-sized carcasses and the further away from the Tarangire gallery forest, the more fleshed the state in which carcasses were abandoned. Those carcasses located in the same area that were hunted and consumed during the earlier part of the dry season (in 2008 and 2010) were much more defleshed, because lions did not have to travel far to get access to water since the Tarangire river had water in those time periods. The sample collected in the north of the Tarangire river, which always contained either running water or ponds, shows a much more defleshed state of carcasses regardless of their size (Fig. 1).

Carcasses with bulk flesh and scraps showed a patterned distribution (Table 2). With the exception of a wildebeest carcass that was hunted very distant from any source of water, all small and medium-sized carcasses are either defleshed or if bulk flesh survived their consumption, it is located on the intermediate bones (radius and tibia). This also applied to large carcasses (only one buffalo had bulk flesh on all upper limb bones). For ten buffalo carcasses and a subadult giraffe carcass, bulk flesh on upper limb bones was only documented on four elements (<10%). Even in



Fig. 5. Juvenile wildebeest (carcass 5, 2009) consumed by two lions. The radio-collared lion is finishing the consumption of the carcass.



Fig. 6. Two zebra carcasses as examples of common defleshing in medium-sized carcasses. Hardly any scrap has survived consumption. The upper image shows defleshing on axial and cranial skeleton (carcass collected at night). The lower image shows typical defleshing of limbs.

those cases where only partial defleshing occurred, femora (with one element exception) were systematically defleshed (Fig. 9). However, bulk flesh was found on >90% of intermediate long bones. Flesh scraps (including small portions of just three of four cm) are also reported in Table 2. Small scraps were documented on upper limb bones of most buffalo carcasses and also on several medium-sized carcasses; although in the latter, almost half of the sample was scrap free. It is important to emphasize that virtually all the completely defleshed (scrap-free) carcasses but one were found at or near the Tarangire River. Therefore, archaeologists modeling hominin scavenging from alluvial environments (e.g., Blumenschine, 1986) should consider using as proxy carcasses consumed by lions in such environments instead of a mixed set of carcasses mostly obtained in other habitats (e.g., Pobiner, 2007), since the former are more commonly defleshed (Fig. 10).

Those upper limb bones from small and medium-sized carcasses bearing flesh scraps also showed a pattern of scrap location. On humeri and femora, most scraps were found on the ends and on femora, some scraps were also documented on the caudal shaft along the linea aspera. Scraps on intermediate bones were located as follows: on the radius, most occurred on the distal end and on the caudal connection with the ulna; on the tibia, most were also located distally and when on the mid-shaft, they occurred on the caudal side.



Fig. 7. Adult buffalo carcass consumed by lions (upper) and totally defleshed upon abandonment (lower).

4.2. Bone damage patterns

Tooth mark frequencies tallied by complete element (MNE) are different from those tallied by number of identifiable specimens to element (NISP). The former show that the number of elements bearing at least one tooth mark is high (Table 3). Humeri and femora are the most frequently tooth-marked bones, followed by the olecranon process of the ulna and tibiae. Radii are the least tooth-marked long bones. About 75% of complete long bones of small and medium-sized carcasses and 83.7% of complete long bones of large carcasses are tooth-marked.

These estimates, however, are inappropriate for evaluating lion bone damage on fragmented assemblages, such as in hypothetical scenarios where humans might scavenge at lion kills by fragmenting long bones to gain access to marrow. When the sample of carcasses consumed by lions is fragmented, the frequencies of tooth-marked specimens drop drastically because most tooth-marked complete elements bear very few tooth marks. This is especially noticeable on shafts, which is the portion that produces more specimens when fragmented and where tooth marks inflicted by lions are scarce or when these are multiple, most frequently they occur in discrete clusters. Almost 99% of all the complete bones in this sample bore less than ten tooth marks on shafts. When considering tooth mark frequencies on the virtually fragmented sample, epiphyses are more highly tooth-marked than shafts on all long bones, irrespective of carcass size (Table 4). It is important to document mark distribution anatomically because a sharp contrast can also be observed when comparing upper versus intermediate limb bones. Humeri and femora are much more highly tooth-marked than radius and tibia both when considering bone portions separately or together. The radius is the least tooth-marked bone in all carcass sizes if excluding the olecranon of the ulna. If it is included (radius–ulna), then the tibia is the least tooth marked element. When using

