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On *in situ* Attrition and Vertebrate Body Part Profiles

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Ungulate body part representation in archaeological sites potentially reflects human foraging decisions. However, because mammal skeleton macrostructure is heterogeneous, its components may not uniformly resist mechanical causes of attrition. Techniques for analyzing vertebrate body part profiles must either address differential resistance among distinct skeletal density classes or compare skeletal representation within a narrower density range that is widely distributed in the vertebrate skeleton. This presentation concerns the benefits of the second approach as developed previously by the author (Stiner, 1991, *Journal of Archaeological Science* **18,** 455–482; 1994, *Honor Among Thieves: A Zooarchaeological Study of Neandertal Ecology*. Princeton; Princeton University Press). Recent attempts to dismiss the approach misuse available standards on variation in structural density, a point demonstrated using the control data said to invalidate the profiling technique. In fact the mid-points and ranges of variation in bone structural density among elements grouped into the cranial and four appendicular skeletal regions are very similar as measured by photon densitometry, and especially for the skeletal portions commonly used to estimate MNE in Mediterranean Palaeolithic archaeofaunas. Region-by-region anatomical comparisons require fewer assumptions than do analyses that focus on differential resistance (''survivorship'') among the full range of bone density classes and thus are limited by fewer unknowns.

Keywords: DENSITY-MEDIATED BONE ATTRITION, VERTEBRATE TAPHONOMY, ZOOARCHAEOLOGY, VERTEBRATE BODY PART PROFILES.

Introduction

Zooarchaeologists often work with data on prey body part representation in the hope that these patterns will reveal something about human foraging behaviour, particularly carcass acquisition, transport and/or processing habits. Human-collected faunas tend to be highly fragmented, so skeletal element counts must be estimated from the frequencies of unique features that can recognized from partial specimens, such as the head of a femur, the nutrient foramen of a humerus, an occipital condyle of a cranium, a pre-zygapophysis of a lumbar vertebra, or the medial face of the distal epiphysis of a tibia. Because the macrostructure of mammal skeletons is heterogeneous, particularly in large mammals, the many components of a skeleton may not resist decomposition forces equally. Zooarchaeologists therefore work in steps, beginning with questions about the agencies of bone collection, modification, and destruction. Later, and assuming that biases introduced by non-human agencies can be excluded or controlled, analysts may take on questions about human behaviour.

Bone destruction from mechanical processes, such as crushing in sediments, ravaging by carnivores, and marrow processing by humans, is thought to be conditioned by the structural ''density'' of bone tissues (*sensu* Lyman, 1994: 235–238), principally its mineral component. Techniques for analysing body part profiles based on fragmented faunal material must either (a) address the differential survivorship of the full range of structural density classes in the skeleton, or (b) stick to comparisons of parts that fall within a narrower, well-defined density range that is widely distributed in the vertebrate skeleton. Both kinds of approaches have found their way into the zooarchaeological literature, usually for different applications and by different research groups. By ''body part profiling'' I refer to almost any systematic comparison of anatomical representation of animals in archaeofaunal assemblages to independent standards based on a natural skeleton model. The results of body part analyses can be portrayed in numerous ways, ranging from standardized bar charts to anatomical indexes to correlation statistics. It is, however, the relation to an accurate anatomical model that determines the reliability of the profiling approach.

An example of the second approach to body part profiling was developed by the author to address questions about niche evolution in Pleistocene humans and the comparative ecology of food transport and processing behaviours of ungulate predators (Stiner, 1991, 1994). This work has come under fire recently, based on the claim that variation in mineral density so

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obscures the original (culturally determined) patterns in ungulate body part representation that the research findings based on the technique are meaningless (Grayson, 1996; Marean & Kim, 1998; Bartram & Marean, 1999). The frequent propagation of this error compels me to unpack the arguments. I begin by describing key differences between the two kinds of profiling techniques. Then I demonstrate where these critics go wrong with respect to the second technique, using most or all of the same control data that were said to invalidate it.

Comparisons Across Major Bone Macrostructure Classes

The more common body part profiling approach in the zooarchaeological literature requires reasonably complete knowledge of structural variation throughout the vertebrate skeletal anatomy in the form of quantitative standards. Skeletal tissues are grouped on the basis of density (=fragility) into major macrostructure[1] types—compact bone, cancellous bone, tooth enamel, dentine—that constitute recognizable features, even in fragmented assemblages. This practice sounds simple in principle but has proved to be a complex problem. Currently there is much variation among investigators in the working definition of density, the structural scale at which resistance to destruction is modelled, and the anatomical standards used as controls. In fact, the extent to which skeletal density explains loss of bone recognizability as defined by zooarchaeological practice is not known (cf. Lam *et al*., 1999; Lyman, 1994).

Many investigators nonetheless have demonstrated a relation between some measure of bone density and observed biases in vertebrate body part representation in faunal assemblages (e.g., Behrensmeyer, 1975; Binford & Bertram, 1977; Brain, 1967, 1969, 1981; Lyman 1984). It is widely assumed, therefore, that variation in bone macrostructure has some explanatory power on questions of skeletal survivorship (for a thorough review, see Lyman, 1994: 235–293). There now is considerable information on the mineral or structural "density" of the skeletons of many vertebrates, although two very different sets of standards are proposed (cf. Lyman, 1984; Lam *et al*., 1998). Lyman's (1984) photon-densitometry standards thus far have proved to be the most successful in application. Even so, less than half of all possible profile outcomes allow investigators to exclude density mediated attrition (Lyman, 1991, 1994: 258–264).

[1]Bone structure is considered to be a hierarchical assembly (Currey, 1984; Weiner & Wagner, 1998), and models of it resistance to mechanical and chemical forces of destruction should vary accordingly. Zooarchaeologists work principally with aspects of skeletal macrostructure for identifying taxa and body parts, on the assumption that microstructure is less relevant to most of the questions they ask. This may be correct with respect to mechanical forces of destruction, but it probably is not correct with respect to chemical dissolution (Karkanas *et al*., 2000; Stiner, n.d.; Stiner *et al*., 2001).

