Bones and Bushes: Soil Carbon Isotopes And Animal Bone Distributions

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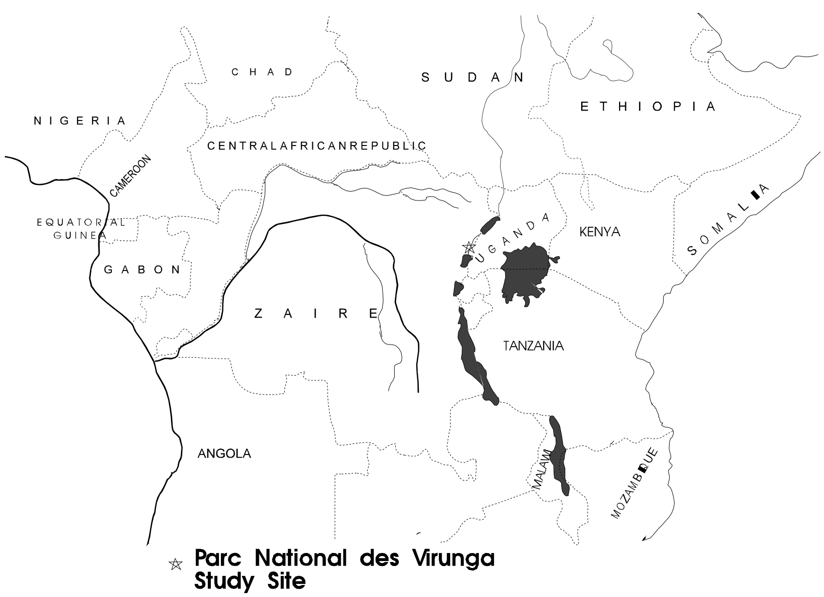
Ancient landscapes are only rarely preserved in the geological record. The contemporaniety of features on such landscapes is difficult to establish. The interaction between plants and animals, and among animals, *should* follow general ecological principles, but are represented as a tangled, time averaged, and generally mucked-up record. However, there do exist laterally extensive paleosols, which by their very nature are in place and not redeposited, and so can be assumed to contain spatially meaningful traces (bones and stone artifacts, etc.) of the kinds of events that we are interested in.

The possibilities are impressive. For example, in the Willwood Formation of Eocene age from the American west, Brown and Beard (1990) found systematic lateral variation in bones across a paleosol. They found variation in species representation from flood plains to inland sediments, thought to represent the habitat preferences of different species, and lateral variation in taphonomic variables, thought to be due to the rate of burial changing across space.

Those who study carbon isotopes in paleosols, and landscape archaeologists who study the distribution and character of bones and stone artifacts on ancient landscapes have many common objectives. We all want to understand the living systems that created the traces we find in the geological record. In so doing, we often turn to modern systems to understand the past, using the methods of taphonomic and actualistic research.

One approach is to study a wide range of modern systems and create a "type collection" of environments to decipher the paleontological record. This approach has been used explicitly by many researchers. But there are several reasons why this is not the best approach.



We cannot assume that every past landscape will be represented in even the most comprehensive "type collection" of modern landscapes. Species evolve, floristic and faunal associations can change dramatically, and certain combinations of climate, altitude, latitude, etc., may simply not be represented in the present day.

Essentially, we recognize the methodological distinction proposed by Tooby and DeVore between "referential models" -- such as a type collection of environments -- and "conceptual models", or models deduced from general principles of biology, behavior, and ecology, obviously preferring the latter.

We have two points to make. First, to draw your attention to a possible avenue of research into ancient ecosystems that incorporates information about bone distribution *and* carbon isotope signatures observed on ancient landscapes. We'll mainly talk about the bones, and those of you who are isotopically inclined can think about the molecules. Second, we wish to point out that while the processes that leave patterning in bones on the landscape may follow general, knowable principles, these principles may result in very different patterns in different settings. Thus, while living systems can teach us about principles and patterns, they do not necessarily serve well as items in a "type collection" for reference in deciphering the past.

We start with observations based primarily on Tappen's study of lateral variation in bone deposition in a Central African savanna, located in Parc National des Virunga, Zaire.

This savanna is located on the floor of the Western Rift Valley, on the northern shores of Lake Rutanzige (ex lake Amin, ex Lake Edward, originally known as Lake Rutanzige).

