

Taphonomic analysis of large mammals recovered from the Pleistocene Rancho La Brea tar seeps

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Abstract.—The asphalt deposits of Rancho La Brea are well known for preserving a prolific and diverse Late Pleistocene fauna. However, little taphonomic research has been done on these collections. To better understand the formation of this impressive assemblage, a taphonomic study of the bones of the large mammals from one asphalt deposit, Pit 91, was carried out, and results are presented here. The predominance of carnivore specimens in the Rancho La Brea deposits has long been explained by a scenario in which a prey animal was trapped in asphalt and attracted large numbers of carnivores who became trapped in turn. Hypotheses generated from this scenario were tested by collecting taphonomic data on over 18,000 specimens. Weathering data indicate that elements were deposited fairly rapidly. However, patterns of skeletal part representation for the seven most common species demonstrate that complete skeletons are not present. Water transport is ruled out as the primary process responsible for removing skeletal elements based on abrasion data. Instead, the feeding activity of carnivores (ravaging) appears to have been an important factor in the formation of the assemblage.

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Introduction

The Pleistocene deposits of Rancho La Brea are world famous for the volume of prehistoric material recovered from them. Millions of specimens ranging in age from 44,000 to 4000 B.P. have been excavated from these deposits over the course of the last 100 years (Marcus and Berger 1984; Stock and Harris 1992). Not only is the material very abundant, but it is also extremely diverse. Representing over 500 species, specimens range in size from insects to mammoth long bones, all well preserved (Akersten et al. 1983; Harris and Jefferson 1985).

The excellent nature of the preservation at Rancho La Brea is due to the sediments from which specimens are recovered—*asphalt-impregnated layers of sand or clay, distributed across an approximately 23-acre area of Los Angeles, California (Woodard and Marcus 1973; Stock and Harris 1992). The sediments were laid down in the late Pleistocene as broad alluvial fans derived from the nearby Santa Monica Mountains (Akersten et al. 1983; Shaw and Quinn 1986; Quinn 1992). Ephem-*

eral streams deposited the sediments that contain the majority of the bones (Shaw and Quinn 1986). Portions of these sediments were permeated by petroleum that seeped upward from deeper, more ancient Tertiary oil sands through strata fractured by movement within the earth's crust (Woodard and Marcus 1973; Shaw and Quinn 1986). In some cases the petroleum reached the surface, and, as the lighter petroleum portion evaporated, sticky pools of natural asphalt were left behind (Akersten et al. 1983). The vertebrate skeletal material is also impregnated with asphalt, which acts to preserve it in its original state (Shaw and Quinn 1986). This process, which continues today, was in progress by at least 45,000 years ago, when animals and plants were mired in these sticky pools and subsequently buried in sediments of the alluvial plain (Harris and Jefferson 1985; Shaw and Quinn 1986; Quinn 1992). In addition to entrapment, bones were also concentrated in the area by fluvial action (Quinn 1992).

What happened to these mammals after they became trapped in the asphalt and before their excavation? Almost all of the skeletons

are entirely disarticulated, obscuring our view of what occurred after death. The question of taphonomic processes in action at Rancho La Brea has only been minimally addressed (Gilbert 1927; Stock 1929; Miller 1969; Scott 1989), and yet a complete understanding of these processes is critical to further paleobiological studies of the collections (Akersten et al. 1983). Without an understanding of the biases that affected preservation, it is premature to use the collections for paleoecological and evolutionary studies. Here, we report on research undertaken to investigate which taphonomic processes affected the Rancho La Brea collection. One reason for the paucity of taphonomic studies at Rancho La Brea is that much of the material was collected before 1930, when excavation techniques were less thorough than is typical today. The preference at that time was for large, complete bones, and little attention was paid to collecting positional or other data (Shaw and Quinn 1986). More recent excavations have addressed this problem. Since 1969, the Los Angeles County Museum of Natural History has been excavating Pit 91, one of the asphalt deposits located in Hancock Park (Shaw 1982). Over 40,000 specimens collected between 1969 and 1980 have been identified and cataloged into a computer database, each with three-dimensional positional information. This collection is the focus of the research presented here.

One of the more unusual aspects of the La Brea faunal collection is the dominance of carnivores (Shaw and Quinn 1986; Stock and Harris 1992). Over 90% of the large mammalian specimens recovered represent members of the order Carnivora (Marcus 1960). This is certainly not the case in living communities, in which carnivores are at the top of the food pyramid and thus are much less abundant than herbivores (Eisenberg 1981). It has been suggested that the disproportionate abundance of carnivores is a result of the following scenario: a single herbivore became trapped in the asphalt and attracted numerous carnivores, some of which were trapped in turn. Such an event need only have occurred once every ten years or so over the course of 30,000 years to account for all the large mammals in

the entire collection (Shaw and Quinn 1986; Stock and Harris 1992).

To investigate taphonomic processes affecting the Rancho La Brea fauna, we explored several hypotheses. First, because the asphalt seeped out through vents, forming a layer of unknown thickness that covered the ground instead of a deep pit, it is possible that the skeletons were exposed for a significant period of time, rather than being quickly submerged in the asphalt. Our first hypothesis is that the bones are likely to exhibit relatively high weathering stages (Behrensmeyer 1978) due to exposure. Second, reconstruction of some of the sediments as deposited by fluvial action suggests that fluvial transport affected the assemblages. If so, then we expect that the majority of the bones' surfaces will exhibit signs of abrasion.