The contrast between compact and cancellous (spongy) macrostructures of bone has received the most attention, and skeletal survivorship normally is compared between these two macrostructure classes to assess the potential severity of *in situ* attrition (e.g., Grayson, 1989; Lyman, 1984; Rogers, 2000). The significant but often weak correlations between bone mineral density and bone survivorship are compelling but also testify to a rather fuzzy understanding of the causal relations that we think should exist between the two phenomena.[2]

Comparisons Within a Single Bone Macrostructure Class

If the relations among observable types of skeletal macrostructure, countable morphologic features, and the processes by which skeletal structures break down are still something of a mystery, then profiling techniques that rely on fewer assumptions about how all of this works should have some obvious benefits. The second of the two approaches to body part profiling outlined above relies principally on compact bone, which is well represented throughout much of the natural vertebrate skeleton. The idea is to control for the possible effects of density-mediated bone attrition on estimates of the minimum number of skeletal elements (MNE) by narrowing the tissue density range to features dominated by compact bone. Teeth, the densest of all skeletal elements, are confined to the cranium and thus are not good choices for this kind of analysis. Spongy structures (a.k.a. cancellous or trabecular bone) dominate much of the axial skeleton, making them the least dense or "least resistant" of elements. Compact bone, on the other hand, is prevalent in the skeletons of all terrestrial mammals and birds. Limb elements, such as the humerus, radius,

[2]Part of the explanation may lie in the extended time over which archaeological bone may be altered. While beyond the scope of this essay, it is important to note that tissue density standards (g/cm^3) for mature skeletons are based principally on the mineral (apatite) component. This proxy measure of resistance comes with some basic liabilities. Fresh bone owes its strength to its fibrous composite structure, a combination of collagen fibrils and small apatite crystals. Degradation of either component, as often occurs post-depositionally, results in significant changes in the mechanical strength of the residual structure; generally, collagen suffers under alkaline conditions that favour the preservation of bone apatite. Destructive processes begin on fresh bone but may not cease as the fibrous component of bone degrades, leaving a much more brittle structure (see also Darwent & Lyman, 2002; Lyman, 1994: 261; Stiner *et al*., 1995). Zooarchaeologists' models of surface-mediated destruction, such as occur in chemical reactions, tend to privilage macrostructure properties. However, chemical exchanges occur at the microscopic or molecular level, such that microporosity is important (Hedges & Millard 1995; Hedges *et al*., 1995). Most compact bone of large mammals possesses many tiny caniculi, and the abundance of these tiny pores increases as the collagen component degrades (Neilson-Marsh & Hedges 2000*a*, *b*). The microporousity of compact and spongy bone may be a good deal closer than many zooarchaeologists realize (Stiner, *et al*., 2001; Stiner, n.d.).

femur, tibia, and metapodials, contain large tracts of compact bone, as do some of the non-dental components of the skull. Certain smaller features of the vertebrae (zygapophyses) and ribs (proximal heads) are also fairly dense, though still less than many limb and cranial features.

The thickness of compact bone varies among elements, but this variation is of a smaller order than that observed among the other tissue classes named above. One simply needs to know the locations of compact bone tissues relative to the distribution of the unique morphologic features (''portions'') normally used to estimate the MNE for each kind of element. Available literature suggests that there is enough information with which to do this, and that a reasonably good correspondence exists between visible and measured variation in the distribution of compact bone in ungulate skeletons (e.g., Elkin & Zanchetta, 1991; Kreutzer, 1992; Lyman, 1984, 1994; Lyman *et al.*, 1992).

The Anatomical Regions Profiling Technique

A regional-based approach to ungulate body part representation in vertebrate faunas circumnavigates much of the variation in mineral density within skeletons by focusing on compact bone. Pooling MNE counts by anatomical region evens-out variation in structural density further still. The technique is directed to interassemblage comparisons from which only the most robust differences in body part representation patterns are sought.

As with other profiling techniques, the minimum number of elements (MNE) must be estimated for each skeletal member of a given taxon from the most common morphologically unique ''portion'' or feature in the assemblage. A variety of unique portions scattered over the surface of an element can and should be considered for estimations of MNE (e.g., Lyman, 1994; Morlan, 1994*a*, *b*). However, some portions will tend to yield higher counts than others, presumably due to their greater inherent resistance to mechanical destruction. Limb end (epiphyseal) and shaft features (e.g., foraminae) are considered in MNE estimates by this author whenever possible, and all fragments, including limb shaft splinters in an assemblage, are examined systematically. For the skull, only bony portions are used in the comparisons to post-cranial MNEs, because tooth enamel is so much denser than any kind of bone (about 95% and 70% mineralized, respectively, Currey, 1984).

The portions of elements typically considered in my studies of Mediterranean Palaeolithic assemblages are listed in Appendix 1. Portion categories tend to be hierarchical, because fragment size varies and a specimen may contain more than one portion suitable for estimating MNE. Ideally, countable portions should be recognizable independent of fragmentation effects.

