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STONE AGE INSTITUTE PUBLICATION SERIES

NUMBER 2

Series Editors Kathy Schick and Nicholas Toth

BREATHING LIFE INTO FOSSILS:

Taphonomic Studies in Honor of C.K. (Bob) Brain



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Front cover, clockwise from top left.

Top left:

Artist's reconstruction of the depositional context of Swartkrans Cave, South Africa, with a leopard consuming a hominid carcass in a tree outside the cave: bones would subsequently wash into the cave and be incorporated in the breccia deposits. © 1985 Jay H. Matternes.

Top right: The Swartkrans cave deposits in South Africa, where excavations have yielded many hominids and other animal fossils. ©1985 David L. Brill.

Bottom right: Reconstruction of a hominid being carried by a leopard. © 1985 Jay H. Matternes.

Bottom left: Photograph of a leopard mandible and the skull cap of a hominid from Swartkrans, with the leopard's canines juxtaposed with puncture marks likely produced by a leopard carrying its hominid prey. © 1985 David L. Brill.

Center: Photo of Bob Brain holding a cast of a spotted hyena skull signed by all of the taphonomy conference participants. © 2004 Kathy Schick, Stone Age Institute.

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CHAPTER 8

CHANGES THROUGH TIME IN CARCASS SURVIVAL IN THE AMBOSELI ECOSYSTEM, SOUTHERN KENYA

A.K. BEHRENSMEYER

ABSTRACT

Bob Brain pioneered using modern bone assemblages to build a body of comparative information that could be used to interpret taphonomic processes affecting faunal remains in the paleoanthropological record. His original research inspired other neo-taphonomic studies that have been used to formulate scavenging vs. hunting models for early hominin subsistence strategies. Study of the Amboseli ecosystem in southern Kenya (1975-2004) demonstrates how decade-scale changes in predator diversity and population dynamics affect the taphonomic features of bone assemblages and carcass survival. Twenty transects in 3 different habitats were surveyed in 1975 and 2002-2003, resulting in a sample of over 800 individuals (MNI) and nearly 10,000 skeletal elements (MNE). Data for each MNI include species, skeletal elements present, bone completeness and other modification features. Relatively high rates of carcass survival occurred during the 1970s and 1980s when lions, spotted hyenas and other carnivores competed for prey and the spotted hyena population was low. Herbivore die-offs during droughts also provided occasional surfeits of carcasses for scavengers. Under such conditions, hominins would have had access to carcasses either through accidental discovery or power-scavenging, as well as ample opportunities to hunt and retain control of their prey. Relative to the 1975 sample, a 75% decrease in bones per individual and higher levels of damage to surviving elements have been the norm in Amboseli from 1990-2004, especially in the prey size range from 25-250 kg. This change correlates with a population increase of Crocuta and low numbers of other predators. Skeletal part survival and bone modification patterns provide direct evidence for these different ecological conditions. The taphonomic changes in Amboseli show that over several decades, the survival of carcasses and bones can vary markedly within the same ecosystem and within the same habitat. Thus, the availability of scavengeable remains could have changed markedly over the lifetime of individual hominins. The results also indicate that differences in habitat–carcass associations can virtually disappear when a bone-consumer such as *Crocuta* becomes the dominant predator. In the fossil and archeological record, unbiased samples of skeletal part abundance and completeness, adult/juvenile ratios, and damage patterns in relation to prey body size could be used to indicate different levels of bone-consuming predator pressure.

INTRODUCTION

A rich history is recorded in the patterns of preservation of animal skeletons. Vertebrate taphonomists work throughout the Phanerozoic fossil record, but the growth in understanding of the meaning of taphonomic patterns has been greatly stimulated by interest in human evolution and the study of bones and stones that our ancestors left scattered on the ancient landscapes. Bob Brain exemplifies this approach and has contributed more than anyone of his generation to the ideas and knowledge that turn evidence from bones into understanding of taphonomic processes, both human and non-human. A major strength of his research has been the actualistic observations and experiments that he conducted to understand taphonomic cause and effect.

Taphonomic studies of bones in modern ecosystems have been championed by Brain (1967, 1969, 1981)

as well as a number of other researchers, starting with Weigelt in the 1920s (Weigelt, 1927) and continuing with the work of Hill (1975; 1980), Gifford (Gifford and Behrensmeyer, 1977), Yellen (1977), Behrensmeyer (Behrensmeyer et al., 1979; Behrensmeyer and Boaz 1980; Behrensmeyer, 1993), Haynes (1985, 1988), Bunn (Bunn, 1982, Bunn et al., 1988, Bunn and Ezzo, 1993), Blumenschine (1989), Dominguez-Rodrigo (2001) and Tappen (1995, 2001). Controlled experiments on taphonomic processes have also contributed to information that can be brought to bear on the past (e.g., Shipman, 1981; Marean et al., 1992, Marean, 1997). Through such actualistic research, paleontologists and paleoanthropologists have built a large body of information on processes that modify bones and leave identifiable traces, allowing us to decode some of the patterns in the fossil record and to distinguish non-human from human damage features. This research has also resulted in a huge leap in understanding of what happens to bones in the post-mortem environment and the realization that different processes can result in similar end-products. The bones themselves, their size, shape and strength, exert definitive though not exclusive control on which body parts, and which bone portions, are most likely to survive to become fossils. Ta-

phonomic "reality checks" provided by experiments and observations in the modern world have shaped many scientific careers, including Bob Brain's, and will continue to challenge and intrigue archeologists, paleoanthropologists, and paleontologists into the future.

Although much has been learned about specific bone-modifying agents and other taphonomic processes over the past century, questions about the relationships of bone assemblages to the ecology of living animals remain unanswered. How faithfully do surface bone assemblages represent the vertebrate species richness, population abundances, and habitat structure of an ecosystem? How stable are the taphonomic features of a bone assemblage, and how is ecological change reflected in these assemblages? Such questions relate to problems of interest to paleoanthropologists, such as whether early hominins might have found some habitats more favorable than others for hunting or scavenging meat from carnivore kills (Blumenschine, 1989; Potts, 2003), and how taphonomic features of fossil bone assemblages correlate with varying levels of predator and scavenger pressure on prey populations.

This paper focuses on the specific problem of carcass completeness and survival in modern East African ecosystems. It builds upon pioneering research by Blumenschine (1989), Tappen (1995; 2001) and Dominguez-Rodrigo (2001), who studied different analogue communities to understand variables and processes that might have controlled carcass availability for early humans. The long-term taphonomic research in Amboseli documents change over several decades in carcass survival and indicates that predator impact as well as overall ecological change likely were important in controlling resources for early hominins living in similar ecosystems.

BACKGROUND: TAPHONOMIC RESEARCH IN AMBOSELI

Amboseli is a national park in southern Kenya that has been under continuous ecological study since the 1960's (Western, 1973, Western and von Praet, 1973; Western and Maitumo, 2004) (Figures 1 and 2). It has a rich vertebrate fauna, supported largely by springs emerging along the base of Mt. Kilimanjaro, which lies to the south on the Tanzanian side of the Kenya-Tanza-



Figure 1. Map of Kenya showing location of the Amboseli Basin in southern Kenya.



Figure 2. Landsat (1997) image of the Amboseli Basin showing the positions of the 20 bone sampling transects analyzed in this paper. Polygon shows the outline of the Amboseli National Park boundary.

nia border. During the past 30-40 years, Amboseli has experienced major ecological change due to the loss of Acacia woodlands and the expansion of grassland habitats. There also has been a substantial increase in the mean annual temperature (MAT) over the past 30 years (Altmann et al., 2002). Human impact has played a role in ecosystem change, with the exclusion of Maasai herds from the central basin, the expansion of tourism and road proliferation, followed by the return of domestic stock to portions of the central basin and increased levels of conflict between animals and wildlife in the areas surrounding Amboseli (Western, 2004, Western and Maitumo, 2004). All of these processes and circumstances have affected the vegetation and the vertebrate community in the park. The Amboseli ecosystem thus is an appropriate natural laboratory for examining how bone assemblages track ecological change and, conversely, how ecological change affects the taphonomic features of these assemblages.