A third set of hypotheses is based on a variety of patterns relating to the effects of carnivores on bone deposits. The predominance of carnivores and the high incidence of carnivore teeth fractured in life (Van Valkenburgh and Hertel 1993) suggest that carnivore modification of carcasses ("ravaging") might have significantly destroyed and dispersed the skeletal assemblages as well. Actualistic studies of bone-modifying behaviors in gray wolves (*C. lupus*) (Haynes 1982, 1983; D'Andrea and Gotthardt 1984) and spotted hyenas (*Crocuta crocuta*) (Blumenschine 1986, 1988; Marean and Spencer 1991) indicate that it is possible to predict expected patterns of bone modification and skeletal representation if carnivore activity was involved. Both these species are appropriate models for this analysis because they share some similarities with dire wolves (*Canis dirus*), a dominant carnivore in the Pit 91 assemblage. Gray wolves are closely related to dire wolves and morphologically similar in many ways, but the slightly more robust dentition of dire wolves indicates greater bone-crushing abilities (Stock and Harris 1992), and thus spotted hyenas are an appropriate analog as well. It is likely that the bone-modifying behaviors of dire wolves were intermediate between those of extant wolves and spotted hyenas. Sabertooth cats (*Smilodon fatalis*) are also abundant in Pit 91, and their feeding activities could also have

modified the fossil sample in some way (Miller 1969), though their postcanine dentition is unsuited for bone crushing (Marean and Ehrhardt 1995).

Both wolves and spotted hyenas tend to leave the skulls and mandibles of their prey behind, but they often remove entire limbs, especially from the upper exposed side of the carcass (Haynes 1982; D'Andrea and Gotthardt 1984; Blumenschine 1986, 1988). They both tend to favor bones that are less dense and contain significant amounts of bone grease and marrow (Haynes 1980, 1982; Blumenschine 1988; Marean and Spencer 1991; Marean et al. 1992). Evidence of their feeding activity can be significant, with 50% to more than 70% of all bones showing tooth marks (D'Andrea and Gotthardt 1984; Blumenschine 1988).

In view of these general patterns, we generated a group of hypotheses concerning carnivore modification of the Pit 91 sample: if carnivore ravaging was significant, then (1) skulls and mandibles should be relatively common elements; (2) limb bones should only be present half as often as expected; and (3) bone density and element frequency should be correlated, because carnivores will preferentially carry away and/or consume the least dense elements of a skeleton. However, because a tar seep is not the same context as a kill site, and carnivores probably did not consume carcasses on site, we predict that (4) bones recovered from the tar seep will be relatively complete, and that (5) tooth mark frequencies will be low. These hypotheses were tested through examination of skeletal part representation and carnivore modification.

Materials and Methods

Sample

To investigate the taphonomic processes that affected the bone collections at Rancho La Brea, we examined a large subset of the cataloged material from the 1969–1980 excavation of Pit 91. Although not all the material from this excavation has been cataloged, we assume that our subset of 18,498 specimens is representative of the entire collection. Elements that might be underrepresented include small el-

ements such as phalanges, because some of these elements have yet to be prepared and cataloged. Consequently, our major conclusions are based on the relative representation of limbs and crania rather than smaller elements. Our subset of 18,498 specimens consisted of material from mammals estimated to have weighed more than 5 kg. Small mammals and nonmammalian species were not included because the smaller, more delicate bones experience different taphonomic processes than bones from larger species. Also excluded from this subset were individual teeth, sesamoid bones, and sloth osteoderms, because none of these element types typically exhibit any surface modification. Table 1 lists the taxa included in this sample, and the number of identified specimens (NISP) for each taxon.

Data Collection and Analysis

For each cataloged specimen, several variables were recorded. These included taxonomic information (order, family, genus and species) and skeletal part (element, side, and, if known, whether the specimen comes from an adult or a juvenile). Also recorded was whether a specimen was complete or partial, and if partial, what portion of the element was present. For example, for all long bones the presence or absence of the following portions was recorded: proximal epiphysis, proximal shaft, midshaft, distal shaft, and distal epiphysis. This information allowed us to generate reasonably accurate MNE (minimum number of element) counts because they were based on the most common portion. Finally, we recorded a variety of taphonomic variables, including weathering, abrasion, pit wear, rodent and insect modification, and carnivore modification. Three of these variables are discussed here:

Weathering.—Bones exposed to the elements experience exfoliation, cracking, and splitting (Miller 1975; Fisher 1995). Behrensmeier (1978) demonstrated that bones lying on the land surface pass through distinct weathering stages. Stage 0: bone surface shows no sign of cracking or flaking; Stage 1: bone surface shows cracking; Stage 2: outermost layers of bone surface show flaking, and deeper cracking; Stage 3: bone surface has large patches of

TABLE 1. Taxonomic information for the Pit 91 sample examined for this project.

Order	Family	Genus	Species	NISP
Artiodactyla				28
Artiodactyla	Antilocapridae			8
Artiodactyla	Antilocapridae	<i>Antilocapra</i>	<i>americana</i>	10
Artiodactyla	Antilocapridae	<i>Capromeryx</i>		3
Artiodactyla	Antilocapridae	<i>Capromeryx</i>	<i>minor</i>	71
Artiodactyla	Bovidae			15
Artiodactyla	Bovidae	<i>Bison</i>		1
Artiodactyla	Bovidae	<i>Bison</i>	<i>antiquus</i>	1002
Artiodactyla	Bovidae	<i>Bison</i>	<i>occidentalis</i>	2
Artiodactyla	Camelidae			2
Artiodactyla	Camelidae	<i>Camelops</i>		1
Artiodactyla	Camelidae	<i>Camelops</i>	<i>hesternus</i>	38
Artiodactyla	Cervidae			7
Artiodactyla	Cervidae	<i>Odocoileus</i>	<i>hemionus</i>	21
Artiodactyla	Tayassuidae	<i>Platygonus</i>		2
Carnivora				22
Carnivora	Canidae			10
Carnivora	Canidae	<i>Canis</i>		36
Carnivora	Canidae	<i>Canis</i>	<i>dirus</i>	6666
Carnivora	Canidae	<i>Canis</i>	<i>latrans</i>	1213
Carnivora	Canidae	<i>Canis</i>	<i>lupus</i>	6
Carnivora	Canidae	<i>Urocyon</i>		1
Carnivora	Felidae			30
Carnivora	Felidae	<i>Felis</i>		19
Carnivora	Felidae	<i>Felis</i>	<i>concolor</i>	29
Carnivora	Felidae	<i>Lynx</i>	<i>rufus</i>	17
Carnivora	Felidae	<i>Panthera</i>	<i>atrox</i>	188
Carnivora	Felidae	<i>Smilodon</i>		2
Carnivora	Felidae	<i>Smilodon</i>	<i>fatalis</i>	7312
Carnivora	Ursidae			9
Carnivora	Ursidae	<i>Arctodus</i>		1
Carnivora	Ursidae	<i>Arctodus</i>	<i>simus</i>	86
Carnivora	Ursidae	<i>Ursus</i>		2
Carnivora	Ursidae	<i>Ursus</i>	<i>arctos</i>	4
Edentata				6
Edentata	Megatheriidae			4
Edentata	Megatheriidae	<i>Nothrotheriops</i>	<i>shastense</i>	52
Edentata	Mylodontidae			1
Edentata	Mylodontidae	<i>Paramylodon</i>	<i>harlani</i>	386
Herbivore				96
Herbivore?				2
Mammalia				204
Pecora				1
Perissodactyla				3
Perissodactyla	Equidae			14
Perissodactyla	Equidae	<i>Equus</i>		14
Perissodactyla	Equidae	<i>Equus</i>	<i>occidentalis</i>	835
Perissodactyla	Tapiridae	<i>Tapirus</i>	<i>californicus</i>	1
Proboscidea				5
Proboscidea	Mammutidae	<i>Mammut</i>	<i>americanum</i>	4
Unknown				6
			Total:	18,498