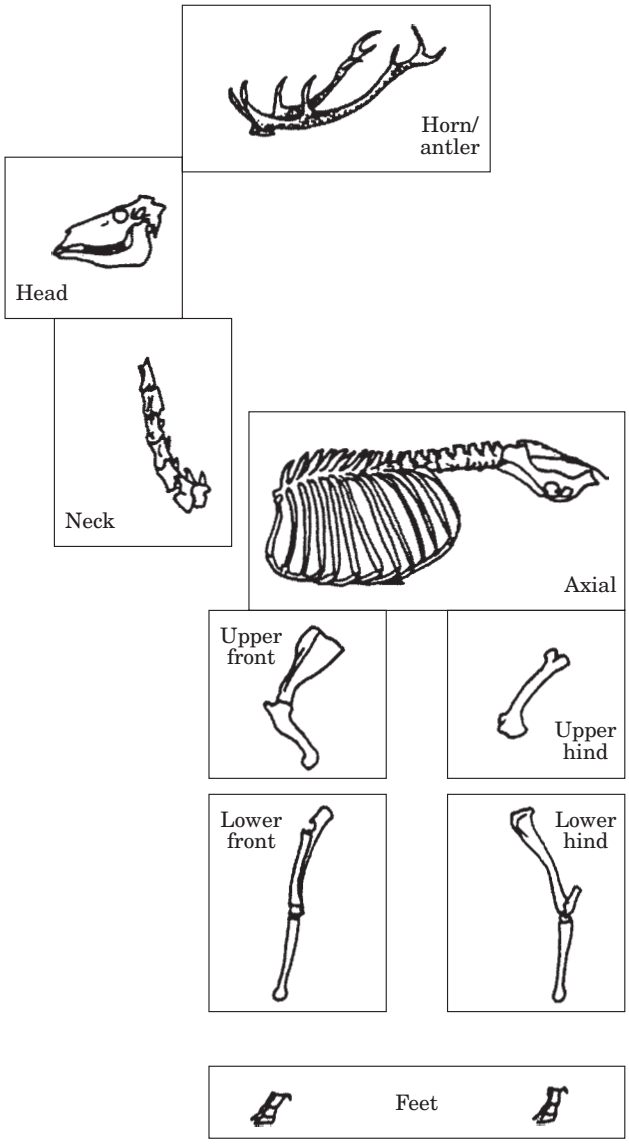

Figure 1. Nine anatomical regions for the ungulate skeleton (from Stiner, 1991).

While this is never perfectly true, it is close to true in reasonably well preserved faunal assemblages. Small, compact features are favoured for counting, and many of these portions coincide with Lyman's photon densitometry scan sites (1994: 234–250).

The MNE counts are then condensed into an array of nine anatomical regions (Figure 1): these are (1) the horn/antler set, (2) head, (3) neck, (4) the rest of the axial column including the ribs and pelvis, (5, 6) upper and lower front limbs, (7, 8) upper and lower rear limbs, and (9) feet (Stiner, 1991, 1994: 240–245). Species-specific identifications are pooled with specimens of the appropriate ungulate body size group to increase sample size and to overcome the fact that some elements and portions of elements are far more diagnostic of species than are others. For bar

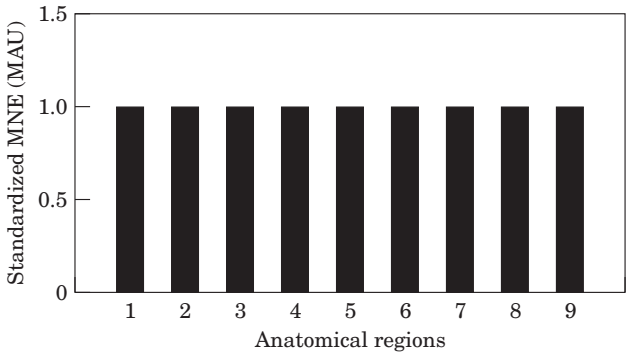

Figure 2. Standardized bar chart for the nine anatomical regions of a theoretically complete skeleton. (1) antler/horn, (2) head, (3) neck, (4) axial, (5) upper front limbs, (6) lower front limbs, (7) upper hind limbs, (8) lower hind limbs, (9) feet. Note that dental elements are not used to calculate frequencies of head parts.

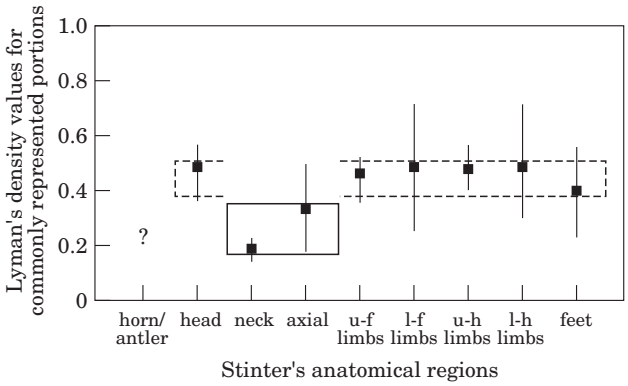

Figure 3. Ranges and midpoints of variation in bone structural density for nine anatomical regions of the artiodactyl skeleton using Stiner's (1991) profiling method and Lyman's (1994) photon densitometry data for deer.

chart comparisons, body part representation can be standardized against a whole skeleton model (Stiner's standardized MNE, 1991; Binford's MAU, 1978) by dividing observed MNE for a skeletal element or group of elements by the expected MNE for the same element or element group in one complete skeleton. If skeletal representation is complete, all standardized values will be equal (Figure 2), making major anatomical biases among regions easy to detect. Observed MNEs for anatomical regions can also be indexed relative to one another, and the total element count (tMNE) compared to the number of individual animals (MNI) represented in the ratio tMNE/MNI.

Test of Density Range Correspondence among Anatomical Regions

How much variation in observed MNE among anatomical regions could be explained by variation in the density of the bone portions used for counting? This comparison begins by considering all possible portions listed in Appendix 1 for which photon densitometry estimates are available irrespective of measured density. Then the comparison is narrowed to include only those portions most commonly represented in my analyses of Mediterranean faunas from 1985 to the present. Control data for deer serve as the skeletal density standards here (Lyman, 1994: Table 7.6), but intra-skeletal variation follows a similar pattern in artiodactyl and perissodactyl species (Lam *et al.*, 1999).

Density value mid-points and ranges in Figure 3, and the pairwise statistical comparisons of density values in Table 1, indicate that the chances for reduced recognizability of bone portions are about the same for the head region and various limb regions. An F-ratio statistic indicates that there are no major differences among pooled cranial, limb, and foot regions ($n=32$, $r^2=0{\cdot}27$, $P=0{\cdot}124$). Upper front limbs and foot bones have a somewhat lower probability of preservation than heads and other limb regions (Table 1b), but these differences are minor (Table 1a).