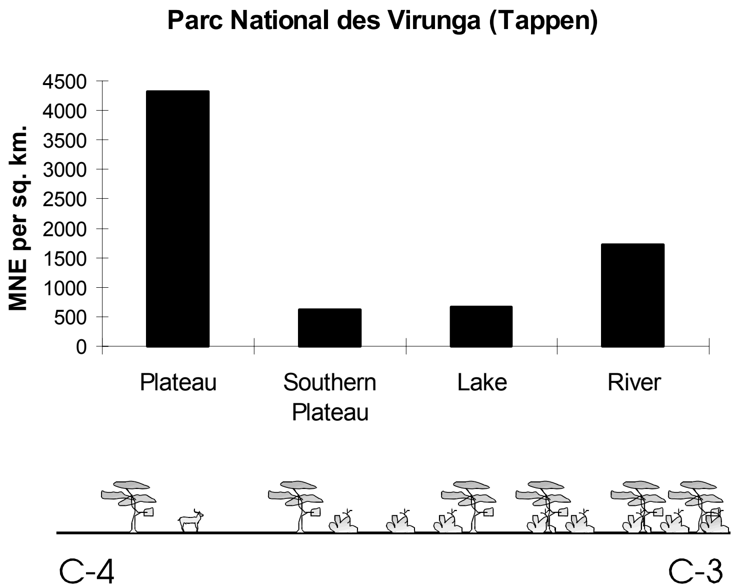
Parc National des Virunga, hereafter (PNV) differs from most East African savanna ecosystems. The dry season is less severe in PNV, and there is abundant permanent fresh water. The antelope and other fauna that live here do not migrate. Average annual rainfall is about 900 mm. There are open plains dominated by C4 grasses, with herds of kob and reedbuck. Also in the grassy plains are kob lekking grounds. Leks are antelope singles bars, where males stand in small well defined territories for most of the day and night munching on the overused grass and hoping that females will choose them for mating before they are eaten by a lion. Leks can be extremely long lived features of the landscape, which has interesting implications for those interested in bone distribution as well as soil processes.

The study area can be broadly divided into two habitats. The grassy plains are one. In contrast, near the river and lake, and across the southern part of the plateau, there is more mixed vegetation including numerous C3 bushes and trees, as well as Euphorbias (Euphorbia calycina) that may be CAM plants.

The open c4 plains have the highest biomass of ungulates. Most of the ungulates are grazers, so they prefer the grassy areas, but also probably prefer open areas for lekking and for increased visibility of predators. And since they are permanent residents, the lions, the dominant carnivore in the area, orient their hunting activities here. Thus, this grassy plain has the highest bone deposition in the study area.

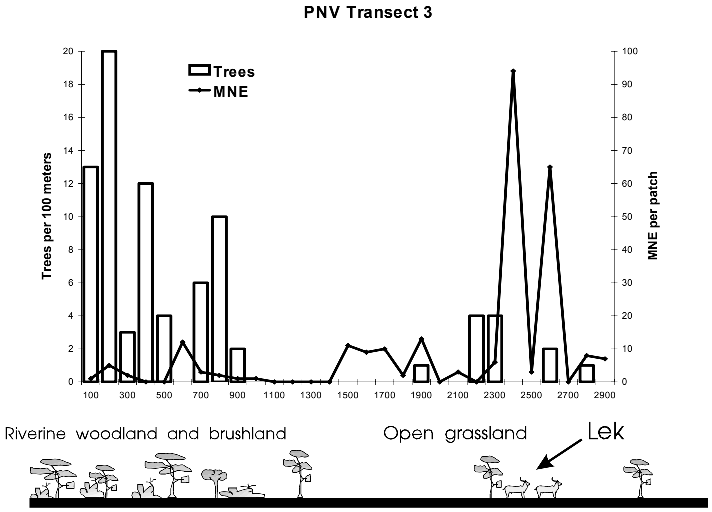
In the more mixed C3-C4 habitats, the ungulate biomass is lower. The lower bone deposition in this habitat is probably due to the lower antelope biomass and also because these areas are habitually used by hyenas, who consume bones and carcasses more completely than do lions.

At a smaller scale, within the open grassland, there are small clumps of C3 plants, often in linear tree lines. These tree lines follow elongated dips in the landscape that drain water from nearby areas, and so have enough moisture for C3 plants to out compete C4 plants. These tree lines are a favorite haunt of the local lion population, who enjoy the shade and possibly the discrete cover provided by the brush.