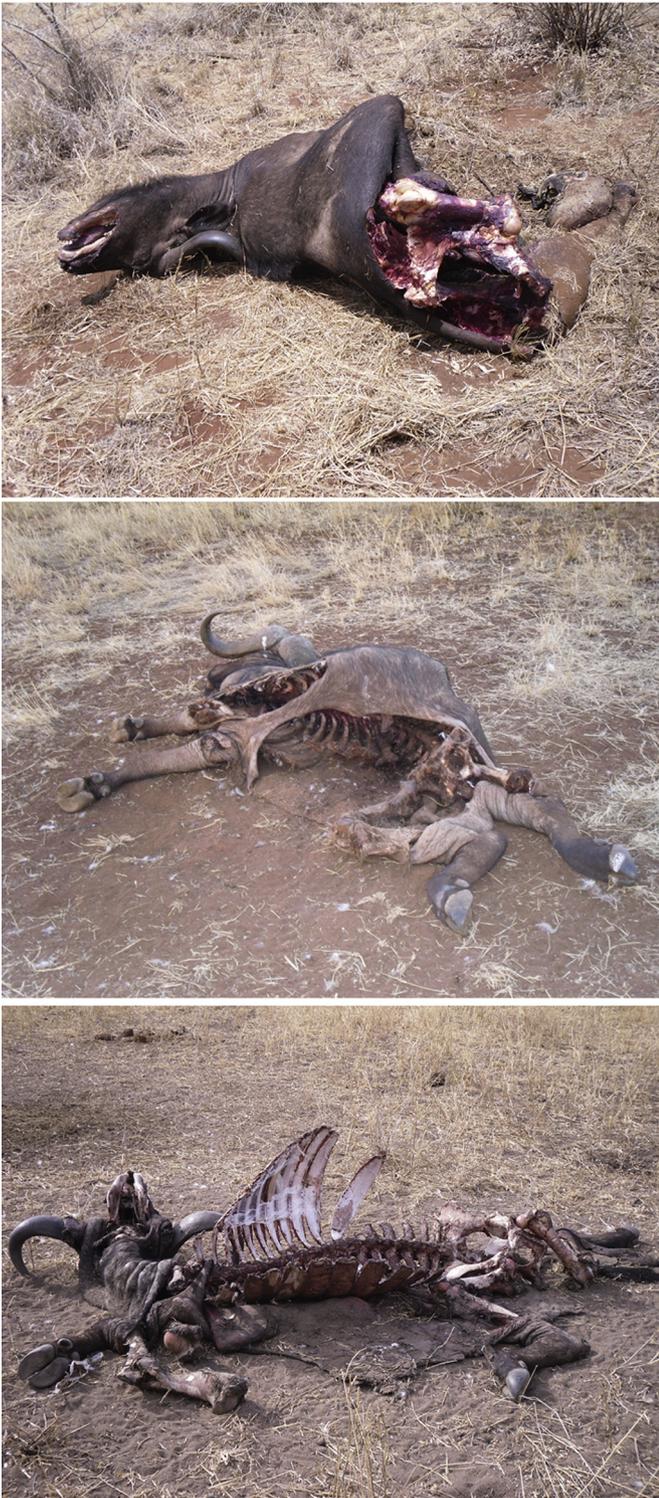


Fig. 8. The three types of buffalo carcass consumption documented in this study. Partially-defleshed (upper), moderately defleshed or bulk fleshed (middle) and completely defleshed (lower). Moderately-defleshed carcasses still exhibited bulk flesh on some parts of the axial skeleton and on the intermediate long bones.

