

Chapter 5

Building Links Between Ecology and Paleontology Using Taphonomic Studies of Recent Vertebrate Communities

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Abstract Ecologists and paleontologists share a common interest in the natural cycles of life and death, but their viewpoints on living organisms and the processes that recycle or preserve their remains are different. The goal of this chapter is to explore the common ground between these fields through taphonomy, the sub-field of paleontology that examines how organisms are preserved as fossils. From studies of recent bone assemblages, taphonomists have assembled information about diversity and abundance, animal behaviour, predator–prey interactions, habitat utilization, mortality (how and where animals die), and nutrient recycling. These studies were initiated to strengthen paleontological understanding of the information content and biases in the fossil record, but the methods and discoveries of taphonomic research in modern ecosystems are also of potential value to ecologists. Both paleontology and ecology would benefit from increased exchange of ideas and perspectives, and this chapter provides examples showing why such exchange is worth pursuing and offers suggestions to encourage future dialogue and collaboration.

Keywords Taphonomy • Vertebrate • Actualistic • Paleoecology • Bone surveys • Diversity • Ecological baselines

5.1 Introduction

Taphonomy focuses on the transition of organic remains from the biosphere to the lithosphere. An important stage of that transition falls squarely in the realm of ecology, specifically the “decomposer” part the natural cycle of life (Fig. 5.1). With an eye

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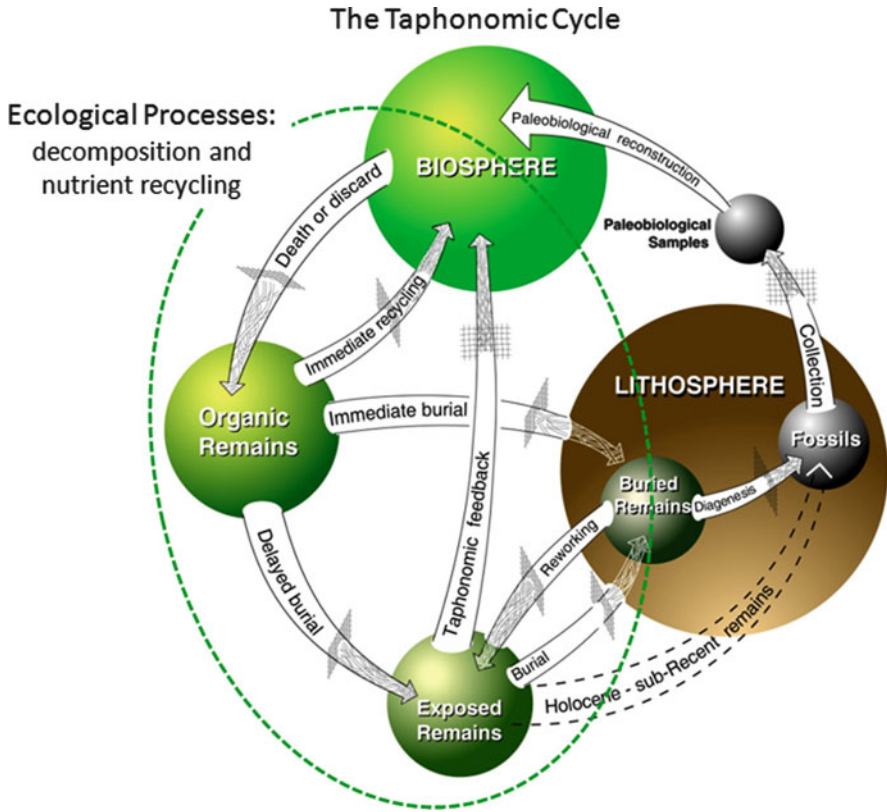