rough bone, from which the outermost surface layer has been removed; Stage 4: bone surface is coarsely fibrous and rough, splinters may be present; Stage 5: bone is falling apart, with large splinters missing, and deep cracking is present. For this study, each specimen was examined and assigned to one of these weath-

ering stages. Because different bones of the skeleton weather at different rates, as do bones of different-sized animals (Behrensmeier 1978), the sample is subdivided into categories of element and taxon.

Abrasion.—Abrasion is commonly defined as the erosion of the bone surface due to the

physical impact of sedimentary particles (Bromage 1984; Lyman 1994; Shipman and Rose 1988). It can occur both in water and on land, though it is much more common in water (Lyman 1994). Often, abrasion can result in a smooth, rounded, and polished surface (Fisher 1995). The erosion of the smooth outer bone surface, however, usually results in a rough texture being exposed. In this study, the degree of abrasion was recorded as follows. Absent: no erosion of surface bone; Minimal: slight erosion at one or two points on the bone; Light: less than 25% of the bone surface shows erosion; Moderate: between 25 and 50% of the bone surface shows erosion; Heavy: more than 50% of the bone surface shows erosion. The presence of a smooth polished surface was also noted.

Carnivore Modification.—Using strong directional lighting, and a low-power microscope when desirable (as advocated in Blumenschine et al. 1996), we carefully inspected every specimen for any kind of surface modification. Three categories of tooth marks were assessed: (1) scores, which are small marks (either circular or linear) with shallow cross-sections; (2) punctures, in which the bone has collapsed under the pressure of the tooth leaving a circular hole in the bone surface; and (3) notches, in which a semicircular-shaped flake is missing from the edge of a bone (Blumenschine 1988). If there were no scores, then a classification of Absent was recorded; one to five scores was recorded as Light; six to ten scores was recorded as Moderate; more than ten scores was recorded as Heavy. For punctures and notches, counts were made and the number of these kinds of modifications was recorded.

Patterns of abrasion, weathering, and carnivore modification present in the skeletal assemblage were summarized by assessing overall frequency (percentage of bones with modification), frequency of different types and levels of modification, and distribution of modified bones by element and species.

Skeletal Part Representation.—The assessment of skeletal part representation was restricted to the most common seven species from the assemblage, which make up more than 98% of the total sample. Table 2 lists these species and

TABLE 2. The seven most common taxa in the sample of specimens from Pit 91 examined in this study. Minimum number of individuals (MNI) is provided for both adults and juveniles.

Taxon	NISP	% Total sample	MNI (adult/juv)
<i>Smilodon fatalis</i>	7312	41%	73 (53/20)
<i>Canis dirus</i>	6666	37%	56 (40/16)
<i>Canis latrans</i>	1213	7%	16 (10/6)
<i>Bison antiquus</i>	1002	6%	12 (5/7)
<i>Equus occidentalis</i>	835	5%	13 (6/7)
<i>Paramylodon harlani</i>	386	2%	6 (4/2)
<i>Panthera atrox</i>	188	1%	6 (4/2)

the minimum number of individuals (MNI) for both adults and juveniles. This sample contains three herbivorous species, all of large (>300 kg) body size: *Equus occidentalis*, the western horse; *Bison antiquus*, the ancient bison; and *Paramylodon harlani*, Harlan's ground sloth. The scarcity of small and medium-sized herbivores suggests that these size classes of herbivores were not well represented in the Los Angeles basin some 30,000 years ago. There is no size bias in the modern collection methods for Pit 91, and the four carnivorous species range in body size from the small coyote (*Canis latrans*) through the medium-sized dire wolf (*C. dirus*) to the large sabertooth cat (*Smilodon fatalis*) and North American lion (*Panthera atrox*).

Skeletal part representation was determined by generating MNE counts for each element of the skeleton. The purpose of this was to assess how complete skeletal representation was for each species. MNE is the minimum number of a particular skeletal element or portion of an element (Lyman 1994). It is a quantitative unit that is useful for illustrating differences between what is found in the paleontological assemblage and the set of skeletal elements found in a complete skeleton. Here, MNE was derived by adding together all the counts for each recorded element portion. Using *Equus humeri* as an example, a NISP of 20 comprised four proximal epiphyses, six proximal shafts, 15 midshafts, 14 distal shafts, and eight distal epiphyses. The MNE is the number of the highest portion, so we recorded an MNE of 15, based on the midshafts represented in this sample. The age of the individ-

ual or side of the element is not taken into account to generate MNEs.