The chances for reduced recognizability among cranial and limb regions are closer still for those portions most commonly used by this author to estimate MNE in archaeological assemblages from Mediterranean shelter sites ($n=23$, $r^2=0{\cdot}330$; F-ratio$=1{\cdot}671$, $P=0{\cdot}195$) (Table 2). Turning to a more stringent non-parametric version of ANOVA, a Kruskal–Wallis statistic yields basically the same answer as the tests above (8·393, df$=5$, $P=0{\cdot}136$).

The conceptual basis for the profiling technique is well supported by Lyman's and others' estimates of variation in bone structural density. The risks of over-interpretation in this technique actually centre on the vertebral column ("neck" and "axial"), anatomical regions which can be excluded from discussion on grounds that their representation is ambiguous. Only the relative abundances of cranial and major limb bones have been used to investigate food acquisition strategies of humans and other ungulate predators in the anatomical index (H+H)/L (Stiner, 1991, 1994). This is the sum of horn/antler MNE and head MNE divided by the total MNE for major limb elements excluding phalanges ("feet"). A related index, HEAD/L, is also largely unaffected by potential variation in bone tissue density.

In examples of early Middle Palaeolithic gazelle (*Gazella gazella*) and fallow deer (*Dama mesopotamica*) assemblages from Hayonim Cave, Israel, one sees a natural balance in the representation of head and limb bones, one of several indications that hominids enjoyed so-called early access to these prey animals some 170,000 years ago, presumably because they were hunting them (Stiner, n.d.). Vertebral elements, particularly below the neck region, are under-represented, as one might expect to occur from higher inherent vulnerability to mechanical destruction of any sort, although differential transport is not refuted. Estimations of limb MNEs in Hayonim Cave are based on limb end

Table 1. Differences in mean structural density for bony portions of elements by anatomical region, based on Lyman's photon densitometry control data for deer

	N-portions considered	Mean density	s.d.	
a. Mean photon densitometry values for cranial and various limb regions				
Anatomical region				
Head	5	0·52	0·09	
Upper front limb	6	0·38	0·11	
Lower front limb	6	0·54	0·13	
Upper hind limb	3	0·42	0·14	
Lower hind limb	7	0·52	0·18	
Feet	5	0·36	0·12	
	t	df	*P*	Difference in means
b. Pair-wise tests for differences in density among cranial and various limb regions				
Anatomical region pair				
Head-upper front limb	2·251	9·0	0·051	0·138
Head-lower front limb	− 0·347	8·7	0·737	− 0·023
Head-upper hind limb	1·075	2·9	0·362	0·100
Head-lower hind limb	− 0·037	9·3	0·972	− 0·003
Head-feet	2·292	7·3	0·054	0·158

Table 2. Pair-wise mean differences in structural density for (a) all potential bone portions, and (b) those portions most commonly used to estimate MNE values in the Mediterranean cave faunas

Anatomical region and code	(2)	(5)	(6)	(7)	(8)	(9)
a. All potential portions						
Head (2)	—					
Upper front limb (5)	− 0·138	—				
Lower front limb (6)	0·023	0·162	—			
Upper hind limb (7)	− 0·100	0·038	− 0·123	—		
Lower hind limb (8)	0·003	0·141	− 0·020	0·103	—	
Feet (9)	− 0·158	− 0·020	− 0·181	− 0·058	− 0·161	—
b. Most commonly used portions						
Head (2)	—					
Upper front limb (5)	− 0·114	—				
Lower front limb (6)	− 0·029	0·085	—			
Upper hind limb (7)	− 0·067	0·048	− 0·037	—		
Lower hind limb (8)	− 0·033	0·082	− 0·003	0·034	—	
Feet (9)	− 0·195	− 0·080	− 0·165	− 0·128	− 0·162	—

Anatomical regions numbered as in Figure 2. No relations among region pairs are signficant based on a Bonferroni adjustment of probability.

and shaft features (Table 3). Shaft MNE estimates tend to agree with at least one end-based estimate for each major limb bone type (see below).

The linear regression statistics in Table 4 evaluate how much of the variation in observed MNE values by portion is explained by independent measures of bone tissue density for the two ungulate body size groups in each of two Mousterian units. For 52 potential portions corresponding to Lyman's scan sites (see Table 3), the relation between tissue density and MNE estimates is essentially random (nonsignificant) in three of the four cases. A very weak relation exists in the fourth case, but structural bone density explains less than 10% of the variation. The nearly balanced representation of head and limb bones is therefore taken to reflect human transport decisions. Vertebral elements are under-represented either because they were destroyed *in situ* or never carried from kill sites to the shelter by Palaeolithic humans: we just cannot know from this analysis.

In summary, portions of elements composed of compact bone can be thick or thin, but many of the components of the skull and limbs have relatively similar chances of resisting mechanical sources of *in situ* destruction. Anatomical indexes that compare head to various limb region frequencies in the manner

Table 3. Lyman's average structural density values for deer skeletal elements as determined by photon densitometry by portion of element, and Stiner's MNE estimates for small and medium ungulates in early Middle Palaeolithic assemblages from Hayonim Cave, Israel