Fig. 5.1 The taphonomic cycle, showing different pathways for dead or discarded organic remains as they are either recycled (destroyed) or survive to go on to the next stage in the transition from biosphere to lithosphere. Filters on the arrows indicate processes that change the biological and ecological information between the different stages. The “decomposer” portion of ecological carbon, nitrogen, and sulphur cycles plays a critical role in determining the nature and effectiveness of these filters (Adapted from Behrensmeier et al. 2000 Fig. 1)

toward understanding biases in the fossil record, taphonomists investigate biological, chemical and physical processes that either destroy remains or transform them into fossils. While ecologists are aware of the functional significance of bones and teeth, they generally are not informed about taphonomic research and its potential for increased understanding of nutrient recycling. In addition, taphonomists are learning that the remains of the dead can provide a wealth of information about the living, some of which is difficult or even impossible for ecologists to sample from current populations. Recent changes in ecosystems over years to decades can be addressed by studying skeletal remains on the ground surface when live census records are incomplete or absent. This is of great potential importance to conservationists as well as ecologists planning long-term strategies to sustain biodiversity, since time-depth is critical to understanding the historical components of community structure and population dynamics.

In spite of many areas of overlapping interest and research, as well as increasing collaboration on late Pleistocene-Holocene paleoecology, ecologists and paleobiologists continue to occupy mostly separate intellectual arenas. Early naturalists were less constrained by the boundaries of scientific fields and more open to what we would now regard as interdisciplinary leaps of insight (Wilkinson 2012). Charles Darwin noted the potential paleontological significance of recently dead animals when he commented on clusters of guanacos that he thought might have perished in bad weather near a river in Argentina.

The guanacos appear to have favourite spots for lying down to die. On the banks of the St. Cruz, in certain circumscribed spaces, which were generally bushy, and all near the river, the ground was actually white with bones. On one such spot I counted between ten and twenty heads. I particularly examined the bones; they did not appear, as some scattered ones which I had seen, gnawed or broken, as if dragged together by beasts of prey. The animals in most cases must have crawled, before dying, beneath and amongst the bushes. . . . I mention these trifling circumstances, because in certain cases they might explain the occurrence of a number of uninjured bones in a cave, or buried under alluvial accumulations; and likewise the cause why certain animals are more commonly embedded than others in sedimentary deposits. (Darwin 1860, p. 168)

The field of taphonomy was named by the Russian paleontologist I. A. Efremov in 1940 (Efremov 1940; see Olson 1980 for a review of its early history). Actualistic study of vertebrate remains was pioneered by Johannes Weigelt, a German paleontologist who surveyed the Gulf Coastal Plain of North America for analogues that would help him interpret fossil vertebrates (Weigelt 1927; translation 1989). The field of “Aktuo-Paleontologie” was further advanced by Wilhelm Schäfer in his comprehensive book on marine ecology and paleoecology (Schäfer 1972). Further advances in actualistic taphonomy (i.e., in modern environments) over recent decades have shown that bone assemblages have much to offer in terms of understanding modern ecosystems. This chapter will provide an overview of information from studies of modern bone assemblages that should be of interest to ecologists as well as to paleobiologists. A thorough treatment of the ecological implications of taphonomic research is not possible within the limits of this chapter. Rather, our goal is to offer examples, commentary, and references that will provide access to the literature and encourage increased exchange among researchers from both fields. We also include an Appendix with guidelines for field surveying of modern bone assemblages.

5.2 Putting the Dead to Work

Using skeletal accumulations to aid understanding of living communities is a relatively new concept for vertebrate ecologists. Karl Flessa of the University of Arizona, Tucson, coined the phrase “Putting the dead to work” for his research on shell beds that record major changes in the ecology of the northern Gulf of California caused by the impact of humans on the flow of the Colorado River

