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Savanna Ecology and Natural Bone Deposition

Implications for Early Hominid Site Formation, Hunting, and Scavenging¹

by Martha Tappen

Modern East African savannas serve as the primary model for the paleoenvironments of early hominids. However, throughout the Neogene there have been cooling and drying trends through time and fluctuations in seasonality. As a result, many modern East African savannas are drier, with more severe dry seasons, than during some periods in the Plio/Pleistocene in which early hominids lived. Our understanding of these moister and less seasonal periods is crucial for reconstructing early hominid lifeways. This paper presents a study of the ecology and bone taphonomy of a savanna less dry and less seasonal than the East African ones, the Central African savanna in Parc National des Virunga, Zaire. The natural bone distributions across the landscape of Parc National des Virunga contain information about the spatial distribution of scavenging opportunities and the effects on bone deposition of ecological variables such as large-herbivore biomass, proximity to water, and tree density. This information is significant for taphonomic interpretation of fossil distributions in paleosols and the paleoecology of hominid scavenging. My results indicate that the Central African savanna differs in bone distributions and scavenging opportunities from the savannas of East Africa. Bone deposition is higher in open grasslands than in wooded areas near rivers, and there is no dry-season glut of carcasses. There is also no evidence for increased bone deposition near permanent water or ephemeral water holes. These differences are ultimately the result of the less seasonal rainfall pattern. For early periods in human evolution, Central African savannas may be a useful analog, and the implications for site formation and the ecology of scavenging are profound.

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Models of early hominid habitats usually use modern African savanna ecosystems as analogs. East African savannas such as in the Turkana Basin, Serengeti, Amboseli, and Ngorongoro Crater have been used particularly often to model the ecological situations that early hominids would have needed to survive in and adapt to (e.g., Behrensmeyer and Dechant-Boaz 1980; Behrensmeyer 1983a; Blumenschine 1986a, 1987, 1989; Blumenschine and Cavallo 1992; Foley 1987; Feibel, Harris, and Brown 1991; Schaller and Lowther 1969; Sinclair, Leakey, and Norton-Griffiths 1986); sometimes South African savannas are also used (Binford 1983; Brain 1981; Vrba 1975, 1980). One purpose of such work is to identify resource distributions in order to assess the possibilities for early hominid diet and land-use systems. Actualistic data on the distribution of plant and animal foods and their seasonal availability and quality are derived from these environments and used to create models of resource exploitation (Blumenschine 1987; Peters and O'Brien 1981; Peters, O'Brien, and Box 1984; Sept 1984; Speth and Davis 1976; Speth 1987, 1989; Foley 1987).

The emphasis on these environments as analogs makes sense. Hominids did, after all, live in eastern and southern Africa, and most of the paleofauna associated with hominid sites is ancestral to species of the savanna communities that exist there today. The basic structure of African savanna large-mammal communities seems to have been in place by the Pliocene (e.g., Barry 1987). Some scientists have stressed the near-identity of these paleohabitats to modern ones, although allowing for shrinkage and expansion of various modern subhabitats, fluctuating with either climatic change or major hydrological changes caused by geological processes (e.g., Feibel, Harris, and Brown 1991).

However, the use of modern eastern and southern African savanna ecosystems to model early hominid paleohabitats demands discrimination and care. Although the simple model of savanna replacing forest in East Africa sometime in the late Miocene or Pliocene probably needs to be abandoned (Kingston, Marino, and Hill 1994), most evidence indicates that climatic patterns and degree of seasonality fluctuated considerably over the Neogene, and this would have affected monsoonal and seasonal rainfall in Africa (Imbrie and Imbrie 1986; Ruddiman and McIntyre 1981; Pokras and Mix 1987; Prell and Van Campo 1986; Rostak et al. 1993; Sarkar et al. 1990). For this reason alone, no single ecosystem can possibly be the "correct" analog for hominid habitats, although one may be better than another for a par-

ticular time and place. Furthermore, the behavior of the plants and animals is likely to have evolved and changed over time. For example, we do not know when the present-day migratory system of some of the major ungulates began; it is possible that such systems are very recent or perhaps came and went with drier or wetter periods (e.g., Marean and Gifford-Gonzalez 1991). Additionally, some members of the bovid tribes that are critical to ecological reconstruction may have evolved habitat and food preferences subsequent to their original radiation (e.g., Plummer and Bishop 1993). Finally, the persistent presence at some paleontological sites of species that are not formally found together or occur in very different proportions in living savanna communities suggests the possibility of real differences in species associations. However, such associations can also be the result of time-averaging, various habitats being represented in one locality because of environmental change through time (Behrensmeyer 1991a).

I do not mean to suggest that anthropologists have uncritically accepted a dogmatic Serengeti-as-analog approach. There has been some acknowledgment that the present is different from the past. The presence of several carnivore species now extinct, including saber-toothed cats and large hyenas, and their hypothetical role in ancient ecosystems have been given considerable attention (Blumenschine 1987, Blumenschine and Cavallo 1992, Marean 1989, Walker 1984). While no habitat today should be used as an all-encompassing model of hominid paleohabitats, we are trapped in the present and must depend primarily upon information about modern ecosystems to develop our models.

Paleoenvironmental interpretation based on analysis of vertebrate remains requires knowledge of the relationship between ecosystems, the mortality of the creatures in the ecosystem, the localities in which skeletons end up, and the condition of the bone. I summarize here the highlights of a survey of modern animal bones (Tapen 1992) across various subhabitats in a savanna in eastern Zaire (Parc National des Virunga, hereafter PNV). I integrate information regarding predator and prey biomass and spatial distributions with the data on bone distribution to begin to develop the correlations between bone deposition and ecology that are required for interpreting fossil bone distributions and paleoecology and for understanding the nature and location of scavengeable carcasses. Until this study, most of our information on these ecological and taphonomic variables came only from relatively drier East African savanna ecosystems. I chose a different type of savanna to study—one with less seasonality, more tall grass, and resident ungulates. Bone deposition patterns, including bone spatial density, degree of scattering, and species representation, are assessed in relation to ecological variables such as predator and prey habitat preferences, proximity to water, and surrounding vegetation. Each of these variables affects bone deposition and by analogy would affect fossil bone distributions across paleosols. These ecological variables likewise affect the distribution of scavengeable resources. The patterns described

show both similarities to those found in previous studies and very important differences.

Patterns in Modern Bone Deposition

The potential for understanding paleoecology through the study of fossil bone distributions across landscapes is beginning to be more fully exploited than in the past. The idea that such information can increase our understanding of hominid habitat preferences and behavior has opened new avenues of research, including actualistic study of modern bone distributions across landscapes with varying ecologies and increasingly detailed mapping and study of fossil bone distributions across lateral facies representing ancient environments (Potts 1989, Blumenschine and Masao 1991, Stern 1993). In well-provenanced fossil localities, especially in paleosols, lateral variation in species representation has helped to reconstruct paleohabitats and habitat preferences (Clark and Keitze 1967, Behrensmeyer 1975, Pickford 1981, Retallack 1988, Bown and Kraus 1981, Bown and Beard 1990). Lateral variation has also been found for taphonomic features of the bone assemblages. Facies can be compared with one another not only in terms of sedimentary features but also in terms of taphonomic characteristics (Badgley 1986; Behrensmeyer 1988, 1991b; Retallack 1988). In the right taphonomic setting, detailed landscape analysis has considerable promise.

Important information can be gleaned from an analysis of bone deposition in relation to ecological variables. Will attritional-death bone deposition ever result in dense bone accumulations in a single spot? If so, are there some situations or environments in which this is more likely to occur? Do bones accumulate in "predation arenas" or "eating areas" where carnivores repeatedly hunt or consume carcasses (Behrensmeyer 1982b, 1983a, 1987; Haynes 1988)? What are the chances of accidental overlap of "background" bones and stone tools, whether by chance or through a "common amenity" such as a shade tree attracting both hominids and carnivores (Isaac 1983) or a water hole (Binford 1983)? Do the geomorphological and faunal associations of hominid fossils represent habitat preferences or other taphonomic factors? How can a relatively undisturbed, cumulative bone distribution across a landscape be characterized, and how will it differ from fossil assemblages found in paleosols (Stern 1993)? Are there ecological variables that can be correlated with certain types of bone deposition? How do areas with differing ecologies differ in bone deposition rates? Where would hominids most likely encounter scavenging opportunities, and how can such opportunities be characterized?

In the savanna landscape, bones are most often dispersed (Isaac and Crader 1981, Behrensmeyer 1983a). A limited number of agents accumulating bones of medium-sized and large animals is known for modern landscapes. Well-known concentrators of bones include, of course, humans (Brain 1967, 1969; Bunn 1983; Bunn, Bartram, and Kroll 1988; Hudson 1993, Yellen 1977).

The questions are when in human evolution we started doing this and whether hominids ever accumulated bones in a way fundamentally different from that of humans today. All three of the living species of hyena collect bone (Mills and Mills 1977), and there have been many studies of their bone-collecting and bone-modifying behavior (see Cruz-Urbe 1991 for a recent review). Leopards' repeated caching of carcasses in the same tree may lead to substantial bone accumulations (Brain 1969, 1981; Cavallo and Blumenschine 1989). There is a surprising lack of information in the literature regarding lion damage to bone or whether the repeated visits by lions to preferred areas mentioned by Behrensmeyer (1983a, 1987) and Haynes (1985, 1988) ever result in substantial numbers of bones. Porcupines collect a large array of bones (Brain 1969, 1981; Bunn 1982), including large bones from many species. Tell-tale gnawing is usually quite abundant in such assemblages. Mass deaths in one spot may occasionally occur because of drought, drowning, or poisonous gas (Dechant-Boaz 1982; Haynes 1988:219; Tazieff 1989; Lyman 1989). Natural traps can also accumulate bones by repeatedly capturing animals over time.

Fluvial processes are commonly thought to be important bone accumulators, but actualistic research and experiments in modern rivers have not borne this out: "Current action *alone* has not been observed to assemble dispersed, unmineralized bones into dense 'lag' accumulations, although this may occur with previously fossilized remains" (Behrensmeyer 1987:432). Instead, some other biological concentrating mechanism usually must occur first. Previously buried fossils exhumed by erosion may become associated with others, creating larger, time-averaged assemblages (Behrensmeyer 1982a, 1983b, 1988b).

Each of these bone-accumulating agents has certain "signature criteria" (Lyman 1987) that help us to recognize it in the fossil record. However, the equifinality of many taphonomic processes sometimes makes distinguishing between them difficult, and this effect is confounded by the fact that many fossil occurrences are affected by more than one taphonomic process. Nonetheless, evidence is usually left behind in patterns of species representation, skeletal frequencies and articulation, and bone modification.

Despite these processes, most bones are dispersed. Animals die of disease or predation usually as individuals, generating clumps of 150 or so bones. The carcasses are consumed and disarticulated and the bones scattered by competing carnivores in a systematic manner based on utility and ease of access (Blumenschine 1985, 1986a), sometimes in a matter of minutes after their death (Isaac and Crader 1981). Carnivores then crack open the bones, completely consuming many elements. Weathering, breakage by trampling, and further consumption by rodents, insects, mosses, algae, and bacteria may follow (Tappen 1994). Bones are further scattered by the kicking of passing animals, movement downslope, or water action (Hill 1979, Hill and Behrensmeyer 1984). Natural death, deposition, and scattering

create a steady "background noise" of bones. It is this attritional-death bone deposition that is the focus of Behrensmeyer's ongoing work in the Amboseli Basin, Kenya (Behrensmeyer, Western, and Dechant-Boaz 1979; Behrensmeyer and Dechant-Boaz 1980; Behrensmeyer 1981, 1983a, 1991a). Her research indicates that the numerous bones distributed across the Amboseli landscape are rarely found in dense concentrations. Species habitat preferences are closely reflected in their bone deposition, bone deposition rates vary among the six habitats defined for the park, and in all habitats bones are relatively dispersed. Hill (1975) examined bones at Murchison Falls, Uganda, and East Turkana, Kenya, and Blumenschine conducted a survey for bone in Tanzania at Ngorongoro Crater and in the Serengeti (1989). Natural fish bone distributions have also been studied (Stewart 1991). Bone deposition has been recorded in the course of Hadza hunting forays in Tanzania (Bunn, Kroll, and Bartram 1991). Recently, Sept (1994) has recorded bone deposition in conjunction with chimpanzee spoor within the gallery forest along the Ishasha River, in PNV's southern sector. The present study differs from these studies in its more detailed spatial analysis, concentrating on microhabitat changes in tree density, topography, and proximity to lake, river, and water-hole situations.

Studying Bone Distributions in Parc National des Virunga

Parc National des Virunga (formerly Prince Albert Park) is located in the Western Rift Valley of eastern Zaire. The park was formed by the Belgian colonial government between 1925 and 1935 and extends 260 km from the Rwenzori Mountains south to the northern tip of Lake Kivu, encompassing 8,900 km². It is a rather isolated pocket of savanna, surrounded by the Rwenzori Mountains to the north, the Virunga Volcanoes to the south, and the Ituri rain forest and the rift wall to the west (fig. 1). Significant elevation changes in the park yield a wide range of rainfall regimes, and both rain forest and savanna zones are represented, as well as sclerophyllous brush, montane forest, bamboo forest, and giant heath (e.g., Bourlière and Verschuren 1960, Verschuren 1986).

The study area within the park is located on the rift floor in the northern sector, on the northern border of Lake Rutanzige (formerly Lake Edward) near the origin of the Semliki River. It is a mostly medium and tall grass savanna with scattered *Acacia* and *Euphorbia* trees (table 1). It differs from East and South African savannas in a few key ways. PNV does not have the migratory system seen in the Serengeti or the dispersal system found in Amboseli, and it is not as dry in the dry season as Ngorongoro Crater. It is similar to the wetter, northwestern corner of the Serengeti and Ngorongoro Crater (Norton-Griffiths, Herlocker, and Pennycuik 1975) in receiving about 930 mm of rain a year (Verschuren 1986), but the seasonal variation in rainfall is not nearly

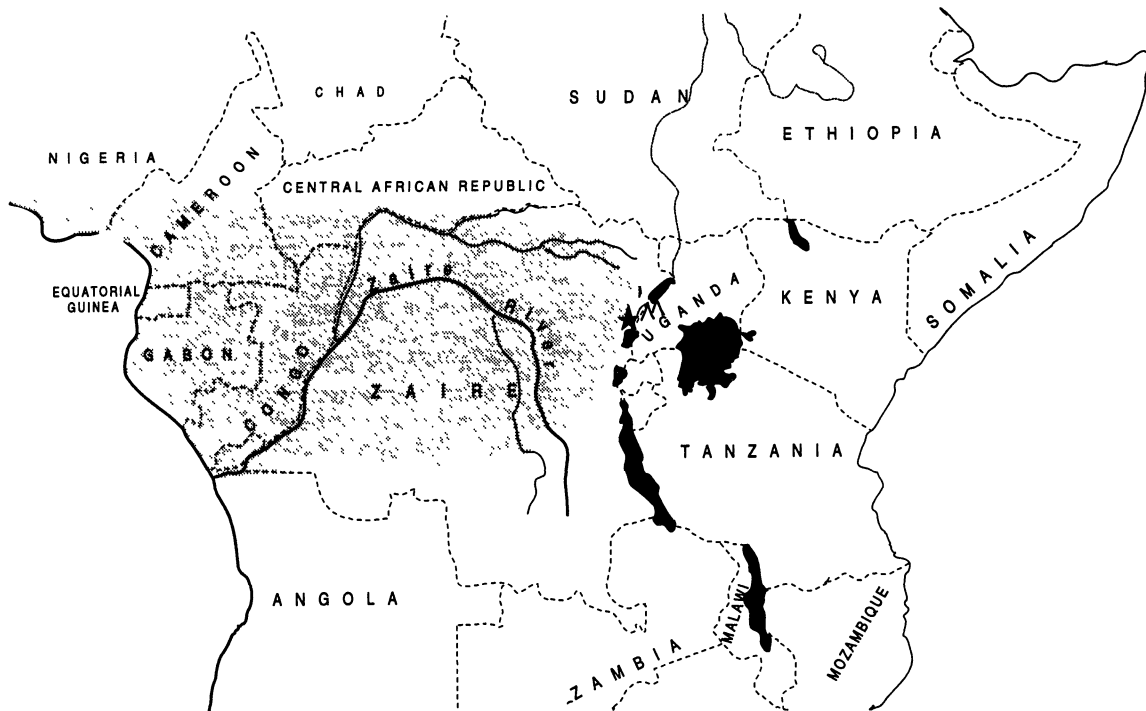


FIG. 1. Location of the Parc National des Virunga (*). Stippled area, rain forest; M, Rwenzori Mountains.

TABLE I
Trees and Grasses Common in the Northern Sector
of the Parc National des Virunga

Trees	
<i>Acacia sieberiana</i>	
<i>A. hockii</i>	
<i>A. gerardii</i>	
<i>A. senegal</i>	
<i>Euphorbia calycina</i> (candelabra tree)	
<i>Cordia africana</i>	
<i>Euclea schimperii</i>	
<i>Olea europaea</i>	
<i>Tarenna graveolens</i>	
<i>Turraea robusta</i>	
Grasses	
<i>Themeda triandra</i> (red oat grass)	
<i>Hyparrhenia dissoluta</i>	
<i>H. filipendula</i>	
<i>Imperata cylindrica</i> (sword grass)	
<i>Sporobolus pyramidalis</i>	
<i>S. robustus</i>	
<i>Cymbopogon</i>	
<i>Andropogon</i>	
<i>Bothriochloa</i>	
<i>Panicum maximum</i>	
<i>Pennisetum</i>	
<i>Microchloa</i>	
<i>Hetropogon</i>	
<i>Cynchrus cillcarus</i>	
<i>Eleusinia indica</i>	

SOURCES: Sept (1990) and field observations with the assistance of Jean-Pierre Kirimunda-Lina.

as intense. Two wet and dry seasons can be distinguished, but the dry seasons are shorter and less severe than those seen in East Africa. In fact, compared with the Serengeti and the Ituri Forest, PNV has the least variation in rainfall from month to month (table 2). This has an important effect on the ungulates in the park, allowing them to remain resident in one area year-round rather than migrating to seasonal food sources. Soils are of a volcanic origin, like many of the valley soils in East Africa, but they tend to have a more neutral pH.

Large-mammal species richness (table 3) is less than in the East African savannas and the Pliocene and Pleistocene fossil record from East Africa, probably because PNV is a relatively isolated and small pocket of savanna (Enama 1989). Despite the lack of variety, large-mammal biomass is very high in the park (e.g., Bourlière and Verschuren 1960, Delvingt 1978, Mertens 1983). The study area is home to one of the largest hippopotamus populations in Africa; they are especially abundant near the origin of the Semliki River (Delvingt 1978).² Over the history of the park, elephant populations have fluctuated greatly; today there remain only about 130 individuals (Conrad Averling, personal communication, 1992). They keep mainly to the western side of the Semliki River, where they can hide in very tall grass and dense brush. Because the bone survey was conducted on the eastern side of the river, elephants are not well represented in the bone survey. Buffalo are common. Re-

2. Since the study was conducted in 1986 and 1988, poaching has become extremely serious and the hippo population has been decimated (Averling, personal communication, 1992).

TABLE 2
Mean Monthly Rainfall (mm) for Rwindi (PNV),
the Serengeti, and the Ituri Forest

	Rwindi	Serengeti	Ituri
January	58.4	87.0	41.6
February	62.5	92.0	63.4
March	81.9	87.0	162.4
April	104.7	118.0	229.0
May	82.1	77.0	174.0
June	64.9	40.0	176.7
July	38.6	17.0	190.8
August	85.4	30.0	195.9
September	73.9	27.0	186.9
October	81.7	42.0	235.2
November	90.6	79.0	178.4
December	52.6	107.0	61.8
Total	877.3	803.0	1,896.0
% variation	25.07	50.76	41.43

SOURCES: For Rwindi, 1963–72, Delvingt (1978); for the Serengeti, based on 62 stations over a period of 5–30 years, Norton-Griffiths, Herlocker, and Pennycuik (1975); for the Ituri Forest, 1977–81 at Angalare, Bailey (1985).

duncines, medium-sized-to-large antelopes that typically live near water, including the Uganda kob, the most common antelope, the waterbuck, and the reedbuck, are the predominant representatives of the Bovidae. Warthog are also abundant. Bush pig, bushbuck, and sitatunga are found in much lower numbers.