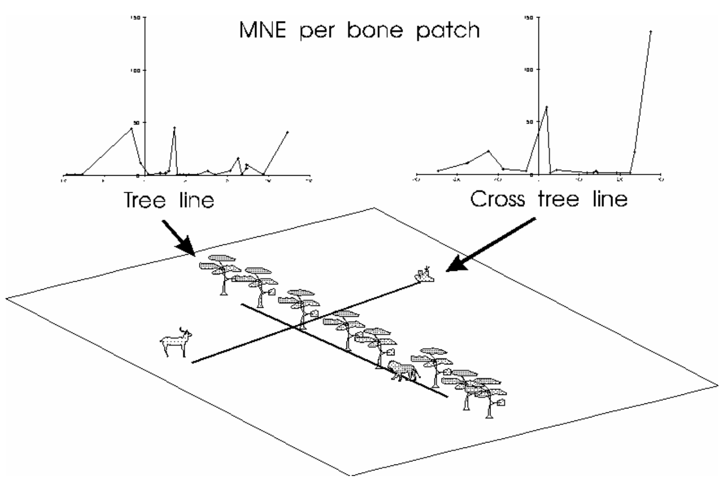


Tappen's bone survey shows that the density of bones, expressed here as Minimum number of elements, or MNE per square kilometer, closely follows the distribution of prey-species biomass, mediated by the hunting behavior of lions and the bone destroying behavior of hyenas. At this scale of spatial resolution, there appears to be a rough correlation between the distribution of bones and the likely Carbon-isotope signatures one would find in a lateral sample, to the degree that carbon isotopes reflect the ambient vegetation of the living system. The degree to which this relationship may hold, and the carbon isotopes may represent it, probably depends on the time depth of the system. Much of the distribution of plants in this area is clearly a function of the local geomorphology, with additional local climatic effects from the nearby lake, so it may be that the relative distribution of vegetation we see today is fairly stable, even if the absolute ratio of brush to grass may vary over decades of time.

We can take a closer look at one of Tappen's transects to see what patterns may be observed at a finer spatial scale. Transect 3 runs from the Semliki River inland across part of the plateau, intersecting a kob Lek near it's end.



The histogram bars represent the number of trees per 100 meters along the 50 meter wide transect, and show a clear distinction between the riverine habitat and the open grasslands. The frequency line represents the MNE for each patch of bones located along the transect. Note that there are more bones in the open plain than in the riverine area, and that the bones in the riverine area occur more often as isolated finds, the result of greater scattering by hyenas. The greatest number of bones is found in close association with the kob lek. All of the bones found in the kob lekking grounds were those of hapless adult male kob.



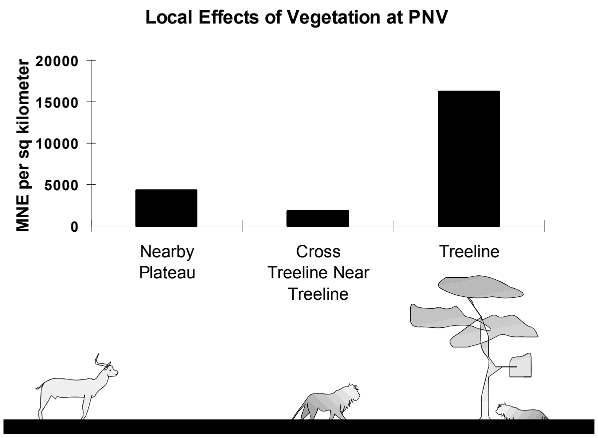
At a smaller scale, we can look at the distribution of bones in relation to one of the tree lines. The graph on the left shows the distribution of MNE per patch along a 25 meter wide transect along the tree line. The graph on the right shows the distribution of MNE per patch along a 50 meter wide transect perpendicular to and crossing the tree line.

There are several things to notice about these data:

There are far more bones per unit area along the treeline, distributed among a larger number of bone patches. (remember that the graph on the left is for a 25 meter wide transect and the graph on the right is for a 50 meter wide transect)

The cross tree line transect has two noticeable concentrations of bone, one as it crosses the treeline, and another as it encounters a single large bush.

Our interpretation of this pattern, based partly on the distribution of bones, and partly on observations and general knowledge about lion behavior, is this: When a lion makes a kill near a tree line, it goes through the extra effort to drag the animal, or parts of it, to the treeline or any other convenient shady spot, to get out of the sun. The very large number of bones under the bush as compared even to the tree line can be interpreted as a more extreme case: If an animal is killed near the tree line, the lions have several options for finding shade. If an animal is killed near a lone bush or tree, there are fewer options, and thus a greater concentration of bones results. The same effect, but more focused in space.