The Amboseli basin covers approximately 600 km², with Amboseli National Park restricted to the central 388 km², which includes a number of spring-fed wetlands and part of seasonal Lake Amboseli (Figure 2). The climate is semi-arid, with average monthly temperatures between 26 and 34°C. There are two rainy seasons,

November-December and March-May, and an average yearly total of 350-400 mm of rainfall. Humidity is generally low, and the dry seasons are both dusty and windy. The permanent springs and accompanying high water table sustain primary productivity in the central basin and support large populations of plant and animal species. Some of the ungulates are resident, but most migrate in during the dry season and disperse during the wet season when there is water and forage elsewhere. Amboseli was known for its beautiful mosaic of woodland, grassland, and bush habitats when the bone study began in 1975. Over 20 different habitat types were originally designated in the 1960s by D. Western (1973), based on characteristic flora. The woodlands are now much reduced in area, and the park is dominated by open plains and salt bush habitats.

The goals of the long-term Amboseli bone study include monitoring bone weathering and destruction rates and patterns, documenting bone frequencies and identities for comparison with live census data, and establishing transects in different habitats for repeated re-sampling over periods of years to decades to record changes in the vertebrate remains (Figure 3). These goals were designed to address the following major questions: (1) What is the relationship of the faunal composition of the



Figure 3. Overview of timing and duration of taphonomic field research in Amboseli through 2003 (darkened bars). Month abbreviations across the top of the chart.

surface bone assemblage to the living community from which it is derived? (2) How rapidly do bones weather under natural circumstances? (3) How do biological, physical, and chemical processes affecting vertebrate remains bias the fossil record, and do bone assemblages have a taphonomic signature that can indicate specific biases? (4) How are bones concentrated and buried in an ecosystem lacking fluvial processes? Because it has been possible to continue this study for nearly 30 years, the results can also be used to examine, (5) How does a bone assemblage track ecological change in the animal community from which it is derived? Results addressing the first four questions have been published, though the research is on-going (See Behrensmeyer, 1978; Behrensmeyer et al., 1979; Behrensmeyer and Boaz, 1980, Behrensmeyer, 1993; Tuross et al., 1987, Koch et al., 2001; Cutler et al., 1999). The results reported below particularly address the fifth question and have not been previously published.

Six major habitat types were sampled for surface bones, based on Western's vegetation map, and three of these are used in the analyses reported here: plains, woodland, and swamp. The latter two categories include several different vegetation types. "Swamp" refers to the accessible swamp margin, within 30 m of the actual water or muddy areas that could not be searched effectively. This swamp margin area still retained considerable bush and tree cover in 1975, resembling a riparian woodland in terms of the structure of the vegetation and the density of cover for the animals. This cover also limited bone visibility and increased our level of caution during the surface surveys. In 2002-03, all of this cover had disappeared on the transects we sampled, transforming the swamp margin into open, grassy habitat more similar to the plains, except for the nearby access to water. Likewise, the Acacia xanthophloea (yellow fever tree) woodland still had many living or partially moribund large trees in 1975, with shrubs and bushes plus a thick ground cover of grass growing in the shade of these trees. This woodland was a favored place for the Maasai and their domestic stock, which limited the number of wild animals. In 2002-03, all of the trees had disappeared, and the terrain can be described more accurately as a saltbush plain, with some low areas moist enough to sustain a healthy grass cover. Although the original habitat names have been retained for the purposes of this paper, readers should be aware that "Woodland-A.x." was no longer woodland in 2002-03. The plains habitat has changed little in terms of vegetation, remaining very open with a variable cover of grasses. The Acacia tortilis woodland was still recognizable in 2002-03 although there were more dead or dying trees than in 1975, the understory of bushes had thinned, and dusty areas had expanded due to the loss of grass cover. Overall, however, the changes were not nearly as pronounced as in the swamp margin or fever tree woodland.

When the Amboseli bone study was initiated in 1975, the land surface of the basin (then a wildlife reserve) was littered with bones and mummified carcasses, and it seemed at the time to be an ideal place to study vertebrate taphonomy. Understanding of the decomposing and recycling components of this ecosystem based on several decades of research have led to the realization that considerable change can occur within the complex of ecological and taphonomic processes and material results that characterize Amboseli. These make up the Amboseli "taphosystem"-a set of biological, chemical and physical processes that shape the living ecosystem but are particularly important in its decomposing/recycling functions, thereby controlling what organic remains and information are available for preservation in the fossil record. Just as every ecosystem has unique features that distinguish it from other similar ecosystems, taphosystems may also have distinctive signatures that are recorded in the assemblages of organic remains.

METHODS

Field methods were originally designed to obtain statistically large samples of the surface (modern) bone assemblage in order to characterize species and skeletal parts and their relative abundances in different habitats (Behrensmeyer and Dechant Boaz, 1980). Transects that were distributed within each of six major habitats, defined originally by Western (1973) based on vegetation types and species. Air photographs and a vegetation map

were used to determine areas to be sampled, and starting points were chosen based on landmarks such as trees, roads, or other features that could aid in later re-location (in 1975, of course, we had no GPS). Transects usually were oriented north-south or east-west to make it easier to keep on a straight line using a compass bearing (Figure 2). In 2002-03, GIS coordinates allow calibration of the area searched and also precisely document the positions of transects for future surveys. However, in 1975, we paced off widths and lengths of the transects. The area to be searched was pre-determined by visibility; in dense vegetation, transect width was 30 meters either side of the midline (i.e., where a vehicle was driven); in open vegetation 50 m either side. During transect sampling, two to four individuals walked the transects, covering as much of the ground as possible. One person (AKB) was responsible for recording all bone occurrences on standardized data sheets; bones that could not be identified without comparative materials or those of special taphonomic interest were collected for later checking. An occurrence was defined as one to many bones belonging to one individual animal in close spatial proximity. Body parts likely belonging to the same individual but dispersed more than 15-20 m away from each other were given separate occurrence numbers. Also, when two different animals occurred at the same place, they were given separate occurrence numbers.

Successful bone surveying requires one or more team members able to identify fragmentary skeletal remains to taxon and skeletal element. Data recorded include: taxon, age (adult, juvenile, state of tooth eruption), skeletal parts present, habitat, weathering stage, breakage and other damage features such as tooth marks and degree of burial. In Amboseli, we continued the transect until we had ~20 individuals ("MNI" = mininum number of individuals). MNI is based on the number of different individual animals that can account for the documented bones; decisions were made in the field, based on body size, species ID, growth stage (juvenile vs. adult), weathering stage, etc. The general approach in Amboseli is to assume that an unknown bone is not a separate individual unless it can be demonstrated to be-a conservative stance that worked against inflation of the MNI count. For more information on the prototype sampling methods in Amboseli Park, Kenya, see Behrensmeyer and Dechant, 1980; Behrensmeyer, 1993.

Generally, a sample of at least 100 MNI is necessary to characterize the presence and relative abundances of common species in a particular habitat (i.e., 5–6 transects), though more may be required to capture the rare species. In Amboseli, we were able to do 2–3 transects in a day, thus it was possible to obtain an adequate sample of several different habitats in a week of bone surveying. This depends, of course, on the density of bones on the ground and the time required by the team to locate and identify these bones.

For the purposes of this study, bones in all weathering stages (WS) (Behrensmeyer, 1978) were used to

provide the largest possible samples of skeletal elements and species for each habitat. Most of the identifiable bone occurrences were in WS 0-3, representing the 10 years prior to the time of transect sampling, i.e., 1965 to1975 and 1992-3 to 2002-03 (Behrensmeyer, 1978). The average WS for the four habitats is between 1.7 and 2.3 for 1975 and between 1.9 and 2.3 for 2002-03. Some of the bone occurrences were WS 4-5 in the 2002-2003 surveys, but it is unlikely that a signifcant number of the same bones recorded in 1975 were identified and recorded again in 2002-03. Thus, these samples represent essentially independent records of skeletal elements and taxa at two successive time intervals, representing a maximum of ~20 years each but dominated by bones that accumulated over the 10 years prior to sampling.

The bone transect data have been entered into electronic databases using a variety of formats since 1976. Analysis in this paper focuses on 20 transects in 4 different habitats (plains, swamp, *Acacia xanthophloea* (yellow fever tree) woodland, *Acacia tortilis* woodland) that were sampled in both 1975 and 2002–03. Table 1. Summary of data from 1975 and 2002-03 surveys of surface bones on 20 transects in 4 different Amboseli habitats. The counts are for all bones and individuals that were identifiable to mammals, birds, reptiles, or fish, and exclude remains that could not be certainly assigned to these groups. Adult/juvenile ratio and percentage > 20 bones per occurrence were calculated for wild mammals only. MNI = Minimum Number of Individuals, MNE = Minimum Number of Elements.