The large carnivores include leopard, lion, and spotted hyena, as well as python and, within the past ten years, crocodile. Competition between lions and hyenas in the park (as in other African savannas) is intense, and lions are clearly dominant over hyenas when they are not too outnumbered (e.g., Cooper 1991, Eaton 1979). The spatial distribution of lions and hyenas in the northern sector is evidently different from that of Serengeti Park. In the Serengeti, lions prefer the bushier habitats to open grassland (Schaller 1972:238). Schaller attributes this to lion hunting techniques: stalking with a short rush and surprise require something to hide behind. Three-fourths of lion kills on the plains observed by Schaller occurred near some cover. Furthermore, because prey is scarce on the plains during the dry season (the residential species tend to be in the more wooded areas), territorial lions cannot live there year-round (Schaller 1972:382). Thirty to forty-one percent of their kills were made in dense vegetation near rivers. Schaller also documents a substantial increase in lion hunting success when grass is taller (over 0.4 m [Schaller 1972: table 56]). In contrast, hyenas keep mostly to the more open plains in the Serengeti (Schaller 1972:345). They travel much greater distances ("commuting") and can therefore remain on the plains even when prey is scarce there. Tsetse flies, which carry trypanosomes, annoy hyenas in the woodlands (Kruuk 1972:22). This spatial parti-

TABLE 3
Large and Medium-sized Mammal Species,
Parc National des Virunga

Proboscidea
<i>Loxodonta africana</i> (African elephant) ^{a,b}
Suidae
<i>Phacochoerus aethiopicus</i> (warthog) ^{a,b}
<i>Potamochoerus porcus</i> (bushpig) ^a
<i>Hylochoerus meinertzhageni</i> (giant forest hog) ^a
Hippopotamidae
<i>Hippopotamus amphibius</i> (hippo) ^{a,b}
Tragulidae
<i>Hyemoschus aquaticus</i> (water chevrotain)
Giraffidae
<i>Okapia johnstoni</i> (okapi)
Bovidae
Bovini
<i>Syncerus caffer</i> (African buffalo) ^{a,b}
Reduncini
<i>Kobus ellipsiprymnus</i> (waterbuck) ^{a,b}
<i>K. kob</i> (Ugandan kob) ^{a,b}
<i>Redunca redunca</i> (reedbuck) ^{a,b}
Tragelaphini
<i>Tragelaphus scriptus</i> (bushbuck) ^{a,b}
<i>T. spekii</i> (sitatunga) ^a
<i>T. euryceros</i> (bongo)
Cephalophini
<i>Cephalophus nigrifrons</i> (black-fronted duiker)
<i>C. sylvicultor</i> (yellow-backed duiker)
<i>C. zebra</i> (black-banded duiker)
<i>C. callipygus</i> (Peters duiker)
<i>C. monticola</i> (blue duiker)
<i>C. grimmia</i> (common duiker)
Alcelaphini
<i>Damaliscus lunatus</i> (topi)
Neotragini
<i>Neotragus batesi</i> (Bates dwarf antelope)
Primates
<i>Papio anubus</i> (baboon) ^a
<i>C. aethiops</i> (vervet) ^a
<i>C. ascanius</i> (red-tailed monkey)
<i>Colobus guereza</i> (black-and-white colobus)
<i>Pan troglodytes</i> (chimpanzee)
Felidae
<i>Panthera leo</i> (lion) ^a
<i>P. pardus</i> (leopard) ^{a,b}
Hyaenidae
<i>Crocuta crocuta</i> (spotted hyena) ^{a,b}

SOURCES: Ungulates, Bourlière and Verschuren (1960); primates and carnivores, Delvingt (1978).

^aCommon in the study area.

^bPresent in the survey bone assemblage.

tioning has had a strong impact on bone deposition and scavenging opportunities (Blumenschine 1987, 1989). In Chobe National Park, Botswana, hyenas also prefer open areas, but when migratory prey are not present in the dry season they hunt in the woodlands more often (Cooper 1990:136). In contrast, hyenas occupy woodland habitat in Timbavati Nature Reserve, South Africa (Bearder 1977). In PNV's northern sector, hyenas are most common in the bushy areas near the lake and along the Semliki River, while lions are habitually in the open plateau. This spatial partitioning is far from absolute, however,

and both species traverse the entire park. One possible explanation for the reverse habitat preference compared with the Serengeti may be the relatively taller, denser grass on the open plateau. *Themeda triandra*, *Hyparrhenia filipendula*, and especially *Imperata cylindrica* often grow very tall and in dense stands in which crouching lions can be completely hidden. Thus, lions can easily hide near where their prey is most numerous. Also, PNV lacks large treeless expanses; even in the open grasslands one is rarely more than 100–200 m from a shade tree. Probably equally important, the lions' most abundant and reliable source of food, the kob, tend to spend more time in the open grasslands than in the treed areas nearer the lake and river.

The study area consists of 100 km² of savanna on the rift floor in the northern sector (fig. 2). I surveyed 42.9 km of transects (1.43 km of them 25 m wide, the rest 50 m wide) on foot with a park guard and at least two trained Zairean workers. Linear transects were the sampling technique chosen to allow observations of changes across space. This method also allowed the sampling of large areas along the Semliki River and assessment of bone-density variation as one moved away from this water source. Transect length was determined either by a natural topographic feature such as the distance from the top to the bottom of a hill or, more often, by dense vegetation that reduced visibility. Vegetative ground cover had some effect on sampling and location of transects. However, the park maintains a burning program to reduce brush and encourage new-growth grass, and burnt areas allowed survey with excellent visibility. Additionally, I obtained permission from the park to burn grassland when necessary, allowing survey of areas that would otherwise have been impossible. Each transect was walked over at least twice and in most cases four times by (usually) three surveyors 10–15 m apart. Exceedingly few previously unrecovered bones were ever found on the fourth walk-over, and most were spotted on the first. Bone-density calculations must, however, be considered a minimum estimate, as clearing of bushy vegetation in a few instances revealed a few missed bones.

Areas of bones surrounded by areas of lower bone density, usually representing the remains of a single individual, are here called *bone patches*. This concept suffers from the same problems as the concept of "site" in archaeology (Ebert 1992, Foley 1981, Isaac, Harris, and Marshall 1981, Thomas 1975), because distribution is quasi-continuous. Bones found singly are called *isolated finds*. For each bone patch, I recorded location,³ vegetation cover, the distance to the nearest tree, the longest dimension of the patch (used to approximate diameter), species represented, minimum number of individuals (MNI), age (neonate, juvenile, adult, old adult), sex (for species dimorphic in horns with the skull present or if

the carcass was fresh), and skeletal elements present.⁴ For each element, side, weathering stage, breakage, burial, and surface modifications were noted. Any flesh, skin, or "potential food" left was recorded, including whether marrow cavities or crania were unbroken, in order to estimate the amount of food that might be available to a late-access scavenger. The analysis is restricted to medium-sized and large mammals.⁵ Bones with evidence of poaching such as cutmarks, burning, and bullet holes were removed from this analysis. A test of the frequency of obvious indications of poaching was conducted by examining patches of known poached bones. It was found that butchery was most often conducted with a machete and often included burning of bones, so poached bone found could be readily identified and removed (Tappen 1992).

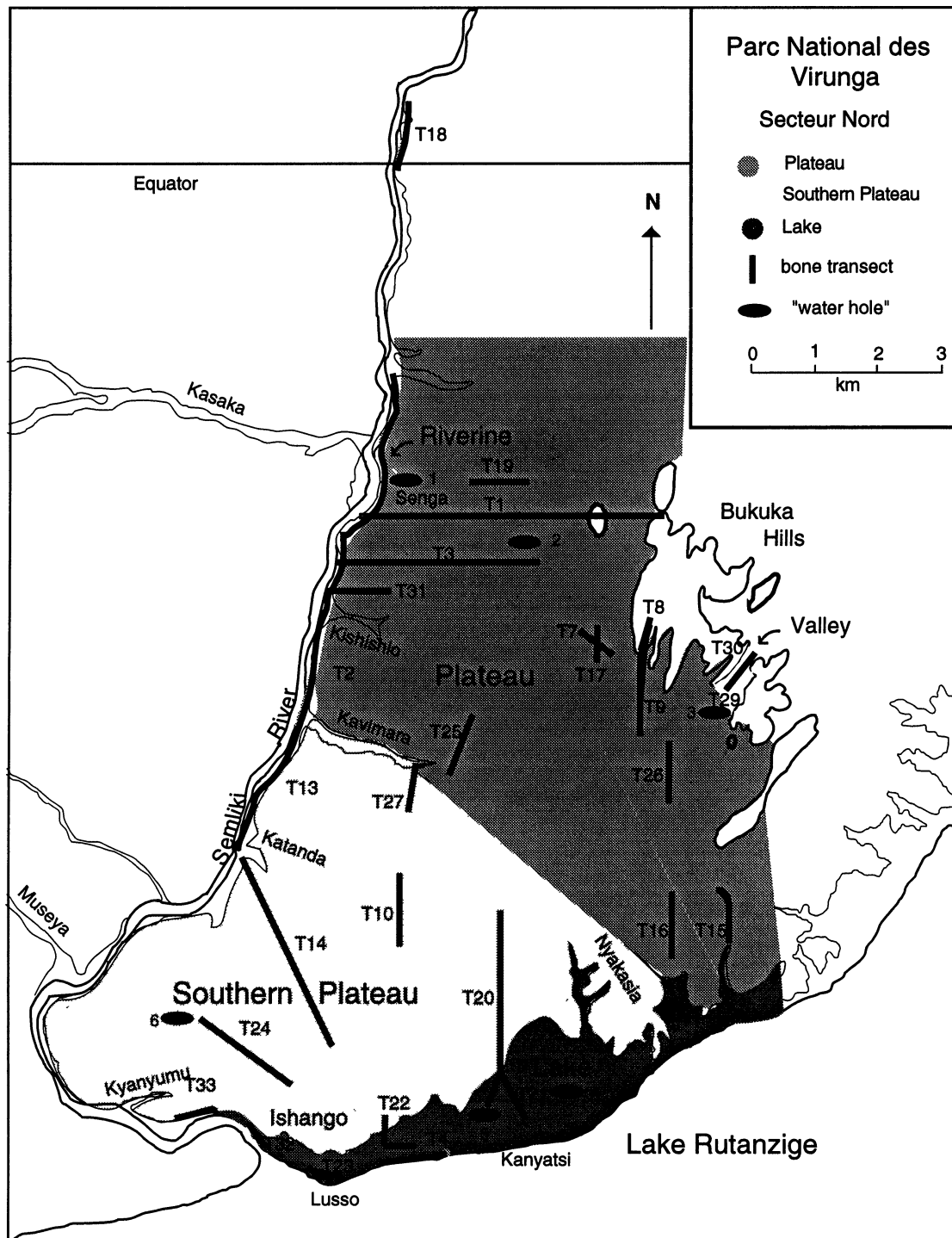
To test the hypothesis that, within a savanna ecosystem, different topographic situations and vegetation physiognomy will effectively "attract" or "discourage" bone accumulation, the survey area was divided into zones. Four main zones were defined: plateau, southern plateau, riverine, and lake (see fig. 2). In addition, I examined four smaller zones representing particular situations that were hypothesized to have distinctive bone deposition patterns: tree lines, cross-tree lines, the Bukuka Hills, and a valley between two hills (table 4).

The *plateau* (fig. 3) is a relatively open grassland with a high biomass of ungulates. In this open area one finds the densest herds of kob and reedbuck and the main kob lek. In contrast, the *southern plateau* has four times the number of trees, with many fewer kob and reedbuck and more waterbuck and warthog. Its proximity to the origin of the Semliki River and Lake Rutanzige results in much more hippopotamus activity. There are also some differences in frequency of grass species (Tappen 1992). The *riverine* zone has a much higher tree and bush density than the plateau but does not form a dense gallery forest. The Semliki River is cutting into the local sediments, and parts of the survey were on cliffs above the river, although most were only a few meters above the water. Ravines occur sporadically and range from a few meters deep and long to over a kilometer long and several tens of meters deep with dense vegetation. They represent unique microenvironments on the rift floor. Most of the bovids in the park are water-dependent and visit the river daily but do not linger. Dense populations of hippos alter the topography with their trails. The areas south of Katanda have high cliffs with no floodplain exposed below and therefore were not surveyed as part of the riverine zone. The *lake* zone includes the sandy beach and the tops of the low adjacent cliffs, as well as

4. Bones were counted as minimum number of elements (MNE). For example, two fragments from the same bone count as one. Following Behrensmeyer (personal communication), at Amboseli each hemimandible and each innominate was counted as one.

5. The bones of small animals such as rodents, rabbits, birds, fish, and reptiles were noted and are included in the species representation table, but including them in the bone-density analysis would have required finer survey techniques for good recovery.

3. Location was recorded using a hip-chain, a small box worn on the belt which trails out string behind it, recording the length of the string.



based on a map by Verniers and de Heinzelin

FIG. 2. The study area, indicating major zones and bone transect locations.

the slopes descending from the southern plateau to the water. In this zone vegetation varies from erosional surfaces with no plant growth to sparse or dense grass and in some areas huge clumps of bushes and trees. Some of these clumps were easy to survey because they are open underneath, while others had to be eliminated from the sample because they were impenetrable. Some very

large, very densely vegetated ravines occur along the lake. Waterbuck and warthog are especially common near the lake (Mertens 1983).

Within the grassy open plateau zone, one finds occasional lines of trees, often 500 m to 1 km long (see fig. 3). Lions are often seen resting in their shade. Three such *tree lines* were surveyed. In one case a perpendicular

TABLE 4
Transects Surveyed

Zone and Transect	Length (m)	Visibility ^a	MNE/ha ^b	LNN ^c
Plateau				
1	4,400	2	30.2	—
3	2,900	2	14.5	0.446
9	1,350	5	42.2	0.454
25	750	1	82.9	0.312*
26	900	1	159.3	0.467
31	900	2	26.0	0.489
Southern plateau				
10	1,240	1	6.4	0.252*
14	3,240	1	6.7	0.420
20	2,600	1	4.5	0.458
24	1,800	3	4.7	0.569
27	600	1	18.3	0.535
Lake				
4 ^d	1,200	4	6.3	0.516
21	1,500	2	18.6	0.691
22	1,230	1	3.9	0.492
23	1,250	4	7.2	0.270
32 ^e	500	4	8.0	0.660
33	1,000	1	3.0	0.785*
Riverine				
2	5,700	2	8.0	—
13	2,650	1	19.5	0.506
18	1,200	1–2	44.6	0.481
Tree line				
7 ^c	430	4	147.9	0.437
15	1,020	1	47.8	0.409
19	975	4	28.0	0.529
Cross-tree line				
17	630	2	69.5	0.628
16	1,100	1	15.4	0.406
Hills				
8	500	3	102.4	0.622
30	550	1	83.6	0.222*
Valley				
29	800	1	15.8	0.569

^a1, excellent, burnt or nearly devoid of vegetation; 2, very good, some bush clumps; 3, good; 4, variable, some bush clumps; 5, poor. Several transects were excluded because of poor visibility.

^bTotal MNE (minimum number of elements) divided by total area surveyed on the transects. (Individual hectares within the transect may be higher or lower.)

^cLinear nearest-neighbor statistic. Values starred (*) differ statistically from random. Transects 1 and 2 have no LNN values because they were surveyed without the hip-chain and therefore produced less accurate spatial data.

^d500 m of this transect is 24 m wide instead of 50 m because of dense brush.

^e24 m wide instead of the usual 50 m because of dense brush.

transect was placed across a tree line, and in another case a transect parallel to the tree line about 300 m away was surveyed; these two are termed *cross-tree lines*. Both types of lines were surveyed to see if carnivores were dragging bones under the trees. Finally, transects were surveyed across the *Bukuka Hills* and in a *valley* between two such hills. The hills are made of resilient Precambrian quartz and quartzite and rise some 100 m above the surrounding plateau (de Heinzelin 1955). The main vegetation is grass, but on some hills there is a ridge of trees and bushes growing along the north-south

axis, appearing much like the dorsal plates of a stegosaur (see fig. 3). Waterbuck are abundant near the hills (Mertens 1983), as are the herds of kob and reedbuck of the surrounding plateau.

The total area surveyed for each zone is given in hectares (1 ha = 10,000 m²) in table 5. The differences in sample size largely reflect the areas of the different zones. The smaller samples are from the tree lines, the cross-tree lines, the hills, and the valley and are considered an exploration of particular situations. They are vulnerable to the problems of small sample size.



FIG. 3. View of the open plateau, with a tree line in the foreground and the Bukuka Hills in the background.

Survey Results

BONE DISTRIBUTION BY ZONE

Bone deposition density is not uniform among the zones (table 5). It is more than six times higher in the plateau than in the more closed southern plateau, and in the more closed habitats along the lake and in the southern plateau it is the lightest; the riverine and valley areas are intermediate in bone deposition rates. Within the

open plateau, tree lines have a slightly higher bone deposition rate than the plateau surrounding them, but notably the cross-tree lines are depleted by approximately the same amount as the corresponding tree lines are increased. It appears that the tree lines are simply low-level concentrators that drain bones from the immediate surroundings. That tree lines accrue background bones, are often located in slight dips in the landscape (where sediment deposition may occur), and because of their

TABLE 5
Bone Density by Zone

Zone	Area (ha)	MNE	MNE/ha	Isolated Finds	Bone Patches	% Area within Bone Patches ^a	MNE per occurrence	
							Mean	S.D.
Plateau	56.00	2,371	42.34	94	143	1.052	10.03	17.68
Southern plateau	47.40	305	6.43	94	44	0.151	2.21	8.02
Riverine	47.75	853	17.86	94	64	0.795	5.40	16.76
Lake	30.90	207	6.69	75	13	0.614	2.35	8.02
Tree line	11.05	557	50.41	57	34	1.438	6.12	11.16
Cross-tree line	8.65	304	35.14	23	20	0.469	7.07	20.80
Hills	5.25	484	92.19	18	20	1.404	11.63	22.01
Valley	4.00	63	15.75	4	5	0.107	7.00	10.56
Total	211	5,151	24.41	459	343			

^aCalculated by modeling bone patches as a circle, using the greatest distance between two bones within a patch as the diameter.

shade may slow weathering suggests that these features might be an important source of fossils in paleosols. By far the densest concentration of bones by zone is in the bushy vegetation lines along the top of the Bukuka Hills, perhaps because they form a special type of tree line.

BONE-PATCH SIZE

Since most bone patches begin with the bones of a single animal, fewer bones per patch indicates scattering, consumption, burial, or destruction. The zones with lower overall bone deposition rates have bone patches with fewer bones and proportionally more isolated finds (fig. 4). The average number of bones per occurrence (includ-

ing both patches and isolated finds) is highest in the hills and plateau, where bone density is highest (table 5). Nonetheless, in all zones the large majority of occurrences contain only a few bones, and in fact the modal value is 1 in each case. There is a complete lack of large patches in the southern plateau, the maximum number of bones being only 15. The lake zone also lacks patches with high MNEs, except a single undispersed hippopotamus skeleton, and the riverine zone has few such patches. Bones in tree lines are very scattered, but there are a substantial number of medium-sized patches. There is a single large patch in the cross-tree transects. The Bukuka Hills have many medium-sized patches, especially between 10 and 30 bones, and several large ones.