We can see this pattern more clearly when we average data from the plateau as a whole, all areas within 100 meters of a tree line, and all of the treellines sampled. There is a small but consistent depletion of bones within 100 meters of the shady treeline, and a concentration of bone within the treeline itself.

This pattern of bone distribution accords with something that we know about carnivore behavior, and predator-prey interaction. It may theoretically be identified on an ancient landscape by careful mapping of bones. If soil isotopes can resolve the distribution of C3 vs C4 plants at this level, then inferences about fine details of the ecology of part of an ancient landscape could be further supported.

The significance of information resolved to this fine scale arises from questions about the formation of patches of bones and stone tools at places like Olduvai Gorge and Koobi Fora. Glynn Isaac's common amenity hypothesis, in this case a shade tree that might attract both predators and hominids, and Kay Behrensmeyer's hypothesis of a "predator arena" -- in this case a Lek, or to the lions, a Kob Automat, with convenient shade trees -- derive from considerations of general principles of behavior, but require finely tuned actualistic and paleontological research to test.

The extent to which this sort of pattern may emerge will depend on the length of time over which vegetative patterning remains stable. In a recent study by Alison Brooks and Laden, we were able to show that two variables that characterize a landscape -- i) the degree to which events are focused in relatively small spaces by the existence of important features, such as trees or natural stone hunting blinds, and ii) the average lifespan of such features -- can determine the visibility in the paleontological record of stone tool using behavioral systems, and probably bone accumulation systems such as this one.

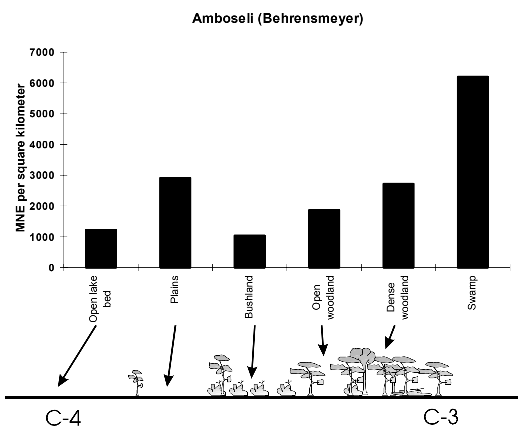
Geomorphological features in some cases may last centuries, creating stable vegetative structure, potentially visible in the soil carbon isotopic signature.

Since the tree lines of PNV are caused by what are probably long-lived geological features, we might hypothesize that high density bone patches and isotopic signals representing small scale lateral variation in vegetation would form in the paleosols here, if all other conditions are favorable.

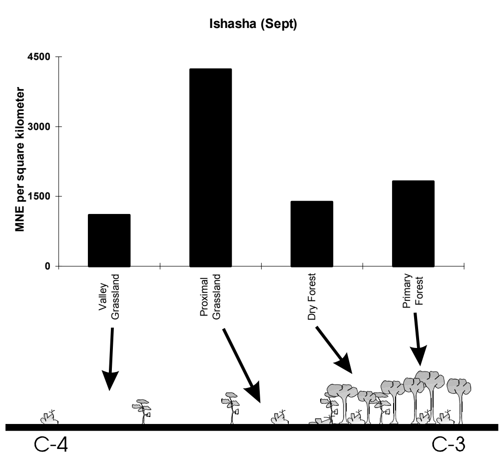
The broad correlation between bone distribution and vegetation shown at PNV -- more bones associated with C4 than with mixed C3-C4 vegetation -- could be one referential model in a type collection of environments. But the photosynthetic pathway of a plant does not determine the likelihood that a bone will be laid down on the landscape more often in one place rather than another.

Feeding and reproductive behavior of ungulates, predator-prey interaction, carnivore - carnivore interaction, and shade seeking behavior of lions, constitute general principles that shape the patterns of bone deposition on the landscape.

In theory, these underlying processes could result in more than one pattern, and in fact, this appears to be the case.