Element	Portion	Lyman's scan site label	Lyman's† value of av. density	MNE est. by portion at Hayonim Cave			
				Unit 3		Unit 4	
				SU	MU	SU	MU
Mandible	Anterior horizontal ramus	DN1	0·55	5	4	20	22
	Anterior-mid horizontal ramus	DN3	0·55	5	4	20	22
	Mid horizontal ramus*	DN4	0·57	5	4	20	22
	Posterior horizontal ramus	DN5	0·57	3	0	15	13
	Mandibular condyle	DN7	0·36	1	2	14	10
Atlas	Complete or nearly complete	AT2	0·15	0	0	2	1
	Anterior articulation*	AT3	0·26	0	1	4	5
axis	Anterior-ventral articulation*	AX1	0·16	1	1	7	7
Other cerv v	Pre-/post-zygapophysis*	CE1/2	0·19 (/0·15)	7	4	16	19
Thor v	Body (centrum)	TH1	0·24	7	2	11	13
	Dorsal spine*	TH2	0·27	8	2	16	21
Lumb v	Pre-zyapophysis*	LU1	0·29	1	1	8	10
	Post-zygapophysis*	LU2	0·30	1	1	8	10
Rib	Head (proximal end)	RI2	0·25	9	2	28	22
	Proximal diaphysis (if long)*	RI3	0·40	~16	~10	~67	~58
Sacrum	Anterior body*	SC1	0·19	1	0	2	3
Innom	Acetabulum (all, ac-il, ac-is, ac-pub)	AC1	0·27	2	1	6	6
	Iliac body*	IL2	0·49	1	1	5	11
	Iscial blade	IS1	0·41	1	0	6	7
Scapula	Distal end (or subset thereof)*	SP1	0·36	5	1	15	14
	Distal diaphysis (narrowest section)*	SP2	0·49	4	1	14	14
	Proximal rim (or subset thereof)	SP5	0·28	1	0	2	5
Humerus	Proximal end (or subset thereof)	HU1	0·24	1	2	8	6
	Diaphysis or fragment w/ foramen	HU3	0·53	2	1	10	8
	Distal end (or subset thereof)*	HU5	0·39	3	0	11	11
Radius	Proximal end (or subset thereof)*	RA1	0·42	2	1	13	8
	Diaphysis or prox. attachment scar*	RA3	0·68	2	2	12	8
	Distal end (or subset thereof)	RA5	0·43	1	3	10	6
Ulna	Proximal end (or subset thereof)*	UL2	0·45	4	2	6	5
Femur	Proximal end (or subset thereof)*	FE1	0·41	2	0	12	4
	Diaphysis or fragment w/ foramen*	FE4	0·57	3	4	5	4
	Distal end (or subset thereof)	FE6	0·28	2	3	7	4
Tibia	Proximal end (or subset thereof)	TI1	0·30	0	1	5	9
	Proximal diaphysis	TI2	0·32	4	5	9	15
	Diaphysis or fragment w/ foramen*	TI3	0·74	4	4	9	14
	Distal end (or subset thereof)*	TI5	0·50	7	4	13	14
Calcaneum	Distal end (or subset thereof)	CA1	0·41	1	3	9	3
	Diaphysis	CA2	0·64	1	2	7	0
	Proximal end (or subset thereof)*	CA3	0·57	3	6	12	9
Astragalus	Complete	AS1	0·47	6	3	13	19
	Middle	AS2	0·59	6	3	13	20
	Distal end (or subset thereof)*	AS3	0·61	5	4	15	22
Metacarpal	Proximal end (or subset thereof)*	MC1	0·56	1	5	10	6
	Diaphysis (long)	MC3	0·72	~1	~4	~2	~7
Metatarsal	Proximal end (or subset thereof)*	MR1	0·55	1	3	6	10
	Diaphysis (long)	MR3	0·74	~6	~3	~2	~16
All metapod	Distal end (or subset thereof)*	MC6/MR6	0·51	8	4	24	17
First phal	Proximal end (or subset thereof)	P11	0·36	5	6	12	25
	Distal end (or subset thereof)*	P13	0·57	8	8	21	32
Second phal	Proximal end (or subset thereof)	P21	0·28	10	2	25	22
	Distal end (or subset thereof)*	P23	0·35	7	5	27	23
Third phal	Proximal end (or subset thereof)*	P31	0·25	10	7	33	27

†Source is Lyman (1994: Table 7.6).
"Subset thereof" means that this area of the element can be subdivided, usually into morphologically unique anterior, posterior, medial, and lateral segments.
*The densest portion for this kind of element.
~The nature of the morphologic feature does not permit a very accurate estimate of MNE.

Table 4. Regression statistics for the relation between estimated MNE in Mousterian archaeofaunas from Hayonim Cave, Israel, and independent measures of bone structural density for 52 potential element portions

Assemblage	Ungulate body size group	r	r^2	P
Mousterian Unit 3	SU	0·009	0·000	0·947
	MU	0·285	0·081	0·041**
Mousterian Unit 4	SU	0·041	0·002	0·772
	MU	0·072	0·005	0·614

**Weak relation; there is no significant relation in all other assemblages.
SU, small ungulates, nearly all mountain gazelle (*G. gazella*); MU, medium ungulates, mostly fallow deer (*Dama mesopotamica*); Mousterian assemblages come from Layer E of the main (central) excavation trench only.

described above are largely immune to the biasing effects of density-mediated attrition. Certain other anatomical indexes may be affected more, such as the horn/antler index HORN/L, because they combine skeletal elements representing a greater range of tissue densities. Yet, horn/antler biases abound in modern hyena dens of Africa and Pleistocene dens of Italy, despite the spongy macrostructure of bovid horn cores and cervid antlers (Stiner, 1991, 1994). An index of parts transported to shelters per carcass source, tMNE/MNI, could be problematic in that it includes vertebral elements along with crania and limb bones. In the Mediterranean cases, however, this effect is levelled by the fact that vertebrae are under-represented in all of the assemblages.

Out of the Pan, Into the Fire?

Experimental evidence on "selective deletion" of skeletal parts by spotted hyenas from human camps suggests that pre-fractured spongy portions are particularly attractive, if the grease component has not already been rendered by humans via crushing and boiling techniques (Bartram & Marean, 1999; Capaldo, 1997; Marean *et al.*, 1992; but see Lupo, 1995). The expectation is that pilfering choices made by hyenas will adhere closely to the cancellous-compact distinction in limb bone macrostructure—essentially shafts vs. ends—because the fats and grease in cancellous bone are more difficult for humans to remove. Hyenas are adapted to eating large quantities of bone and have little difficulty breaking down cancellous tissues (Sutcliffe, 1970), although it requires energy.