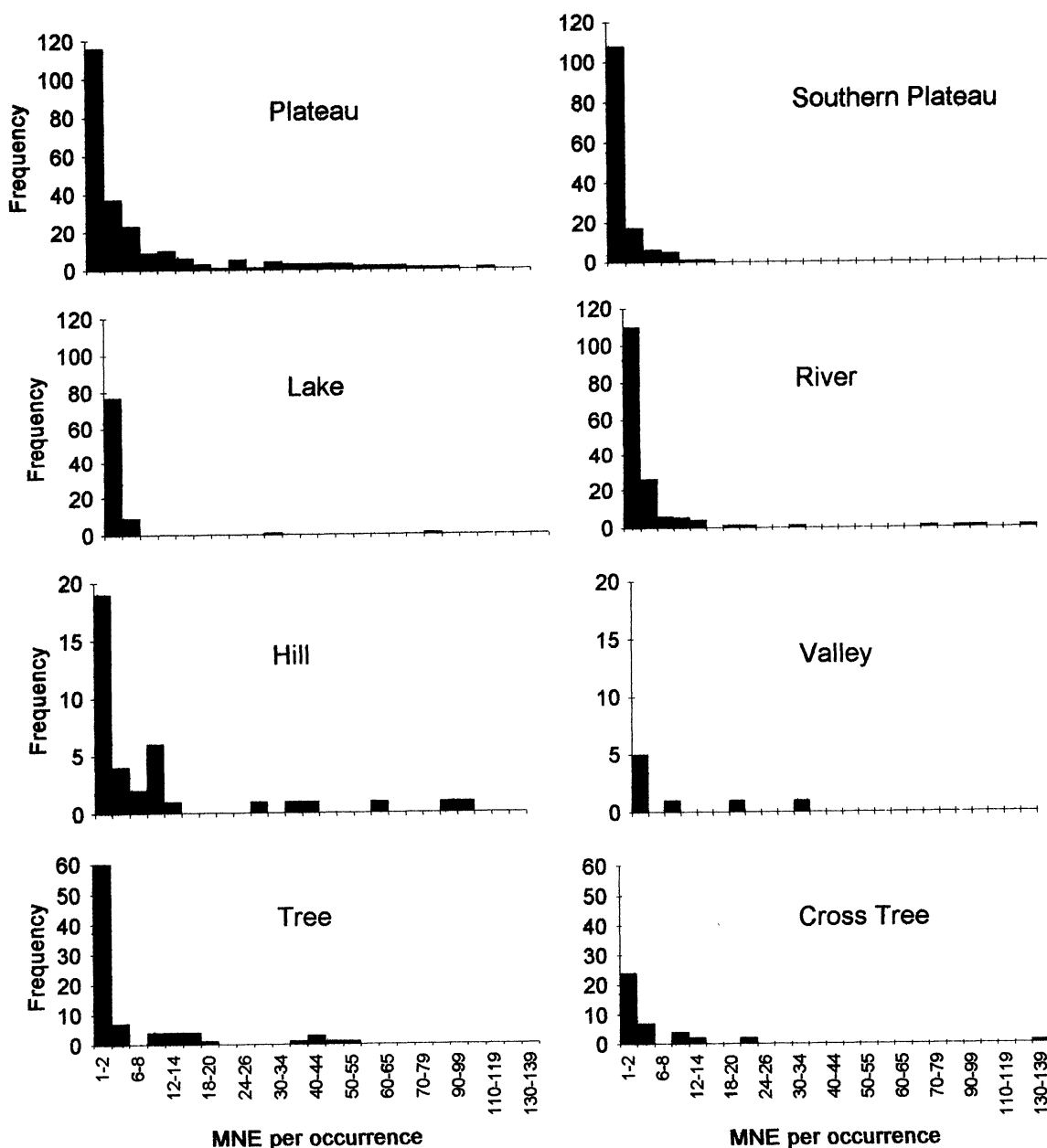


FIG. 4. Bone-patch sizes (MNE) by zone. (Y-axes are not all to the same scale.)

Taking the ratio of isolated bones to bone patches as a measure of the degree of scattering, the lake zone is by far the most scattered, with 6 isolated bones found for every bone patch, while areas of high bone deposition along the hilltops and on the plateau have fewer isolated finds than bone patches. The only area with high bone densities and a high ratio of isolated finds is the tree-line zone. The increased scattering reflected in small patch sizes in areas of low bone deposition probably reflects intense feeding competition among the carnivores. Another way to view bone densities across the landscape is in terms of the total area of bone patches. Table 5 shows what a tiny portion of the landscape this is. Only in the three densest zones, hills, tree lines, and plateau, do bone patches cover more than 1% of the land surface.

RANDOM, UNIFORM, OR CLUMPED?

Differences in the patterning of bone spatial distribution should reflect differences in the agents of deposition and scattering, particularly differences in herbivore and carnivore distributions. It is useful to think of the three basic types of spatial distribution recognized by ecologists: random, uniform, and clumped. For living organisms, random distributions usually imply either environmental homogeneity or nonselective spatial patterns, while clumping implies environmental heterogeneity, with more favorable and less favorable areas; uniform distributions are thought to indicate competition between individuals (Ludwig and Reynolds 1988:14). At the death of an animal, bones are clumped in groups of over 100. This level of clumping is easily recognized in the fossil record and therefore uncomplicated to interpret. Such a clump is unremarkable in that relatively little has happened to the animal taphonomically. An entire skeleton will usually represent an animal that died and was not subsequently scattered by carnivores or other dispersing agents. It was therefore probably buried rapidly. Such a find is unusual in the fossil record, however, and *very* unusual in the bone assemblage of this study. (In fact, whole animals may be more important in the fossil record than in surface assemblages accumulated over time because of the overrepresentation of catastrophic events in the fossil record.)

Bone patches from single individuals usually get dispersed, creating several smaller patches and several isolated finds. This can be the result of the competition among the consumers of the carcass and bones. Thus the bone dispersers, all things being equal, tend to influence the distribution toward a uniform one. However, competition between carnivores would lead to a uniform distribution only if all the competitive feeding events occurred at the same time. Because the carcass parts of different individuals found in the surface bone assemblages were mostly dispersed as separate events, the bone distribution, though the result of competition, cannot in any simple way be predicted from the ecological model of competitive individuals. Nonetheless, the model is instructive in explaining the high degree of dispersion of bones. The question, then, is what type of

distribution results from carnivore activity and whether the processes can result over some period of time in a rather large accumulation.

A linear nearest-neighbor (LNN) statistic (Pinder and Witherick 1975) was calculated for each of the transects (table 4), counting each bone occurrence equally regardless of the number of bones present in each patch instead of weighing each by the number of bones in a patch. The vast majority of patches represent a single individual, and the latter method would place unwanted stress on the few undispersed skeletons rather than on different bone occurrence events. While the method employed causes some loss of clumping information, it more accurately measures the proximity of separate individuals. Thus the LNN statistic equals the average distance between bone occurrences (isolated finds and bone patches) divided by the length of the transect and will always be between 0 and 1 (0.5 representing a random distribution, near 0 a clumped distribution, and near 1 a uniform pattern). Assuming the distribution of nearest-neighbor distance to be normal, an LNN statistic that differs from 0.5 by a *Z* score of greater than the absolute value of 1.96 is unlikely to be the result of chance ($p > 0.05$).

The vast majority of transects, 22 of 26, have LNN statistics indicating random spatial distributions. Four transects differ significantly from random ($p < 0.05$). Two of these transects, 10 and 33, have very low bone deposition rates (fig. 5). Transect 10 (LNN = 0.252; $Z = -1.981$) represents a clumped pattern because of a single small clump at about 200–400 m along the transect. All but 7 of the bones occur between 150 and 450 m along the transect. Although the total is only 33 bones, three species are represented (kob, waterbuck, and warthog). Transect 33 (LNN = 0.785; $Z = 2.133$) has a more uniform distribution of bones. It has the lowest bone deposition rate of all the transects and is the only transect without any bone patches. Many of the isolated bones are groups of long bone flakes (counted as an MNE of 1 in isolated finds). This transect is likely to be affected by the presence of several families that live year-round at Ishango. Nonetheless, its uniform pattern is interesting because the transect traverses the cliff above a hyena den. The large numbers of hyenas in the area appear to be dispersing and fragmenting bones to a high degree, producing the uniform pattern predicted by the ecological model of competition.

The other two transects with LNN statistics indicating patterns different from random, 25 and 30, have relatively high bone deposition rates (fig. 6). Transect 30 (LNN = 0.222; $Z = -2.425$) approaches a clumped distribution. It is a densely packed transect with several clusters of isolated finds and bone patches, including relatively undispersed skeletons. Transect 25 (LNN = 0.312; $Z = -2.093$) is also statistically clumped. The clump at 700–725 m along the transect is around a large shade tree.

Thus bone density varies with the zone, but within zones the spatial distribution of bone occurrences is in nearly all cases random and clusters are rare.

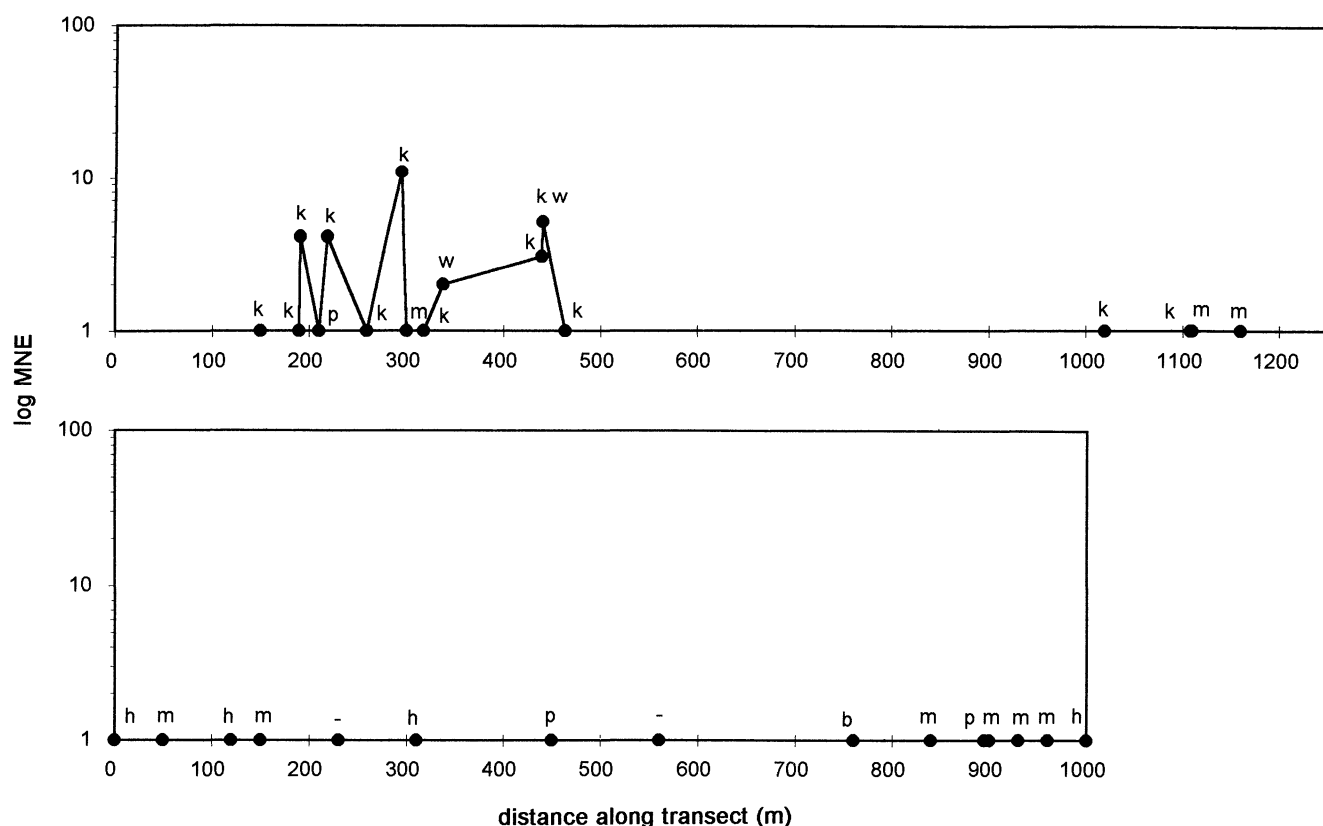


FIG. 5. Two low-density transects with nonrandom distributions of bone occurrences (patches and isolated finds): transect 10 (top), from the southern plateau, with a low-density "clump," and transect 33 (bottom), from the lake zone, with a more uniform distribution. Number of bones is presented in a log scale because otherwise the few individual animals whose bones have not been dispersed skew the graphs. b, *Syncerus caffer* (buffalo); h, *Hippopotamus amphibius* (hippo); k, *Kobus kob* (kob); m, unidentified medium-sized species; p, *Phacochoerus aethiopicus* (warthog); w, *Kobus ellipsiprymnus* (waterbuck); -, unidentified.

MINIMUM NUMBER OF INDIVIDUALS

Across the study area, 80.7% of the 343 bone patches contain the bones of a single individual; 16.6% have an MNI of 2 and 1.75% have an MNI of 3 (fig. 7). The predominance of single individuals is consistent with Behrensmeyer's observations in Amboseli, where no sampling quadrant of 20×30 m contained an MNI over 3 (1983:96). This supports the hypothesis that bone distribution processes result in random and possibly uniform rather than clumped distributions. This predominance of single individuals per patch is consistent across all zones. The valley zone ranks highest, with 100% of its bone patches showing an MNI of 1, but with such a small sample (5 bone patches) this is probably sampling error. In all the zones except the riverine and the lake between 79% and 85% of the patches have an MNI of 1. This concordance is remarkable because the bone deposition rate for the southern plateau is so much lower than for the plateau. By chance, much more overlap of individuals should occur in the plateau on the basis of density alone. The reason for this similarity may be the higher rate of scattering in the southern plateau, which would increase the relative rate of bone overlap from

different individuals. The lake and riverine zones have the highest percentages of bone patches with an MNI of more than 1 and the highest percentages with an MNI of 2 (one-third and one-quarter of patches, respectively). This also seems to be because of the great amount of scattering in these zones and occurs in spite of the low bone density. If one were to include smaller animals, such as fish, birds, rodents, lizards, turtles, and snakes, the overlap of individuals in a patch would be highest for the riverine zone.

Only three bone patches had 4 or more individuals. At the end of transect 17, around a large bush, was a patch of bones strewn in a doughnut shape with a diameter of 15 m and an MNI of 6. This patch had bones from 4 kob or reedbuck juveniles and 2 adult kob with a total MNE of 136. This patch probably formed through the repeated carnivore (especially lion) activity in the area, the bush probably serving at different times as an ambush site or as a divider for competing carnivores consuming carcass parts.

A patch under a large *Acacia siberiana* in transect 19 had an MNI of 5, including 2 adult and 1 immature kob, much of a mongoose still articulated by skin and tendons, and the weathered and splintered jaw and cranium

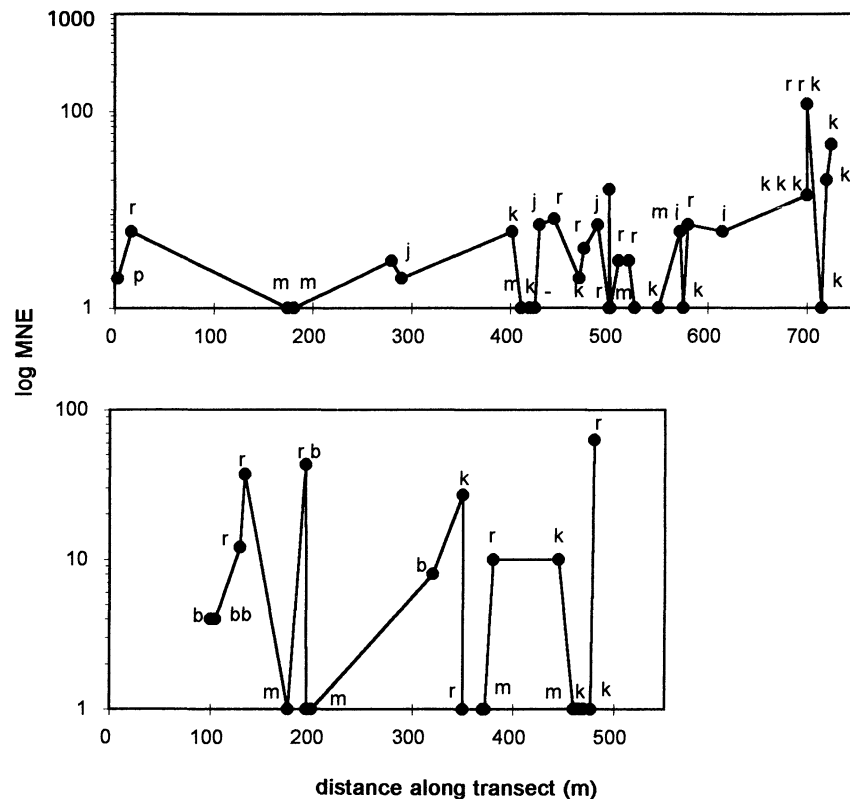


FIG. 6. Two high-density transects with nonrandom distributions of bone occurrences (patches and isolated finds): transect 25 (top), from the plateau, with a high-density clump of patches occurring around an isolated tree near 700 m, and transect 30 (bottom), from the hills. b, *Syncerus caffer*; j, juvenile kob or reedbuck; k, *Kobus kob*; m, unidentified medium-sized species; p, *Phacochoerus aethiopicus*; r, *Redunca redunca*; –, unidentified.

of a very old hyena. The presence in the patch of two rare species (mongoose and hyena) was clearly unusual, but the total number of surface bones was not unusually high (MNE = 12, not including the mongoose). This acacia tree is a good climbing tree with large horizontal branches that also provide shade. The fact that the individuals represented under the tree had a wide range of weathering stages (0–3/4) indicates that the bones accumulated over some time. It is likely that over several years carnivores made a series of visits, bringing bones to the tree. To find out if more bones were buried around the tree, vegetation was cleared completely and 21 1 × 1-m squares were excavated to 5–10 cm below the surface. Only a few additional bones were found, including 3 more kob bones within the first 3 cm below surface, 2 small rodent bones, a small falconiform femur, and 2 reedbuck long bones.

The third large patch occurred under an isolated large *Euphorbia* tree in transect 25. Initially, the bones of two individuals were found under the tree, but continued search revealed a total MNI of 5 on the surface. Surrounding this, within 20 m of the edge of the tree canopy, four additional bone patches were found: (1) 18, 10 m away, with an MNI of 3, including the bones of a juvenile reedbuck, an adult kob, and a very old kob;

(2) 20, 9 m away, with the remains of an adult kob; (3) 21, 20 m away, a kob neonate; and (4) 23, 6 m away, some bones of an old kob (total MNI = 6). An additional adjacent patch was of a poached waterbuck. Excavation under the tree revealed that buried bones were confined to the first 10 cm below surface. The presence of many isolated kob teeth indicates that bones were probably being destroyed in situ. Many small, unidentifiable fragments and long bone flakes were also found. The soil under the canopy in the bushes was very soft, promoting burial. A few test pits surrounding the tree indicated that bones were not being buried outside of the tree canopy.