	1975	2002-03	Decrease	
Occurences	641	575	10%	
Individuals (MNI)	458	365	20%	
Bones (MNE)	8160	1700	79%	
Bones/MNI	17.82	4.66	74%	
Adult/Juvenile	1.73	3.04		
>20 bones/Occurrence (Wild only)	21%	2%		
Occurrences with 1 bone	22%	57%		
By habitat (all mammals)	1975			
	MNE	MNI	MNE/MNI	
Plains	2307	116	19.89	
Swamp	2658	105	25.31	
Woodland - A x.	848	69	12.29	
Woodland - A t.	2347	168	13.97	
	2002-03			
				Decrease
	MNE	MNI	MNE/MNI	in ratio
Plains	630	106	5.94	70%
Swamp	702	139	5.05	80%
Woodland - A x.	75	31	2.42	80%
Woodland - A t.	293	89	3.29	76%

RESULTS

Characteristics of the surface bone assemblage

There are striking changes in the bones recorded in 2002-03 compared with 1975 (Table 1). The number of occurrences and individuals has decreased, but the most notable difference is in the total number of bones (MNE = Minimum Number of Elements), which has declined by 79%. This translates into a 74% decrease in the average number of bones per individual. The decrease is MNE/MNI has occurred in all transects except T1-8 in the central plains habitat (Table 2, Figures 4 and 5), with the greatest average difference in the swamp habitat. The higher variability of the MNE/MNI ratio in 1975 also contrasts with lower variability in 2002-03; not only has the number of bones per individual decreased, but the surface bone assemblages in the sampled habitats have become much more homogeneous in this respect.

The major shift in carcass and bone survival between 1975 and 2002–03 is further underscored by the lack of complete or partial skeletons in the later sample and the dominance of isolated bone occurrences. In 1975, 21% of the recorded occurrences of wild species had more than 20 associated bones, whereas in 2002–03, this dropped to only 2% (Table 1). Moreover, in 1975, only 21% of the wild species occurrences were singleton bones, but this increased to 56% in 2002–03. These figures indicate wider dispersal as well as increased destruction of skeletal elements in the later sample. The numbers of bones that could be assigned to adult versus juvenile changed as well, with increases in the number of adults and decreases in juveniles, both for the total wild mammal sample and for the two most common species, wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*) (Table 1, Figure 6).

The shift in bone survival between 1975 and 2002– 03 is most pronounced in the middle body sizes between 25 kg (Thompson's Gazelle) and 500 kg (Cape buffalo), with category 3 (Brain, 1981) showing the biggest change (Figure 7). There is also a marked decrease in MNE/ MNI for elephant. Exceptions to the overall trend occur in body size category 5 (giraffe, rhino, hippo), which is the only one that increases in bones per individual, and category 1 (< 25 kg), which shows little change.

Behrensmeyer > 143

Table 2. Bone survey data for 1975 and 2002-03. A. Summary of 1975 MNE (Minimum Number of Elements) and MNI (Minimum Number of Individuals) data by transect and break-down for each major vertebrate group. B. Summary of 2002-03 MNE and MNI and break-down for vertebrate groups. T1=Plains, T5=Woodland (Acacia xanthophloea), T8=Woodland (Acacia tortilis), T21=Swamp; habitat number designations based on Western (1973) and some no longer apply to the 2002-03 sample areas (see text)

A. 1975 sum	nary			Major	vertebra	ate grou	ıps						
	MNE 1975	MNI 1975	MNE/ MNI 1975	MNE 1975	MNE 1975	MNE 1975	MNE 1975	MNE 1975	MNI 1975	MNI 1975	MNI 1975	MNI 1975	MNI 1975
TRANSECT	Total	Total		Fish	Reptile	Bird	Mam- mal	Total	Fish	Reptile	Bird	Mam- mal	Total
T1-3	430	24	17.92				430	430				24	24
T1-4	504	24	21.00				504	504				24	24
T1-5	447	21	21.29	•	•	•	447	447	•	•	•	21	21
T1-7	550	24	22.92	•	•	26	524	550	•	•	1	23	24
T1-8	89	10	8.90		•	•	89	89		•		10	10
T1-14	287	13	22.08		3	•	284	287		1		12	13
T5-3	337	33	10.21		•	3	334	337		1	1	31	33
T5-4	291	20	14.55		•	3	288	291	•	•	1	19	20
T5-5	220	16	13.75		•	3	217	220		1	1	14	16
T8-1	310	34	9.12	•	•	2	308	310	•	•	2	32	34
T8-2	647	31	20.87	•	•	•	647	647	•	•	•	31	31
T8-3	157	25	6.28	•	•	•	157	157	•	•	•	25	25
T8-4	266	23	11.57	•	•	•	266	266	•	•	•	23	23
T8-5	120	25	4.80	•	•	3	117	120	•	•	1	24	25
T8-6	847	30	28.23	•	•	•	847	847	•	•	•	30	30
T21-5	747	29	25.76	14	•	7	726	747	4	•	1	24	29
T21-6	377	18	20.94	•	•	•	377	377	•	•	•	18	18
T21-7	814	32	25.44	•	•	60	754	814	•	•	2	30	32
T21-13	202	12	16.83	•	•	•	202	202	•	•	•	12	12
T21-14	518	14	37.00		•	•	518	518			•	14	14
	8160	458	17.82	14	3	107	8036	8160	4	3	10	441	458

B. 2002-03 Summary

Major vertebrate groups

			MNE/										
	MNE	MNI	MNI	MNI	E MNE	MNE	MNE	MNE	MNI	MNI	MNI	MNI	MNI
	2002-	2002-	2002-	2002	- 2002-	2002-	2002-	2002-	2002-	2002-	2002-	2002-	2002-
	03	03	03	03	03	03	03	03	03	03	03	03	03
							Mam-					Mam-	
TRANSECT	Total	Total		Fish	Reptile	Bird	mal	Total	Fish	Reptile	Bird	mal	Total
T1-3	38	12	3.17			•	38	38		•		12	12
T1-4	147	26	5.65			•	147	147		•		26	26
T1-5	120	16	7.50			•	120	120	•	•	•	16	16
T1-7	34	8	4.25		•	•	34	34		•	•	8	8
T1-8	196	21	9.33		•	•	196	196		•	•	21	21
T1-14	95	23	4.13		•	•	95	95		•	•	23	23
T5-3	29	9	3.22		•	•	29	29		•	•	9	9
T5-4	13	7	1.86	•	•	1	12	13	•	•	1	6	7
T5-5	33	15	2.20	•	•	•	33	33	•	2		13	15
T8-1	120	28	4.29	•	•	•	120	120	•	2	0	26	28
T8-2	3	2	1.50	•	•	•	3	3	•			2	2
T8-3	35	15	2.33	•	•	5	30	35	•		3	12	15
T8-4	57	19	3.00	•	•	•	57	57	•			19	19
T8-5	40	14	2.86	· ·	•	3	37	40	•		2	12	14
T8-6	38	11	3.45	•	•	•	38	38	•			11	11
T21-5	243	36	6.75	•	•	•	243	243	•			36	36
T21-6	126	25	5.04	9	•	•	116	126	5			20	25
T21-7	58	15	3.87	•	•	•	58	58				15	15
T21-13	138	38	3.63	· ·	•	•	138	138	.			38	38
T21-14	137	25	5.48	•		•	137	137				25	25
	1700	365	4.66	9	0	9	1681	1700	5	4	6	350	365



Figure 4. Change in bone survival for 20 transects sampled both in 1975 and 2002-03, for all bone occurrences identifiable to major vertebrate group (fish, reptile, bird, mammal).



Figure 5. Summary of change in bone survival in different habitats (data from Table 1). There was a 74% decrease overall in the number of bones per individual between 1975 and 2002-03.



Figure 6. Comparison of age group representation for 1975 vs. 2002-03 in the wild mammal samples. A. Results for the total sample that could be categorized to relative age (1975: MNI=320, 2002-03: MNI=339) showing decrease in numbers of juveniles and increase in adults in 2002-03. Individuals were counted as adults if they had fused epiphyses and/or adult dentition, and juveniles were counted if they had unfused epiphyses and/or sub-adult dentition. B. Results for wildebeest only. C. Results for zebra only. Note that scales for B and C are the same to show the absolute lower numbers of zebra MNI.



