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Raining more than cats and dogs: Looking back at field studies of noncultural animal-bone occurrences

Gary Haynes

University of Nevada, Reno, United States

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ABSTRACT

This paper summarizes the context and results of long-term actualistic field studies of mammal bones at carnivore kills and mass death sites on three continents; it also updates analyses and data from the work. The main topics are variability – such as in bone representation and carnivore effects on bones – and the possible ecological implications of the variability. An important feature of bone rains is their punctuated nature, especially the disproportionate inputs from infrequent mass deaths such as drownings in flood events or drought-caused starvation.

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1. Introduction

Here I review and update information from a 40 year-long (and continuing) study of animal-bone rain in North America, Australia, and southern Africa. The term “bone rain” denotes the pre-burial and pre-fossilization process of bone input to the Earth's surface from noncultural deaths in various landscapes. These materials and experimental specimens are the subjects of study in the field of neo-taphonomic/actualistic research.

A.K. Behrensmeyer (1993), Behrensmeyer and Dechant (1980) and Faith and Behrensmeyer (2006) have shown that long-term actualistic studies provide important lessons for taphonomists, paleontologists, and archeologists. The spatial and taphonomic characteristics of noncultural bonesites at least partly result from ecologically meaningful features, such as diversity in prey types, prey abundance and mobility, carnivore density and competition, the distribution of water and forage, and geomorphic changes in landscapes. Different landscapes have distinctive sources and intensities of bone inputs. By learning how bone rains represent modern variability in ecosystems we may be better able to decipher fossil bone rains.

My field studies began in 1968, and were intended to be longitudinal, with return visits planned to the bonesites discovered in the early years. Tables 1 and 2 provide updated numbers of carcass and skeletal sites in North America and Africa where the most detailed records were gathered. I also had free access to data from hundreds more ungulate deaths not in these tables, recorded during sustained work by wildlife researchers.

2. Captive carnivore studies

Before beginning field studies, I did what other researchers had been doing, feeding defleshed ungulate limb bones to a range of captive animals (Haynes, 1981: 66–107). I also collected gnawed or broken ungulate bones from the enclosures of captive wolf packs which had been fed livestock body parts and whitetail deer carcasses, and received shipments of prey bones from field researchers studying wild wolf packs. These projects introduced me to the effects different carnivore species have on large-mammal bones. I soon saw that captive carnivores, without a need to hunt and with no competition from other species, affected bones differently than did wild conspecifics (Haynes, 1981: 102–103; Haynes 1982: 268–269). This kind of observation is important because it shows that carnivore effects on fossil bones also need not have been unimodal, and would have varied for ecologically significant reasons, such as differential predation success due to changing prey vulnerability, changes in the intensity of gnaw-damage to carcass bones due to varying prey availability (see Nagaoka, 2015), or carnivore reactions to greater or lesser feeding competition.

The recent re-discovery of differences between modifications made by wild and captive carnivores is briefly discussed below in this paper's last section.

3. Fieldwork: background

3.1. North America and Australia

My actualistic fieldwork in North America was a twice-yearly search for carnivore killsites of large mammals. Fig. 1 shows the

E-mail address: gahaynes@unr.edu.

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Table 1
North American carcasses or skeletal occurrences studied most intensively in the 1970s and 1980s, updated from Haynes (1983b: 104, Table 1).

Taxon	Cause of death	Number of bone sites
Alces alces (moose)	Confirmed wolf kill	14
A. alces	Suspected wolf kill	2
A. alces	Winter death; scavenged by wolves and black bear	2
A. alces	Unknown	7
Bison bison (bison)	Confirmed wolf kill	27
B. bison	Suspected wolf kill	9
B. bison	Mass drowning	43 (and 15 other suspected drowning occurrences)
B. bison	Poached, disease deaths, died during disease control activities	95
Ursus americanus (black bear)	Killed by wolves? Partly eaten by wolves	2
Canis lupus (wolf)	Killed by wolves, uneaten	5
Vulpes vulpes (grey fox)	Killed by wolves, uneaten	4
Urocyon cinereargenteus (red fox)	Suspected wolf kill, uneaten	3
Total		**228**

Table 2
Carcass and skeletal sites examined in most detail in African wilderness areas, from a wide range of mostly natural deaths (predation, disease, starvation, intraspecific conflict, etc.) plus elephant-control shootings, occurring 1972–1987. The counts do not include many other bonesites that were only briefly observed, including >200 more elephant carcasses and skeletons.