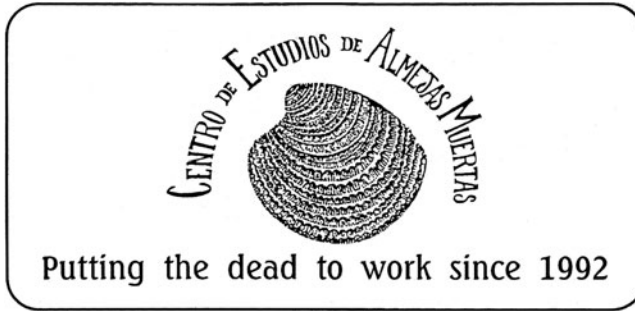


Fig. 5.2 Bumper sticker created by Karl Flessa for his actualistic research project on the invertebrate and vertebrate taphonomy of the Colorado River Delta, Baja, California (Dietl and Flessa 2011)

over the past century (Fig. 5.2) (Dietl and Flessa 2011). Numerous other studies of marine organisms (including “live-dead” research) are being used to document human impact on marine ecosystems (Schöne et al. 2003; Rowell et al. 2008; Flessa 2009; Kidwell 2007, 2009; Kowalewski 2009; Lybolt et al. 2011). This, and earlier research by paleobotanists (Davis 1989, 1991; Huntley 1990, 1991) have established the independent discipline of “Conservation Paleobiology” (Flessa 2002; Dietl and Flessa 2011). The idea of putting the dead to work to increase understanding of recent ecological history and processes applies equally well to vertebrate remains, from small mammals (e.g., Smith et al. 1995; Hadly 1999; Reed et al. 2006; Hadly and Barnosky 2009; Blois et al. 2010; Terry 2010a, b) to large terrestrial mammals (e.g., Lyons and Wagner 2009; Western and Behrensmeier 2009; Miller 2011a) and marine mammals (e.g., Liebig et al. 2003; Pyenson 2011). Simultaneously, such research informs vertebrate paleontologists about ecological processes that control recycling vs. preservation in the early post-mortem environment and how to interpret information that got through these filters. Understanding the taphonomic impact of early post-mortem ecological processes allows paleobiologists to assess biases in fossil assemblages, providing necessary tools for distinguishing ecological signals contained in these assemblages from overprints and noise imposed by processes that lead to destruction and (sometimes) preservation.

The viewpoints of ecologists and paleontologists on processes that interact with dead organisms are two sides of the same coin. Thus, taphonomy can be a unifying conceptual bridge to bring these fields into closer collaboration and mutual understanding. In an effort to help stimulate this discussion, we will describe a series of topics relating to vertebrate taphonomy and examine their implications from both points of view. We will emphasize what has been learned through recent actualistic studies of bone assemblages, as this provides a readily accessible foundation for increased dialogue between ecologists and paleontologists.