Figure 7. Bones per individual (MNEs / MNIs) by body size category for wild mammals (domestic species omitted), showing the greatest change for sizes 3, 4 and 6 between 1975 and 2002-03. Size categories based on Brain (1981). Key to abbreviations on X axis: WB=wildebeeste, ZB=zebra, BF=Cape buffalo, CW=cow, GG=Grant's Gazelle, TG=Thompson's Gazelle, HP=hippo, WH=warthog, EL=elephant, IM=impala, GF=giraffe, RH=black rhino, OR=oryx, PP=porcupine, MG=mongoose.



Figure 8. Skeletal part representation in the Amboseli surface bone assemblage, for all 20 transects. A. Comparison of 1975 and 2002-03 for all vertebrates (Table 3). B. Comparison of 1975 and 2002-03 for size 3 wild mammals only (mainly wildebeest and zebra; domestic cows and donkeys not included) and the proportions of skeletal parts in a single average ungulate skeleton (zebra + wildebeest).

Differences in the relative proportions of skeletal parts are not pronounced for the vertebrate sample as a whole between 1975 and 2002–03 (Table 3; Figure 8A). There is a relative increase in cranial and limb elements. with the latter biased toward resistant limb-ends such as distal humeri, proximal radius-ulnae, distal tibiae and metapodials in the 2002-03 sample. Considering only the most common wild ungulate species in Brain's body size category 3 (Brain, 1981) (Tables 3 and 4, Figure 8B), it is notable that there is a disproportionate number of vertebrae relative to other elements in 1975, making a much stronger peak for this size group than for the vertebrate assemblage as a whole. The 1975 skeletal part sample retains more overall similarity to the proportions of a single average skeleton (Figure 8B), than the 2002-03 sample, indicating that the taphonomic processes operating in Amboseli have shifted to stronger overprinting of

the body-part signal from the original whole skeletons.

Skeletal part representation for size 3 wild mammals varies across the 4 different habitat samples (Table 3, Figure 9). In 1975, the patterns are similar among the habitats, except that proportionally fewer vertebrae occurred in the Acacia xanthophloea woodland. In 2002-03, however, the two woodland samples retain a higher proportion of vertebrae and also show increased numbers of durable limb elements, which is characteristic of the more open habitats in 1975 and the 2002-03 sample as a whole. Of all the habitats, the Acacia tortilis woodland has changed the least in terms of the relative abundance of the different body segments.

The degree of bone modification by predator/ scavengers has yet to be quantified in the two samples (1975 vs. 2002–03), and a thorough treatment is beyond the scope of this paper. Data collected on tooth marks and other damage to individual bones was more systematic in the 2002-03 sample than in 1975, making a detailed level of comparison problematic. However, skeletal part representation, limb element completeness

and the survival of different bone portions (proximal, distal, shaft only, etc.) were recorded in the same way in the two samples (Table 4). Analysis of skeletal element survival and damage in one species (zebra) reduces cross-taxon variability and serves to demonstrate the major taphonomic changes between 1975 and 2002-03. Skeletal parts were tallied from a subset of 11 transects (swamp and plains) and analyzed in terms of observed versus expected numbers of different elements (Figure 10). In 1975, there is clear evidence of post-mortem deletion of bones in certain body segments, such as distal limbs, vertebrae and ribs, caused by destruction and/or burial of bones. Overall, however, the pattern reflects relatively predictable survival based on bone strength and size, with cranial elements dominating and relatively lower survival of vertebrae and ribs, forelimb relative to

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Table 3. A. Counts of bones from all vertebrate remains on the 20 transects, grouped by skeletal region. B. Totals for Amboseli Size 3 wild mammals only, including both adults and juveniles. Numbers may differ from Table 1 because totals here include only bones that could be identified to the specified skeletal element. Note: podials include fibulae, innominate = left or right half of the pelvis, and forelimb includes radii, ulnae, and fused radius-ulnae.

A. All vertebrates

	All Ha	HabitatsProportionsINE)MNE		By Habit	at		WD-	WD-	WD-	WD-		
	1975	2002- 03	1975	2002- 03	PLAINS 1975	PLAINS 2002-03	SWAMP 1975	SWAMP 2002-03	A.x. 1975	A.x. 2002-03	A.t. 1975	A.t. 2002-03
Skull	155	68	0.020	0.070	37	26	49	21	15	4	54	17
Jaw (hemi)	287	78	0.037	0.081	60	26	89	37	44	1	94	14
Vertebrae	1993	248	0.259	0.256	592	78	756	105	179	17	493	48
Ribs	1250	118	0.163	0.122	327	56	458	46	127	3	338	13
Scapula	193	52	0.025	0.054	58	20	55	26	25	5	55	3
Forelimb	365	134	0.047	0.138	98	41	97	62	63	14	107	17
Innominate	242	52	0.031	0.054	72	21	68	26	35	5	67	3
Hindlimb	362	97	0.047	0.100	118	27	106	47	34	7	104	16
Metapodials	201	63	0.026	0.065	72	28	458	23	36	2	61	10
Podials	366	40	0.048	0.041	140	20	112	13	51	0	110	7
Phalanges	297	18	0.039	0.019	122	8	80	4	48	0	47	6
MNE	7686	968			1696	351	2328	410	657	58	1530	154
MNI	458	365			116	106	105	139	69	31	168	89
MNE/MNI	16.78	2.65			14.62	3.31	22.17	2.95	9.52	1.87	9.11	1.73

B. Size 3 wild mammals

	All Ha	abitats NE)	Prop M	ortion NE	By Habit	at			WD	WD		WD
	1975	2002- 03	1975	2002- 03	PLAINS 1975	PLAINS 2002-03	SWAMP 1975	SWAMP 2002-03	WD- A.x. 1975	WD- A.x. 2002-03	WD- A.t. 1975	WD- A.t. 2002-03
Skull	67	39	0.02	0.07	27	23	32	11	2	0	6	5
Jaw (hemi)	134	57	0.05	0.11	50	22	69	24	3	0	12	11
Vertebrae	1073	114	0.40	0.21	492	49	524	30	17	8	40	27
Ribs	576	47	0.21	0.09	279	28	286	8	6	0	5	11
Scapulae	77	33	0.03	0.06	41	15	28	15	3	2	5	1
Forelimb	135	91	0.05	0.17	67	29	52	37	8	11	8	14
Innominate	113	36	0.04	0.07	59	16	46	15	5	2	3	3
Hindlimb	151	57	0.06	0.11	81	18	61	29	2	4	7	6
Metapodials	98	36	0.04	0.07	58	17	32	14	4	2	4	3
Podials	156	13	0.06	0.02	102	9	47	4	7	0	0	0
Phalanges	135	8	0.05	0.02	95	1	36	3	4	0	0	4
MNE	2715	531			1351	227	1213	190	61	29	90	85
MNI	226	342			110	133	78	129	10	24	28	56
MNE/MNI	12.01	1.55			12.28	1.71	15.55	1.47	6.10	1.21	3.21	1.52

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Table 3. (continued)

	PLAINS	PLAINS	SWAMP	SWAMP	WD-A.x.	WD-A.x.	WD-A.t.	WD-A.t.
	1975	2002-03	1975	2002-03	1975	2002-03	1975	2002-03
Skull	0.020	0.101	0.026	0.058	0.033	0.000	0.067	0.059
Jaw (hemi)	0.037	0.097	0.057	0.126	0.049	0.000	0.133	0.129
Vertebrae	0.364	0.216	0.432	0.158	0.279	0.276	0.444	0.318
Ribs	0.207	0.123	0.236	0.042	0.098	0.000	0.056	0.129
Scapulae	0.030	0.066	0.023	0.079	0.049	0.069	0.056	0.012
Forelimb	0.050	0.128	0.043	0.195	0.131	0.379	0.089	0.165
Innominate	0.044	0.070	0.038	0.079	0.082	0.069	0.033	0.035
Hindlimb	0.060	0.079	0.050	0.153	0.033	0.138	0.078	0.071
Metapodials	0.043	0.075	0.026	0.074	0.066	0.069	0.044	0.035
Podials	0.076	0.040	0.039	0.021	0.115	0.000	0.000	0.000
Phalanges	0.070	0.004	0.030	0.016	0.066	0.000	0.000	0.047
MNE	1351	227	1213	190	61	29	90	85