The MNE data (Table 3) were used to generate MAU (minimum animal unit) and %MAU values. To generate MAU values, the MNE for each element was divided by the number of times that element appears in a skeleton (e.g., humerus = 2). For each species, the MAU values were then standardized by dividing each MAU value by the greatest MAU value. In the *Equus* example, the axis yielded the highest MAU value, eight, and so the MAU of each element was divided by eight. The humerus thus had a %MAU value of 94%, showing that the survivorship of the humerus midshaft was very high relative to the most common element, the axis. The %MAU values for the seven most common taxa are listed in Table 4.

To assess whether patterns of skeletal part representation are mediated by such factors as bone density and the quantity of within-bone nutrients (e.g., marrow, grease), %MAU values of *Bison* and *Equus* limb element portions were plotted against structural density data for extant bovids (wildebeest, *Connochaetes taurinus*) and horses (*Equus* sp.) (Lam et al. 1998), and against bone grease or marrow cavity volume data for *Bison* and *Equus* (Brink 1997; Outram and Rowley-Conwy 1998). Unfortunately, comparable density data and within-bone nutrient data do not exist for *Paramylodon* or any carnivores.

Results

Weathering.—The overwhelming majority of the specimens (93%) are in Stages 0–2, showing either no weathering or some cracking and exfoliation of the outermost bone surface (Table 5). This pattern is consistent across different subsets of the sample, whether it is broken down by taxon, by element, or by age. Very few bones display Stage 5, yet these heavily weathered specimens are from four different species and were scattered throughout the deposit, so they do not represent a coherent group. Clearly, the large mammal bones from Pit 91 were buried fairly rapidly.

Abrasion.—Almost half of the specimens (48%) show no or minimal erosion of the surface bone (Table 6). Only 14% of the specimens

show moderate or heavy degrees of abrasion, in which more than 25% of the bone surface shows erosion. This pattern is consistent across different subcategories, including both bone type and mammalian order. However, when the sample is broken down by age, there is a shift in the frequencies for bones from juvenile individuals. The number of juvenile specimens showing moderate or heavy degrees of abrasion increases to 24%. It seems likely that the spongier nature of juvenile bone is more vulnerable to the effects of abrasion. Only 4% of the entire sample has a smooth polish and the rounded edges characteristic of water transport. Because almost half of the specimens examined show no or minimal abrasion, it is likely that fluvial transport did not significantly influence the composition of the Pit 91 bone assemblage.

Carnivore Modification.—As we predicted, very few specimens, 2% of the total sample, show carnivore modification. The number of specimens exhibiting carnivore scores is low ($n = 243$), and the majority of these show light scoring (Table 7). The same pattern is found for the other categories of carnivore modification. The number of specimens that have notches is lower ($n = 136$), and the number of specimens that show carnivore punctures is lower still ($n = 95$).

Limb bones, ribs, and vertebrae make up the majority of elements that show carnivore modification (Table 7). Specimens that show carnivore modification come from a variety of taxa (Table 8). In raw numbers, the most common taxa in the total sample also show the highest frequency of carnivore modification (bison, dire wolf, and sabertooth cat). However, when these values are scaled to NISPs, it is specimens that cannot be identified to genus that show higher frequencies of carnivore modification (Pecora, Edentata, Unknown, and Cervidae). These specimens cannot be identified to genus because they are so fragmentary, suggesting that these bones were intensively modified by carnivores at or near the tar seep.

Skeletal Part Representation.—If complete or mostly complete skeletons were recovered for the seven most common species, then most of the %MAU values in Table 4 would be at or

TABLE 3. Data on NISPs and MNEs for the most common seven taxa in the Pit 91 assemblage. See text for definitions.

Element	Bison		Equus		Paramylodon		C. dirus		Smilodon		C. latrans		Panthera	
	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE
Cranium	129	35	59	14	28	5	405	99	393	80	77	30	8	4
Dentary	35	32	15	13	7	7	175	140	168	143	34	31	7	6
Atlas	2	2	2	2	1	1	57	52	64	57	11	6	1	1
Axis	2	2	8	8	0	0	69	55	50	44	11	10	1	1
Cervical vertebra	28	13	45	16	6	3	247	175	318	202	40	34	2	2
Thoracic vertebra	120	65	183	110	56	23	473	320	666	464	54	35	14	12
Lumbar vertebra	58	21	48	22	0	0	314	197	458	264	44	31	13	6
Sacral vertebra	17	11	14	12	4	2	31	24	70	55	4	3	3	2
Caudal vertebra	9	9	23	18	28	21	249	231	256	247	42	37	10	6
Scapula	23	18	9	8	8	7	113	87	121	83	13	11	4	4
Rib	229	123	196	108	73	48	834	620	940	773	119	72	14	14
Sternebra	0	0	6	6	10	10	99	89	106	87	8	8	3	3
Innominate	39	18	24	14	9	7	112	78	153	96	23	18	4	3
Humerus	20	15	20	15	10	5	140	98	122	61	24	10	5	4
Radius	38	11	15	12	6	4	134	95	121	72	36	18	5	3
Ulna	17	15	5	5	3	2	165	100	124	80	39	25	1	1
Metacarpal	16	15	12	12	10	10	340	331	256	254	96	95	5	4
Carpal	35	35	21	21	14	14	333	329	353	346	60	60	6	6
Femur	20	13	21	10	9	5	154	81	172	87	18	10	6	3
Tibia	18	12	12	8	7	6	137	89	154	87	18	10	6	4
Fibula	8	7	2	1	7	5	103	62	109	68	32	18	9	6
Patella	5	5	5	5	0	0	58	58	42	42	11	11	6	6
Metatarsals	9	9	6	14	4	4	260	255	272	271	57	56	7	5
Metapodials	34	24	4	26	n/a	n/a	685	663	584	528	192	152	n/a	n/a
Astragalus	8	8	14	6	6	5	90	89	65	63	27	27	2	2
Calcaneum	13	12	30	4	3	3	106	90	77	49	25	17	5	2
Other tarsals	19	19	12	12	6	5	182	179	241	236	25	25	12	12
Phalanx	78	64	29	26	43	n/a	1017	949	1235	1110	216	160	27	26

TABLE 4. Skeletal part representation data (%MAU) for the seven most common taxa. Each value represents the MAU scaled to the element that had the highest MAU value, to indicate the completeness of the skeletal remains.