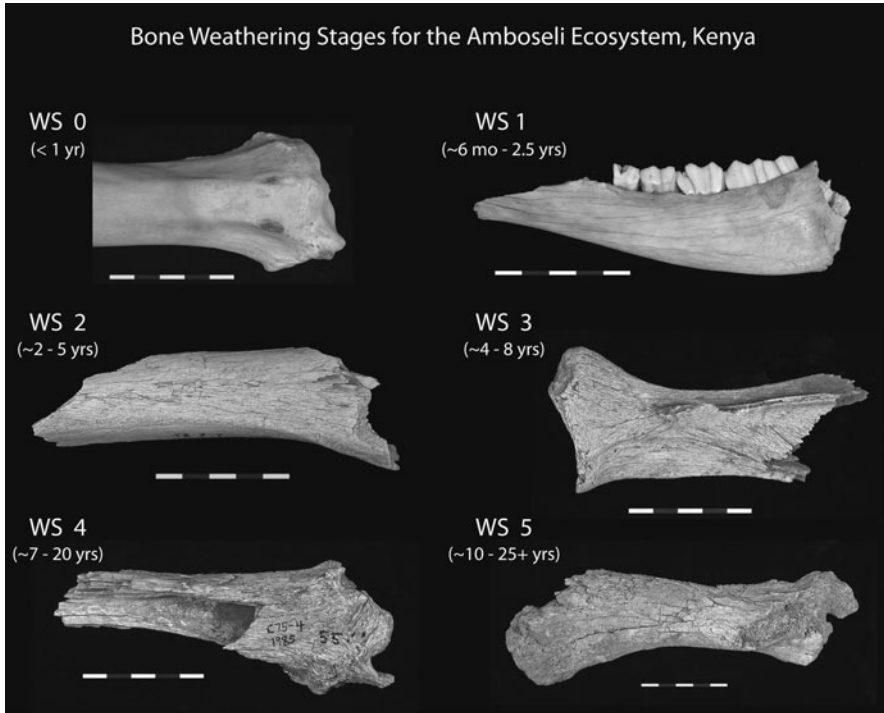


Fig. 5.3 Bones showing the progressive weathering stages: WS 0 (unweathered), WS 1 (fine cracking), WS 2 (flaking of surface bone), WS 3 (revealing fibrous inner bone), WS 4 (spalling and deep cracking), and WS 5 (fragile, degraded, falling apart); see Behrensmeier 1978 for details and other examples. The approximate years represented by each weathering stage are for bones exposed to full sun on the ground surface in Amboseli's tropical, semi-arid climate (Behrensmeier and Faith 2006 and Behrensmeier unpublished data). Scale in centimetres

5.3 Useful Information from Bone Taphonomy

5.3.1 Bone Weathering

Bones on the ground surface weather or decompose at rates that are predictable for a given climate and exposure situation. Sequential weathering stages based on simple morphological criteria can be used to estimate the years since death (Behrensmeier 1978) (Fig. 5.3). This makes bone weathering stages rough but useful “taphonomic clocks”—a tool that allows ecologists and conservationists to assess change over years to decades in animal populations. The descriptive weathering stages reflect the gradual weakening of bone structural components that are similar across vertebrate classes. Mammals are best known in this respect, but limited research on birds, reptiles, and bony fish indicates that, with some caution, the six-stage weathering classification can also be applied to these groups as well (e.g., Brand et al. 2003; Behrensmeier et al. 2003).