Marean & Kim (1998) assert from these actualistic experiments that extensive pilfering may have occurred at many Pleistocene sites. However, the proposition that head-biased and in some cases head-and-foot-biased faunas reported by other zooarchaeologists can be explained by density-mediated bone attrition clearly is falsified by available control data. Moreover, the causal link that these authors infer between observed skeletal biases in the fauna from Kobé Cave, a rockshelter in Iraq, and modelled bone deletion by hyenas appears to have been exaggerated. A Spearman's *rho* statistic indicates only a weak relation (0·403, $n=30$, $0{\cdot}05>P>0{\cdot}02$) between MNE estimates by long bone portion (each end, mid-shaft, and two intermediate locations on each long bone element) in Kobé Cave against photon densitometry data that Marean & Kim (1998, Table 5) borrow from Lyman. Structural density explains about 16% of all variation in portion of element representation for limb bones in this Palaeolithic site.

How much more resistant are limb shafts than spongy (soft) limb ends? Empirical observations provide some reality checks on this question. In Table 5 MNE estimates based on long bone shaft portions versus end portions are about the same in the spotted hyena-collected assemblages from Buca della Iena in west-central Italy, as in two completely recovered human-collected assemblages of Middle and late Upper age in the same region. The same is true for human-collected faunas from Hayonim Cave in Israel. At most, only one end of a long bone was destroyed regardless of assemblage history, some involving hyenas and others involving humans, all in regions where hyenas were once prevalent. Because these archaeological assemblages were completely recovered and examined, there is no observer bias against limb shafts. Surface damage in the form of tooth drag marks on compact bone, salivary rounding, crenelation, and punctures in spongy tissues are widespread in the hyena-collected assemblages. Yet this kind of damage seems not to have rendered many elements of the head or limb regions of red deer, fallow deer or aurochs unrecognizable. The absence of limb ends in the Middle Palaeolithic fauna from Kobé Cave, where shaft MNE is said to be up to eight times that for *either* end of any long bone therefore seems peculiar. To the extent that more vulnerable, softer or greasier portions were lost from Pleistocene sites in Italy and Israel, the ratio of compact to spongy bone portions tends to be no more than double that of portions dominated by cancellous bone. In other words, the scale of biasing effect proposed by Marean and Kim for pilfering hyenas can not be generalized to Middle and Late Pleistocene Mediterranean settings, regardless of acknowledged variation in bone recovery by excavators working in peninsular Italy in the 1930s–1950s (Stiner, 1994: 37–56).

If bone tissue density has anything at all to do with mechanical processes of bone attrition, some degree of correlation must be expected *a priori*. Thus it is the strength of that relation that is most relevant to explaining anatomical biases in faunal assemblages (Grayson, 1989). The weak relation in the Kobé case indicates remarkably limited power of mineral density—and by extension grease distributions in

Table 5. Comparison of limb MNE counts based on unique shaft features and epiphyseal (end) features for the more common end in completely recovered assemblages collected by Pleistocene spotted hyenas, Middle Palaeolithic humans, and Epipalaeolithic humans in Mediterranean caves

	Riparo Salvini† MU		Grotta Breuil‡ MU		Buca della Iena• MU			LU
Element	Shafts	End	Shafts	End	Shafts	End	Shafts	End
a. Italian sites (from Stiner, 1991)								
Scapula	1	5	0	1	0	0	1	2
Humerus	6	8	4	4	1	2	4	5
Radius	1	3	3	3	2	3	4	5
Femur	3	7	2	3	1	1	1	3
Tibia	5	7	5	4	2	3	6	6
Humerus/femur	(4)							
Total MNE	20	30	14	15	7	9	16	21

	SU‡		MU‡	
Element	Shafts	End	Shafts	End
b. Middle Palaeolithic layers in Hayonim Cave, Israel				
Scapula	18	20	15	15
Humerus	12	14	9	11
Radius	14	15	10	9
Femur	8	14	8	7
Tibia	13	20	20	18
Total MNE	57	83	62	60

•Collectors were mainly or exclusively spotted hyenas; †Epipaleolithic humans exclusively; ‡Middle Palaeolithic humans exclusively. Humerus and femur could not always be distinguished on basis of foraminae in the highly fragmented material from Riparo Salvini. (SU) small ungulate, (MU) medium ungulate, (LU) large ungulate.

trabeculae—for explaining portion representation for ungulate limb bones there or elsewhere in the Palaeolithic record. Recent and very different standards of density variation in limbs obtained by computed tomography (CT) (Lam *et al*., 1998) are of little help here, as Lam *et al*. (1999) are ambivalent about what these data are measuring; the CT standards are also incomplete, prohibiting comparisons of cranial bone and limb bone representation.

Marean and colleagues insist that one can only evaluate original element frequencies by completely refitting all remaining shaft fragments. However, they are unable to provide a replicable structural basis (i.e., differential distributions of bone grease or bone mineral density) for why the unique features on shafts used by zooarchaeologists can not suffice for total reconstruction in accurate estimations of shaft-based MNE. A related source of confusion in their arguments has been the misapplication of hyena feeding experiment data involving relatively small ungulates to Pleistocene cases involving much larger ungulates (Horwitz, 1998; Klein & Cruz-Uribe, 1998; Klein *et al*., 1999). Spotted hyenas of Late Pleistocene Italy and many wild populations today (Henschel *et al*., 1979; Hill, 1980; Kruuk, 1970, 1972: 80–81; Mills, 1984*a*, *b*, 1989; Mills & Mills, 1977; Skinner *et al*., 1986; Tilson *et al*., 1980) tend to concentrate on larger prey, usually 6 to 14 times greater than the hyenas' body weight (Stuart, 1991) and roughly an order of magnitude greater on average than the domestic caprovines used in Marean and Spencer's (1991) captive feeding experiments.