Element	<i>Bison</i>	<i>Equus</i>	<i>Paramylodon</i>	<i>Smilodon</i>	<i>C. dirus</i>	<i>C. latrans</i>	<i>Panthera</i>
Cranium	100	88	71	100	71	97	100
Dentary	91	81	100	89	100	100	75
Atlas	11	25	29	71	74	39	25
Axis	11	100	0	55	79	65	25
Cervical	15	40	17	50	50	44	10
Thoracic	27	76	41	44	35	17	23
Lumbar	24	46	0	47	40	29	21
Sacral	13	21	6	23	11	6	17
Caudal	3	12	29	24	16	11	6
Scapula	51	50	100	52	62	35	50
Rib	25	38	26	37	34	18	13
Sternebra	0	9	41	14	16	6	9
Innominate	51	88	100	60	56	58	38
Humerus	43	94	71	38	70	32	50
Radius	31	75	57	45	68	58	38
Ulna	43	31	29	50	71	81	13
Metacarpal	43	75	29	32	47	61	10
Carpal	17	19	29	31	34	28	11
Femur	37	63	71	54	58	32	38
Tibia	34	50	86	54	44	32	50
Fibula	20	6	71	42	64	58	75
Patella	14	31	0	26	41	35	75
Metatarsal	26	88	14	42	46	45	16
Astragalus	23	38	71	39	64	87	25
Calcaneum	34	25	43	30	64	55	25
Other tarsal	18	19	18	29	26	16	30
Phalanx	15	27	n/a	27	24	18	13

close to 100. However, examination of Table 4 shows that for each species there are many elements missing, relative to the most common element recovered for each (see also Fig. 1). Among the seven species, *Bison* shows the most missing elements, with all but two of the elements showing %MAU values at or below 50%. The two cranial elements, cranium and dentary, are the most common, and small elements such as sternebrae and caudal vertebrae are almost completely absent. In contrast to *Bison*, *Equus* shows better survival of elements, with many %MAU values above 75%. Those elements that tend to be underrepresented in the *Equus* sample are small bones such as fibulae, sternebrae, and caudal vertebrae. *Paramylodon* shows a pattern of %MAU values intermediate between *Bison* and *Equus*. The innominate, scapula, and dentary all yield values of 100%, and six other elements (cranium, humerus, femur, tibia, fibula, and astragalus) have %MAU values between 50 and 75%.

Among the carnivores, the dire wolf shows the most complete pattern of skeletal repre-

sentation. *C. dirus* has %MAU values that fall between 50% and 75% for most of the appendicular bones, whereas bones of the axial skeleton (ribs, sternebrae, and vertebrae) tend to be underrepresented, although not to the extent seen in *Bison*. For *C. latrans*, cranium, dentary, astragalus, and ulna are well represented, with %MAU values over 75%. Underrepresented elements include thoracic, lumbar, sacral, and caudal vertebrae, and sternebrae. *Smilodon* exhibits a fairly even pattern of representation, with most of the elements showing %MAU values between 30 and 60%. The elements that are most underrepresented are sternebrae and the small vertebrae. Finally, *Panthera* specimens are not common in the assemblage, and many of the elements are underrepresented. The only elements that show high %MAU values are crania, dentaries, fibulae, and patellae.

The %MAU values for the seven species were pooled so that we could examine the range of values for each element (Fig. 1). It is consistently the skull elements (crania [especially maxillae] and dentaries) that yield the

TABLE 5. Weathering data for the Pit 91 sample. Regardless of taxon, bone type, and age, the majority of the bones exhibit the first three weathering stages. Numbers in parentheses refer to percentage of the total.

Taxon	Stage 0	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5
Artiodactyla						
Skull	16	108	43	48	2	1
Axial bone	24	389	122	67	7	0
Long bone	11	154	59	52	7	1
Compact bone	6	66	26	2	0	0
Perissodactyla						
Skull	9	51	15	15	2	0
Axial bone	28	427	67	40	2	0
Long bone	3	65	34	32	4	1
Compact bone	0	42	6	2	2	0
Edentata						
Skull	4	28	10	6	0	0
Axial bone	10	136	54	38	6	0
Long bone	10	72	16	12	1	0
Compact bone	5	29	10	2	0	0
Carnivora						
Skull	220	834	278	149	10	1
Axial bone	553	4793	732	353	27	0
Long bone	747	4254	582	265	24	3
Compact bone	418	1303	89	13	2	0
Other Mammalia						
Skull	28	82	15	13	1	0
Axial bone	11	91	21	21	1	0
Long bone	6	13	4	1	0	0
Compact bone	0	4	0	0	0	0
Total	2109 (11)	12,941 (70)	2183 (12)	1131 (6)	98 (1)	7 (0.03)
Age						
Adult	945 (11)	5931 (69)	1182 (14)	471 (5)	52 (0.6)	3 (0.03)
Juvenile	425 (9)	3302 (71)	470 (10)	406 (9)	26 (0.6)	1 (0.02)

highest %MAU values (mean = 0.9, range = 0.71–1.0), whereas small elements such as sacral vertebrae, caudal vertebrae, sternebrae, carpals, tarsals (other than astragalus and calcaneum), and phalanges have the lowest %MAU values (mean = 0.18, range = 0.14–0.24). The limb elements have %MAU values that tend to be around 50% (mean = 0.51, range = 0.45–0.57).

Completeness of Skeletal Elements.—Only data from adult individuals are used in this analysis, as juveniles were scored as partial even if only unfused epiphyses were missing. Out of a total of 8586 unequivocally adult specimens from all taxa, 76% were complete. This indicates that, of the bones that were deposited at the tar seep, fully three-quarters of them were unmodified before burial.