Blumenschine's (1988) approach of assigning specimens to part irrespective of element, 52% of epiphyses from small and medium-sized carcasses are tooth-marked (95% confidence interval: 30.95–71.14) and only 8% of shaft specimens bear at least one tooth mark (95% confidence interval: 4.45–11.29). Similar frequencies can be



Fig. 9. Partially-defleshed carcass (upper) showing complete defleshing of the lumbar area, pelvis and femora (lower). No scrap was documented on the femoral shafts.

documented in larger carcasses: 35% of epiphyses are tooth marked (95% confidence interval: 11.13–60) and 6.1% of shafts bear tooth marks (95% confidence interval: 1.13–11.66). Therefore, this shows that lion-consumed carcasses usually bear few tooth marks when



Fig. 10. Different stages in the consumption of buffalo in the Tarangire riparian habitat. Main: Buffalo carcass partially defleshed in the process of consumption. Insert: Buffalo carcass completely defleshed upon abandonment.

long bones are broken. This result is similar to that documented by Domínguez-Rodrigo et al. (2007b) on carcasses consumed by leopards and cheetahs.

Table 4

Frequency of tooth marked specimens per element and bone portion according to carcass size.

	Epiphyses	Shafts	Epiphyses plus shafts
Small/medium-sized carcasses			
Humerus	71/136 (52.2)	31/340 (9.1)	102/476 (21.4)
Radius—ulna	49/116 (42.2)	17/290 (5.8)	66/406 (16.2)
Femur	101/128 (78.9)	47/384 (12.2)	148/512 (28.9)
Tibia	34/110 (30.9)	17/385 (4.4)	51/495 (10.3)
Total	255/490 (52)	112/1399 (8)	367/1889 (19.4)
Large carcasses			
Humerus	19/32 (59.3)	8/80 (10)	22/112 (10.5)
Radius—ulna	10/40 (25)	4/100 (4)	14/140 (10)
Femur	21/40 (52.5)	14/120 (11.6)	35/160 (21.8)
Tibia	2/36 (5.5)	0/126 (0)	2/162 (1.2)
Total	52/148 (35.1)	26/426 (6.1)	73/574 (12.7)



Fig. 12. Lion eating a warthog (upper). Notice how in carcasses this size, conspicuous damage to bones can also include bone breaking, especially on proximal epiphyses of upper limb bones (lower).

Bone damage is probably related to the intensity with which carcasses are consumed. Therefore, the degree of defleshing may determine how much a bone may be modified. This means that bone damage can also be understood within the ecological context where carcass consumption takes place. A multiple correspondence analysis using as explanatory variable bone damage on humeri and femora ends and as predictor variables some of the ecological variables described in the Method section shows that the main factor determining carcass modification is carcass size in combination with open/closed environment (Fig. 11). The smaller the carcass, the more intensively it is modified by lions (Fig. 12). The least relevant variable is the number of lion consumers. Closed habitats contained carcasses that exhibited less damage than those from open habitats, but this may be biased by open habitats having yielded a higher number of smaller carcasses.

Tooth pit dimensions on a sample of 406 tooth marks, showed size differences between dense cortical shafts and cancellous ends (*U*-test *p*-value <0.05). The mean length of tooth pits on the former is 2.8 mm versus 6.1 in the latter. Differences for score breadths are similar; the average on shafts is 0.86 mm and 2.7 mm on ends. This indicates that marks left on dense cortical bone by lions are on average very small; smaller than previously reported by Domínguez-Rodrigo and Piqueras (2003). The ratio of score to pits on shafts is 4:1, which shows that the abundance of scores and the underrepresentation of pits could also be used as a diagnostic feature differentiating lions from more durophagous carnivores such as hyenas and canids, where pits are always more frequent than scores (Egeland et al., 2008; Yravedra et al., 2011).

4.3. Carcasses processed with stone tools

A total of 12 carcasses initially consumed by lions were processed with lithic artefacts to remove the available flesh, either in the form of bulk meat or flesh scraps (Tables 5–7). The resulting cut marks show that upper limb bones are the least cut-marked appendicular portion of all the meat-bearing long bones. Intermediate bones displayed a higher frequency of cut marks. Likewise, a contrast was observed when comparing bone section types. Shafts were substantially less cut-marked than ends. The sample of medium-sized carcasses processed with stone tools provide even lower estimates of cut marks than previously reported for field-defleshed carcasses butchered at Maasai Mara and at Galana & Kulalu (Kenya) (Domínguez-Rodrigo et al., 2007a). The contrast with carcasses initially defleshed by humans is sharp (Fig. 13). The