This patch of patches appears to be a “predation arena” as hypothesized by Behrensmeyer (1983a, 1987), where repeated carnivore activity through time allows some bone concentration. There are several reasons that predation and/or bone transport are high around this tree. It is the only protection and shade for several hundred meters, and, located on a small rise, it is also a good vantage point for ambush. This rise in elevation makes it a very windy spot, and prey are unlikely to smell (or hear) predators if they are upwind of them here. During the course of excavation under the tree we had to shoo away a buffalo, and young kob and reedbuck came near

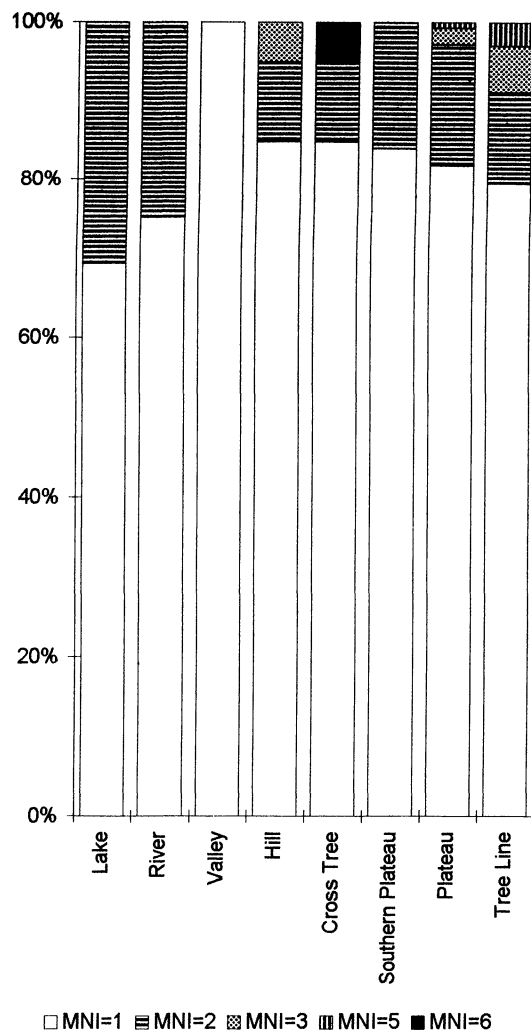


FIG. 7. MNI (1-6) per bone patch by zone (percent).

us much more than usual. It appears that these animals, who are normally very wary, did not smell us until they were quite close. This large isolated tree also fits Isaac's (1983) hypothesis of a "common amenity." The presence of poached waterbuck bones in a patch a few meters from the tree and a few poached bones under the tree itself indicates that the tree attracted both humans (poachers) and carnivores. It appears to be mainly a predation area of lions, but since the deaths and consumption of the ungulates represented were not observed, hyenas cannot be ruled out. The evidence for the predominance of lions in forming these patches is (1) lion claw marks all over the trunk of the tree; (2) lion footprints under the tree, indicating that lions were climbing it; (3) frequent sightings of lions in the area; (4) the killing of a kob by lions 25 m from the transect on which this tree is located while we were surveying; and (5) far more frequent sightings of lions than hyenas in the open plain.

SPECIES REPRESENTATION

Presence or absence and relative proportions of species are of primary importance for reconstructing paleoecology, but one cannot simply equate proportions and representations of living species in different ecological situations with fossil assemblages. The relationship between habitat preferences, the location of death, and the location to which bones are transported and/or destroyed was therefore examined for the different zones. Across the zones, six species account for the vast majority of the bone patches, and these species are also the most abundant in the living community. Species representation in the bone patches closely conforms to habitat preferences (fig. 8). Hippopotamus is the most common species in bone patches near the river and lake and is present in the southern plateau but is absent or very poorly represented in the other zones. Kob are present in all the zones and especially common in the cross-tree lines, tree lines, and plateau. These areas, several kilometers inland from the river and lake, are where one finds their largest herds. Reedbuck bones are most common in the hill and valley zones, where living reedbuck are abundant (Enama 1989). The habitat preferences of warthog are evident in their bone distribution (common in lake and riverine areas), although I expected more in the southern plateau. Bones of waterbuck are similarly abundant in their preferred zones, near the Bukukas and in the southern plateau. They are present in the riverine zone, though not in large numbers, and surprisingly absent from the lake zone. The high rates of destruction and scattering in the southern plateau and lake may have caused the dearth of warthog and waterbuck bones there. Buffalo usually roam as a single large herd over the entire area, spending more time in the southern plateau than elsewhere.

Table 6 lists the species present in the bone assemblages of each zone, including the smaller animals excluded from the bone density analysis and the species occurring as isolated finds. The fish, reptiles, birds, and microfauna included in this table are present in 54 bone patches (37 of which are fish). The riverine zone is the richest, partly because it includes aquatic species (hippopotamus, turtle, fish). Animals with low population densities are rare in the bone sample. Primates are completely absent from the surface assemblage sample, although small and scattered baboons and vervet populations are present in the living community. Other rare species, such as the sitatunga, bush pig, and duiker, are missing from the bone sample. Carnivores are also rare; the lion is absent from the bone sample, the leopard is represented by a single radius from the lake zone, and *Crocota* is represented by a cranium and mandible found under a tree in the plateau.

Number of species in archaeological assemblages has been shown to correlate closely with sample size (Grayson 1984). However, Cruz-Uribe (1988) has empirically demonstrated that the Shannon species diversity index does not correlate with sample sizes over 25 in Southern

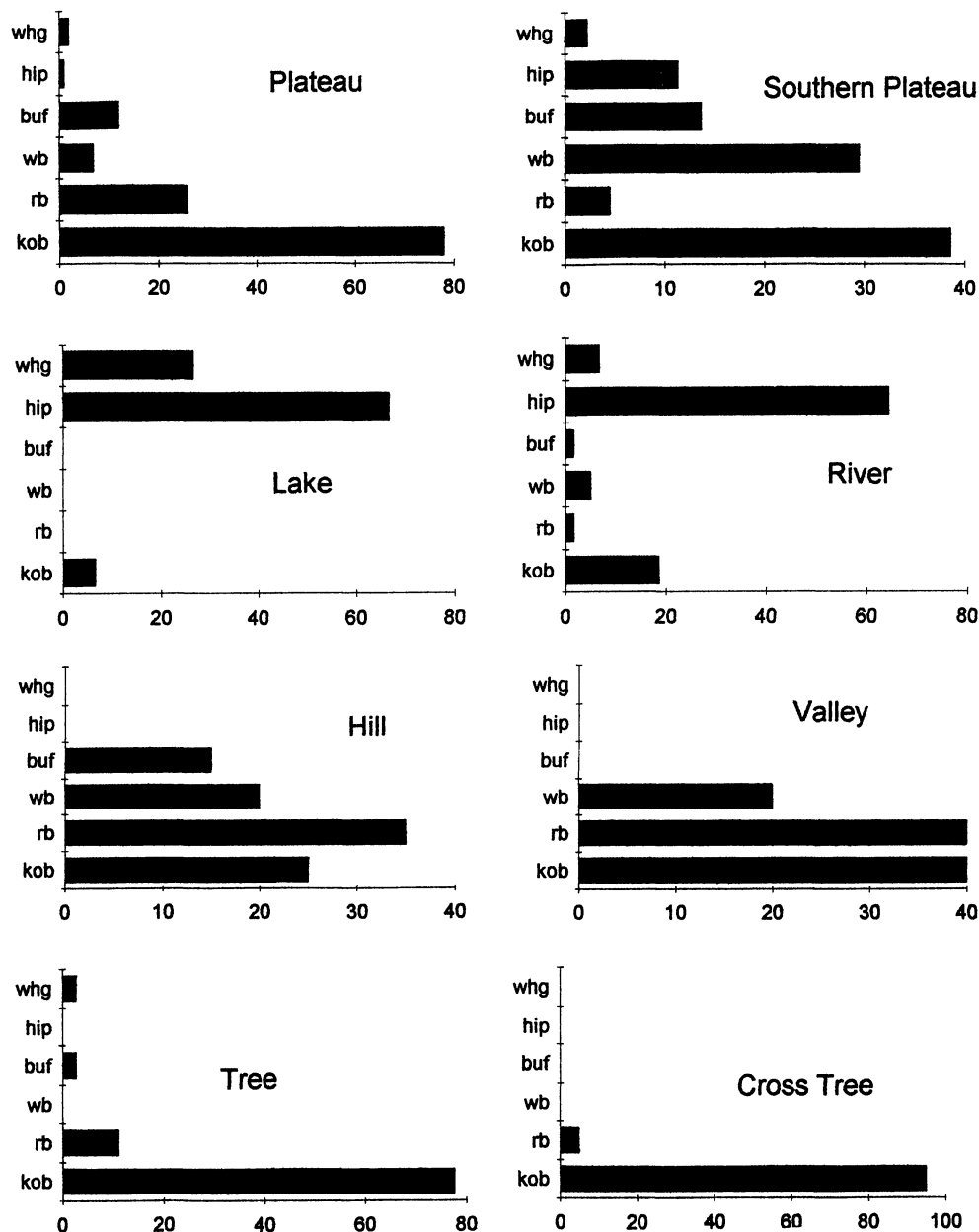


FIG. 8. Representation of the six most common species in bone patches by zone (percent). whg, warthog; hip, hippopotamus; buf, buffalo; wb, waterbuck; rb, reedbuck; kob, kudu.

African assemblages. Such diversity indexes take into account not only the number of species but also their relative abundance. The Shannon index was computed only for species found in bone patches, because the scattering in isolated finds would greatly inflate the apparent abundance of some species. The southern plateau has the highest index not because it has a large number of species but because they are more evenly represented than in the other zones. The hills and valley both have sample sizes under 25 (21 and 20, respectively) and so should be regarded with more caution.

Despite the fact that the study area is surrounded by

rain forest, no strictly rain-forest species were represented in the surface assemblage.

Ecological Effects on Bone Deposition

WATER

The least bone deposition *and* the most scattering occur near the lake and the river, the habitats in which fossilization is most likely to occur. However, if all of the northern sector were suddenly buried (for example, in an ashfall) and all the bones fossilized, archaeological

TABLE 6
Species Representation by Zone

Species	Plateau	Southern Plateau	Lake	River	Hills	Valley	Tree Line	Cross-Tree Line
kob	x	x	x	x	x	x	x	x
reedbuck	x	x	—	x	x	x	x	x
waterbuck	x	x	(x)	x	x	x	—	—
buffalo	x	x	—	x	x	—	x	—
bushbuck	—	—	—	—	x	—	—	—
warthog	x	x	x	x	—	—	x	(x)
hippopotamus	x	x	x	x	—	—	—	—
elephant	—	—	—	x	—	—	—	—
spotted hyena	—	—	—	—	—	—	x	—
leopard	—	—	(x)	—	—	—	—	—
mongoose ^a	—	—	—	—	—	—	x	—
cane rat ^b	—	—	—	x	—	—	—	—
rabbit ^c	x	—	—	—	—	—	x	x
turtle ^d	—	—	—	x	—	—	—	—
python ^e	x	x	—	—	—	x	—	—
lizard (monitor) ^f	—	—	—	x	—	—	—	—
lizard (chameleon) ^g	—	—	x	—	—	—	—	—
fish ^h	—	—	x	x	—	—	—	—
bird ⁱ	x	—	—	—	—	—	x	—
Total	9	7	7	10	5	4	8	4
<i>H'</i> (Shannon diversity index)	0.998	1.388	0.302	0.463	1.189	0.697	0.424	0.054

NOTE: (x), isolated finds only.

^a*Mungos mungo*.^b*Thyromys swinderianus*.^c*Lagamorpha* gen. et sp. indet.^dGen. et sp. indet.^e*Python*.^f*Varanus* sp.^g*Chamaeleo* sp.^hIncluding *Clarias*, *Tilapia*, *Bagris*.ⁱIbis (plateau) and gen. et sp. indet.

sites along the river and especially the lake would be relatively free of contaminating background bones, while the treeless plateau might contain accidental co-occurrences of stone and bone (figs. 9–11). This light bone deposition rate near water is contrary to the widely held view that water sources are often associated with large bone accumulations. This view is held for several reasons. For one, the majority of fossil sites are preserved because they were buried by flowing water. Time-averaging in fluvial situations is likely to be very high because of the reworking and redepositing of buried bones as the channel migrates (Behrensmeyer 1982a, b, 1983b, 1988, 1991b). In addition to this, bones are considered to accumulate gradually near water because of the biological interactions between carnivores and prey animals. In PNV large predators do not seem to hunt preferentially near water sources (personal observation and Verschuren 1972:48), and the tall grass inland allows lions to hunt just as effectively there as near water. Most of the prey animals also spend less time near the water. Although most do drink daily, they are very vigilant in the dense brush. In addition, in PNV droughts are rare, so concentrations of starved ungulates around water sources are rare or nonexistent. The riverine bone

deposition rate is higher than near the lake, probably because the large numbers of animals living on the plateau go there to drink. All the common ungulates are water-dependent.

In addition to the lake and riverine zones, six ephemeral water holes were searched for bones to examine if in this less dry environment they were magnets for predation and bone deposition as hypothesized by Binford (1983). These water holes are very small, ranging from about 350 m to 10 m in length. Because 1988 was a very wet year, they persisted the entire time we were there (June–December), which includes the main dry season; in July and August 1986 most of these water holes were absent. Four (numbers 2, 3, 5, and 6) were completely devoid of bones. At water hole 1, on the Holocene terrace very close to the Semliki River, large numbers of kob and reedbuck, warthog, and a few vervets were seen drinking daily, but no bones were found. Later a freshly dead reedbuck found half-submerged in it remained there for three days even though it was within about 200 m of a hyena den; finally, three juvenile hyenas were seen dragging it away, dispersing the limbs, which we found part-way down the ravine in which they den, and leaving no bones behind. Water hole 4 was the largest

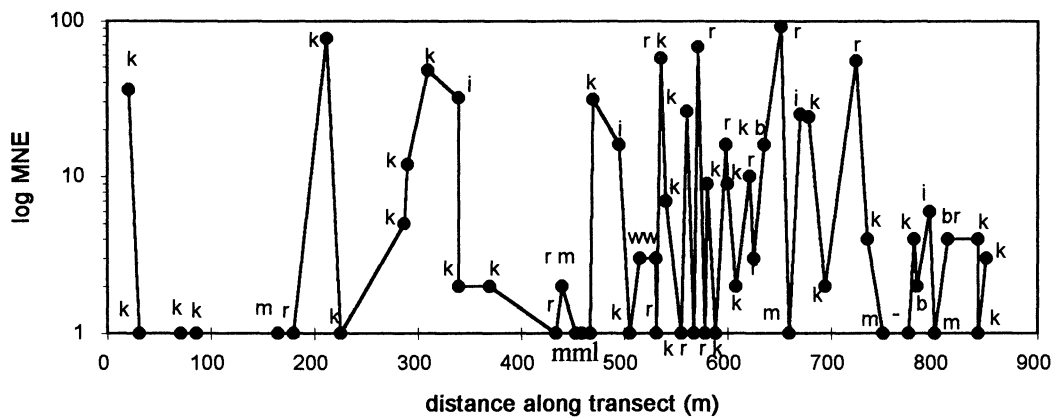


FIG. 9. Bone distribution in plateau transect 26, 5 km from the river, the densest transect in the survey. b, *Syncerus caffer*; i, juvenile kob or reedbuck; k, *Kobus kob*; m, unidentified medium-sized species; r, *Redunca redunca*; w, *Kobus ellipsiprymnus*; –, unidentified.

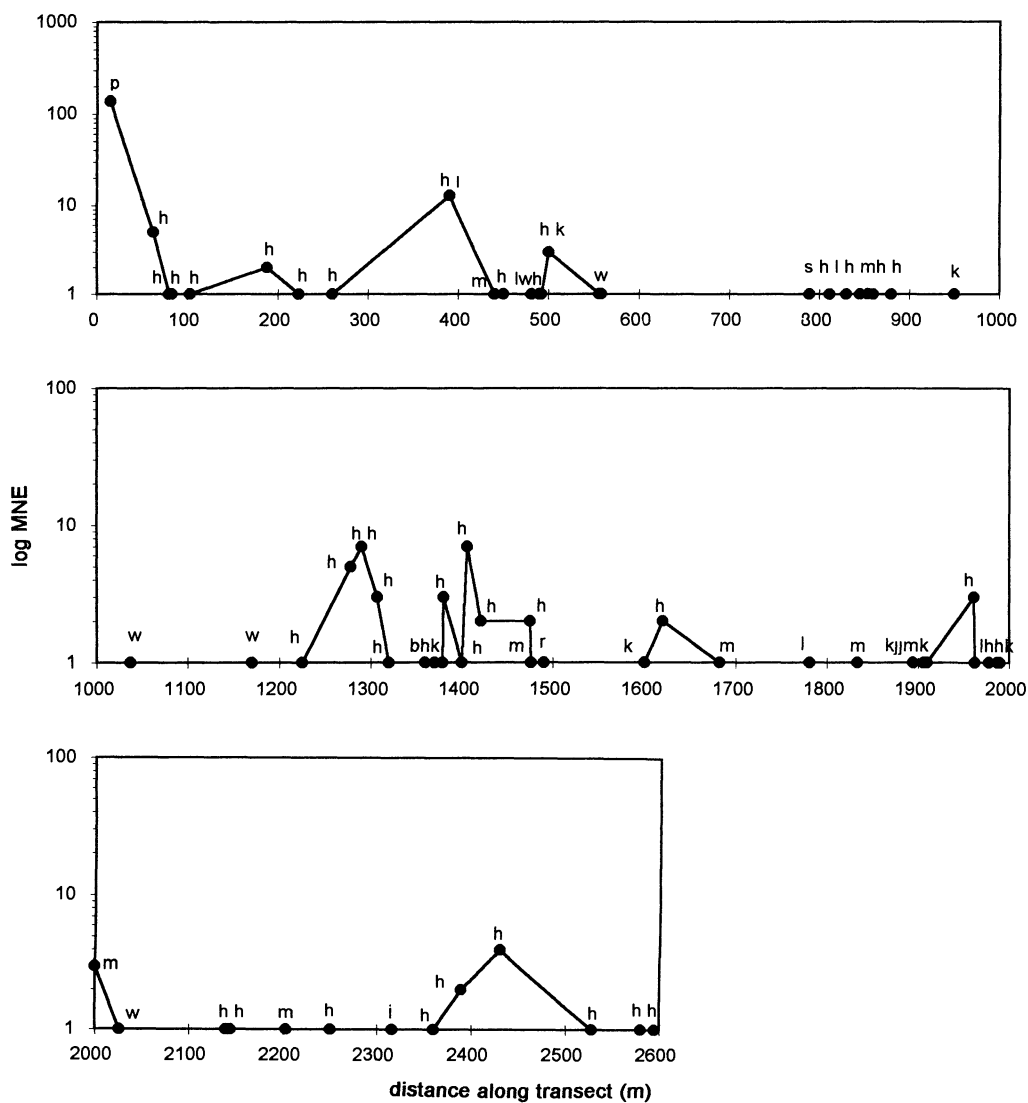


FIG. 10. Bone distribution in riverine transect 13. b, *Syncerus caffer*; h, *Hippopotamus amphibius*; j, juvenile kob or reedbuck; k, *Kobus kob*; m, unidentified medium-sized species; p, *Phacochoerus aethiopicus*; r, *Redunca redunca*; s, unidentified small species; w, *Kobus ellipsiprymnus*.