C.	Pro	portions	from	B :	size	3	wild	mammals
				_ 7		_		

D. Single whole skeleton

	Single ZB	Single WB	Average Size 3	Proportion MNE
Skull	1	1	1	0.01
Jaw (hemi)	2	2	2	0.02
Vertebrae	32	27	29	0.24
Ribs	36	26	31	0.25
Scapula	2	2	2	0.02
Forelimb	6	6	6	0.05
Innominate	2	2	2	0.02
Hindlimb	4	4	4	0.03
Metapodials	4	4	4	0.03
Podials	26	20	23	0.19
Phalanges	12	24	18	0.15
MNE	127	118	122	
MNI	1	1	1	

hind limb, and distal versus proximal limb bones. In the 2002-03 sample, cranial and mandibular elements are similar in terms of observed vs. expected ratio (~20%), axial elements are nearly absent, and fore- and hind-limb bones are similar in terms of survival rates. Overall, the survival of zebra remains is reduced by about 80% although the number of individuals on the sampled transects is only 20% less than in 1975. Damage to individual bones, based on humeri and femora, also changed markedly from 1975 to 2002-03 (Figure 11), with a decrease in the number of whole elements accompanied by an increase in durable portions such as distal humeri. Based on more detailed examination of bone modification features, there is an accompanying shift in the amount of moderate to heavy chewing and fragmentation in the 2002-03 sample (Figure 11B).

Species diversity in the bone assemblage

The diversity of species represented in the surface bone assemblages likely reflects the diversity of the living populations in the different habitats, which was probably important to early hominin scavengers or hunters. Based on field and laboratory identifications of the fragmentary remains on the 20 transects, there are a total of 19 mammal, one fish, one reptile, and several bird species in the sampled bone assemblage (Table 5; Figures 12 and 13). A total mammal species richness of 14 in 1975 increased to 17 in 2002-03. Species abundance is based on field assessment of MNI rather than on the most common skeletal element (Behrensmeyer and Dechant Boaz, 1980). Comparison of the MNI abundances for mammals highlights the impact of the removal of domestic animals from the park in the 1980s and also indicates a shift to a somewhat different abundance distribution in the 2002-03 sample, with a stronger dominance of wildebeeste in the bone assemblage. Fisher's alpha, which characterizes diversity in terms of abundance distribution for a given number of species, is very similar for the top 12 species -2.412 (1975) and 2.581 (2002-03). This indicates surprising stability in this ecological parameter, in spite of major changes in the ecosystem.

The four habitats show different patterns of change



Figure 9. Line graphs showing differences in skeletal part survival between 1975 and 2002-03 in the 4 habitats sampled in Amboseli, for size 3 wild mammals only (Table 4).

Table 4. Data for Amboseli adult and juvenile zebra remains recorded on transects in the plains and swamp habitats, for 1975 and 2002-03 (Figures 10-11). A. Counts of MNEs for different elements, and proportions of observed over expected based on the number of bones in a single zebra, B. Counts of humeri and femora in different stages of completeness, C. Counts of MNEs in carnivore damage categories of B. Pobiner (Pobiner and Blumenschine, 2003; pers. comm. 2004): A: Minimal = toothmarks, both ends still present, B: Moderate = one end missing, C: Heavy = both ends missing, shaft only, D: Fragments only.

A. Skeletal representation											
		Single		Proportion		Single		Proportion			
	1975	Zebra	Expected	Ō/E	2002-03	Zebra	Expected	O/E			
Skull	18	1	45	0.40	7	1	36	0.19			
Jaw (hemi)	28	2	90	0.31	15	2	72	0.21			
Vertebrae	236	32	1440	0.16	9	32	1152	0.01			
Ribs	95	36	1620	0.06	3	36	1296	0.00			
Scapula	19	2	90	0.21	7	2	72	0.10			
Humerus	20	2	90	0.22	11	2	72	0.15			
Radius/ulna	29	4	180	0.16	14	4	144	0.10			
Metacarpal	8	2	90	0.09	8	2	72	0.11			
Innominate	32	2	90	0.36	10	2	72	0.14			
Femur	28	2	90	0.31	7	2	72	0.10			
Tibia	26	2	90	0.29	9	2	72	0.13			
Metatarsal	16	2	90	0.18	5	2	72	0.07			
Patella	2	2	90	0.02	0	2	72	0.00			
Podials	41	26	1170	0.04	8	26	936	0.01			
Phalanges	18	12	540	0.03	3	12	432	0.01			
MNE	616	129	5805		116	129	4644				
MNI	45	1	45		36	1	36				

B. Completene	SS		C. Damage		
	1975	2002-03		1975	2002-03
Whole	26	3	No Damage	20	1
Prox-Dist Pair	2	1	А	17	2
Shaft only	5	3	В	11	11
Prox only	1	0	С	0	2
Prox+Shaft	1	0	D	0	1
Dist only	9	7			
Dist+Shaft	4	3	Total	48	17
Total	48	17			



Figure 10. Skeletal part representation for Amboseli zebra remains from 20 bone survey transects in 1975 and 2002-03, as a proportion of the expected number of bones for the observed MNI. Teeth are not counted.

in the common mammal species (Figure 14, Table 6). The removal of cows from the central area of the park in 1981 has a clear signal in the bone assemblages, especially in the two woodland habitats preferred by the Maasai herdsmen, where the MNIs for cow drops by 85->90%. Interestingly, the species richness in each of the 4 habitats changed little between 1975 and 2002-03, in spite of the removal of domestic stock. There are shifts in abundance of some species, such as decreased numbers of impala, Grant's gazelle and giraffe in the woodland habitats in 2002-03 accompanied by slight increases in wildebeest and zebra. Rhinoceros have been extinct in the Amboseli ecosystem since the mid-1980s, but their bones continue to be found on the transects in low numbers. MNIs for zebra decreased in the plains habitat, while buffalo and warthog increased. Slightly larger MNIs occur for all wild species in the swamp habitat 2002-03 transects, except elephant and rhino. Overall diversity, as measured by Fisher's Alpha, increases for the two woodland habitats and slightly for plains but remains approximately the same for swamp. However, if cows are removed from the calculations, diversity remains stable in the bone assemblages of the four habitats between 1975 and 2002-03, with only plains showing a slight increase in the evenness of the abundance distribution (Table 6).

The most common species in Amboseli are plotted on Figure 14 in order of body size, providing an overview of the dominance of size 3 herbivores in the bone assemblage (zebra, wildebeest, and cow). The relationship of this distribution to abundances in the living populations has yet to be determined, but the MNI counts are known to be affected by taphonomic as well as sampling biases in the low numbers of size 2 species (Behrensmeyer et al., 1979). The ecology of all the species—their habitat preferences, seasonal movements, turnover rates, and areas of high vs. low mortality—also affect the distributions and numbers of MNIs in the different habitat samples (Western, 1980; Behrensmeyer and Dechant Boaz, 1980), resulting in a complex relationship between the living animal community and the information recorded in the surface bone assemblage.

Comparison of skeletal element survival in Amboseli and the Serengeti

Data from the bone transect surveys in Amboseli and the Serengeti ecosystem (Blumenschine, 1989) can be used to investigate similarities among the different habitat samples based on the proportions of different body parts (MNEs) (Table 5, Figures 15 and 16). The survey methods were comparable, although bone visibility may have been less in the Serengeti surveys due to denser ground cover. The size and shape of Blumenshine's transects also differed from those in Amboseli. Sample sizes (MNEs and MNIs) are generally similar (Table 5a), especially for the woodland habitats.

The cluster diagram (Figure 15) groups Serengeti riparian woodland most closely with the Amboseli's *Acacia tortilis* woodland (1975 sample). The other Serengeti



Figure 11.Change in bone modification patterns for zebra humeri and femora from 1975 to 2002-03, based on MNE from the 20 Amboseli transects. A. Proportions of more and less complete individual elements. B. Damage levels for same bone sample as in A., based on categories of Briana Pobiner (Pobiner and Blumenschine, 2003; pers. comm. 2004): Minimal = toothmarks, both ends still present, Moderate = one end missing, Heavy = both ends missing, shaft only.