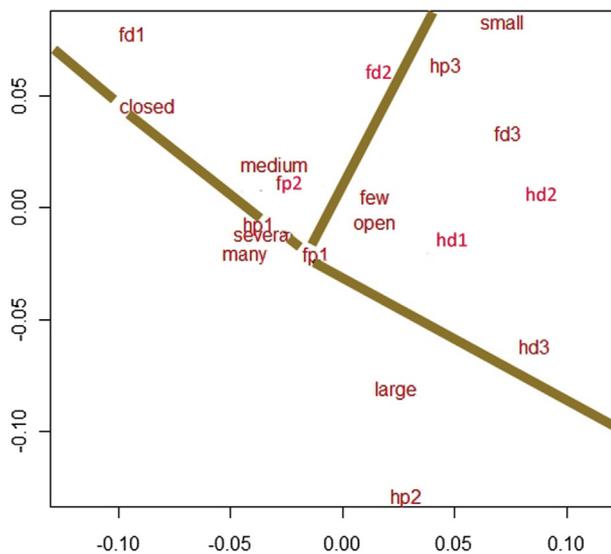


Fig. 11. Multiple correspondence analyses showing the distribution of the factors of each variable. Numbers indicate degree of modification with 1 being slight and 3 being intense. Key: h, humerus; f, femur, p, proximal; d, distal. Number of lions: few, consumption by a maximum of 6 lions; several, consumption by 7–12 lions; many, consumption by a pride larger than 12 individuals. Habitat type: open, closed. Carcass size: small (Bunn's (1982) sizes 1–2), medium (Bunn's (1982) size 3), large (Bunn's (1982) size 4–5).

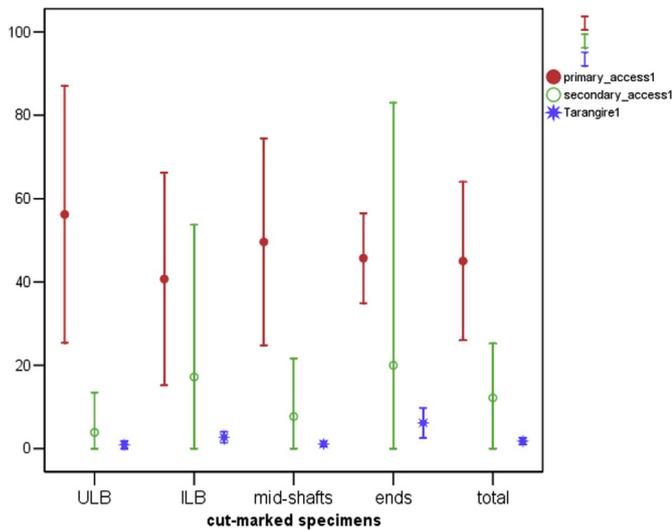


Fig. 13. Percentages of cut marked specimens (Y-axis) in the reported samples of small/medium-sized carcasses experimentally butchered with stone tools. Range of variation (95% confidence intervals) for experiments simulating primary and secondary access to fleshed carcasses (Table 5). Data for experiments replicating primary and secondary access are from Domínguez-Rodrigo (1997a, 1997b). The latter were collected at lion kills in Maasai Mara and Galana & Kulalu (Kenya). The ranges of variation of the Tarangire experiments, also replicating secondary access to lion kills (this study) are also displayed and show an even lower frequency and more restricted range than previous experiments butchering carcasses at lion kills. ULB, upper limb bones; ILB, Intermediate limb bones.

contrast is also sharp when compared to previous experiments butchering carcasses from felid kills (Domínguez-Rodrigo, 1997a, 1997b), because in those experiments complete removal of every single flesh scrap was targeted, irrespective of its size (most were extremely small), whereas in the present study, scavenged carcasses were butchered by removing the most conspicuous scraps, disregarding those that were smaller than 1–2 cm.

Table 5

Distribution of cut-marked specimens from the medium-sized carcasses butchered with stone tools according to total number of identifiable specimens of each part. Percentages are shown in parentheses. Lower table shows mean, standard deviation, sample number and 95% confidence interval where two-tailed alpha is 0.025.