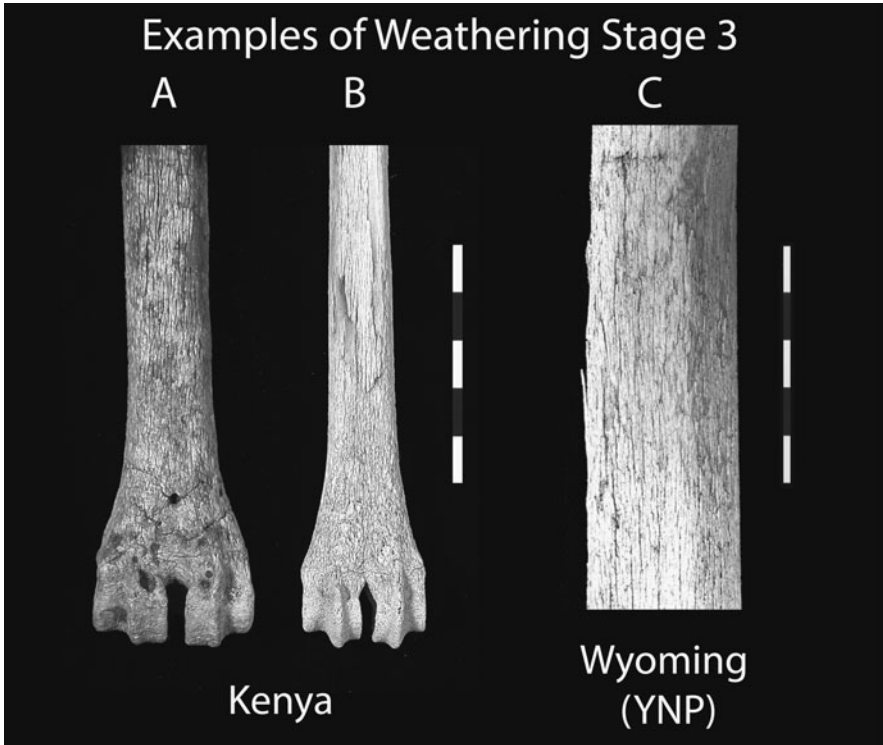


Fig. 5.4 Examples of bones in Weathering Stage 3. (a) Fossil artiodactyl metapodial from East Turkana, Kenya (Pleistocene); (b) Modern metapodial with WS 3 surface very similar in surface texture to (a) note remaining patch of WS 2 on shaft; (c) Modern elk metatarsal from the temperate climate of Yellowstone National Park, Wyoming, showing characteristic WS 3 surface texture. Scales in centimetres

Bones weather much faster in tropical environments than in temperate or arctic ones (Andrews 1995; Andrews and Armour-Chelu 1998; Meldgaard 1986; Sutcliff and Blake 2000; Janjua and Rogers 2008; Miller 2009), but the descriptive stages are more-or-less consistent across latitudes (Fig. 5.4). In Amboseli National Park, a semi-arid tropical ecosystem, surface bones are subjected to intense sunlight and seasonal fluctuations in moisture and temperature (Behrensmeier 1978) (Figs. 5.3 and 5.4). Rates of weathering differ across body size; in medium-sized ungulates (25–200 kg), bones usually proceed to Weathering Stage (WS) 3–4 within 5–10 years. Bones of very large animals (elephants, rhinos) can last in identifiable form for at least 35 years. Weathering of medium to large mammals in the temperate climate of Yellowstone National Park appears to stall at WS 3 (Miller 2009) and bones may survive, without burial, for over a 100 years (Miller 2011a). The effects of relatively consistent moisture and seasonal freezing on bone weathering have yet to be experimentally studied. Variation in the micro-environment of surface bones can greatly affect weathering rates, including the up versus down side (with respect

to the substrate) of the same bone. Protection from direct sunlight (and associated UV damage to organic components) slows down the weathering process, while precipitation of salts from the underlying substrate can accelerate weathering (Behrensmeyer 1978).

Paleontologists and archeologists originally studied weathering stages in order to determine natural rates of destruction of bones on land surfaces (Isaac 1967; Behrensmeyer 1978; Lyman 1994). Paleontologists are interested in recognizing pre-burial weathering in fossil bones as evidence of surface exposure prior to burial. Weathering stages can be problematic in fossils because post-burial weathering, diagenetic cracking, and post-exposure damage on outcrop surfaces can cause similar surface damage or obscure original weathering features. In modern bones, however, the descriptive categories have been tested by many different workers, are reproducible, and could be readily adopted by ecologists. Two important caveats regarding the method are: (1) rates of weathering should be calibrated within each study area (not assumed based on other areas), and (2) only exposed (not shaded) bones should be used to calibrate the maximum weathering rates for any given climatic regime.

5.3.2 *Natural Bone Concentrations*

Bone concentrations in dens, lairs, pellets, or faeces represent a point source of information about species in an ecosystem as well as predator size and behaviour. The remains of small vertebrates accumulated by predators in owl pellets are a relatively faithful sample of prey species within the size range and geographic area accessible to any particular species (Andrews 1990; Reed 2007; Terry 2010a, b). This may also be true for prey species found in other raptor bone concentrations (Stewart et al. 1999; Trepani et al. 2005) or in carnivore faeces but has not been documented as well as for owls. These bone accumulations may be time-averaged over days to decades or even millennia in the case of cave accumulations (Terry 2008; Graham et al. 2011). In situations where bones are exposed to natural weathering, the time-averaging interval should be shorter for small bones than for large ones because of slower destruction rates for the latter. Hyena dens and leopard lairs have received considerable taphonomic attention as analogues for past bone concentrations, both in terms of the species represented and damage patterns displayed by skeletal parts (e.g., Brain 1981; Hill 1989; Pickering et al. 2004; Lansing et al. 2009).