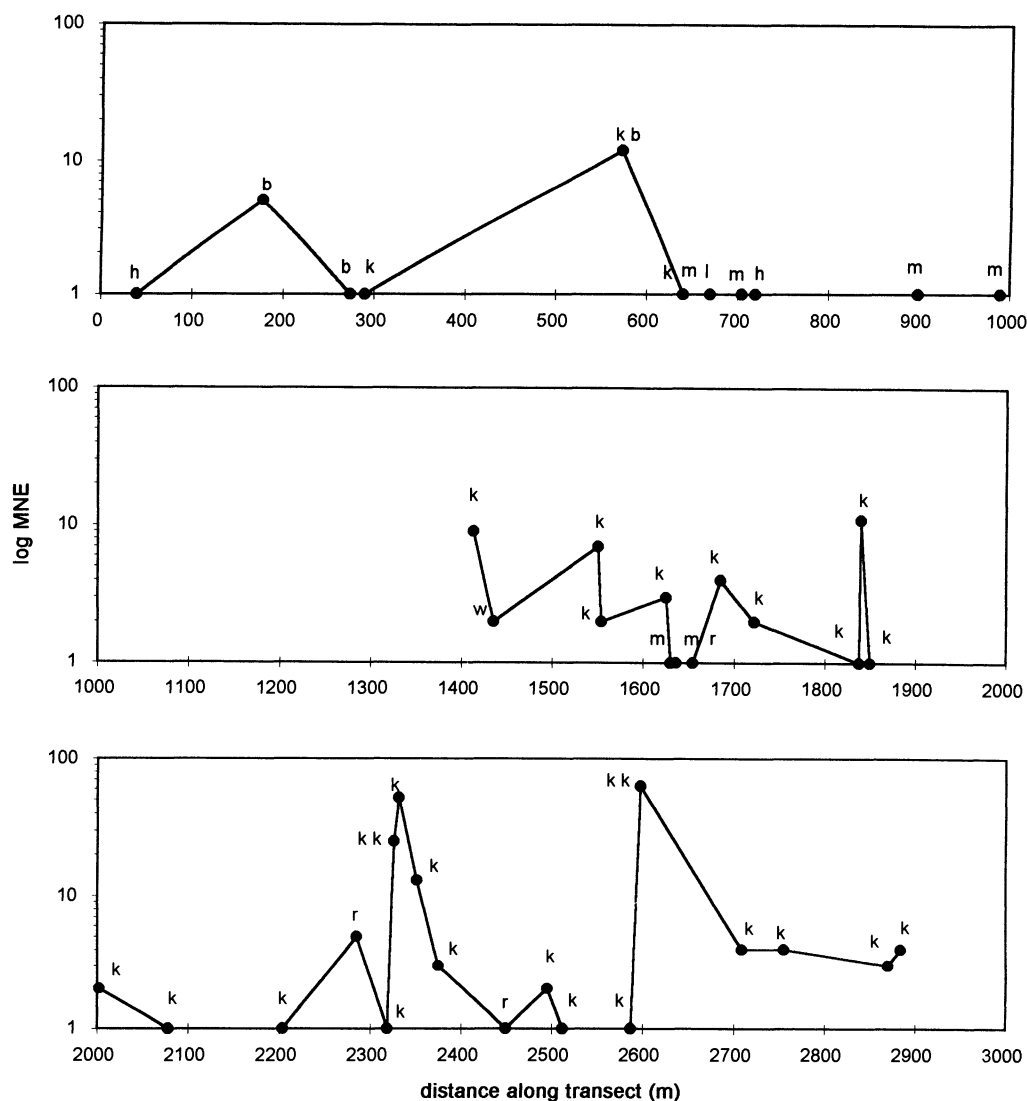


FIG. 11. Bone distribution in transect 3, from the river to 3 km inland. b, *Syncerus caffer*; h, *Hippopotamus amphibius*; j, juvenile kob or reedbuck; k, *Kobus kob*; m, unidentified medium-sized species; r, *Redunca redunca*; w, *Kobus ellipsiprymnus*.

examined, approximately 350×150 m, and was located on the slope about 1 km from the lake. Two isolated finds (a long bone flake and a deciduous kob molar) and one patch of two bones (a buffalo femur and tibia) were found in a 30-m-wide swath around this hole. The hole was surrounded by footprints of buffalo, primate (vervet or baboon), and hippopotamus.

Water holes are evidently not attracting large amounts of bone in PNV. Plentiful year-round water in the lake and river reduces the attraction for animals of any single one of these spots. All the water holes are, however, heavily used by the fauna. In drier years it is necessary to make the trek all the way to the lake or river; water holes reduce the amount of travel time required in relatively denser vegetation near the lake and river, where bovids are probably more cautious because of reduced visibility. Because of the abundance of available water,

no single source in PNV is able to attract animals from all around as occurs in more arid East and Southern African savannas. There is clearly no concentration of attritional bones around water holes in a relatively moist savanna such as at PNV, and for times and places in the past that may have been analogous to today's PNV in availability of water and vegetation cover Binford's (1983) water-hole hypothesis seems not to be supported by these observations.

Not surprisingly, rates of attritional bone deposition around a water hole may be significantly higher in drier climates or during a severe dry season or drought (e.g., Conybeare and Haynes 1984; Haynes 1985, 1988, 1991; Senzota and Mtahko 1990). Diagnostic criteria for identifying such an assemblage might include high rates of trample marks (depending on substrate [Behrensmeyer, Gordon, and Yangai 1986, Fiorillo 1989]) and a high pro-

portion of grazing species which obtain their moisture from water rather than browse (Western 1975). Positional characteristics such as might result from being stuck in mud may also be evidence for water holes (Weigelt 1989). An important point is that if there is such a fossil assemblage caused by attritional death formed around a water hole, its paleoenvironmental setting is probably not an environment analogous to Parc National des Virunga, and it may be evidence for a severe dry season or drought. Conversely, if paleoenvironmental evidence strongly indicates a wetter, less seasonal situation, attritional buildup of bones around a water hole is less likely to be an important site formation factor. The use of water holes as ambush sites by carnivores needs to be examined in more habitats, as there may be a critical ecological point (say, in dryness) at which the holes become significantly more profitable for hunting (and therefore bone buildup).

RAVINES

The large erosional ravines in PNV are a special subhabitat relevant for three main reasons. First, the microenvironment is densely wooded; a large ravine near Ishango is even referred to as a forest by Sept (1990), who studied its vegetation. This habitat includes some species with closed-vegetation preferences (for example, forest hog and bush pig) and so might be expected to have some different species in its attritional bone assemblage. Second, ravines form adjacent to main sources of water. The high rates of erosion from the ravines into the main bodies of water could be a potentially important source for input of bones into the fluvial environment. The third taphonomically relevant feature of ravines is the frequent denning of hyenas in them.

Active erosion in the ravines is apparent. Ravines are being cut back, getting larger and larger at their heads. Many are straight-walled, tens of meters deep, and range from short (tens of meters) to long (several kilometers). The large ravines rush with water when rainfall is high, and the bottoms are flat, with loose, fluvially deposited sediment and little vegetation. Large collapses of the walls are common, and presumably many dens, along with their inhabitants and any bones inside, are buried in this way.

Several ravines, some wide cuts near the Ishango Park station, and four smaller ravines just north of Senga were surveyed for bones. Only one north of Senga contained bones, and this one also had two hyena dens.⁶ I did not enter the dens because they were occupied and den bone accumulations are not the subject of this study, but there were hyena feces at the top of the ravines in this area, and on the trails entering the ravine with the dens there were hyena feces, long bone flakes, and digested bone fragments. This is where the legs of the reedbuck found dead in water hole 1 were deposited.

6. A hyena den was also located in the cliff below (and to the west of) the Ishango Park Station but was extremely difficult to reach and was not explored extensively.

The low rate of bone deposition in the ravines, with the possible exception of the hyena dens, probably reflects the infrequent use of these areas by the herd animals that are the main bone producers in the park. Bones may also be removed or buried during flash floods. The large number of hyena dens in the ravines could of course be visible in the fossil record if they stopped eroding and became buried. Such locations for dens could also be a significant contributor to the assemblages of bones in the fossil record presumed to have been accumulated by fluvial processes (see Behrensmeyer 1987) and an attritional source for bones entering the river through flowing water during storms.

TREE DENSITY, PREY, AND PREDATORS

The location and density of trees has one of the strongest influences on bone deposition in PNV. The southern plateau, with a high tree density, has a much lower density of bones than the more open plateau. This is because the major bone producers in the area, kob and reedbuck, prefer open areas and are vulnerable to predation in their habitual grazing areas. As we have seen, bone deposition closely reflects the distribution of living animals. The species producing the most bones congregate in the open habitat of the plateau near the Bukuka Hills and are less common near the river, the lake, and the southern plateau, where tree density is higher. These bovids are grazers, and the open grassland is where their food grows. The relative abundance of *Themeda triandra* and *Hyparrhenia* spp. increases away from the lake and river, where *Sporobolus* is more abundant (Tappen 1992). Hippopotamus grazing near the water may actually increase the abundance of *Sporobolus* (Field 1968), and the kob and reedbuck may be avoiding these areas because of this habitat modification by and food competition with hippopotamus. Other factors, such as availability of soil nutrients and the distribution of other grass species (McNaughton 1988, 1990), may be involved.

The lions distribute themselves near their main food supply, kob, and dominate the open areas, which therefore have heavier bone deposition. Within the plateau, however, they tend to draw bones to trees, preferring to consume their kills in the shade (fig. 12). Isolated small patches of trees, which in PNV usually occur as tree lines, provide shade, refuge, and ambush points for the lions adjacent to the kob. The combined average bone density for the tree lines and the adjacent or perpendicular transects is the same as for the plateau as a whole; the concentration in tree lines is a local effect. In other words, bone deposition rates are about the same as in the surrounding plateau, but they are depleted from the area immediately surrounding trees and deposited in the tree lines. Thus it seems that the bovids are being killed at about the same rate near the tree lines as in the open but some bones are transported to the tree line if the kill is near it. In the southern plateau, where there are 15 or 20 trees per hectare, the ungulate population is small and therefore the lion population is small and

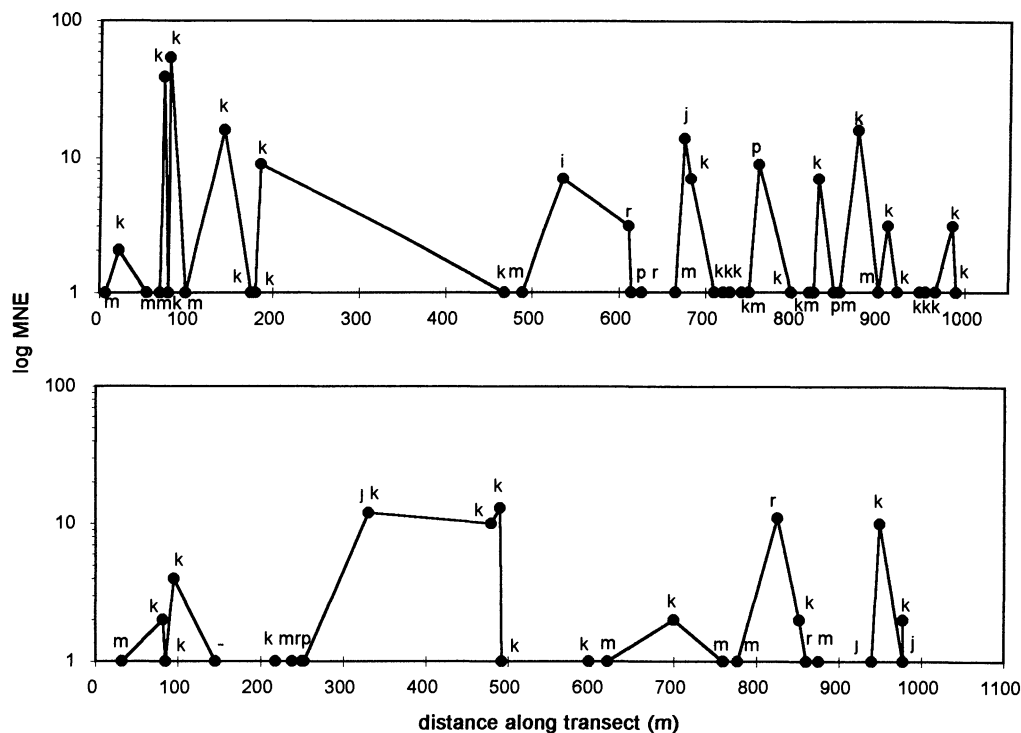


FIG. 12. Bone distributions in transects from a tree line (transect 15) (top) and a cross-tree line (transect 16) in the open plateau 300 m away (bottom). j, juvenile kob or reedbuck; k, *Kobus kob*; m, unidentified medium-sized species; p, *Phacochoerus aethiopicus*; r, *Redunca redunca*; –, unidentified.

there are more hyenas. Consequently, bone deposition is light. In contrast, in open areas (the plateau has on average fewer than 5 trees per hectare) the resident herds of kob and reedbuck provide a consistent and reliable source of food for the lions. The relatively large number of bones in the lions' main area compared with that in the hyenas' makes sense in terms of the lions' lesser ability to consume bones and is consistent with findings in the Serengeti, where lion-dominated habitats have more bones and carcasses (Blumenschine 1986a, 1987, 1989).

The hyenas traverse the entire study area, but they are clearly based in the bushy treed habitats of the southern plateau, lake, and riverine zones. In addition to the abundance of denning sites, the intense competition between the hyenas and the lions on the plateau surely contributes to their preference for these zones. In these habitats bone density is low, bone patches are small, and scattering is high. The well-known intense exploitation of bones by hyenas may be the main cause of the high degree of bone scattering and destruction in these areas. These parameters are intermediate in the area where lions predominate, and in the Bukuka Hills, where it is believed leopards are common, patches of individual animals have more bones and are less scattered.

The high rate of bone deposition in the bush and tree lines on hilltops seems to result from similar processes as seen for the tree lines elsewhere. The tops of some of these hills have dense vegetation, again providing secrecy and protection for carnivores consuming carcass

parts. Evidently, it is the dense vegetation on top of these hills rather than simply topography that leads to high bone deposition rates here. This hypothesis is supported by evidence from transect 1; unlike the other transects running over the hills, it ran east-west along the steep banks of a hill with no trees whatsoever, and this portion contained no bones. The open, steep hill-sides have very few bones compared with the densely vegetated hill crests. In addition to a higher overall number of bones, the hilltops have significantly larger numbers of bones per patch, suggesting less scattering and perhaps less hyena activity.

I suspect that in addition to the treed habitats near the lake and river, leopards may favor the Bukuka Hills as they do the kopjes in the Serengeti. The presence of the elusive leopard is generally made known by its spoor, and this spoor is more obvious near the river and lake, where the ground is more often bare and soft. However, many trees in the Bukukas have leopard scratch marks on them (Leith Smith, personal communication). This evidence of leopard activity may explain the higher bone density, as bones would be scattered less. Additionally, the high percentage of reedbuck in the hills' bone patches is consistent with the interpretation that leopards deposited much of the bone here, as leopards have a smaller prey-size than the social-hunting lions and hyenas. Since leopards are solitary creatures, eating and hunting alone, they do not need to transport carcass parts away from competitive conspecifics as do lions and hyenas. At the same time, their tendency to stash prey

in trees (Brain 1981, Cavallo and Blumenshine 1989) is certainly an adaptation for guarding their kills against scavengers, and it would concentrate bones in the tree-lines of the hills. The leopards near the lake and the river would also be expected to create larger bone patches because of less scattering and less destruction, but this is not the bone deposition pattern for these zones. It appears that the overprint of hyena behavior masks the predicted leopard pattern here. There may also be areas near favored hyena spots along the river and lake where leopards are excluded because of competition, but sightings and footprints indicate that leopards are not rare in this area.

Thus, the distributions of both the prey and the predators in a living animal community leave a strong impression on the distribution of bones in PNV's northern sector. Habitat preferences of both predator and prey are clearly reflected in the character of the bone deposition, and these preferences are closely tied to tree density and distribution.

Comparisons with East Africa

Understanding the relationship between bone deposition and ecology in PNV may be interesting and useful, but comparison with other ecosystems should provide the deeper understanding required for interpreting the past. An initial overview directed toward this problem is presented in table 7, where the bone deposition rate for the PNV survey area is compared with bone-density data from other surveys. What are the causes of the similarities and differences, and are there any correlations

with interesting ecological variables? We might expect there to be correlations, considering that factors affecting attritional bone deposition in most areas are probably qualitatively similar. The relationship of the main variables is $R = (hmn) - (d + b)/a$, where R = annual number of bones added to the surface per km², h = number of herbivores (bone producers), m = annual mortality rate, n = number of bones in an animal, d = annual number of bones destroyed (by carnivores, weathering, trampling), b = number of bones buried, and a = area in km². Carnivores are effectively present in the equation twice, as major influences on mortality and as bone destroyers. Not all these variables are known for any of the environments that have been examined for attritional-death bones, but the best-known, because of extensive ecological and census studies conducted over the years, are Amboseli, PNV (northern sector), the Serengeti, and Ngorongoro Crater. A comparison of bone-counting methods indicates that in all these studies bones were tallied in similar ways (using MNE). Recovery rates during survey could have had some effect on bone counts, but this is difficult to assess (Tappen 1992).

PNV (northern sector) has the highest bone densities, Amboseli has 30% less, and bone density at the Serengeti and Ngorongoro is an order of magnitude lower. The similarity of PNV and Amboseli is at first glance surprising, because these are in several ways the most dissimilar ecosystems and Ngorongoro Crater and PNV the most similar. PNV and Ngorongoro have similar amounts of annual rainfall (although they differ in degree of seasonality) and no migratory species. Amboseli is very dry, with a wet-season dispersal and a dry-season concentration of ungulates (Western 1975). The Ser-

TABLE 7
Bone Density in Four Savanna Parks

	MNE	Area Surveyed (km ²)	Bone Density (km ²)	Medium-sized Mammal Biomass (kg/km ²) ^a
PNV				
Northern Sector	5,151	2.11	2,441.23	3,030
Ishasha	165	0.0763	2,162.5	—
Amboseli	14,687 ^b	8.75	1,678.51	2,255 ^b
Serengeti	986	4.299	229.42	4,222 (total), 1,568 (resident)
Ngorongoro	250	2.475	101.01	10,363
Lake Eyasi	1,200	2.264	530.03	—

SOURCES: For PNV, Mertens (1983), with a rough estimate for warthog and reedbuck; for Amboseli, Behrensmeyer and Dechant-Boaz (1980), Behrensmeyer, personal communication, May 1992, and (for biomass) Western (1973:table 6), which is based on 12 aerial censuses around the seasons of the dry-season concentration area and therefore takes seasonality into account; for the Serengeti and Ngorongoro, Blumenshine (1989) and (for biomass) Schaller (1972:428–29); for Lake Eyasi, Bunn, Kroll, and Bertram (1989); for Ishasha, Sept (1994a).

^aElephants, hippos, and rhinos are excluded because their weights skew biomass and their low turnover rate means a relatively small contribution to bone deposition (Tappen 1992).

^bExcluding domesticated cattle, which inflate both biomass and number of bones.

engeti, of course, is dominated by migratory ungulate herds (Sinclair and Norton-Griffiths 1979).

Large-mammal biomass seems likely to be one of the most important variables in the attritional-death bone deposition equation and one of the most useful ones we might reconstruct for the past. Biomass is strongly correlated with rainfall in African savanna ecosystems ($r = 0.877$ for large-herbivore biomass and mean annual precipitation [Coe, Cumming, and Phillipson 1976:348]), but this correlation breaks down with the existence of permanent water, which allows biomass to be much higher than rainfall predicts at Amboseli and PNV. Thus annual rainfall alone cannot be used to predict bone deposition rates for these four parks (Tappen 1992). A straightforward correlation between biomass and bone density is difficult even for these relatively well-studied parks. Problems include fluctuation in animal populations due to natural and anthropogenic factors and differences in the timing of the bone surveys and the animal censuses. For example, for the PNV northern sector some animals were censused in the early 1980s and later, but their populations have clearly changed even since then (see Mertens 1983, 1985; Delvingt 1978; Enama 1989; Verschuren 1986). Rapid fluctuations and censuses based on only some species make it difficult to produce an accurate estimate of the PNV northern-sector biomass. In addition, correlations with bone density would be confounded by the presence of large animals (elephant, hippopotamus); although they may be overrepresented in surface bone assemblages (because of slower rates of destruction), they increase biomass even more while retaining the same number of bones as smaller animals. The PNV study area probably has a medium-sized mammal (prey-sized) biomass near 3,000 kg/km², based on a 1981 census (Mertens 1983), although this did not include some common species such as warthog and reedbuck, and a 1990 buffalo census by Averling (personal communication). It may be a bit higher because of recent increases in kob and reedbuck populations (Enama 1989).

A comparison confined to medium-sized herbivore biomass shows that bone deposition does not increase with published biomass estimates (table 7). For example, Ngorongoro Crater has the highest biomass and the lowest bone deposition rates. For the Serengeti, it may be more realistic to use total resident biomass plus a portion of the migratory biomass rather than total biomass, as 73% of the medium-sized herbivores are migratory. Serengeti total biomass is the second-highest of the parks (though resident biomass is nearer the range of PNV and Amboseli), yet it has only a fraction of the bone deposition of these two parks. Amboseli and PNV, however, have similar medium-sized mammal biomass and similar bone densities. In fact, the MNE per km² is 0.756 and 0.744 per kg of biomass for PNV and Amboseli respectively (Tappen 1992).