	Carcass 1	Carcass 2	Carcass 4	Carcass 5	Carcass 6	Carcass 7	Carcass 8	Carcass 9	Carcass 10	Carcass 11	Carcass 12
Upper limb bones	0/46 (0)	1/46 (2.1)	0/46 (0)	0/46 (0)	0/46 (0)	1/46 (2.1)	0/46 (0)	2/46 (4.2)	1/46 (2.1)	0/46 (0)	0/46 (0)
Intermediate limb bones	0/50 (0)	2/50 (4)	0/50 (0)	2/50 (4)	2/50 (4)	1/50 (2)	3/50 (6)	1/50 (2)	3/50 (6)	1/50 (2)	0/50 (0)
Mid-shafts	0/80 (0)	2/80 (2.5)	0/80 (0)	2/80 (2.5)	1/80 (1.2)	1/80 (1.2)	2/80 (2.5)	1/80 (1.2)	1/80 (1.2)	0/80 (0)	0/80 (0)
Ends	0/16 (0)	1/16 (6.2)	0/16 (0)	0/16 (0)	1/16 (6.2)	1/16 (6.2)	1/16 (6.2)	2/16 (12.4)	3/16 (18.6)	1/16 (6.2)	0/16 (0)
Total	0/96 (0)	3/96 (3.1)	0/96 (0)	2/96 (2)	2/96 (2)	2/96 (2)	3/96 (3.1)	3/96 (3.1)	4/96 (4.1)	1/96 (1)	0/96 (0)
	Mean		s.d.		n		95% c.i.				
Upper limb bones	0.92		1.42		11		0.08–1.76				
Intermediate limb bones	2.72		2.24		11		1.40–4.05				
Mid-shafts	1.11		1.03		11		0.50–1.73				
Ends	6.18		5.84		11		2.55–9.80				
Total	1.81		1.40		11		0.99–2.64				

Table 6

Distribution of cut-marked specimens for the two buffalo carcasses from lion kills and the two experimental fleshed carcasses butchered with stone tools according to total number of identifiable specimens of each part. Percentages are shown in parentheses.

	Carcass 3 (2010)	Carcass 11 (2009)	Fleshed buffalo	Fleshed cow
Upper limb bones	1/50 (2)	0/50 (0)	7/50 (14)	2/41 (4.8)
Intermediate limb bones	4/46 (8.7)	2/46 (4.3)	7/46 (15.2)	4/47 (8.5)
Mid-shafts	2/80 (2.5)	0/80 (0)	9/80 (11.2)	4/72 (5.5)
Ends	3/16 (18.7)	2/16 (12.3)	5/16 (31.2)	2/16 (12.3)
Total	5/96 (5.3)	2/96 (2.1)	14/96 (14.5)	6/88 (6.8)

Table 7

Mean, standard deviation and 95% confidence intervals of both types of butchery experiments simulating secondary access and primary access to lion-defleshed size 4 carcasses. Analysis of 95% C.I. for both sets of experiments are included. They were calculated using the *t* distribution, where $t_{0.025}$ is the critical value of *t* with *n* – 1 degrees of freedom.

	Mean	s.d.	n	95% c.i.
Lion kills (carcasses 3 and 9)				
Upper limb bones	1	1.41	2	0–3
Intermediate limb bones	6.5	3.11	2	2.18–10.81
Mid-shafts	1.25	1.76	2	0–4.71
Ends	15.5	4.52	2	9.22–21.77
Total	3.7	2.26	2	0–6.9
Primary access butchery experiments				
Upper limb bones	9.4	6.50	2	0–22.15
Intermediate limb bones	11.85	4.73	2	2.56–21.13
Mid-shafts	8.35	4.03	2	0.45–16.24
Ends	21.75	13.76	2	0–47.94
Total	10.65	5.44	2	0–21.32