Bone Density.—To determine if any density-mediated processes of destruction might have influenced the Pit 91 assemblage, the repre-

sentation of elements relative to their density was examined for bison and horse, the only two of the fossil species for which there are pertinent density data. A regression of the *Bison* %MAU limb data against wildebeest (*Connochaetes taurinus*) bone density data revealed a significant ($p < 0.0001$) relationship between the density of an element portion and %MAU value (Fig. 2). The elements included in this analysis are the proximal end, proximal shaft, midshaft, distal shaft, and distal end of the humerus, radius, metacarpal, femur, tibia, and metatarsal. To determine if carnivore ravaging was likely to have created the pattern of representation seen in the Pit 91 *Bison* assemblage, the %MAU values of limb portions were plotted against the mean fat content of those limb portions (Fig. 3). The highly significant relationship between these two variables ($p < 0.0001$, Spearman's $\rho = -0.854$) suggests that *Bison* carcasses were ravaged by carni-

TABLE 6. Number of specimens assigned to each category of abrasion, separated by taxon, bone type, and age. The number in parentheses is the percentage of the total.

Taxon	Absent	Minimal	Light	Moderate	Heavy
Artiodactyla					
Skull	22	32	126	33	5
Axial	40	96	327	134	11
Long bone	44	51	123	53	13
Compact bone	25	26	30	16	3
Carnivora					
Skull	283	349	623	203	34
Axial	720	1708	3031	868	131
Long bone	1539	2201	1618	459	57
Compact bone	465	742	525	84	9
Edentata					
Skull	6	9	21	11	1
Axial	12	61	114	47	10
Long bone	16	31	40	19	5
Compact bone	9	12	17	6	2
Perissodactyla					
Skull	8	15	52	16	1
Axial	35	104	300	114	31
Long bone	20	22	52	39	6
Compact bone	13	12	20	5	2
Other Mammalia					
Skull	26	38	60	15	0
Axial	12	24	79	33	7
Long bone	0	4	11	6	3
Compact bone	0	0	4	0	0
Total	3295 (18)	5537 (30)	7173 (39)	2161 (12)	331 (2)
Age					
Adult	1895 (22)	2937 (34)	2950 (34)	686 (8)	114 (1)
Juvenile	369 (8)	874 (19)	2276 (49)	966 (21)	144 (3)

vores who either dispersed or consumed the greasiest portions of the limb elements.

However, a similar analysis of *Equus* limb bone density and representation does not show such a strong relationship. Regression of *Equus* %MAU limb data against modern *Equus* bone density data showed a weaker correlation (Fig. 4). Although it is significant ($p = 0.0004$), the bivariate plot shows a general

scatter of points. These data suggest that unlike *Bison*, the representation of *Equus* limb element portions was not strongly influenced by a density-mediated process. Mean fat content of *Equus* limb elements has not been published, but marrow cavity volume for the limb bones (Outram and Rowley-Conwy 1998) plotted against %MAU values show a weak, nonsignificant relationship (Fig. 5). Of course, marrow cavity volume is not the same as either marrow mass or quality, but Outram and Rowley-Conwy (1998) found that it provides the same rank order of elements, and is more consistently measured than marrow mass. Notably, their study indicated that the femur, humerus, and radius had the greatest cavity volumes and marrow masses. These elements are not underrepresented in Pit 91 (all have %MAU values greater than 0.60), and thus the skeletal-element representation of *Equus* limb bones does not appear to be indicative of car-

TABLE 7. A summary of the quantity of carnivore modifications found on the various types of skeletal elements from the entire sample of bones ($n = 18,498$).

Bone class	n	Score	Puncture	Notch
Compact bone	19	10	6	5
Innominate/scapula	45	27	14	18
Long bone	132	90	22	34
Rib	114	70	26	23
Skull	23	7	4	12
Vertebra	98	39	23	44
Total:	431	243	95	136

TABLE 8. Taxonomic information for the specimens that exhibit carnivore tooth marks.

Order	Family	Genus	No. of tooth-marked specimens	Total NISP	Proportion of NISP with tooth marks
Artiodactyla			1	28	0.04
Artiodactyla	Antilocapridae	<i>Capromeryx</i>	1	71	0.01
Artiodactyla	Bovidae	<i>Bison</i>	75	1004	0.07
Artiodactyla	Camelidae	<i>Camelops</i>	2	38	0.05
Artiodactyla	Cervidae		1	7	0.14
Artiodactyla	Cervidae	<i>Odocoileus</i>	2	21	0.10
Carnivora	Canidae	<i>Canis</i>	112	7915	0.01
Carnivora	Felidae	<i>Panthera</i>	5	188	0.03
Carnivora	Felidae	<i>Smilodon</i>	155	7312	0.02
Carnivora	Ursidae	<i>Arctodus</i>	3	86	0.03
Edentata			2	6	0.33
Edentata	Megatheriidae	<i>Nothrotheriops</i>	1	52	0.02
Edentata	Mylodontidae	<i>Paramylodon</i>	14	386	0.04
Herbivore			8	96	0.08
Mammalia			3	204	0.01
Pecora			1	1	1.00
Perissodactyla	Equidae	<i>Equus</i>	44	849	0.05
Unknown			1	6	0.17

nivore ravaging, at least, not to the extent seen in the *Bison* assemblage.

Discussion

The taphonomic data collected for this study can be used to identify the postmortem

processes that affected the larger animals that became trapped in the Pit 91 asphalt deposit. The majority of the more than 18,000 specimens examined showed little or no weathering, indicating that skeletal elements were not exposed on the surface for long. Abrasion data