In addition to biomass differences there are differences in mortality between the parks. In the Serengeti and Amboseli there is dry-season attrition caused by starvation, lack of water, and, for the wildebeest, drowning

while crossing rivers during the migration. This can cause a seasonal glut in carcasses that would only incompletely be consumed by carnivores (Western 1980, Blumenshine 1987). This type of mortality is not found in PNV. Predation rates may also differ, as may the proportion of large carnivore species. Blumenshine has suggested that the absence of bones in various environments in Tanzania is related to large numbers of hyenas that destroy and disperse bones and that areas with lions have greater bone deposition. Estimates of predator and prey ratios for the parks in question (table 8) show no simple relationship. Predators increase bone deposition but are also great bone destroyers. The rate of bone destruction will increase as the density of hyenas relative to prey increases because of increased competition and consumption (Blumenshine 1985). Unfortunately, there are no censuses available for number of hyenas in PNV, and the estimates in table 8 are only educated guesses.⁷ Ngorongoro is famous for its large numbers of hyenas, and Kruuk (1972) noted that predation pressure on ungulates is higher there than in the Serengeti, resulting in earlier maturation rates of wildebeest. No simple linear relationship between these predator-prey ratios is evident.

Other factors in the bone deposition equation may have effects on bone deposition rates but are likely to be less significant than biomass and prey:predator ratios. For example, bone weathering rates appear to be similar (Tappen 1994). Some factors do show substantial differences; for example, PNV was found to have more than twice the burial rate of Amboseli (Tappen 1992). Equids, which have fewer bones than bovids, also make up a substantial portion of bone deposition at the East African sites and are not present in PNV.

Although bone densities on the modern landscape are patterned by the same ecological variables that we may want to reconstruct for hominid habitats, such as large-mammal biomass and predator density, data from the four parks compared here indicate that such relationships are very complicated and difficult to interpret. Studies of bone deposition patterns and ecology in other parks would probably help elucidate the relationships of some of these variables. Computer modeling of nonlinear relationships such as the increase in competition between carnivores as they increase in number might also be useful.

Within-Park Variation

The results of several published surface bone density studies are presented in figure 13. Although habitats were not all defined in exactly the same way, some information can reasonably be gleaned from such a comparison. No single type of microenvironment (e.g.,

7. For the study area, my guess is that there are approximately 0.5 hyenas per km², perhaps between 25 and 100 individuals. This is fewer than at Ngorongoro but many more than in Amboseli or the Serengeti.

TABLE 8
Prey and Predator Numbers and Proportions (Individuals/km²) at PNV, Amboseli, the Serengeti, and Ngorongoro

	Prey/km	Lions/km ²	Prey:Lions	Hyenas/ km ²	Prey/Hyena	Hyena + Lion/km ²	Lion:Hyena	Prey: Predator
PNV	~19.0	0.13–0.25	76.0–146.0 ^a	0.25–0.5	38.0–70.9	0.38–0.75	?	25.3–50.0
Amboseli	11.5	0.083	160.0	0.16	83.12	0.243	0.5187	54.7
Serengeti All	37.5	0.086	436.0	0.12	312.5	0.206	0.7166	182.0
Resident	10.1	0.086	117.4	0.12	84.16	0.206	0.7166	49.0
Ngorongoro	91.0	0.26	350.0	1.7	53.5	1.96	0.1529	46.4

SOURCES: For PNV, lions based on 13 seen at one time and considered a minimum; number of hyenas estimated; for Amboseli, Western (1973:177); for Serengeti and Ngorongoro, Schaller (1972) and Kruuk (1972).

^aBourlière (1965) estimated 326 prey per lion in the savanna portions of the park, but populations have fluctuated greatly since then.

woodland versus grassland, near water versus away) consistently has higher bone densities than any other. Amboseli, Ishasha, and the PNV northern sector all have more bones in their grasslands than in more wooded areas, but the opposite is true for the Serengeti. Both Zairean sites have fewer bones near water, but at the Serengeti there are more bones in the riverine area. Amboseli has highest bone deposition in the swamp and much less in the lake bed. These differences in bone deposition by microhabitat reflect differences in the location of the highest prey biomass and the distribution of carnivores within each park. For the East African sites, the location of dry-season deaths is also influential (Behrensmeyer and Dechant-Boaz 1980).

Discussion

TAPHONOMY AND PALEOENVIRONMENTS

The attritional-death bone assemblage from the PNV northern sector has several implications for paleoenvironmental interpretations. It is in accord with Behrensmeyer's (1981) discovery in Amboseli of a very high correlation between the habitat preferences of species and their location and representation in modern surface bone assemblages. The PNV pattern is similar to that of Amboseli but with different habitats and species. This study strengthens our confidence in the robustness of this observation and in its general applicability. Paleosols representing ancient land surfaces should represent very specific subhabitats of the ancient ecosystem. The proximity of forest to the PNV northern-sector savanna is not in any way represented in the surface bone assemblage, and this raises questions about the association of rain-forest species with savanna dwellers in the Neogene fossil record of Africa. If the bones at such sites are autochthonous, there are several possible interpretations: (1) that the vegetation may have changed in situ with the succession of a new community, for example, a forest moving in where a savanna once was, with the

bones of species from the new community being added to that of the old (making the assemblage a time-averaged one [Behrensmeyer 1991a]); (2) that community structure was different in the past, and species that are not found together today were once sympatric; and (3) that a gallery-forest bone accumulation may include savanna and forest species. In a recent study of bone deposition in the gallery forest along the Ishasha River, Sept (1994) found only savanna-dwelling species, except for the giant forest hog. Additional landscape bone deposition studies in gallery forests are needed to provide information about the relative proportions of forest versus savanna species in this context.

Comparison of PNV bone-deposition densities with those from other environments indicates that although ecological and taphonomic principles must be driving these systems, the factors are complex and interrelated. Rainfall, biomass, and predator:prey ratios have not yet been shown to predict bone densities. Better data on the living ecosystems and bone deposition are required.

CLUMPING AND SITE FORMATION

Bones are preferentially deposited in certain zones in PNV, being especially common in open, grassy plateau areas away from permanent water. *Within* any given zone, however, bone patches are typically small, consisting of isolated occurrences or only a few bones that are almost always distributed in a random fashion. There are few situations in which bones from attritional deaths accumulate to form large patches that would imitate the densities seen in archaeological sites. Even time-averaging simulations predict relatively low densities (Behrensmeyer 1983a). The research presented here, in a savanna very different from that of Amboseli, is in agreement with Behrensmeyer's observations in that most bone patches are small and few patches overlap with the bones of more than one individual. However, 20% of the bone patches in PNV do contain an MNI of 2 or more, and several contain 3 or more. Also, PNV

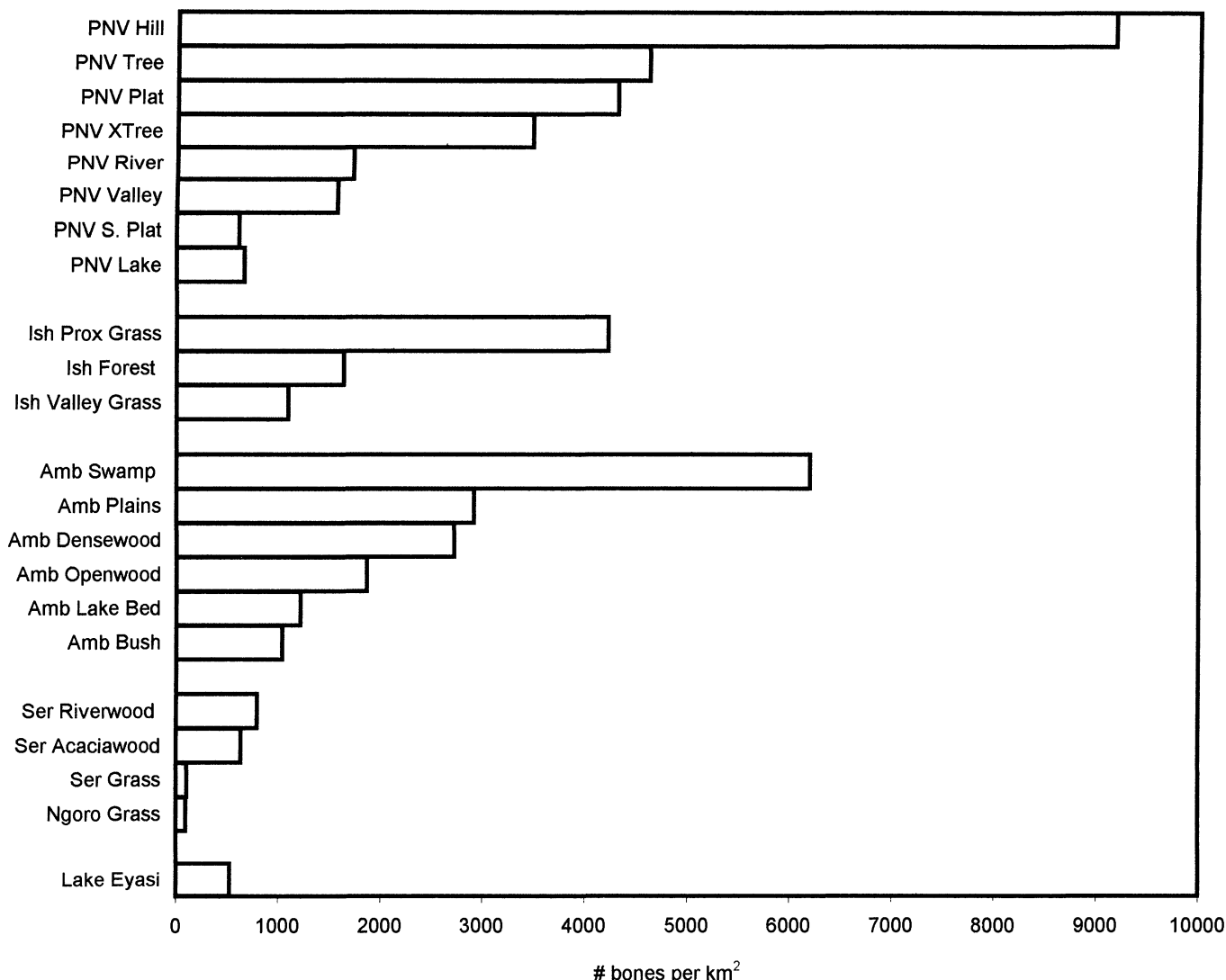


FIG. 13. MNE per km² in various habitats of East and Central African parks. PNV, Parc National des Virunga, northern sector, zones identified in this study; Ish, Ishasha River, proximal grassland, galley forest, and valley grassland (Sept 1994a); Amb, Amboseli, swamp, plains, dense woodland, open woodland, lake bed, and bush (Behrensmeyer and Dechant-Boaz 1980); Ser, Serengeti riverine woodland, acacia woodland, and grassland (Blumenschine 1989); Ngoro, Ngorongoro Crater grassland (Blumenschine 1989); Lake Eyasi, Hadza hunting area (Bunn, Kroll, and Bertram 1989).

has a higher burial rate than Amboseli (Tappen 1992), indicating perhaps a greater likelihood of time-averaging or a greater percentage of bones potentially surviving to become part of the fossil record.

The probability of palimpsests of artifacts and behaviorally unrelated fossil bones has been a nagging problem for archaeologists attempting to interpret Plio/Pleistocene archaeological occurrences of stone and bone (e.g., Isaac 1983, 1984; Bunn 1982; Potts 1988; Stern 1991, 1993). Binford (1981, 1983) has contributed to this concern by suggesting that the probability of such palimpsests is very high. About 1% of the total area across the PNV landscape is within bone patches. If these patches are randomly distributed and if one adds a random distri-

bution of artifacts, the probability of a simple overlap will depend on the density of artifact patches and the manner in which they are scattered. In a scenario in which artifacts are as common as bones (i.e., stone tool patches take up 1% of the landscape), the probability of overlap in a random distribution would be on the order of $0.01 \times 0.01 = 0.0001$. Of course, stone tools are probably not randomly distributed across the landscape (e.g., Isaac 1980, 1981; Stern 1991, 1993), and there are a few situations (predation arenas) in which cumulative bone deposition is also clumped. At sites as large as FLK Zinj there must have been a feature of the landscape that focused activity there (Laden and Brooks 1994).

As a heuristic device, Isaac (1983, 1984) defined four

site types: A, concentrations of artifacts without bone; B, the bones of a single large animal and associated artifacts; C, larger concentrations of artifacts intermingled with the bones of many animals of several species; and M, bones with stone-tool-caused modifications but without stone artifacts. If an attritional-death bone patch did “accidentally” overlap with a stone tool occurrence, it would much more likely look like a type-B site than like a type-C site. Type-B sites are usually interpreted as kill or at least butchery sites (Isaac 1983, 1984; Crader 1983). They are more likely to be a fortuitous association of stone tools and bones than the other site types simply because single-animal bone patches make up 85% of attritional-death bone assemblages. Therefore, these sites especially need confirming evidence of hominid bone modifications, such as cut marks, to establish the behavioral link between the bones and artifacts.

The vast majority of attributional bone deposition is not in dense patches and so is more realistically compared with the ancient “scatter between the patches” (*sensu* Isaac, Harris, and Marshall 1981), the “background” scatter of artifacts and bones between sites, than with the patches (archaeological sites) themselves. Early Stone Age archaeological sites from Olduvai Gorge, Tanzania, and from East Turkana, Kenya, usually have bone densities from over a hundred to several thousand bones per 100 m² (Potts 1988:table 3.2; Stern 1993:table 2). The average “scatter” bone density on the surface of the Lower Okote Member between Fxj 20 and Fxj 37 was 4 per 100 m² (Stern 1991:table 8.1), ranging from 0 to 15 per 100 m² (Stern 1991:347), depending on depositional environment. Stern argues that the scatter of bone in the Lower Okote Member was deposited over a period of 90,000 years and is therefore not equivalent to a cumulative bone assemblage such as the one studied here. The mean “scatters” density as calculated by Stern would be 400 bones per hectare, over four times higher than represented in the highest-density zone found in PNV (the Bukuka Hills) and two and a half times the density of the densest individual transects. Furthermore, the Okote scatters’ bones tend to be hard, durable elements of high density, indicating that the assemblage is the remainder of a larger assemblage that went through severe taphonomic destruction (Stern 1993:211). Had the destruction been less severe, bone densities presumably would have been even higher. The bone densities in the Lower Okote Member are much higher than normal attritional-death bone deposition at PNV, Amboseli, or other areas studied. This is consistent with Stern’s interpretation that they in fact are time-averaged and are not analogous in a straightforward way to modern short-term surface bone assemblages. One expected difference is that fossil assemblages will contain elements more likely to be buried quickly while modern surface assemblages will contain more bones that are buried more slowly. Modeling long periods of time and specific skeletal-element burial and destruction rates on the basis of actualistic data is the next step in comparing paleontological and actualistic scatters of bone, as one cannot

simply multiply the PNV landscape assemblage by some number to get something comparable to the Okote paleontological “scatters” assemblage. It would be useful for more fossil data to be collected in rigorously controlled stratigraphic levels and for the reporting of bone densities to become routine, as is increasingly the case with regard to early hominid strata in East Africa (Potts 1989, Blumenschine and Masao 1991, Stern 1993).

The taphonomic processes affecting a bone after deposition, during burial, diagenesis, and especially postfossilization reworking and transport, are obviously important in shaping the paleontological record and need to be incorporated into models of its formation. Bones found in paleosols should be autochthonous—at or very near their original location of deposition (Behrensmeyer 1982b)—and at worst time-averaged, but in most soil conditions there will be continuous breakdown of bone through chemical and biological processes even after burial. Stone tools are much more likely to be time-averaged than bones. In most situations bones need to be rapidly buried to avoid destruction through weathering, and the continuous or quasi-continuous burial (by sedimentation) through time required for time-averaging will allow minimal soil formation. Although the depositional hiatus represented by a paleosol may be thousands of years long, the bones that may become fossils in this situation will probably represent only a portion of that hiatus—a much shorter period of time just prior to the burial of the soil (Behrensmeyer 1982b)—while the stone tools will represent the entire time span (Stern 1993). Models of site formation should incorporate more time averaging for stone tool distributions than for bones in subaerial situations.

IMPLICATIONS FOR SCAVENGING MODELS

If the distribution of bones across the landscape can be used as an indicator of the distribution of scavenging opportunities (e.g., Blumenschine 1989), then PNV exhibits a very different pattern from the Serengeti. This is largely because in the Serengeti the woodlands are lions’ preferred habitat because of greater hunting success in the taller grass near the trees and bushes that are often near rivers and the presence of resident prey providing a stable food supply (Schaller 1972). Because lions leave more food behind after eating than do hyenas, woodland and riverine areas will provide more scavangeable food according to Blumenschine’s model. In the savanna of PNV, grasses are taller and evidently dense enough to provide lions with enough cover to hunt successfully away from the river, where their favorite prey, the Uganda kob, is habitually located. It is there, in the open grassland, that more bones, more carcasses, and more scavenging opportunities are found (Tappen 1992). Thus availability of scavenging opportunities is not *always* better in wooded areas near water, and we should be cautious in applying this as a simple ecological rule (e.g., Blumenschine 1987). Instead, there may be more scavenging opportunities for hominids where lions dominate the landscape and fewer where

hyenas do, as is noted by Blumenschine for the Serengeti and here for PNV. If the dominant carnivores (today usually lions when numerous enough) choose to be in the areas with the densest or most predictable prey biomass and are not bone destroyers, such areas will provide the most scavenging opportunities. More work on these habitat preferences in a variety of environments is needed to test this hypothesis. Because the bone-producing prey biomass and lions are not always in the same zone in all savanna ecosystems (e.g., near water in wooded areas), it is more complicated to incorporate them into simple models of hominid land use. Additional problems lie in our lack of understanding of the extinct carnivores. Along with body size, whether a species is social or solitary continues to elude us (Janis and Wilhelm 1993) but is a major determinant of which species was dominant. If the relatively large sabertooth cats that, from their tooth morphology, were apparently not bone crunchers (e.g., Marean 1989, Blumenschine and Cavallo 1992) usually dominated over bone-crunching species, a pattern of areas of high and low bone deposition similar to today's may have existed in the past. Where the scavenging opportunities on the landscape were located would have been determined by the habitat preferences of the most abundant and stable prey populations.

Furthermore, PNV is not nearly as strongly seasonal in herbivore location and mortality, and so a seasonal glut in carcasses is not available for scavenging. If PNV can be used as an analog for early hominid environments (perhaps especially early ones, before about 1.6 million years ago, which would have been more humid and less seasonal), a different hominid strategy for exploiting carcasses would be predicted. Carcasses would be available year-round but at much lower densities than in the dry season in dry periods. The ungulates would not go through the severe seasonal stress that depletes fat levels in the highly seasonal environments of East Africa (Brooks, Hanks, and Ludbrook 1977, Jones and Metcalfe 1988, Speth 1989; but see Bunn and Ezzo 1993). In less seasonal habitats, late-access scavenging would provide a low-level, relatively constant although not totally predictable source of fat, which might be extremely important for hominid nutrition in such an environment (Speth 1989). However, the lower density of carcasses compared with those for an East African dry season would make scavenging a less profitable foraging strategy.

If scavengeable food is found mostly in habitats preferred by lions, then we have to question whether early hominids would habitually have sought such scavenging opportunities. Bunn and Ezzo (1993) also question the idea of this habitat preference. The abundance of hominid fossils with carnivore gnaw marks attests to much carnivore-hominid "interaction." Australopithecines and even some species of early *Homo* retained many arboreal adaptations (e.g., McHenry 1991) which would have been useful for escaping from predators, but this was probably not a major strategy for *H. erectus*. Throw-

ing stones or branches may have served to intimidate carnivores as chimps are sometimes able to frighten off leopards and lions (Kortlandt 1980, Hiraiwa-Hasegawa et al. 1986). There are several points that need to be reiterated regarding "the scavenging niche" (see also Bunn and Ezzo 1993). One is that there are no mammalian carnivores that live solely by scavenging, probably because of the sporadic nature and low density of "opportunities" (Houston 1979). Another is that in confrontational or early-access scavenging, typically the larger, more numerous, and/or dominant species scavenges from the kills of the smaller, more subordinate species (e.g., Cooper 1991, Eaton 1979). Thus, cheetahs and leopards rarely scavenge, lions often scavenge from hyenas quite a bit more than vice versa (Kruuk 1972:129; but see Cooper 1991), and modern human hunter-gatherers scavenge from lions (O'Connell, Hawkes, and Blurton-Jones 1988). The overlap of hominid and large-carnivore habitats in the savanna may have been so extensive that while confrontational scavenging would have increased risk for hominids dramatically, late-access scavenging might not have increased it very much. If early hominids had early access to carcasses, as Bunn and Kroll (1986) have convincingly argued was the case at FLK Zinj (although this debate is far from settled) [see, e.g., Blumenschine 1991, Blumenschine and Selvaggio 1994]], and they were scavenging, it is likely that they were also predominantly hunting and able to stand their ground with other large carnivores in interference competition.