The distribution of cut marks documented in the two buffalo carcasses is similar to those documented in medium-sized carcasses. The frequencies are, however, substantially lower, if sample size in the former is not biasing this estimate (Fig. 14). A safe assumption that such is not the case is that both butchered carcasses are representative of most of the remaining buffalo carcasses studied between 2008 and 2010 in Tarangire in terms of flesh availability after felid consumption. The main differences when butchering fleshed versus largely defleshed buffalo carcasses are documented in the former bearing a few more cut marks on upper limb bones and more specifically on shafts. The latter show fewer specimens with cut-marked shafts on upper limb bones. There are differences also on average values of cut marked specimens from intermediate bones between both scenarios. However, confidence intervals show a strong overlap, which renders the mean values statistically non-significant, probably because felids frequently abandoned bulk flesh on radius and tibia, whose processing created

a similar frequency of cut marks on those bones as when butchering complete elements. In addition, an even more influential reason could be that when defleshing such large amounts of bulk flesh, the butcher does not need to scrape the final scraps of meat off bones and as a result substantially fewer cut marks are produced when compared with smaller carcasses. Therefore, despite the shortcomings of such a small sample size for both types of butchery experiments, cut mark frequencies could be heuristically used to differentiate both scenarios, although not as well as they can for small and medium-sized carcasses, if considering the 10% cut-

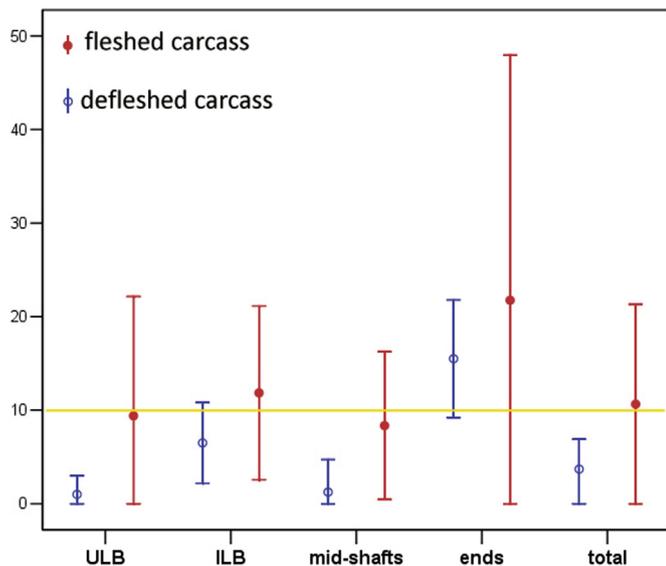


Fig. 14. Percentage of cut-marked specimens (Y-axis) and range of variation (95% confidence intervals) for experiments simulating primary and secondary access to fleshed (red; mean = filled circle) and defleshed (blue; mean = open circle) size-4 (Bunn, 1982) carcasses (Tables 6 and 7). ULB, upper limb bones; ILB, Intermediate limb bones. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

marked specimen boundary. Any assemblage with more than 10% of cut-marked specimens (total) or more than 10% cut-marked specimens from upper and intermediate limb bones, as well as shafts, would be more susceptible of being interpreted as access to fleshed carcasses rather than secondary access to mostly defleshed remains.

5. Discussion

The present study expands and further confirms results of previous studies on flesh availability of small and medium-sized carcasses in Serengeti (Blumenschine, 1986), Maasai Mara, Galana and Kulalu (Domínguez-Rodrigo, 1996, 1999; Domínguez-Rodrigo et al., 2007a). It also adds arguments to the critique of those studies carried out in highly anthropogenically-impacted environments, such as private properties or ranches, where the number of carnivores is insignificant compared to national parks or reserves and their trophic dynamic is further altered by humans either by removing specific carnivore taxa (e.g., hyenas) or shooting lions and, thus, conditioning how these consume their prey (Domínguez-Rodrigo, 2008, 2012).

The present study has also shown how variability in the manner in which carcasses are consumed by lions is ecologically-influenced. Lions, irrespective of the size of the pride, remain more time at kills when they are closer to water. This results in a more thorough defleshing of carcasses than when they are distant from water sources. Some of the evolutionary scenarios of hominins scavenging from felid kills have posited that such scavenging opportunities would be higher in riparian/alluvial environments where water is close (e.g., Blumenschine, 1986). However, previous data for scavenging opportunities have been collected from carcasses found in various types of habitats, several of them distant from water (Blumenschine, 1986; Pobiner, 2007). The results displayed here advice to construct experimental scenarios for such a hypothesis using the anatomical distribution of resources from carcasses found near or at alluvial environments. They are more completely defleshed than carcasses found in open habitats or in

bushy environments far from water in certain times of the year, and their processing with stone tools will potentially leave fewer cut marks on bones.