Table 5. Comparison of skeletal part representation in the 1980s Serengeti bone surveys of Blumenschine (1989; 16 transects) and Amboseli, based on data in Table 3. A. Raw MNE counts. B. Proportions based on total MNEs for each habitat. C. Contingency Table of similarity (Pearson correlation coefficient) for data in 5B (MNE Proportions) organized by habitat; all cells in bold have significant values at the level of significance alpha=0.050 (two-tailed test). D. Contingency Table (Pearson correlation coefficient) for data in 5B (MNE Proportions) organized by year; all cells in bold have significant values at the level of significance alpha=0.050 (two-tailed test).

A. MNE

Counts	Seren	geti		Ambosel	i						
Skeletal Parts (MNE)	NGO	AW& GP	RW	PLAINS 1975	PLAINS 2002-03	SWAMP 1975	SWAMP 2002-03	WD-A.x. 1975	WD-A.x. 2002-03	WD-A.t. 1975	WD-A.t. 2002-03
Skull	40	44	11	27	23	32	11	2	0	6	5
Hemi-Mandible	32	27	9	50	22	69	24	3	0	12	11
Vertebrae	64	111	76	492	49	524	30	17	8	40	27
Ribs	5	14	13	279	28	286	8	6	0	5	11
Scapula	12	25	9	41	15	28	15	3	2	5	1
Forelimb	18	23	3	67	29	52	37	8	11	8	14
Innominate	4	32	9	59	16	46	15	5	2	3	3
Hindlimb	13	30	8	81	18	61	29	2	4	7	6
Metapodials	7	21	4	58	17	32	14	4	2	4	3
Podials	2	4	3	102	9	47	4	7	0	0	0
Phalanges	0	1	0	95	1	36	3	4	0	0	4
MNE	197	332	145	1351	227	1213	190	61	29	90	85
MNI	46	51	12	110	133	78	129	10	24	28	56
MNE/MNI	4.28	6.51	12.08	12.28	1.71	15.55	1.47	6.10	1.21	3.21	1.52

B. MNE Proportions

Skeletal Parts (MNE)	NGO	AW& GP	RW	PL 75	PL 02-03	SW 75	SW 02- 03	WD-Ax 75	WD-Ax 02-03	WD-At 75	WD-At 02-03
Skull	0.203	0.133	0.076	0.020	0.101	0.026	0.058	0.033	0.000	0.067	0.059
Hemi-Mandible	0.162	0.081	0.062	0.037	0.097	0.057	0.126	0.049	0.000	0.133	0.129
Vertebrae	0.325	0.334	0.524	0.364	0.216	0.432	0.158	0.279	0.276	0.444	0.318
Ribs	0.025	0.042	0.090	0.207	0.123	0.236	0.042	0.098	0.000	0.056	0.129
Scapula	0.061	0.075	0.062	0.030	0.066	0.023	0.079	0.049	0.069	0.056	0.012
Forelimb	0.091	0.069	0.021	0.050	0.128	0.043	0.195	0.131	0.379	0.089	0.165
Innominate	0.020	0.096	0.062	0.044	0.070	0.038	0.079	0.082	0.069	0.033	0.035
Hindlimb	0.066	0.090	0.055	0.060	0.079	0.050	0.153	0.033	0.138	0.078	0.071
Metapodials	0.036	0.063	0.028	0.043	0.075	0.026	0.074	0.066	0.069	0.044	0.035
Podials	0.010	0.012	0.021	0.076	0.040	0.039	0.021	0.115	0.000	0.000	0.000
Phalanges	0.000	0.003	0.000	0.070	0.004	0.030	0.016	0.066	0.000	0.000	0.047
MNE	197	332	145	1351	227	1213	190	61	29	90	85
MNI	46	51	12	110	133	78	129	10	24	28	56
MNE/MNI	4.28	6.51	12.08	12.28	1.71	15.55	1.47	6.10	1.21	3.21	1.52

Table 5. (continued)

C. Contingency Table organized by habitat.

		NGO	AW& GP	RW	PL 75	PL 02-03	SW 75	SW 02-03	WD-Ax 75	WD-Ax 02-03	WD-At 75	WD-At 02-03
Serengeti	NGO	1.000	0.897	0.809	0.539	0.805	0.626	0.519	0.555	0.394	0.879	0.770
	AW&GP	0.897	1.000	0.941	0.699	0.842	0.761	0.522	0.709	0.497	0.941	0.781
	RW	0.809	0.941	1.000	0.884	0.820	0.912	0.377	0.843	0.427	0.961	0.828
Amboseli	PL 75	0.539	0.699	0.884	1.000	0.734	0.988	0.190	0.867	0.338	0.804	0.806
	PL 02-03	0.805	0.842	0.820	0.734	1.000	0.814	0.642	0.723	0.614	0.869	0.899
	SW 75	0.626	0.761	0.912	0.988	0.814	1.000	0.264	0.845	0.352	0.853	0.853
	SW 02-03	0.519	0.522	0.377	0.190	0.642	0.264	1.000	0.351	0.844	0.573	0.635
	WD-Ax 75	0.555	0.709	0.843	0.867	0.723	0.845	0.351	1.000	0.603	0.807	0.801
	WD-Ax 02-03	0.394	0.497	0.427	0.338	0.614	0.352	0.844	0.603	1.000	0.543	0.639
	WD-At 75	0.879	0.941	0.961	0.804	0.869	0.853	0.573	0.807	0.543	1.000	0.905
	WD-At 02-03	0.770	0.781	0.828	0.806	0.899	0.853	0.635	0.801	0.639	0.905	1.000

D. Contingency Table organized by year.

		NGO	AW& GP	RW	PL 75	SW 75	WD- Ax75	WD- At75	PL 02- 03	SW 02-03	WD- Ax02-03	WD- At02-03
Serengeti	NGO	1.000	0.897	0.809	0.539	0.626	0.555	0.879	0.805	0.519	0.394	0.770
	AW&GP	0.897	1.000	0.941	0.699	0.761	0.709	0.941	0.842	0.522	0.497	0.781
	RW	0.809	0.941	1.000	0.884	0.912	0.843	0.961	0.820	0.377	0.427	0.828
Amboseli	PL 75	0.539	0.699	0.884	1.000	0.988	0.867	0.804	0.734	0.190	0.338	0.806
	SW 75	0.626	0.761	0.912	0.988	1.000	0.845	0.853	0.814	0.264	0.352	0.853
	WD-Ax75	0.555	0.709	0.843	0.867	0.845	1.000	0.807	0.723	0.351	0.603	0.801
	WD-At75	0.879	0.941	0.961	0.804	0.853	0.807	1.000	0.869	0.573	0.543	0.905
	PL 02-03	0.805	0.842	0.820	0.734	0.814	0.723	0.869	1.000	0.642	0.614	0.899
	SW 02-03	0.519	0.522	0.377	0.190	0.264	0.351	0.573	0.642	1.000	0.844	0.635
	WD-Ax02-03	0.394	0.497	0.427	0.338	0.352	0.603	0.543	0.614	0.844	1.000	0.639
	WD-At02-03	0.770	0.781	0.828	0.806	0.853	0.801	0.905	0.899	0.635	0.639	1.000

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Table 6. Numbers of individuals for all vertebrate species found on the 20 transects. A. Data for the 12 most common mammals. Key: EL = elephant (Loxodonta africana), HP = hippo (Hippopotamus amphibious), RH = black rhino (Diceros bicornis), GF = giraffe (Giraffa camelopardalis), BF = Cape buffalo (Syncerus caffer), ZB = zebra (Equus burchelli), WB = wildebeest (Connochaetes taurinus), CW = cow (Bos taurus), GG = Grant's gazelle (Gazella granti), IM = impala (Aepyceros melampus), WH = warthog (Phacochoerus aethiopicus), TG = Thompson's gazelle (Gazella thompsoni). B. Data for additional 7 rare mammals. C. Data for non-mammals. D. Rank order (based on 2002-03).