Paleontologists are especially interested in causes of mortality that generate dense bone concentrations – i.e., bonebeds (Rogers et al. 2007). Bonebeds are often sources for more complete anatomical information as well as clues about population demography, herding behaviour and other attributes and vulnerabilities of extinct species. Many bonebeds represent mass mortality events (e.g., Voorhies 1969, 1992), but others are formed through attritional bone accumulation and sedimentary processes or circumstances that concentrate the remains in restricted areas, such as caves and fissures, as well as stratigraphic condensation of reworked skeletal material at sedimentary (sequence) boundaries (Rogers and Kidwell 2000).

Although mass mortality events may be uncommon by ecological standards, they likely contribute a disproportionate amount of information to vertebrate paleontology and paleoecology, mainly because unusual death events overwhelm the recycling capacity of decomposers, resulting in relatively complete specimens. Such events also may be associated with uncommon geological processes (e.g., flooding, volcanic eruptions) leading to rapid burial.

5.3.3 Demographic Information

Ecologists can assess the demography of a standing population of live animals through direct examination of individuals or general categorization of juveniles vs. adults, males and females. Capturing or observing the living is considerably more time and labour intensive than surveying the dead and recording skeletal fusion and dental eruption stages. Many ecologists, of course, are well aware of the value of examining the remains of dead animals for evidence of health issues, predators and age at death, but they generally work with individual species rather than taking a broader approach to learning from multi-species mortality patterns (see Green et al. 1997 for an exception). There is a wealth of information about the living population as well as the dead in skeletal remains and teeth, and this could be a valuable resource for ecologists and conservationists. Under stable conditions of turnover (balanced birth and death rates), the dead provide information on the age structure of the living population (Lyman 1994) and also which age cohorts may be more vulnerable to predation (Behrensmeyer 1993). Live and dead census data for the same community can be compared to look for shifts in the mortality profiles that indicate a species in decline vs. increase (Terry 2010a; Miller 2011a).

5.3.4 Discarded Skeletal Remains

Mammals lose deciduous teeth as they grow, and reptile and fish (e.g., shark) teeth are shed and replaced constantly during life. Cervid antlers are shed and regrown annually, and elephants lose their molars and often parts of their tusks throughout their lives. Broken elephant tusk fragments are an indicator of intra-species conflict and have been linked to population stress, as can happen during times of drought around waterholes (Haynes 1988). Female caribou lose their antlers within days of giving birth, thus concentrations of shed antlers are a taphonomic signature of birthing grounds (Miller 2011b, c). Such accumulations occur in different places in different stages of decomposition (weathering), which can show how calving grounds have shifted over time. Most cervids grow and shed antlers in particular seasons, thus providing evidence for seasonal habitat utilization (Miller 2008). Basal measurements of shed crocodylian teeth can be used to track habitat use by individuals of different size and life stage (Bir et al. 2002). It is important to

remember, when considering relative abundance of species in either the actualistic or fossil record, that some species may produce many more preservable parts per individual than others that only lose their hard parts when they die.

5.3.5 Bone Modification

This term refers to many different types of damage that alter bones and bone surfaces, including breakage, tooth and tool marks, insect excavations, etching by acid (gastric and otherwise), trampling, various types of physical abrasion (by wind, water, or sediment), and internal microscopic tunnelling by fungi and bacteria. Many of these modifications represent distinctive signatures of a particular agent or process while others are harder to interpret. Single bones may bear the marks of one or many different types of modification that occurred soon after death, and depending on how long they remain on the surface, can acquire a succession of modification traces. Thus, a single bone may be broken and chewed by carnivores, weathered to WS 1, gnawed by rodents, and have its lower side burrowed into by termites prior to burial. Such features can be used to reconstruct the post-mortem history of a bone or carcass, analogous to a forensic investigation of human remains, and the resulting information is useful to both paleobiologists and ecologists. Early post-mortem surface modification is best recorded on unweathered bones and gradually disappears as the bone is weathered or abraded. In the fossil record, there are added complications: (1) bone modification features may have no modern analogue, representing extinct bone-modifying agents, and (2) burial, diagenesis, and destructive processes that occur as bones are naturally exhumed onto outcrop surfaces or uncovered by excavation can overprint pre-fossilization modification traces. In any quantitative assessment of bone modification on recent or fossil bones, such as the frequency of tooth marks on limb elements, it is critical to control for the specimens, and parts of specimens, that are well-preserved enough to record the presence or absence of such modification (e.g., Marean and Spencer 1991; Blumenschine et al. 1996; Faith 2007; Faith et al. 2007).