An important conclusion of this study is that contrary to previous statements (e.g., Selvaggio, 1994; Blumenschine, 1995; Capaldo, 1995; Pobiner, 2007), tooth marks on bones from carcasses from felid kills exhibit drastically fewer tooth marks than on bones from carcasses modified by hyenas (e.g., Faith, 2007; Egeland et al., 2008). Blumenschine's (1988) experiments constitute the basis for the assumption that any carnivore-first scenario will be conducive to creating more than 70% of shaft specimens with tooth marks. The multi-patterned (felid-hominin-hyaenid) models proposed by some authors (e.g., Selvaggio, 1994; Capaldo, 1995) and used by others (e.g., Pante et al., 2012) systematically to argue that any carnivore (felid included) having primary access to carcasses subsequently exploited by hominins will leave a high number of tooth-marked specimens is unsupported. An extensive critique to this interpretation was presented by Domínguez-Rodrigo (2009, 2012). The reason why felids are believed to leave many tooth marked long bones is that the frequency of complete long bones bearing at least one tooth mark is high (Table 3). However, in most cases this is reflected in one or two tooth marks on the shafts (ends are more highly tooth marked), which once the bone is hypothetically broken by hominins to gain access to marrow, most of the resulting fragments are tooth mark free. Therefore, intensity of tooth marking (i.e., the number of tooth marks per each complete bone) is also different from that documented in hyenas.

The present study has also documented that whereas tooth pits are more abundant than tooth scores on ends, the reverse is true on shafts in a proportion of four scores per each pit. This intense scoring is also different from what is documented in hyenas (Egeland et al., 2008). Although it has not been described in detail, the survival of flesh scraps on long bones is similar to that documented by Domínguez-Rodrigo et al. (2007a) for other lion-consumed carcasses, mostly concentrated in areas of muscle attachment or insertion (a.k.a, cold zones).

The butchery experiments with large buffalo carcasses has shown that butchery of such large animals results in substantially fewer cut marks than reported for smaller carcasses. Despite the different states of buffalo carcass abandonment by lions, the experiments show a strong overlap in frequency and anatomical distribution of cut marks when butchering buffalo carcasses at lion kills and when butchering complete carcasses. The presence of bulk flesh is partly accountable for that since it survives mostly on intermediate limb bones and such overlap also affects the more intensively defleshed upper limb bones. However, the only potential diagnostic feature that might enable some differentiation is that hindquarters are defleshed early in the consumption sequence, showing utterly defleshed femora even in those cases in which most bulk meat survives in the remainder of the carcass (e.g., partially defleshed carcasses). Only the removal of the small surviving scraps could in these cases create cut marks on femoral shaft surfaces.

The present study stresses the importance of environmental variables in shaping carnivore behavior and the resulting bone modification patterns. Therefore, actualistic studies on carnivores should contemplate the selection of the right environments for modeling prehistoric predators. Bunge (1981) criticized that most analogical reasoning was either undefined or too narrowly defined under isomorphic (and sometimes homomorphic) applications of the concept. He developed a qualitative concept of analogy embedded within the concept that most analogical reasoning in science occurs in dynamic systemic structures. These systems depend on the tight interaction of three components: composition, structure and environment. Composition refers to the collection of

components in any of two given systems. Structure refers to the relationship of those components within each system. Environment impacts the structure by determining how the system components interact. This third element is of utmost importance because it shows that when comparing two systems (as analogical reasoning does), even if both systems have similar composition their structure may be different on account of the environmental differences of each of them.

From this point of view two systems are “substantially analogous” when they share the same components, “structurally (or formally) analogous” when they share similar structures and “environmentally analogous” when their contexts are similar.

To emphasize that not all analogical reasoning is equally valid, Bunge (1981) stressed that there were different (heuristic and epistemic) degrees of analogy. The degree of similarity between system A and system B could be proportional to their similarity in composition (degree of substantial analogy), structure (degree of structural analogy) and environment (degree of environmental analogy). The most important criterion in using degrees of analogy lies in the combination of the three types of intertwined parts of analogical reasoning, which is what Bunge (1981) identified as the degree of total analogy defined as the average of the degree of substantial, structural and environmental analogies shared between two systems.