Genus (common name)	Number of bone sites
Loxodonta (elephant)	821
Giraffa (giraffe)	39
Syncerus (Cape buffalo)	274
Hippopotamus (hippo)	2
Ceratotherium (White rhino)	4
Taurotragus (eland)	4
Equus (zebra)	27
Aepyceros (impala)	62
Papio (baboon)	12
Tragelaphus (kudu)	28
Hippotragus (sable)	8
Sylvicapra (duiker)	3
Oryx (gemsbok)	6
Antidorcas (springbok)	13
Phacochoerus (warthog)	14
Crocuta (hyena)	7
Panthera (lion)	3
Connochaetes (wildebeest)	51
Canis (jackal)	5
Lycaon (Wild dog)	1
Ictonyx (polecat)	1
Mellivora (Honey badger)	2
Total	**1387**

main fieldwork areas. I began with a study of whitetail deer (*Odocoileus virginianus*) killed by packs of wolves (*Canis lupus*) having 3–6 members in northern Minnesota, where often few bones were left at kills (Fig. 2) (Haynes, 1980), and progressed to moose (*Alces alces*) in Isle Royale National Park and bison (*Bison bison*) in Wood Buffalo National Park killed by wolf packs with up to 16 members. I also examined skeletal sites from winter deaths and mass drownings. The North American fieldwork was facilitated by wildlife researchers who had been monitoring wild wolves with radio-telemetry for years to determine their impact on ungulate populations (Mech, 1970, 1973a,b; Mech and Frenzel, 1971; Peterson, 1975, 1977 [and many later annual reports authored/co-authored by R.O. Peterson]; Carbyn et al., 1977, 1981; Mech and Karns, 1977; Allen, 1979; Peterson and Scheidler, 1979; Oosenbrug and Carbyn, 1980; Oosenbrug et al., 1980a,b; Carbyn and Trottier, 1988).

During the field work I often flew in the one-passenger airplanes used to track the radio-collared wolves, and from the air I observed wolves chasing and attacking prey animals or feeding on fresh kills. Figs. 3 and 4 are maps of winter wolf-kills analyzed in my doctoral dissertation (Haynes, 1981: 108–336).

Most of my North American fieldwork took place in Wood Buffalo National Park, the second largest national park in the world (~45,000 km^2) and the last place on earth (at that time) where wolves preferentially and regularly preyed on free-roaming bison. I was in the field in winters when wolf predation was frequent and easier to observe, and I traveled by snowmobile to record the carcasses as soon as wolves left the killsites (Fig. 5). I also made repeat visits on foot to prey sites later in the year to map and record bone modifications and skeletal part representation (Fig. 6). I was mostly alone in summers, on foot and unarmed, in roadless country where I had to be dropped off by single-engine airplane or helicopter, and picked up again in a week or two. I had no radio, no cellphones in those days, and no GPS. At times I watched wolves testing or chasing bison groups, and every now and then I came face to face with curious but cautious wolves which backed off when I spoke to them. I walked dozens of miles, filled up two field notebooks each year, and spent hours boiling water to make it safe to drink. I collected gnawed and broken limb bones and also a sample of bison hemi-mandibles, from which I extracted first molars to section for counting cementum annuli, so I could reliably determine the ages of dead bison (Haynes, 1984).

Two short seasons of fieldwork on bonesites were also undertaken in central Australia, where wildlife officers had recorded large drought-related die-offs of feral horses (*Equus caballus*) in 1984–1986, and behavioral studies were being done of feral camels (*Camelus dromedarius*) (Dörges and Heucke, n.d.). Haynes (1985: 10–14) briefly summarized results of the Australian study.

3.2. Africa

After 1982, I spent more time on studies of the animal-bone rain in parts of southern Africa, particularly Hwange National Park, Zimbabwe, one of Africa's largest protected areas (Fig. 7). In the 1980s and into the 1990s most of it was still very remote wilderness. The difference between bone rain there and in the North American study areas was immediately noticeable. While wet-season predation was mostly done on individual large ungulates in Hwange's upland locales, away from water bodies, a common pattern also in North America, much more predation in the dry season was done serially around Hwange's point sources of water, frequently producing overlapping and commingled skeletal sites.

I used a 4-wheel drive vehicle to visit as many water sources as possible, and walked many kilometers of transects, streamway borders, and quadrats. Bone dispersal at predator kills was greater in Africa, due to aggressively competitive feeding by carnivores such as spotted hyenas (*Crocuta crocuta*) and jackals (*Canis mesomelas* and *C. adjustus*). Table 2 shows the number of bone sites that I examined in most detail, usually more than once, during the most intensive period of actualistic fieldwork in Africa, up to 1987. Table 2 includes natural deaths and also a sample of elephants that I witnessed being shot and butchered during government-

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