Conclusions

The research summarized here is important for three reasons. First, if PNV is a good analog for some habitats in hominid evolution, then the pattern of bone deposition found there should contribute to the interpretation of Plio/Pleistocene landscapes. Second, comparison and analysis of data from various parks have revealed certain principles governing the patterning of natural bone deposition, specifically regarding the dominance hierarchy of large carnivores and the location of the most predictable prey. Third, the analysis of PNV and the comparisons made here demonstrate that a number of alleged relationships between the ecology of living systems and the deposition of bones across the landscape are not obvious and require further investigation.

It is clear that attritional-death bone deposition closely reflects herbivore and carnivore population densities and habitat preferences. Certain areas, differentiated by proximity to permanent water, topography, and tree density, accumulate many more bones than others. At the scale of specific habitats or zones, bones tend to be distributed randomly and are almost never naturally clumped. Although trees (important for shade and protection) "attract" bones at a much higher rates than do surrounding open areas, they have not been observed to collect bones in quantities as large as found at large

type-C sites. The addition of time averaging could change this, but time averaging is not as likely in paleosol situations as in other depositional environments. Contrary to ideas stemming from dry areas in eastern and southern Africa, neither permanent water nor ephemeral water holes accumulate significant quantities of bones. The fact that bone deposition is highest in the open habitats reflects a different spatial distribution of hyenas and lions than is found in the study areas reported from the Serengeti and suggests that different strategies of scavenging would be required by hominids using such a habitat.

Each of the contrasts between the better-watered, less seasonal PNV and the East African study areas requires that we move away from specific analogies to develop general principles that describe the distribution of bones on the basis of knowledge of a larger number of ecological variables. It should be obvious that the topographical and edaphic characteristics of a landscape shape the vegetation, which in turn shapes (and interacts dynamically with) the distribution of herbivores, which in turn shapes (and interacts dynamically with) the distribution and behavior of carnivores. This study shows that a simple descriptive, referential analogy (Tooby and DeVore 1987) based on a limited number of environments is insufficient to support conclusions about this complex set of causal relationships. The spatial (and bone-affecting) behavior of leopards, lions, and hyenas in the Serengeti has been used to explain the distribution of bones and scavenging opportunities for hominids in earlier times. Having observed the difference between the Serengeti and PNV and other study sites, we are required to broaden our analytical approach to take into account the relationship between seasonality and distribution of water, patterns of vegetation, and the behavior of large mammals.

Comments

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I applaud Tappen's attempt to provide new data for testing the characteristics of scavenging opportunities developed by my team in the Serengeti/Ngorongoro ecosystem (e.g., Blumenschine 1988b, Blumenschine, Cavallo, and Capaldo 1994, Cavallo and Blumenschine 1989). These data, however, do not warrant the conclusions she reaches about modern scavenging opportunities or hominid subsistence ecology.

Tappen does not demonstrate that, in contrast to the situation in the Serengeti, scavenging opportunities in PNV are better in open areas than in riverine woodlands. The only quantitative support for the claim—density

distributions of bones—is indirect. Even here, Tappen provides no corresponding data for PNV on the habitat-specific persistence of carcasses as scavengeable food or the completeness of fresh carcass consumption. These data are essential for establishing landscape bone densities as an accurate proxy for the scale of scavenging opportunities. I have documented three material proxies in landscape bone assemblages whose meaning for scavenging was calibrated through direct observations on the consumption of over 250 fresh carcasses by Serengeti carnivores: the number of bones per individual (MNE/MNI), the skeletal parts preserved, and their completeness (Blumenschine 1989). Tappen provides neither side of this middle-range equation for PNV.

As it turns out, bone density may be a fourth proxy for the scale of scavenging opportunities. Although several intervening variables have not been controlled for, my data on habitat-specific bone densities for the Serengeti region (Tappen's fig. 12) correspond directly to fresh carcass persistence and completeness there. Nonetheless, reliance on my fresh-carcass data to calibrate the bone-density proxy from PNV would undermine Tappen's call to avoid "Serengeti-centric" interpretations of early hominid subsistence ecology.

Tappen mistakenly assumes that a high carcass input necessarily denotes better scavenging opportunities. This equation omits several more important variables. We have emphasized scavenging of abandoned lion and leopard kills in riparian woodlands because they are safe (*contra* Tappen's agreement with Bunn and Ezzo 1993), predictably located in time and space, high-yielding, and congruent with other adaptations of Oldowan hominids. Yet these carcasses are vastly outnumbered in absolute terms and probably also per unit area by ungulate mortality in more open settings of the Serengeti. Indeed, carcass density is irrelevant to the riparian scavenging prescription beyond showing that carcasses there are not rare.

Contrary to Tappen's concluding paragraph, I have documented many ecological variables affecting the scale of scavenging opportunities and its landscape bone proxies (reviewed in Blumenschine, Cavallo, and Capaldo 1994). The most fundamental is the ratio of spotted hyena biomass to the biomass of large mammal carcasses. Though operating also at the ecosystemic and the annual time scale, it is on a local, habitat scale and on a time scale measured in hours that the spotted-hyena: carcass ratio has the greatest relevance for a hominid scavenging niche. Riverine woodlands are a focus of good opportunities in the Serengeti because discovery of carcasses by spotted hyenas is delayed over that in more open settings. The brevity but uncontested nature of this rich feeding opportunity for would-be hominid scavengers remains unappreciated (e.g., Bunn and Ezzo 1993) and would be a critical PNV datum for evaluating Tappen's suggestion that the apparent preference by PNV hyenas for riverine woodland translates into poor scavenging opportunities in this habitat. Tappen would also need to provide habitat-specific information, as we

have for the Serengeti, on the risk of predation to a would-be hominid scavenger, the availability of refuge, the predictability of carcass locations in time and space, the degree of competition for carcass tissues by other scavengers, and seasonal changes therein.

If Tappen could substantiate her claims in these ways, we would have an interesting contrast to the Serengeti. Yet the mechanism I have proposed to explain the patterns of bone deposition and scales of scavenging opportunities—the degree of competition for carcasses by bone-crunching carnivores such as spotted hyenas—would be the same for both ecosystems and, as I have argued, for Amboseli, Manyara, and Plio/Pleistocene savanna woodlands.

The paleoanthropological implications of my Serengeti work are not arguments based on referential modeling (Tooby and DeVore 1987) or formal analogy (Gifford-Gonzalez 1991) as Tappen asserts. Formal analogies have no demonstrated common mechanism responsible for alleged similarities between the phenomena being compared. This is the case with the oft-repeated but groundless criticism of the idea of hominid scavenging echoed by Tappen—that hominids could not have relied solely on scavenging because no mammalian carnivore does. This formal analogy ignores the different anatomical, physiological, and technological mechanisms mediating scavenging behavior in Carnivora and hominids, including, most basically, that hominids are not obligate carnivores. In contrast, the relational analogy (Gifford-Gonzalez 1991) I proposed as a basis for modeling prehistoric hominid scavenging is rooted in a fundamental ecological mechanism with distinct and fossilizable traces. The contexts (e.g., riparian woodlands vs. more open settings) within which the mechanism operates may prove to be variable, and I agree with Tappen that tests of the robustness of such explanations against independent samples will strengthen our confidence in, and the resolution of, models of hominid subsistence ecology. Unfortunately, Tappen's paper does not provide us with the information needed to achieve these ends.

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It should be self-evident that any modern ecosystem and the particular, complex interrelationships among its predators, prey, habitats, and bone distributions did not exist at the beginning of the Pleistocene. Yet recent observations of modern Serengeti lions, leopards, hyenas, and habitat-specific bone distributions and recent observations by researchers posing as marginal hominid scavengers of abandoned, predator-killed carcasses have been used as though they were valid as stand-alone substitutes for direct observations of life in the Plio/Pleistocene. An approach involving direct analogies of a single modern ecosystem does not allow for variability in modern behavior and interrelationships or for change

through time. The valuable observations from the Serengeti need to be analyzed in combination with comparable data from other ecosystems.

Paleoanthropologists and other researchers interested in reconstructing unobservable events in the remote past, whether involving hominid subsistence or dinosaur social behavior, rely on uniformitarian principles. The question is one of threshold: When is our understanding of observable pattern and process in modern contexts sufficient to warrant its use in analogies and models about the past? In a discussion of uniformitarianism, Simpson (1970) distinguished between inherent properties or characteristics and their position, arrangement, and activity at any one time. Similarly, Tooby and DeVore (1987) have criticized referential models using narrow, direct analogies based on particular modern animals; instead, they favor conceptual models based on specified interrelationships among a range of relevant variables.

Tappen's project is, thus, important and timely. At Virunga, lions, prey animals, bone residues, and scavenging opportunities are more abundant in open savannas than in riparian woodlands. By describing patterns that contrast with those of the Serengeti, Tappen shows that one modern savanna ecosystem is not adequate for generalization about savanna paleoecosystems of the Plio/Pleistocene, and she demonstrates some of the modern range of variation.

Trees, for example, have long been a key ingredient in models of the foraging and site-forming activities of Plio/Pleistocene hominids (e.g., Isaac 1978, 1983; Kroll 1994; Kroll and Isaac 1984; Potts 1988). As Tappen shows, lions at Virunga accumulate bones of prey animals at trees, which raises the need to distinguish such residues from those attributable to hominid subsistence activities. It would be informative if Tappen were to summarize trends in skeletal proportions and bone condition at trees and tree lines at Virunga.

As for scavenging opportunities, the Virunga ecosystem seems to provide a very limited availability of intact marrow bones for marginal scavenging (see also Sept 1994). This finding is consistent with those for the Lake Eyasi ecosystem, where Hadza foragers obtain approximately 20% of the carcasses they consume through scavenging, mostly active confrontations with carnivores yielding relatively complete carcasses (Bunn, Bartram, and Kroll 1988; O'Connell, Hawkes, and Blurton Jones 1988), and where a hominid forager reliant on marrow bones from defleshed carcasses abandoned by predators would either starve (Bunn, Kroll, and Bartram 1991) or move to the Serengeti. Is the narrowly defined niche for marginal scavenging of marrow bones from abandoned, defleshed carcasses (Binford 1981, 1983; Blumenshine 1987) realistic and consistent with the known archaeological and hominid fossil record? Its test implications—relative abundance of the nonmeaty lower limb bones (metapodials) that carnivores consume last or abandon and low frequency of defleshing cut marks on upper limb bones that carnivores eat first—are both contradicted by archaeological evidence from Ol-

duvai (Bunn and Kroll 1986, 1988). Hominids did break open limbs and mandibles for marrow fat. If they were most interested in fat, why would they have restricted their utilization to marrow bones when most fat is located on other body parts to which they also had access (Bunn and Ezzo 1993)? Advocates of the marginal scavenging niche have even linked carcass acquisition to the supposed arboreal activities of early *Homo*, arguing that abandoned, tree-stored leopard kills could have been obtainable in riparian woodlands (Blumenshine and Cavallo 1992). But if the prevalent open-country scavenging opportunities of the Virunga ecosystem instead characterized Plio/Pleistocene Olduvai, then it is hard to see the adaptive advantages of arboreality. Another alternative is that the fossil remains of early *Homo* include a smaller, arboreally adapted species, *H. habilis*, and a larger, more terrestrially adapted species, *H. rudolfensis* (Wood 1992). It is certainly possible that the arboreally adapted *H. habilis* had little to do with the formation of the archaeological record, while *H. rudolfensis*, as a more formidable hunter and scavenger, formed most of the sites. Although the larger species has not yet been found at Olduvai, its remains are known from deposits of comparable age several hundred kilometers to the north at Koobi Fora.

Finally, as Tappen notes, a hominid scavenger capable of confronting large carnivores was probably also a hunter. Although scavenging dominated the literature of the 1980s, hunting needs to be reincorporated into alternative models of carcass acquisition by Plio/Pleistocene hominids. There seems to be a growing interest in this direction (e.g., Tooby and DeVore 1987, Boesch and Boesch 1989, Stanford et al. 1994). By documenting variability in predator-prey interrelationships and bone distributions in a Central African savanna ecosystem, Tappen emphasizes the need for additional studies of landscape taphonomy so that more realistic models of ancient hominid lifeways can be developed.

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Much of the comparative taphonomic information on bone deposition and the formation of bone assemblages derives from semiarid, seasonal grassland ecosystems. These studies have shown that several ecological parameters operate systematically to condition the formation of bone assemblages, and these parameters include vegetation density, carnivore:herbivore ratios, and types of carnivores (bone crushers in particular). To develop laws on bone assemblage formation, in the uniformitarian sense, ideally we would conduct experimental studies that manipulated the critical parameters with the goal of understanding their causative effects. This is not possible, but it is possible to sample many ecosystems in which the critical parameters differ. Tappen's important paper begins that task. It provides new and valuable data

on the formation of bone assemblages in a previously unsampled vegetative context. This research expands our knowledge greatly, and I hope that it will be followed by more studies sampling other ecosystems.

Tappen's discussion of several problems that are raised by a reliance on the semiarid grasslands ecosystems of East Africa as analogs for Plio/Pleistocene environments is very useful, but I think we need to take this issue even farther. Tappen states that the basic structure of African savannas was in place by the Pliocene, citing Barry's (1987) description of the fossil carnivores of Laetoli. However, when we look carefully at what we mean by "savanna" and seek evidence of its existence, problems begin to arise. "Savanna" is a very imprecise term. Its original use derives from descriptions of New World vegetation, and its usage differs from continent to continent (Lind and Morrison 1974). In Africa "savanna" typically includes any vegetative mosaic that has a substantial grass association, thus including everything from open grassland to woodlands. Furthermore, most African ecologists recognize that these grassland associations are nearly all secondary vegetation caused by regular burning. It is now clear that natural sources of fire are insufficient to result in many grassland associations we see today. If one removes regular burning, the natural succession to bush and woodland begins (Pratt and Gwynne 1977, Talbot and Kesel 1975, Vesey-FitzGerald 1970). This is why many national parks have burn units, Tappen notes that her research area has one.

The primary source of burning derives from agriculturalists and, in East African grasslands, the pastoralists who burn off dry, fibrous grass to stimulate a burst of green regrowth for their cattle (Lemon 1968, Norton-Griffiths 1979). This regular burning has the added effect of pushing back the tsetse fly. Pastoralists did not enter eastern Africa until about 4,000 B.P., and before that the so-called savannas must have been much more wooded and the vegetative mosaic much different (Marean 1992). When we attempt to model Plio/Pleistocene habitats we need to consider this important problem. African savannas, as we picture them, are the result of 4,000 years of occupation by peoples that modified their environment. I think we would be better off if we just discarded this imprecise term and used the more precise descriptive nomenclature constructed by the range ecologists (Pratt, Greenway, and Gwynne 1966).

Species diversity in paleoecology has received increasing attention in the literature, and Tappen conducts a preliminary diversity analysis of her data. She notes that species richness often correlates strongly with sample size but then cites Cruz-Urbe's (1988) finding that in southern African fossil assemblages there is no sample-size-diversity correlation in samples over 25. More recently Meltzer, Leonard, and Stratton (1992) have shown that Cruz-Urbe's analysis is flawed: the generalization is true neither of the original data set nor of others. The best way to test for the sample-size effect is to examine the relationship between sample size and richness using linear regression. A linear regression of the number of species vs. logMNE (MNE is logged because the residuals

of a non-logged regression indicated a partially curvilinear relationship) is nearly significant ($r = .66$, $p = .07$), showing that sample size is an issue with these data. Perhaps more important is the issue of sampled area: as sampled area per habitat type (zone) increases, so does the likelihood of adding another species. This is a perpetual problem with wildlife studies that census modern populations and attempt to analyze diversity (Smith 1966). The relationship between sampled area for each zone (area in hectares in table 5) and number of species per zone is significant ($r = .78$, $p = .02$). This suggests that much of the variation in species richness per zone is a product of the size of the area that Tappen sampled per zone. When such a relationship occurs it is useful to examine the residuals around the regression line (Rhode 1988) to see if any cases have a species richness significantly above or below the value predicted by the independent variable (sampled area). My calculation of standardized residuals (residuals expressed as units of standard deviation from the predicted value) shows that only the tree-line zone had a residual greater than two standard deviations (2.3). Therefore tree lines, given the small amount of sampled area, have very high species richness. Perhaps Tappen could comment on this.

Tappen concludes that bone preservation in her study area differs significantly from that documented by Blumenschine in the Serengeti and Ngorongoro Crater. In this context it is important to make a distinction between bone burial and deposition (see Lyman 1994). Deposition is the placement of the bone on a land surface, while burial is the ultimate covering of the bone by matrix. Taphonomic models for interpreting fossil assemblages typically assume a close relationship between deposition and burial, but the time between deposition and burial is perhaps the most taphonomically active period. Tappen's work does not really measure the amount of bone deposited. Rather, it measures a combination of what was deposited and what survived between the time the bone hit the ground and the time it was observed by Tappen. Thus her study focuses on the time between deposition and burial, and I believe it is in this interval that significant interecosystem variability could occur.

For example, whereas Blumenschine found more bones in riparian woodlands, Tappen finds more in grasslands. A key causal agent for bone destruction in the grasslands studied by Blumenschine was the common presence of spotted hyenas, which quickly discover bones in grasslands but not in woodlands. If we discard the vegetative descriptions (grasslands versus woodlands) and consider ground-level visibility, the results of Tappen and Blumenschine are more similar. The grasslands sampled by Tappen are generally tall grassland, where ground visibility is very low; she often needed to burn off the grass to collect the bones. The Serengeti and Ngorongoro grasses are short to medium-sized, and visibility is high, while the riparian woodlands have low ground visibility due to taller grasses and bushy vegetation. The two studies taken together show that bones survive long enough for a researcher to count them in thickly vegetated substrates, and presumably these sur-

living bones will ultimately be buried. Tappen's results clearly show how increasing the sampled environments results in refinement of our understanding of assemblage formation processes.

I am not completely convinced that we can use bone survival on the landscape to measure scavenging opportunities. Tappen assumes, pointing to Blumenschine's (1989) arguments, that the density of bones on the landscape correlates with scavenging opportunities—the amount and survival time of flesh and within-bone tissues. If carnivores kill many animals in the grasslands and rapidly consume flesh and major marrow bones, bones may still be abundant on the landscape if, as in Tappen's area, hyenas do not discover the remaining fragmented bones. In contrast, if carcasses killed in the woodlands are rare but consumed slowly and less completely, then the woodlands may actually provide better scavenging opportunities, although bones will be more abundant on the grasslands. The only true measure of scavenging opportunities is observational data on the frequency of kills, the speed of consumption, and the completeness of consumption (Blumenschine 1987).

Tappen should be commended for carrying out and presenting the results of this important study. By adding just one very different ecosystem to the sample, she has significantly increased our knowledge of the ways in which bone assemblages form.

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Understanding the taphonomic processes that influence bone accumulation and destruction on modern land surfaces is a critical step towards the interpretation of fossilized bone assemblages in paleontological or archaeological sites. Tappen's survey of ancient bone distribution near the Semliki River in eastern Zaire (PNV) is a welcome contribution to this field. It broadens the range of habitats and faunal communities sampled by landscape studies, which have with few exceptions (e.g., Sept 1994a) been confined to more arid environments in the eastern Rift Valley. It sets standards for future research through the use of systematic foot surveys of large transect samples (although, unfortunately, some of the transects were terminated when dense thicket was encountered). It develops innovative approaches to the investigation of bone distribution patterns in special microhabitats, such as excavating under target trees. However, this paper suffers from gaps in data presentation and in places confuses both the logic and the substance of Tappen's arguments.