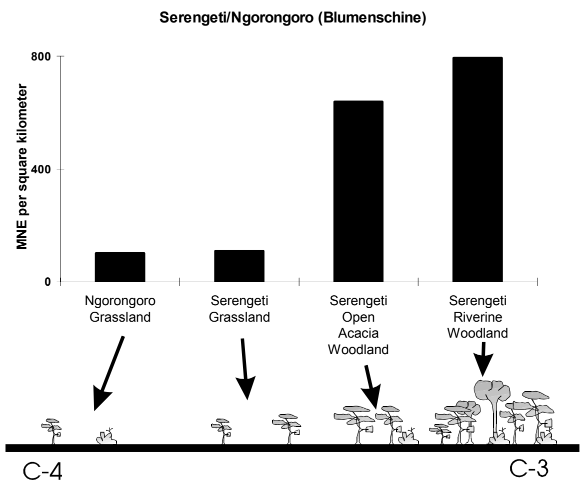


One of the earliest and most important surveys of modern bone on an African landscape is that of Kay Behrensmeyer at Amboseli Park, Kenya. Amboseli is a closed-basin ecosystem at the base of Mt. Kilominjaro. It is much more arid than Parc National des Virunga, with only 350 mm of rain each year, and severe dry seasons. Much of its ungulate population disperse seasonally and then concentrate in the dry season. At Amboseli, by far the highest density of bone occurred in the swamp environment, due to seasonal mortality caused by drought related starvation chiefly of migratory species. This type of death assemblage is not observed from PNV. At Amboseli, the open plains tend to have more bone deposition than the woodlands, though not much more than the dense woodlands.



Sept studied bone deposition across a riverine gallery forest and the adjoining open C4 plains along the Ishasha River, which runs into the south end of Lake Rutanzige along the Zaire-Uganda border. Here she found an interesting pattern: Very low bone deposition in the gallery forest itself, adjoining a strip of higher bone deposition on the proximal grassland, and farther out, a drop in deposition. This should not be interpreted as a similar pattern to the concentration of bone along tree lines in PNV. According to Sept, it was difficult to separate the effects of large mammal density and predator behavior here (Sept 1994:223).

More gallery forests should be studied, and more attention paid to carnivore behavior in these settings. Gallery forests are good candidates for early hominid habitats: No one has ever found an East African australopithecine site without some evidence for forest, possibly often gallery forest, in the same assemblage. Bone and possibly carbon isotope patterning on landscapes with gallery forests may reveal important clues to the ecology of these habitats, including risks associated with large carnivore activities.



The correlation documented by Tappen between C4 and C3 environments and bone deposition at PNV can be interpreted in terms of general principles of predator and prey behavior, but these underlying principles may be revealed in different patterns in different settings. Blumenschine's surveys at Serengeti and Ngorongoro illustrate this. Here, bone deposition is an order of magnitude lower than in the other studied areas. The Serengeti is famed for its migratory herds, zebra,- a million and half wildebeest, and Thomson's gazelle migrate hundreds of miles seasonally. Here lion territories center on the mixed woodlands, largely because resident antelope have territories here. This allows hunting of predictable prey year-round, which is required for lions with their altricial young.

Blumenschine has shown that because lions do not consume carcasses as completely as do hyenas, who are marginalized to the open plains by the lions, there are more bones to be found in the woodlands. The contrast with PNV is evident, as at PNV the stable prey biomass is out on the C3 plains, and so therefore are the Lions. Thus, the habitat preferences of lions and hyenas are the opposite of PNV, and thus the deposition of bones is different, as presumably is the correspondence between bone rich land surfaces and any isotopic signature that may indicate vegetative cover.

Grazers eat grass, browsers eat bushes, lions are often dominant over hyenas and like to dine in the shade, and hyenas don't leave much behind when they ravage a carcass. We know that these behavioral high-points of the modern savannas of Africa have not always been the same. Plumber and Bishop's taxon free analysis of ancient ungulates seems to demonstrate that these beasts have indeed evolved with respect to their feeding behavior and habitat preferences. Lions and hyenas may have changed their behavior too, and they were not the only "supercarnivours" on the African landscape of the Miocene and Plio-Pleistocene. Nonetheless, we can significantly refine our analytical toolkit by recognizing that general principles demonstrated to work in modern systems are better than simple referential models, and by studying a wider range of modern habitats. Moreover, there seems to be a significant potential for combining the analysis of "bone rain" as represented in ancient paleosols with the study of variation in vegetative patterning as indicated by isotopic and geomorphological studies.

Nota Bene

This presented paper represents a work in progress. We reproduced only a selection of the graphics used during the presentation in this copy, and do not provide a list of references. Most of the ideas presented in this paper and a bibliography on this subject can be found in a forthcoming paper by Tappen in Current Anthropology.