Ramifications

If one kind of explanation for body part biases does not hold, are analysts merely delivered into the other hand? That is, having solved issues of *in situ* attrition, is one bound to be defeated by the possibility of selective deletion by hyenas? Is documented variation in bone tissue density as measured by photon densitometry made pointless by newer CT-based density standards? Perhaps confirmation of these fears—"shaft anxiety"—will be had in the future, but current standards fail to do so:

(1) There is considerable fallacy to the assumption that shafts are more persistent in Palaeolithic archaeofaunas than *every* end of long bone elements. Most indications are that mean shaft persistence is about the same or nearly the same as one end, but often greater than that of the other end of the same element. The maximum loss differential between soft ends and harder portions of limb bones appears to be 2:1 or at most 3:1 (compare, for example, cases in Lyman, 1994). Photon densitometry data predict this well, at least where mechanical forces are concerned.

Perhaps with the advent of milling and boiling technologies of some later archaeological records, spongy bone fared much worse than compact bone (e.g., Bar-Oz & Dayan, 2002; Brink, 1997; Munro, 2001), but this does not apply to much of the Palaeolithic.

(2) The assertion that head-dominated patterns, or head-and-foot-dominated patterns, in ungulate remains are likely to be the product of density-mediated attrition is not supported by documented variation in structural density in the skeletons of vertebrates. If anything, foot bones as a group are slightly less dense than the countable compact bone portions of the head or limb groups, and the latter regions are composed of many portions of roughly equivalent densities. None of the differences in bone density of head and limb regions is of the order needed to greatly bias MNE estimates in the region-by-region profiling technique. Compact bone is the most widely distributed tissue class in vertebrate skeletons, literally head to toe, with the partial exception of the vertebral column.

(3) Some authors argue that two other sources of bias may work together to obscure archaeologists' perceptions of prey body part representation. These factors are selective deletion by hyenas or other carnivores, and human observer error arising from the practice of ignoring shaft fragments during data collection. The selective deletion concept is based on actualistic experiments, some in ethno-archaeological contexts, and others in which investigators break and discard bones as they think early hominids would have done in open settings and then observe what local predators (mainly hyenas) carry off. Hyenas' choices are said to follow the compact-cancellous tissue distinction for pre-broken bones: when bones are broken and still greasy, they are attracted to spongy parts. One problem with this application of experiment data is that not all limb bone ends are spongy or greasy; some are quite dense, such as the distal tibia and humerus, proximal radius and metapodials, and so on. From a palaeontological point of view, at least in the Mediterranean region where spotted hyenas were once common, there are no indications that hyenas spirited off large or disproportionate quantities of limb bone ends of all sorts from human sites. Instead there is good quantitative agreement between MNE estimates for the shaft and at least one end of most limb bone elements. The larger point is that the experiments cited by these authors explain, at most, missing portions of particular elements. They explain less about why certain elements are missing, and much less about disproportionate representation of most regions of the body other than the vertebral column. Anatomical regions are arguably closer approximations than portions of elements to what people and other large predators generally decide to carry away from procurement sites outside of some rather special foraging circumstances.

(4) Archaeological recovery biases are a trickier matter, as is variation in how analysts treat faunal specimens not readily identified to species or element. Shaft fragments generally fall into this category, yet they may carry much information about bone processing behaviours and assemblage formation history, including burning damage, tool marks, and gnawing marks. However, it does not appear that the majority of faunal analysts ignore shaft fragments (cf. Brain, 1981; Binford, 1978; Bunn & Kroll, 1986, 1988; Delpech, 1998; Stiner, 1991, 1994, 1998; Morlan, 1994*a*, *b*; Todd & Rapson, 1988). Even if one does not like to estimate MNE from shaft features (e.g., Klein & Cruz-Uribe, 1984), the negative impact of the latter practice on profiling of the sort described here seems to be rather weak.

(5) Finally there is the complication of differing standards of relative density of limb shafts and ends (Lam *et al.*, 1998, 1999). The jury is still out on this one. CT is a relatively new technique designed for, among other things, studying the influence of variation in calcium metabolism on bone structure and bone strength. As a new and exciting development in bone tissue research, it is unlikely that any one understands well what this technique measures with respect to the issues of macrostructure recognizability and bone survivorship in archaeofaunal assemblages. Photon densitometry has a longer track record, and its strengths and limitations are better understood. Indeed, the skeletal density standards obtained from photon densitometry appear to better describe the scale of differential survivorship observed in archaeological and palaeontological records in general.

Conclusion

The anatomical region profiling technique described above (Stiner, 1991) is not for every one and every problem. However, it is reliable and appropriate to research on food transport behaviour , and the results obtained via its application remain valid. This technique controls for variation in bone tissue macrostructure density by confining comparisons of element representation principally to features rich in compact bone tissue, a point entirely missed by detractors of the technique. This outcome may be good news in the increasingly baroque world of vertebrate taphonomy, an exciting but conceptually messy science.

This exercise demonstrates that (a) there is more than one way to cope with the possibility of *in situ* bone attrition, and (b) different ways of grouping data

associate with significantly different risks of misinterpretation. Experiments and many zooarchaeological studies concerned with the relative rates of loss of head and limb parts have tended to focus on why certain portions of elements may be missing from an assemblage. Such analyses may say little about the probability of imbalances at the level of anatomical regions in prey. The latter are much coarser divisions of the anatomy of large prey animals yet they are arguably closer approximations, however imperfect, of the butchering and transport units that humans commonly create.

Macrostructure tissue classes of large mammal skeletons each have limited structural density ranges. Mature teeth are uniformly dense but concentrated in the skull; spongy bone dominates the axial skeleton, and for this reason the axial skeleton remains an area of ambiguity with respect to interpreting patterns of *in situ* attrition. Because compact bone is so prevalent in vertebrate skeletons, its utility for inter-regional analyses of body part representation is great.

The region-by-region approach to body part profiling is simpler than most, requiring less information about density variation and its relation to portion identifiability. Approaches that involve fewer assumptions and shorter chains of inference should be preferred, if only because there are fewer ways to be wrong. Many of the potential biases noted by investigators of *in situ* attrition over the last few decades must be taken seriously. Yet we still know little about how bone destruction processes translate to declining identifiability in archaeofaunal assemblages. That the consequences of chemical and mechanical decomposition are routinely equated in models of bone attrition is but one symptom of a science with few reliable principles. (This discussion concerns only mechanical forces.) Inroads to these long-standing problems are made each year, and well designed experiments continue to be crucial to the learning process. However, some recent arguments that call upon measures of skeletal tissue density are baseless, and, in their more reductionist forms, distract archaeologists from the real problems still to be solved.