														Fisher's	Alpha
A. Common Mam	mals	(MNI)												Wild
Habitat, Year	EL	HP	RH	GF	BF	ZB	WB	CW	GG	IM	WH	TG	N (MNI)	All	Only
Plains1975	0	1	0	3	2	30	45	4	6	1	0	3	95	2.441	2.113
Plains02-03	0	1	0	2	7	16	41	1	1	1	3	2	75	3.099	2.685
WoodA.x.1975	0	0	1	3	3	3	2	24	1	5	0	1	43	3.468	5.205
WoodA.x.02-03	1	1	1	2	2	4	7	1	0	0	0	1	20	6.296	5.205
WoodA.t.1975	1	0	3	6	3	10	9	62	9	18	1	2	124	2.915	3.374
WoodA.t.02-03	2	0	1	1	3	13	14	9	3	6	4	1	57	4.057	3.843
Swamp1975	9	1	3	0	9	15	37	8	2	0	0	1	85	2.543	2.245
Swamp02-03	5	8	1	0	9	21	50	0	5	0	2	6	107	2.341	2.341
1975	10	2	7	12	17	58	93	98	18	24	1	7	347	2.412	2.355
2002-03	9	10	3	5	21	54	114	13	11	7	10	10	267	2.581	2.343

B. Rare Mammals

	SHEEP-							
	ORYX	DONKEY	BUSHBUCK	HYENA	GOAT	PORCUPINE	MONGOOSE	N (MNI)
Plains 1975								0
Plains 02-03								0
Wood A.x. 1975								0
Wood A.x. 02-03	1		1	1				3
Wood A.t. 1975		1			3			4
Wood A.t. 02-03			1	1		1	1	4
Swamp 1975								0
Swamp 02-03								0
1975	0	1	0	0	3	0	0	4
2002-03	1	0	2	2	0	1	1	7

C. Non-Mammals

FISH (Catfish)	REPTILE (Tortoise)	BIRD (non- Ostrich)	OSTRICH	N (MNI)
	1			0
	2	1		1
		3		3
	2	1		1
		3		3
	2	4	1	4
4		3		3
5				0
4	2	10	0	10
5	4	5	1	5

	1975	2002-03
WB	93	114
ZB	58	54
BF	17	21
CW	98	13
GG	18	11
TG	7	10
HP	2	10
WH	1	10
EL	10	9
IM	24	7
GF	12	5
RH	7	3
N (MNI)	347	267



Figure 12. Abundances of all 19 mammal species identified on 20 sampled transects in 1975 and 2002-03, rank order based on 2002-03 sample. The number of species increased from 14 in 1975 to 17 in 2002-03 on these transects, while the proportion of domestic stock (CW, SH, DK) markedly decreased. Key: WB = wildebeeste, ZB = zebra, BF = cape buffalo, CW = cow, CG = Grant's gazelle, TG = Thompson's gazelle, HP = hippo, WH = warthog, EL = elephant, IM = impala, GF = giraffe, RH = black rhino, BU = bushbuck, HY = spotted hyena, OR = oryx, PP = porcupine, MG = mongoose (white-tailed), SH = sheep/goat, DK = donkey



Figure 13. MNI counts of non-mammals in the 20 Amboseli bone transects for fish (catfish), reptiles (tortoise), and birds, with ostrich plotted separately.







Figure 15. Cluster analysis using Pearson correlation coefficient for MNE bone data from Amboseli and the Serengeti, based on skeletal parts of Size 3 mammals (excluding cow). See Table 6; Serengeti data from Blumenschine, 1989. Habitat abbreviations for Serengeti: NGO = Ngorongoro, AW&GP = Acacia woodland and grassy plains, RW = riparian woodland; all other branch ends are Amboseli data: WD-A.t. = Acacia tortilis woodland, WD-A.x. = Acacia xanthophloea woodland.



Figure 16. Correspondence Analysis comparing habitats in the Serengeti (gray diamonds) and Amboseli (double line (1975) and black (2002-03) diamonds), based on proportional MNE skeletal part data of Size 3 mammals (excluding cow). Skeletal parts plotted on the diagram show which of these have the most impact in the distribution of the 7 habitat samples on the two major axes. Based on data from Table 5; Serengeti data from Blumenschine (1989). Habitat abbreviations: Serengeti: NGO = Ngorongoro, AW&GP = Acacia woodland and grassy plains, RW = riparian woodland. Amboseli: WD-A.t. = Acacia tortilis woodland, WD-A.x. = Acacia xanthophloea woodland, PL = Plains, SW = Swamp (1975 and 2002-03).

samples form a cluster with these two woodlands, and together they are associated with Amboseli's plains and A. tortilis woodland in 2002–03. The Pearson coefficient of similarity values (Table 5C, 5D) shows that most of these samples are significantly alike, and slight differences in the numbers are only an indication of which pairs are more or less similar based on the skeletal part data. The correspondence analysis in Figure 16 provides more insight into which skeletal elements are responsible for the observed hierarchy in the cluster diagram. The high relative abundance of skulls and mandibles groups the Serengeti samples and 1975 Amboseli A. tortilis woodland, abundant distal limb elements (podials and phalanges) group the other three 1975 Amboseli samples, and a higher proportion of hind- and forelimb elements pull the 2002–03 Amboseli swamp and Acacia xanthophloea woodland away from the others.

The 2002–03 Amboseli samples are the outliers on the cluster diagram, while the 1975 samples group with each other and with the three Serengeti habitats. These patterns show that there is no dominant habitat signal in the Amboseli surface bone assemblages—instead, greater differences occur between the same habitats in the 1975 vs. 2002–03 samples than among the habitats themselves.

DISCUSSION

Changes in the Amboseli bone assemblages over nearly 30 years provide a basis for considering the potential impact of resource fluctuations that might have affected predator/scavengers in the Plio-Pleistocene. What would be the impact of predator-prey cycles or climatedriven habitat changes over decades, on the availability of species for scavenging or hunting? Blumenshine (1989) proposed that woodland habitats in the Serengeti ecosystem provide more opportunities for hominin scavenging than open plains habitats because there are lower numbers of other carcass consumers (e.g., hyenas) in woodlands. Recent work by Domingquez-Rodrigo (2001) indicates that competition with other predators is lower in riparian woodland vs. open plains habitats, further supporting Blumenschine's hypothesis. Tappen (1995, 2001), in contrast, has countered that in the savanna ecosystem of the western rift valley of Zaire, there are few scavenging opportunities in any of the habitats she sampled, indicating that deliberate foraging for carcasses would not have been a productive use of time and energy for early homnins.

The results of the Amboseli analysis show that, from 1975 to 2002–03, bones per individual have decreased

by nearly 75%, skeletal part survival has shifted toward higher proportions of the more durable limb elements, and the degree of damage to individual bones has increased, with fewer whole elements and more partial or fragmentary remains. These changes are particularly marked for species in body sizes 3 and 4 (wildebeest, zebra, cow, buffalo). Isolated identifiable bone fragments have shifted from 21% to 57% of the recorded occurrences, and variability in bones per individual has evened out across the different habitats. There also is a higher proportion of adult vs. juvenile remains in the later sample. All of these results indicate a marked increase in the impact of taphonomic processes that disperse and destroy skeletal remains over the past several decades. In contrast, the numbers of bone occurrences and MNIs on the transects have changed relatively little (10% and 20% decreases, respectively) and wild species diversity recorded in the bone assemblages in the four habitats has remained remarkably stable. This implies that shifts in the ecology of the basin, including the removal of domestic stock and the loss of woodlands, have had less of an effect on the changes in the bone assemblages than destructive processes acting on these assemblages.

Changes in the predator populations in Amboseli over the past 15 years, combined with an unusual drought die-off in the early 1970s, provide an explanation for the marked shift in the taphonomy of the bone assemblages. In 1975, lions were the dominant predator in the basin, spotted hyena (Crocuta crocuta) was relatively uncommon, and leopard and cheetah also were present. A severe drought weakened the ungulate populations, resulting in large numbers of dead wild and domestic animals in 1972-73; a number of these mummified and were still partially intact when transect sampling began in 1975. In the late 1980s, lions were temporarily absent from the ecosystem and the Crocuta population began an increase that has continued into the 21st century, with estimates of 250-300 individuals, one of the highest densities of spotted hyena thus far recorded (Watts, Personal Communication, 2004). Intense intra-specific competition for carcasses means that hyenas disperse and consume much more of their own kills and those of other predators, leaving behind primarily the most durable portions of the skeleton. Species in body size categories 2-3 are the preferred prey for Crocuta, which is able to completely consume most parts of the skeleton. Crocuta is less capable of destroying the bones of larger species, resulting in a gradient of decreasing damage from size categories 3 through 6. Fresh kills can attract up to 40 hyenas at a time, and for body size 3 and smaller animals, there is virtually nothing left at the kill site after 10-20 minutes of feeding frenzy; much is consumed on the spot but any hyena that can tear off a portion of the carcass takes it away immediately for less stressful feeding elsewhere.