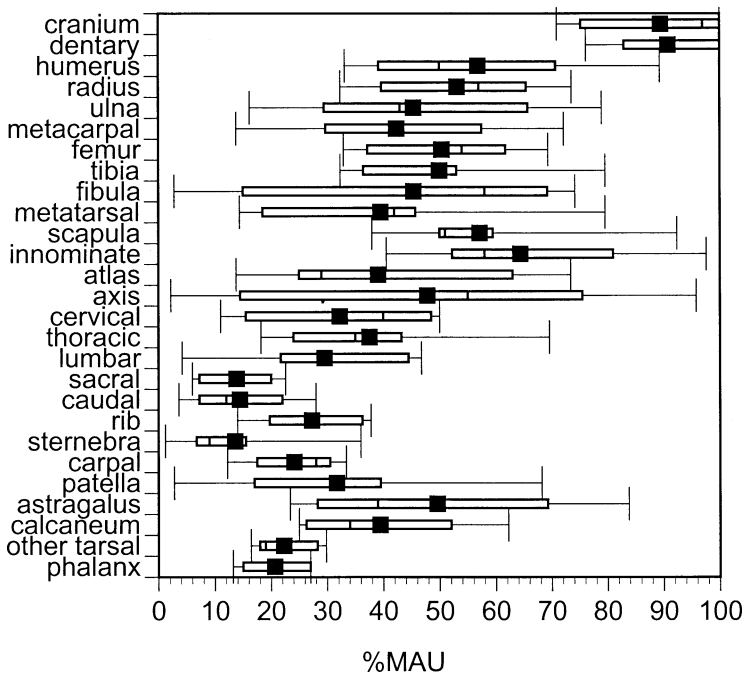


FIGURE 1. The %MAU values for each element pooled for the seven most common large mammals from Pit 91. The black box represents the means, and the vertical lines represent the endpoints of the ranges. The open horizontal box encloses the central 50% of the data.

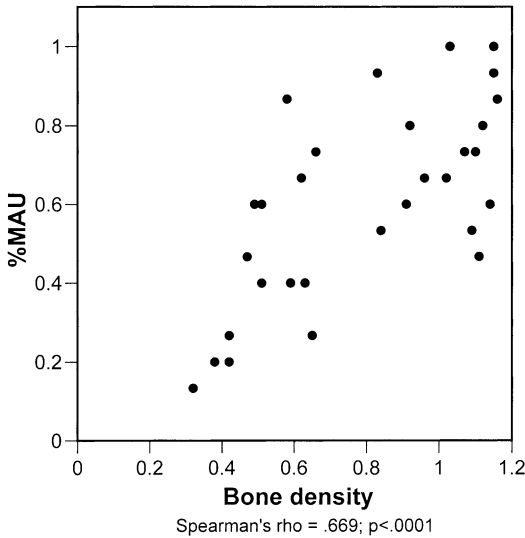


FIGURE 2. *Bison* %MAU values for limb portions (proximal epiphysis, proximal shaft, midshaft, distal shaft, and distal epiphysis of the humerus, radius, metacarpal, femur, tibia, and metatarsal) plotted against *Connochaetes* bone density values from Lam et al. 1999.

suggest that fluvial action did not significantly influence the composition of the bone assemblage from Pit 91. The erosion of surface bone is not common in this assemblage, as 86% of the specimens examined show little, minimal, or no abrasion at all. Although the area of deposition includes stream channels, it

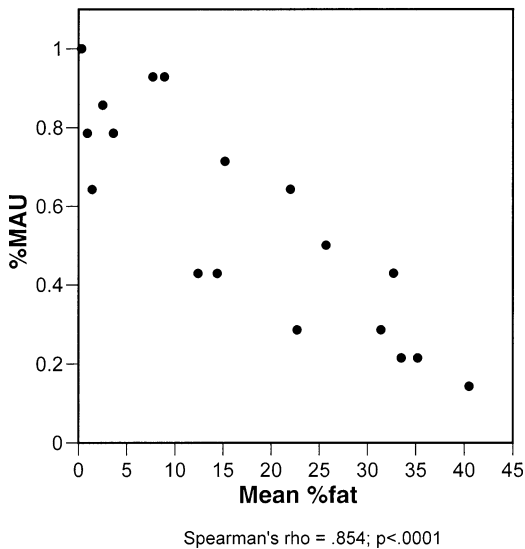


FIGURE 3. *Bison* %MAU values for limb portions (same as in Fig. 2) plotted against mean percentage of fat values found in *Bison* limb bones from Brink 1997.

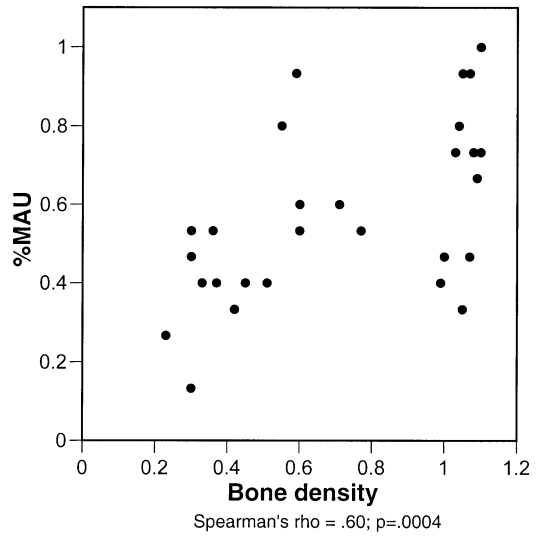


FIGURE 4. *Equus* %MAU values for limb portions (same as in Fig. 2) plotted against *Equus* bone density values from Lam et al. 1999.

seems that once partial or entire carcasses were mired in asphalt, they resisted movement by water. The abrasive effects of asphalt on bone are unknown, and future actualistic studies might indicate that the small amounts of observed abrasion are the result of erosion of surface bone by asphalt rather than water.