When comparing different types of carnivores and their effects on bones, analogies must be substantially and structurally similar (using the same types of bones from the same carcass type: as opposed to using similar bones from different carcass sizes). Ideally, the analogy should also be environmentally similar. A recent study shows the importance of the environmental part of analogy by comparing how the same bone modifying agent (lions) could produce different modification patterns on the same bones from the same carcass type depending on the context (Gidna et al., 2012). Gidna et al. (2012) showed that the Tarangire wild lions and a group of captive lions in Spain produced different bone modification patterns. This is of utmost relevance because it casts doubt on analogical frameworks made with carnivores in captivity, but also because it underscores the need of understanding carnivore behavioural variability in the wild. By having selected the Tarangire ecosystem, which differs from Serengeti, Maasai Mara and Galana & Kulalu, where previous neo-taphonomic research on lion behaviour was done, this study increases our understanding on lion behavioural variability and its analogical application to the past.

6. Conclusions

Current interpretations on Early Pleistocene hominin subsistence, with special emphasis on the hunting and scavenging debate, revolve around adequate understanding on how felids consume their prey and the resulting bone modification patterns. The present study supports previous ethological observations carried out in other East African natural parks regarding lion behavior (Blumenschine, 1986; Domínguez-Rodrigo, 1999). These felids consume their prey thoroughly leaving only occasional bulk flesh remains and limited scraps. Scavenging from their kills does not allow regular access to flesh but to long bone marrow and head contents. This contrasts with Pobiner's (2007) study of lion behavior in a private ranch. A recent study by Gidna et al. (2012) clearly shows that the environmental component of analogies is determinant as can be documented in significantly different bone modification patterns documented in lions in captivity when compared to wild lions.

The present work has also shown that lion bone modification is limited and anatomically patterned. It has also shown that lions produce a different proportion of tooth mark types when compared to durophagous carnivores such as hyenids or canids. Although the

frequency of tooth marked complete bones is high, it is shown that in hypothetical scenarios of hominins scavenging these bones by breaking them open to gain access to marrow the resulting tooth mark frequency (measured by fragmented specimens in contrast with complete elements) is substantially lower as previously documented with other felid-modified bone collections (Domínguez-Rodrigo et al., 2007b) and undifferentiated from tooth mark frequencies reported in experiments where hyenas have secondary access to human-fragmented bones.

The expanded sample of carcasses butchered with stone tools provides a more reliable estimate of cut mark frequencies and anatomical distribution than in previous experiments and shows that cut mark frequency tallied by bone section and element type is a heuristic tool to discriminate primary from secondary access in small and medium-sized carcasses. Experiments modeling butchery of large carcasses scavenged at lion kills provides a more ambiguous analogical framework but also stresses that differences between primary and secondary access can be better understood when comparing cut mark frequency and distribution the heavily fleshed upper limb bones, more intensively defleshed by lions than intermediate long bones.

In addition, an ecological understanding of the variables which determine the degree of exploitation of carcasses by lions show that the more defleshed carcasses are ecologically located close to water sources, especially in riparian and alluvial environments. This underscores the need to use this type of carcass consumption by lions when modeling hominin scavenging from lion kills in riparian environments, as in the felid-hominin-hyenid interpretive model suggested by Blumenschine (1995), instead of using carcasses from heterogeneous habitats (as in Selvaggio, 1994) or non-alluvial environments or even in captivity (as in Pobiner, 2007).

This study represents the largest longitudinal research carried out on carcasses consumed by lions to date, with a tighter control of the documented consumption processes, which can be confidently used as an analogical framework to understand lion behavior in prehistoric African savannas. The detailed description of bone modification patterns provides a good tool to identify lion bone damage. The butchery experiments on lion kills also provides comparative results with previous similar experimental work and improves our understanding of cut mark frequency and anatomical distribution according to carcass size when carcasses are accessed secondarily by humans. By having diversified the ecological context where this type of studies has been previously carried out, the present work also contributes to knowing the range of variation of carcass consumption behavior by lions. It is expected that its application to prehistoric contexts will strengthen our interpretations of early hominin behavior.

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