Significantly, Tappen does not present the empirical evidence necessary to link patterns of bone density to the ecological processes she discusses. While she mentions recording data on bone breakage patterns and surface modification important for diagnosing the agents responsible for dispersing bones, these data are not dis-

cussed. Lacking ecological information on variation in species density, predator/prey ratios, or predation rates between different habitats sampled in the study, she simply *alleges* differential competition between the large carnivores based on a few observations of lion and hyena ranging patterns and some traces of carnivore behavior (e.g., claw marks on trees). Her statement "In the southern plateau . . . the ungulate population is small and therefore the lion population is small and there are more hyenas" is not supported empirically and makes little ecological sense in terms of hyena predation patterns. While she refers to tree density as a key habitat variable (with few supporting data), tree density by itself is little guide to the relative dominance of trees vs. grazeable grass in this region. Shrubs are not mentioned at all, but they are a dominant growth and form important thickets in three of the sampled regions—along the river, near the lake margins, and in the southern plateau (Sept 1990, 1994b).

While Tappen focuses on the distribution of "bone patches" in her samples, the criteria for recognizing a patch of bone in the field are left ambiguous, and this makes it impossible to compare her patch data with other bone survey data (e.g., Bunn, Bartram, and Kroll 1988). Analyzing the distribution of bones along the length of transects, she notes that 22 transects have random spatial distributions, including their patches, but then subsequently identifies a transect area 300 m long (1,500 m²), containing 33 bones from three species, as a "small clump." She needs to address the theoretical relationship between the "bone patches" defined in the field and the "clumps" or other distribution types identified through statistical analysis, because this issue of spatial scale is fundamental to effective comparisons of surface bone assemblages with the paleontological or archaeological record. To link her analysis of bone density to ecological context, she tries to explain a few uniformly patterned samples of bone distribution in terms of what she calls "the ecological model of competition." But a land-surface bone distribution is the cumulative by-product of many carnivore feeding events, conditioned by prey distribution and other variables, and cannot be directly compared with the frequency of negative interactions between individual organisms which might influence their territorial spacing. This is a misapplication of Ludwig and Reynolds's (1988:14) short summary of spatio-ecological patterning.

Finally, I was looking for a discussion of the relevance of this study to bone accumulation in sedimentary environments—the analogs most relevant to fossil assemblage formation. The Semliki environments sampled by Tappen include few sites of active sedimentation, and the plateau and hill slopes most prominent in her analyses are rarely sampled in the East African Plio/Pleistocene sedimentary record that provides the rationale for her study. While she argues effectively for the need to diversify the existing sample of modern analogs for ancient environments and makes useful comparisons between her sample and the Serengeti and Amboseli ecosystems (in terms of quality of grasslands, for example),

Tappen still confounds her comparative analyses by lumping together dissimilar habitats. Riverine environments of the Serengeti, Semliki (PNV), and Ishasha (PNV), for instance, are very different types of habitat in terms of geomorphology, vegetation structure, and mammalian community (Sept 1992, 1994b). With its focus on sampling the entire landscape near the Semliki River rather than just sedimentary environments, Tappen's study is arguably more useful for defining the range of scavenging opportunities in different savanna habitats than it is for interpreting the depositional patterns of fossil bone assemblages. However, despite the implications of its title, no actualistic data on scavenging (such as samples of seasonal carcass availability, bone fragmentation, body-part distributions, marrow yields, etc.) are presented in this paper.

Reply

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I thank the commentators for their careful consideration of the bone distributions and ecology of Parc National des Virunga. I designed this research project to explore the effects on bone deposition patterns of ecological and environmental variables such as broad vegetation structure, topography, and herbivore-carnivore populations and specifically to test the hypothesis that some ecological variables are observable in bone distributions. In terms of the classic taphonomic flow diagram developed by Clark and Keitze (1967; fig. 14), my study focused mostly on biotic, thanatic, and perthotaxic processes. I agree with the commentators who point out that the other three processes—taphic, anataxic, and sullegic—are equally important to the formation of the fossil record.

Although considering the implications for scavenging was only part of my work, it is a very interesting part because they may directly pertain to hominid behavior. An important criticism, expressed by Blumenshine, Marean, and Sept, is that the information I have provided may not be directly linked to the availability of scavenging opportunities in PNV. This study was not designed to duplicate Blumenshine's ground-breaking study of scavenging opportunities and carcass persistence in East Africa. Nonetheless, my observations in PNV raise important questions about the variation of scavenging opportunities in different habitats. My arguments regarding differences in the spatial and seasonal distributions of carcasses between East and Central Africa are based on both ecological differences and bone distributions. The less severe dry season and permanent water of PNV create a situation in which the ungulates do not migrate, are not more reliably available in riverine or woodland areas, and do not suffer severe seasonal deaths. Most PNV ungulates are not even seasonal

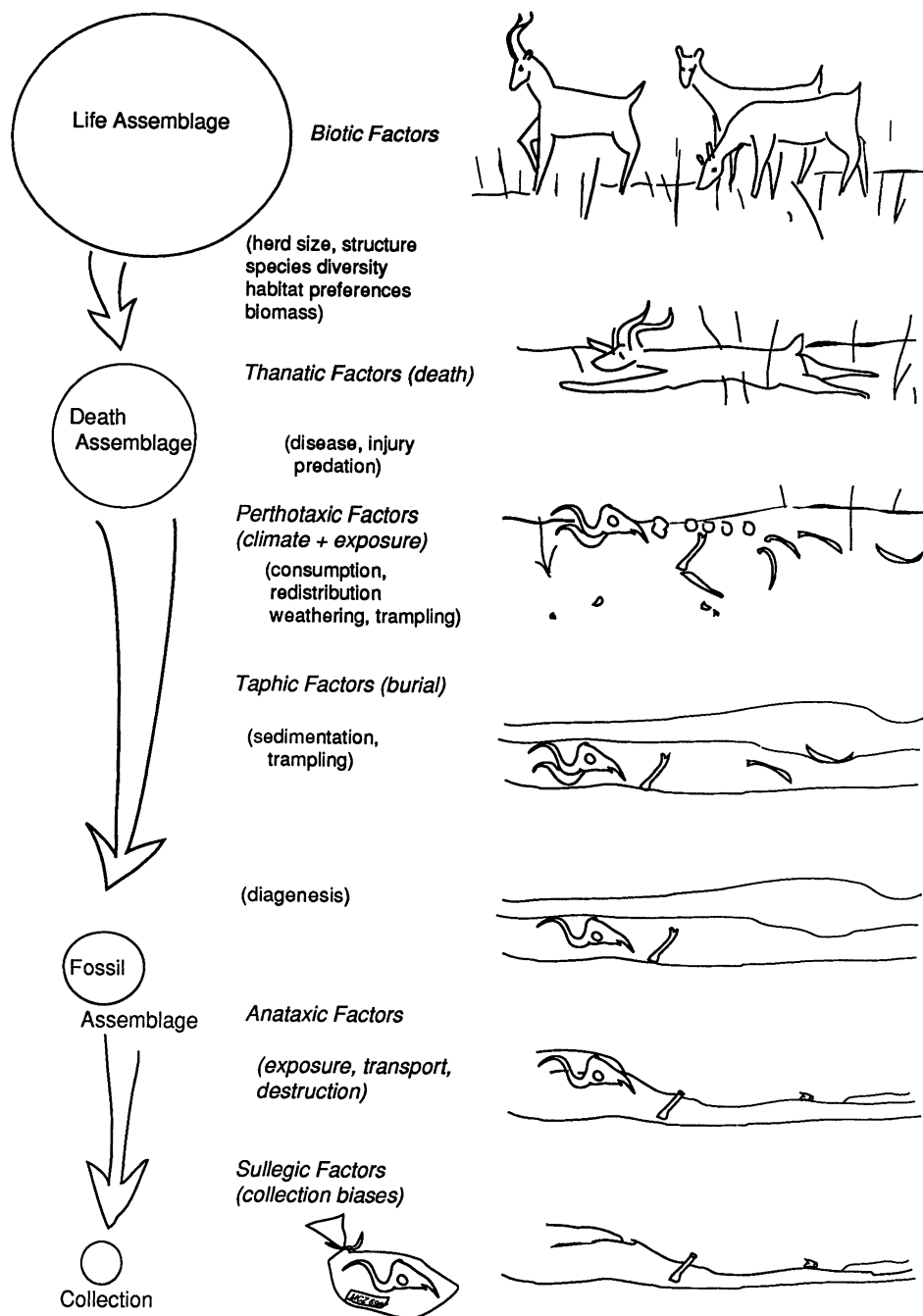


FIG. 14. A taphonomic flow diagram adapted from Clark and Keitze (1967).

breeders. Blumenschine is probably correct in stating that ecological considerations such as these are some of the main causes of seasonal variation in scavenging in the Serengeti (1987:387–88), yet the Serengeti is different from PNV in all of them. Thus, it is reasonable and logical that seasonality in carcass availability will not be the same in these two parks.

I have built upon Blumenschine's work (as well as the work of other taphonomists, especially Behrensmeyer) but have not attempted to replicate that work. I found that many of the agents that Blumenschine attributes

to spatial and temporal variation in scavenging opportunities that he observed in East Africa are very different in PNV. He has made convincing ecological and behavioral arguments for why hyena-dominated areas will have fewer scavenging opportunities than areas dominated by lions: among these are body size, tooth morphology, and gut morphology of the carnivores, which result in more complete consumption by hyenas. These factors are probably reasonably constant for all ecosystems. Contrary to Blumenschine's comment, I have documented a correlation between "hyena habitats," de-

struction of bone, and completeness of prey based on bone distributions, even though I did not study carcass persistence. The very scattered distribution of bones in the riverine, lake, and southern plateau, presented here as MNE per patch, is a similar statistic to his MNE/MNI ratio (Blumenschine 1989), as most patches represent the bones of a single animal. (This is also indicated by a ratio of isolated finds to bone patches and by the diameter of patches, which are larger in the "hyena areas" [Tappen 1992].) The very low MNE per patch and extensive scattering of bone and the dearth of bone in the hyena-dominated and more heavily treed areas indicate, as they do in the open areas in the Serengeti, that animals are more completely consumed and scattered where hyenas are most common. Although Blumenschine suggests that I am using a Serengeti-centric approach by referring to his work to use bone density as an indicator for scavenging opportunities, this is not true. In criticizing a Serengeti-centric approach I am arguing not against the use of information gleaned from the Serengeti but rather against the use of the Serengeti ecosystem, lock, stock, and barrel, as an analog for Plio/Pleistocene hominid habitats. It is our responsibility to decipher, on the basis of a broad understanding of the modern world, what makes useful analogy. Blumenschine's research has provided much excellent information. His carcass consumption sequences, the relative completeness of hyenas' consumption of carcasses, and the comparative ease with which stashed leopard kills could be scavenged by hominids are very important observations. Relevant here is Bunn's observation that the application of uniformitarian principles is a question of threshold. His query "When is our understanding of observable pattern and process in modern contexts sufficient to warrant its use in analogies and models?" is not easily answered. With all the ecological processes that Blumenschine has documented that may nearly universally affect the distribution of scavenging opportunities, improved scavenging in woodlands or riparian woodlands compared with open grasslands is not one of them.

A very minor portion of my field research in PNV included observations on a few fresher carcasses (Tappen 1992). On the few occasions that I followed vultures in search of scavenging opportunities, I could never find them in the southern plateau or riverine area because the trees blocked the view of where they had landed. I have spent hours searching for carcasses in woodlands to no avail. In contrast, in the open plateau, one can easily see where a vulture lands from several kilometers away and walk straight up to a carcass. If hyenas, with their additional keen sense of smell, have a hard time finding carcasses in riverine areas, how could hominids have found them? Nonetheless, hominids are water-tethered, and therefore riverine and lacustrine areas would doubtless have been important habitats for them.

If we wish to reconstruct hominid habitats and behavior, then we must deal with ecological variability, and no such reconstruction can ignore Marean's observation of how much the modern savanna has changed because

of anthropogenic factors. This important point will become ever more central to studies of hominid paleoecology as the forest-savanna dichotomy, often oversimplified, breaks down (Kingston, Marino, and Hill 1994, Sikes 1994) and we face the probability that the origins of the Hominidae may not have taken place in a "Serengeti-like savanna" (in the sense of an open grassland with a few scattered acacias [WoldeGabriel et al. 1994]). Defining more specifically what we mean by "savanna" and how it has changed through time is a real problem for anyone studying modern ecosystems in the hope of elucidating past hominid ecology. For example, what plant species (some may have been critical resources to hominids) are currently excluded from savanna areas not because of lower rainfall than in forests but because they are not fire-adapted (Laden 1991)? How has the character of rain-forest edges, possibly critical habitats among the "mosaics" in hominid ecology, been altered by cutting and burning over recent centuries (Laden 1991)?

Finally, an extremely important subject brought up by Bunn is that, if we are accurately to construct models of the behavior of hominids that created early archaeological sites, we must address the question of which species created the sites. In the Plio/Pleistocene, for example, at the time of Bed I at Olduvai, there may have been four species of hominids, with different body sizes, degrees of arboreality, brain sizes, and manipulative abilities, in East Africa. Although *Homo erectus* has not been found in Bed I of Olduvai, this is probably sampling bias, because by Middle Bed I times it is already present at East Turkana. Furthermore, it may be that *Paranthropus boisei* was quite encephalized (McHenry 1994). *H. habilis sensu stricto*, small-bodied and evidently quite arboreal, would have interacted with carnivores in a very different manner from *H. erectus* and probably *H. rudolfensis*. Did all of them create archaeological sites? Encompassing behavioral models demand an explicit hypothesis for each species.

Marean suggests an interesting correlation between bone survival and vegetation: that bone survival is longest in thick vegetation, whether that vegetation is grassland or woodland and whether it is in East or Central Africa. However, there is no evidence of such a correlation's causing variation in bone density in PNV. For example, many parts of the southern plateau have very thick grass despite the higher density of trees. In this area burning was required to find bones, and then, with near-perfect visibility, there were very few. Likewise, the riverine and lake zones do not uniformly have less vegetation than the plateau (although there are patches of erosional surfaces devoid of vegetation).

I reported Shannon diversity indexes more for comparative purposes than to make a specific point. Marean points out that the reported variation in Shannon index values across the zones in my study area may be due to either sample-size or sample-area effects. He also points to Meltzer, Leonard, and Stratton's (1992) criticism of Cruz-Uribe's (1988) assertion that diversity indices are not affected by sample size when they approach 25. One may indeed question the utility of diversity indices as

opposed to richness indices in the first place. Measurement of actual species diversity and richness (in a living system) and the correlation between this and diversity and richness as reflected in a faunal record are important, and further research is needed in this regard. Meltzer et al. purport to show that sample size and diversity indices can be correlated across a very wide range of sample sizes. This is a perennial problem in analysis of species richness or diversity. Typically, as the area sampled increases, so does the number of species—but at a diminishing rate (Ludwig and Reynolds 1988). Meltzer et al.'s analysis seems to show that sample size and species diversity can be correlated across a wide range of sample sizes. Although their work is interesting and thought-provoking, it is possible that their results are an artifact of their particular method of analysis. The number of species represented in a sample is most likely to increase under two separate conditions: with increasing sample size, up to a point, and with increasing number of different habitats included in the sample. Meltzer et al. do not distinguish between these two effects in their analysis, and both are likely to have been important in that case. Thus, their admonition about sample size may be questionable.

Marean's suggestion and demonstration that species richness is probably correlated, in the case of the PNV data, with the area sampled is important and welcome. He shows, using regression analysis and examining residuals, that the tree-line zone may have greater species richness than predicted by the simple correlation between sample size and the species-richness measure. This zone contains two species not recovered from any other zone: mongoose and spotted hyena. There is a lot of lion activity in tree lines, and carnivores are well known for killing each other in competition. It may be that this is the reason that these species are represented in the surface assemblage despite the small sample size in this zone. Also, the tree lines form special microhabitats within relatively open grassland, and they may concentrate activities of some smaller species such as the mongoose, some rodents, and some birds.

Sept raises the issue of the thoroughness of my survey, noting that I report terminating some transects because of poor visibility. This is an important issue and one that should always be considered. I have outlined the methods that I used to insure maximum visibility (for more detail see Tappen 1992) and will not reiterate them here; it is likely that I have made the most thorough search for bones over a large area to date. In this case, a more thorough inspection would have required more extensive cutting of dense vegetation than would have been appropriate in this park.

Sept asserts that my characterization of the bovid and predator ecology of PNV is faulty or based on anecdotal information. It is true that one must always question assumptions about natural process, and assumptions based on anecdotal information can be very misleading. However, my conclusion about the habitat preferences of prey species is based not on anecdotal information but on nearly eight months of observation in two differ-

ent field seasons in the PNV northern sector and on censuses and observations by Averling (personal communication), Mertens (1983, 1985), and Enama (1989) of kob, reedbuck, waterbuck, buffalo, and elephant distributions and habitat preferences, as well as conversations with the conservator and park guards. The preferences and locations of the main kob and reedbuck herds in the plateau are not in the least subtle. However, the reasons for these preferences remain unknown. In addition to the abundance of preferred grass species in the plateau (and, as Sept points out, in the southern plateau) there may be factors such as soil nutrient status and increased visibility for predator avoidance and lek behavior (discussed more extensively in Tappen 1992). Although it is unfortunate that there have not been thorough studies of the PNV lions and hyenas (as is the case for the Serengeti and Ngorongoro [e.g., Kruuk 1972, Schaller 1972]), there is no question of the habitat preferences of these predators in PNV. The ungulate population is significantly smaller in the southern than in the northern plateau, and it makes perfect ecological sense that the lions would prefer to situate themselves nearest the largest and most predictable prey biomass. This explanation for lion habitat preferences is based on the logic and observations of Schaller (1972), who hypothesized that lions in the Serengeti preferred woodlands because the most predictable prey sources (resident ungulates) were there. In contrast, the habitat preferences of leopards are entirely inferred, as I made clear. Sept suggests that riverine areas are not the same in every savanna environment, which is correct, but mistakenly claims that I have confounded different habitats in my analysis. In fact, I emphasize the ecological variability between different ecosystems and the need for great care in creating environmental analogies.

Defining a bone patch is a little like defining an archaeological "site"—often intuitively obvious but technically difficult. At PNV, bone patches are typically small, with an MNI of 1 (see figs. 5, 6, 9–12). Usually patches have a diameter of 3–11 m (see Tappen 1992 for more details). This definition reflects my interest in studying the overlap in space of individuals that died independent deaths. One can, however, also compare my bone-density data by unit area rather than density of bone patches by using the appendix in my thesis.

Sept is concerned about the use of the ecological model of competition to explain bone distributions. I agree with her and have said so. Because the carcass parts of different individuals found on the surface were mostly dispersed as separate events, the spatial distribution, though the result of competition, cannot in any simple way be predicted from the ecological model of competitive individuals.

Sept echoes my statements that the river is currently eroding into sediments rather than depositing a large floodplain that would bury bones and similarly comments that conditions in the Bukuka Hills would never result in the fossilization of bones. As I have said, rather than studying the effects of depositional facies on bone distributions, which I agree is worthy of study, I was

studying the *ecological* and *behavioral* effects of proximity to permanent water and water holes and of topography and vegetation on bone deposition.

Sept correctly points to the need for clarification of the calculation of tree density. Tree density was calculated by counting trees along 14 bone transects (see Tappen 1992:99). (Bushes were also counted but not included in the final numbers of trees; there are more bushes in the southern plateau than in the plateau.) The tree counts were intended to provide an order of magnitude of the differences between the plateau and the southern plateau. For more detailed analysis of vegetation, I refer readers to Sept (1990).

In the end, we are going to have to create theoretical models that are applicable to the past and to test their applicability through empirical studies of a broad base of ecosystems. I am glad that my paper has produced spirited comment, and I look forward to future research and discussion. As more ecosystems are studied, they will surely provide insight into the relationship between ecology, bone deposition, and the probability of an early hominid scavenging niche.

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