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Appendix

Stiner's faunal coding keys for skeletal elements and portions of elements in research on Mediterranean faunas (Italy, Turkey, Israel). Portions can occur singly or in combination with others, and thus the coding system is hierarchical

Elements

Horn/antler (10s):
11 horn core
12 antler

Skull (20s):
21 half cranium, L or R
22 half mandible, L or R

Neck (30s):
31 atlas
32 axis
33 cervical vertebra

Main axial column+(40):
40 vertebra, type unknown
41 thoracic vertebra
42 rib
43 lumbar vertebra
44 sacral vertebra
45 innominate (1/2 pelvis)
46 caudal vertebra
47 sternal segment

Front limb (50s and 60s):
51 scapula
52 humerus
53 coracoid (birds only)
61 radius
62 ulna
63 carpal (type unknown)
64 metacarpal (bird=carpometacarpus)
65 cuneiform
66 magnum
67 lunate
68 scaphoid
69 unciform

Hind limb (70s and 80s):
71 femur
81 tibia
82 patella
83 astragalus
84 calcaneum
85 tarsal (type unknown)
86 metatarsal (bird=tarsometatarsus)
87 naviculo-cuboid
88 external and middle cuneiform
89 lateral malleolus

Feet (90s):
90 sesamoid
91 first phalanx

Elements *(cont'd)*

Feet (90s) *cont'd:*
92 second phalanx
93 third/terminal phalanx

General element categories:
1 metapodial (type unknown)
2 long bone (type unknown)
3 flat bone (skull or scapula fragment)
4 carpal or tarsal (type unknown)
5 spongy element (axial?)
6 auxiliary third phalanx
7 auxiliary second phalanx
8 auxiliary first phalanx
9 auxiliary metapodial
10 eggshell (bird)

Teeth (100s, mammals only):
9000 deciduous tooth
100 from upper jaw
200 from lower jaw
300 dental position unknown
010 incisor (type unknown)
011 first incisor
012 second incisor
013 third incisor
020 canine
030 premolar (type unknown)
031 first premolar
032 second premolar
033 third premolar
034 fourth premolar
040 molar (type unknown)
041 first molar
042 second molar
043 third molar

Portion Codes (general types):
1 complete
2 nearly complete
56 half
80 short diaphysis (tube)
81 short proximal diaphysis (tube)
82 short mid-diaphysis (tube)
83 short distal diaphysis (tube)
85 long diaphysis (tube)
86 diaphysis w/ foramen
90 shaft fragment
93 epiphysis fragment
95 spongy bone fragment
97 flat bone fragment

Appendix

Continued

Portions (*cont'd*)

Horn/antler:
10 rosette (base)
11 pedicel-braincase
12 shaft/rosette-pedicel-braincase
13 tip/tine

Cranium:
19 hyoid
20 premaxilla
21 nasal
22 zygomatic (jugal-squamous)
23 maxilla (complete half)
24 maxilla fragment
25 petrous
26 auditory bulla
27 braincase fragment
28 occipital
29 occipital condyle
30 frontal fragment
31 orbit
32 lacrimal (foramen)

Mandible, base missing:
33 middle horizontal ramus
34 mid-anterior horizontal ramus
35 anterior horizontal ramus
36 mid-posterior horizontal ramus
37 posterior horizontal ramus
38 "dip" between condyle-coronoid
39 base of horizontal ramus
40 condyloid process
41 coronoid process
42 condyle and coronoid
43 ascending ramus with lingual foramen

Mandible, base intact:
44 horizontal ramus (whole)
45 middle horizontal ramus
46 anterior horizontaontal ramus
47 posterior horizontal ramus
48 mid-anteror horizontal ramus
49 mid-posterior horizontal ramus

Innominate:
57 acetabulum fragment
58 acetabulum section-pubic body
59 acetabulum, complete
60 acetabulum and ilium (complete)
61 acetabulum section-iliac body fragment
62 acetabulum-iscium (complete)
63 acetabulum section-iscial body fragment

Portions (*cont'd*)

Innominate *cont'd*:
64 iliac body (diaphysis)
65 iliac blade
66 ilium
67 iscial body
68 iscial blade
69 iscium

Vertebrae:
50 epiphysis
51 centrum (body)
52 transverse process
53 pre-zygapophyses (5353=intact pair)
54 post-zygapophyses (5454=intact pair)
55 dorsal spine
56 half
57 anterior-ventral articulation
58 zygapophysis (type unknown)

Limb ("long") bones:
70 proximal (P) epiphysis
71 P epiphysis fragment (see also 91–94)
72 P<1/2
73 P 1/2
74 P>1/2
75 distal (D)>1/2
76 D 1/2
77 D<1/2
78 D epiphysis fragment (see also 81–84)
79 D epiphysis

Long bone epiphysis portions:
81 medial distal (D) epiphysis
82 lateral D epiphysis
83 anterior D epiphysis
84 posterior D epiphysis
91 anterior proximal (P) epiphysis
92 posterior P epiphysis
93 medial P epiphysis
94 lateral P epiphysis

Shaft and other features:
990 w/ foramen present
991 w/ attachment scar (proximal end of radius feature)
994 anterior "angle" (tibia)
995 muscle insertion scar
996 posterior rugosities (tibia)
997 interior diagonal lattice (humerus)
998 anterior groove (metapodials)
999 posterior groove (metapodials)

Note: This is not a perfectly complete list, since the requirements and potential for identification shift with site and regional conditions, as well as with the range of taxa represented. This list is intended only to be a relatively complete example for purposes of discussion. Note also that foramen position varies with species, and that its position tends to be fixed in the wild species to which this author has applied this coding system, but is known to be more variable in some domesticated animals.