In summary, the shift from relatively complete carcasses in 1975 to dispersed, highly processed, fragmentary remains in 2002–03 represents a contrast between low and high scavenging pressure on the Amboseli bone

assemblage. The most reasonable explanation is that this has been caused by a major shift in the predator structure, from diverse species dominated by a meat-consumer (lion) to super-dominance by a meat+bone consumer (spotted hyena), combined with a drought-generated carcass surfeit in 1975, when scavenging pressure on the bone assemblage was unusually low. There have been important changes in the vegetation of the Amboseli Basin during the same time interval, and the increase in open habitats probably contributes to the current dominance of spotted hyena, which is primarily a pursuit predator. There is less cover for ambush predators such as lion, although they again are present in moderate numbers; cheetah numbers also appear to be increasing in the central park area (Personal observation; H. Watts, Personal Communication, 2004).

If there were a strong habitat signal in the Amboseli skeletal part data, one would expect that the woodlands to be similar in both 1975 and 2002-03, and that the other habitats would retain characteristic taphonomic signatures distinct from the woodlands and consistent through time (1975 to 2002–03). Contrary to this expectation, however, results indicate that the dominant signal reflects major changes over three decades in biological taphonomic processes affecting the bone assemblages across all habitats. Even between contemporaneous woodland samples in 1975 (i.e., Acacia xanthophloea and Acacia tortilis woodlands), there is no indication of a distinctive taphonomic "imprint" of this habitat type. All habitat samples were fairly similar in 1975 (Table 5C, 5D), and this similarity actually decreased among some sample pairs in 2002–03, suggesting that the impact of hyena consumption may be somewhat variable among the different habitats, with the most intense carcass destruction in the 2002-03 swamp habitat and the saltbush plain that replaced the former A. xanthophloea woodland. The A. tortilis woodland assemblages remained the most alike between 1975 and 2002-03. Thus, it is clear that shifts in skeletal survival rate can be controlled by the changes in the dominant predator and are expressed across all the Amboseli habitats analyzed in this study.

Comparisons with the data of Blumenschine (1989) indicate that the proportions of recorded skeletal parts in all three Serengeti habitats are most similar to the 1975 Amboseli A. tortilis woodland, but beyond this, there is no particular pattern of clustering with other Amboseli habitat samples of either time interval (Figure 15). The relatively high proportions of cranial remains (skull and mandible) that are responsible for grouping all three Serengeti habitats with the Amboseli, 1975 A. tortilis woodland (Figure 16) could relate to visibility of remains in these habitats (i.e., a sampling bias signal), and/ or to actual similarity in skeletal part survival patterns in these two ecosystems. The proportions of innominates, also a large and visible skeletal element, are somewhat higher the Serengeti AW&GP and RP habitats vs. the A. tortilis woodland samples, but low in the NGO (more open) habitat. This suggests that there may indeed be a sampling bias toward more visible elements in the more densely vegetated habitats. (It should be noted, however, that visibility may also be a factor in predator scavenging and could have affected the foraging strategies of early hominins as well.)

Returning to the question of scavenging opportunities for hominins in woodlands vs. other habitats, the results from Amboseli demonstrate that while there may be a tendency for less destruction and deletion of skeletal parts in relatively stable woodlands (e.g., the Amboseli Acacia tortilis woodland), a major shift to bone-consuming predator dominance could overwhelm this pattern, leaving little that would be worth scavenging for periods of years to decades. Therefore, woodlands were not necessarily the optimal habitat for hominin scavenging activities through the Plio-Pleistocene because other processes could intervene to upset the balance of foraging benefits vs. risks. If hominins were more involved in hunting than scavenging, they would also have been affected by the population dynamics and habitat preferences of other predators, and it is unlikely that early hominins would have been effective competitors as scavengers or hunters in habitats, or times, dominated by either felids or hyenids. However, the cycle of carcass abundance vs. scarcity over three decades in Amboseli also points to the periodic opportunities for meat-eating during the times when predator pressure was relatively low. An omnivore with the ability to shift dietary and foraging strategies seems ideally suited to take advantage of changes through time in available resources as well as recognizing and effectively utilizing differences among habitats and their resident predators at any given point in time.

CONCLUSIONS

The overall goal of the Amboseli study was to determine how a bone assemblage tracks decade-scale ecological change in the animal community from which it is derived. Results were also used to test the hypothesis that more complete animal remains typically occur in woodland habitats in the African savanna ecosystems, which has been used in support of a model for early hominin foraging strategies in woodland versus grassland habitats (Blumenschine, 1989). Analysis of the Amboseli data involved counts of skeletal elements and other evidence for carcass modification and bone completeness to determine: 1) the degree of correlation between skeletal part survival and habitat, 2) the impact of ecological change through time on skeletal occurrence patterns and survival. The taphonomic changes in Amboseli show that over several decades, the survival of carcasses and bones can vary markedly within the same ecosystem and within the same habitat. This suggests that the availability of scavengeable remains for hominins not only may vary from habitat to habitat (Blumenschine, 1989), but also change over time-spans shorter than or comparable to the lifetime of individual hominins. The results also

indicate that predator pressure exerts a major control on carcass completeness and bone survival patterns in Amboseli and that differences in habitat—carcass associations can disappear under increased abundance of a bone-consuming carnivore. Thus, it is not likely that any particular habitat, such as woodlands, would have been consistently the best place for early hominins to forage for carcasses or hunt for animals. Rather, hominins and other predators or scavengers would have had to adjust their foraging strategies to cycles of shifting abundance in both prey and competing predator/scavenger species, as well as environmentally induced changes in habitat structure.

It is possible that the changes observed in the bone assemblage of Amboseli are a unique result of the combination of human impact, environmental change, and chance, making the shift from carcass glut to scattered fragmentary bones limited as an analogue for taphonomic cycles of the past. However, some variability would be expected over ecological and geological time in biological and ecological processes affecting skeletal remains in any ecosystem. It is clear that changes in the predator populations can have major impact on bone assemblages in tropical East Africa, and the same would likely hold true for other vertebrate communities that have both meat and bone-consuming carnivore species. Predator diversity and dominance patterns are unlikely to be stable for long periods of time because they are linked to alternating periods of abundant vs. scarce prey, disease, changes in interspecific competition, or shifts in vegetation structure affecting hunting success.

An unexpected outcome of this study is the relative stability of species richness and evenness (as measured by Fisher's Alpha) through time in the Amboseli habitats, in spite of the loss of woodlands and other habitat changes and the increase in destructive taphonomic processes. This indicates that although the Amboseli surface bone assemblages were greatly reduced in quantity and quality between 1975 and 2002-03, the taxonomic and ecological information in the fragmentary but identifiable remains would show the same basic species abundance distribution for each habitat. The evidence for ecological change (i.e., shift to bone-consuming predator dominance) is in the skeletal element assemblages themselves, and in differences in rank order reflecting more subtle increases and decreases in the abundance of particular species (e.g., increase of wildebeeste and zebra and decline of giraffe and impala remains in the woodlands). If the past 30 years of Amboseli's history were preserved in two successive, stratified assemblages with minimal additional diagenetic bias, there likely would be sufficient evidence to reconstruct the major taphonomic and ecological processes that formed this record.

Skeletal part abundances and completeness, adult/ juvenile ratios, and damage patterns and how these vary in relation to prey body size can provide evidence for different levels of predator pressure on bone assemblages. Similar information on skeletal elements and bone modification is preserved in the paleontological/archeological record, but the value of such data depends on collecting strategies that control for taxonomic, taphonomic, and sampling biases in both excavated and surface assemblages. If such controlled samples could be documented, then the actualistic evidence from Amboseli, the Serengeti, Zaire and other ecosystems could be used to develop and test hypotheses regarding predator pressure and scavenging and/or hunting behaviors that affected ancient bone assemblages. This approach would be particularly appropriate for fossil assemblages that can be sampled in the context of preserved paleolandscapes. Given the problems of time-averaging and variability in the ecological and taphonomic processes that may have affected skeletal survival rates in the past, it will be essential to develop and compare as many actualistic studies as possible to obtain a realistic sense of variation in predator/scavenger impacts on bone assemblages during the Plio-Pleistocene.

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