However, in the short time between death

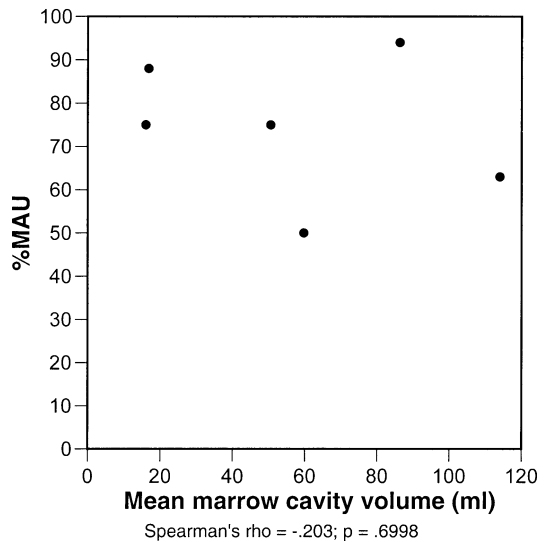


FIGURE 5. *Equus* %MAU values for limb elements (humerus, radius, metacarpal, femur, tibia, metatarsal) plotted against mean marrow cavity volume (ml) from three modern horses; data from Outram and Rowley-Conwy 1998.

and burial, it is clear that some taphonomic process was affecting carcasses, because complete skeletons are rare, if not entirely absent. Among the seven most common species, cranial elements (skull and mandible) predominate (Fig. 1). Skeletal elements that are most often missing from these species are the small bones, (such as sternbrae, tarsals, carpals, and smaller vertebrae such as sacral and caudal elements), though larger elements such as limb bones tend to be represented only half as often as expected.

Carnivore ravaging can produce patterns of skeletal representation similar to that documented for Pit 91. If intense carnivore ravaging occurred during the formation of the Pit 91 assemblage, skulls and mandibles are expected to be the most common elements, and that is indeed the case. When the MNE values for each of the seven most common species were scaled to reflect completeness of skeletons, all but one species had either cranium or dentary as yielding the highest MAU. The single exception is *Equus*, in which the axis yields the highest MAU value. This cervical vertebra is so tightly attached to the skull by ligaments that it is often considered part of the head complex (Haynes 1982), and so does not nullify our hypothesis.

Many observers of carnivore ravaging behaviors at kill sites have noted that carnivores often remove a limb from a carcass and transport it to a safer place for feeding (e.g., Haynes 1982; Blumenschine 1988). Therefore, we predicted that limb bones would be present only half as often as expected, and indeed, the %MAU values for most of the limb bones of the seven species tend to be around 50%. We suggest that only half of the limb elements are represented in Pit 91 because the other half, representing the half of the carcass that was not in contact with the ground, was carried off by carnivores. The limbs on one side of the carcass were presumably mired in the asphalt, and thus could not be carried off or were not desirable because of the asphalt contamination. Notably, skeletal representation data do not show that distal limb bones are better represented than more proximal elements. This might be expected if trapped animals usually sank in feet first, leaving their torsos and

heads exposed to carnivores. However, Table 4 does not show a pattern of greater representation of distal relative to more proximal elements (compare radii with humeri, tibiae with femora, metapodials with femora or humeri). Instead, it seems that animals usually fell to one side as they struggled in the asphalt.

The predominance of half skeletons implies that many of the carnivores that came to feed on trapped animals at Rancho La Brea were successful at removing elements from the asphalt and did not become trapped themselves. Interestingly, Haynes (1982) noted that wolves carry carcass parts back to their dens in the summertime, when their young, born in early spring, are old enough to eat meat. Speculating that dire wolves had a similar reproductive schedule, we might expect that they also were removing parts from carcasses trapped in asphalt deposits during the summer, when the seeps are at their stickiest (Shaw and Quinn 1986; Quinn 1992).

The overall pattern of skeletal part representation indicates many missing elements for the most abundant species from Pit 91, especially the bison. The significant correlation between bone density and element representation in this species suggests that carnivores were responsible for eliminating the least dense elements. This conclusion is further supported by the relationship between element representation and bone grease content, which showed that the least common elements were those that contained the most bone grease. However, a different pattern is seen in the skeletal part representation of the other common herbivore, the horse. *Equus* elements show higher %MAU values, and weaker correlations between the elements present and both bone density and marrow content. Lam et al.'s 1999 study of bone density among species of bovids and equids concluded that "the similarity in bone density patterns [between these two groups]. . . indicates that differences in bone survivorship between them are far more likely to be attributable to behavioral agents than to density-mediated destruction (Lam et al. 1999: p. 359). We therefore conclude that the different pattern of skeletal-element representation at La Brea is more likely the result of carnivore preference for *Bison*.

Apparently, La Brea carnivores were less interested in consuming *Equus* skeletal elements, perhaps because the marrow content in their limb bones is of lower yield relative to that of artiodactyls (Blumenschine and Madrigal 1993; Outram and Rowley-Conwy 1998). The nutrient content of *Paramylodon* bones is unknown, but their pattern of more complete representation in the Pit 91 assemblage suggests that, compared with the other herbivore species, sloth carcasses were less attractive and less vulnerable to carnivores. Because many elements are missing from the four carnivore species profiles and a small percentage of carnivore bones exhibit tooth marks, it appears that these species were also consumed, which is intriguing because extant carnivores rarely feed on other large carnivores even when they are available.

Our expectation of little on-site ravaging was supported by data on carnivore modification and completeness of skeletal elements. The actual amount of carnivore modification on the bones is low, less than 2%, and the majority of the adult bones are complete. A tar seep was not likely to have been a comfortable place for a carnivore to consume a carcass, and the low %MAU values for many elements suggests that carnivores were more likely to have taken body parts away from the tar seep for consumption. These data highlight the unique nature of this depositional environment, emphasizing its differences from modern kill sites.

Conclusion

The wealth of material recovered from the asphalt deposits of Rancho La Brea has long been appreciated for providing information about late Pleistocene fauna and flora of southern California. However, research using the collections has been limited by a lack of data on the taphonomic history of the fossil deposits. Our taphonomic analysis of a sample of over 18,000 specimens from Pit 91 indicates rapid burial and a strong overprint of carnivore activity. Rapid burial is supported by the fact that over 90% of the bones exhibit little or no weathering. Although the bones themselves have few carnivore tooth marks, the patterns of skeletal-element abundance in-

dicating that many elements are missing from the assemblage. Moreover, those elements that are missing appear to be those that are most attractive to carnivores because of their low density and high nutrient content (at least for the most common herbivore for which such data are available). Carnivores and herbivores show a comparable lack of complete preservation, suggesting that both were similarly subject to carnivore feeding activity. From these results we conclude that the large mammal assemblage of Pit 91 has been substantially biased by the activities of carnivores.

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