Bone breakage imparts distinctive features that can indicate the agent and timing of fracturing. Bones of large animals (e.g., >15 kg) are physically tough and not easily broken; it takes considerable force to fracture an unweathered limb element of a wildebeest or other ungulate. Agencies capable of such force include bone-crushing carnivores, humans with implements, or trampling on a firm substrate. These processes can also preferentially destroy low density limb ends, resulting in characteristic patterns of survival of proximal, distal, and shaft components (e.g., Marean et al. 2004; Faith et al. 2007). Fracture surfaces of fresh bones have distinctive morphologies, such as spiral and saw-toothed patterns resulting from the retained tensile strength of their organic matrix. Once bones are weathered to WS 2 and beyond, bone collagen has decayed to the point where breaks tend to follow cracks and become more stepped (perpendicular to bone fiber direction) and splintered. Contrary to popular belief, fluvial transport generally does not break

relatively fresh bones, whatever their size or major taxonomic group (Aslan and Behrensmeyer 1996). However, once weakened by sub-aerial weathering or sub-aquatic decay, transport by wind, water, or mudflow can break bones as well as disperse and abrade them (Behrensmeyer unpublished data).

5.3.6 *Footprints and Trackways*

Animal tracks are worth including in this overview because they are instantaneous records of animal behaviour and faunal associations, and because they are of interest to both ecologists and paleontologists. Actualistic research on tracks and their taphonomy include both experimental and field studies (e.g., Laporte and Behrensmeyer 1980; Cohen et al. 1991). In modern ecosystems, it is usually not too difficult to identify the track-maker, whereas in the fossil record, tracks are given their own Latin names (ichnotaxa) because of the uncertainties in positively identifying the track-maker. Ecologists value the knowledge of expert trackers in studies of animal behavior, and there have been a number of collaborations between trackers and paleontologists seeking to understand tracks and trails left by extinct species (including early humans) (Hay and Leakey 1982; Leakey and Harris 1987). This is yet another point of contact between ecology and paleontology that could be explored in the future.

5.4 Ecological Information from Dispersed Surface Bones

5.4.1 *Species Richness*

The most basic measure of diversity is the number of species present in a community – i.e., species richness. Aside from the newly developed method of assessing diversity using aDNA in soils (“metagenomics”; e.g., Poinar et al. 2006), measuring diversity involves counting animal species in a community or ecosystem using systematic visual censuses (air and ground), collecting and trapping, and/or compilation of anecdotal sighting and historical records. Rarely are censuses taken of all vertebrate species in an ecosystem; rather, target groups are usually vertebrate classes, or orders within a single class, such as Mammalia, and often further restricted to size ranges within these (e.g., macro vs. micro-mammals). Taphonomic surveys, in contrast, can theoretically sample the remains of all species dying in an ecosystem, as well as document shed or discarded materials such as eggshells, antlers, tusk fragments, regurgitated pellets and faeces. In recent taphonomic surveys in Africa, species that were unknown from live census data turned up in the bone assemblage, including domestic animals that were illegally brought into national parks to graze (Odock 2011).

There are, of course, limitations on diversity sampling using dead and discarded skeletal remains. These include differential rates of bone recycling (how fast they disappear), their visibility in different types of habitats, and the observer’s ability to

identify the original owner of any given skeletal part, tooth, or other trace. The latter issue is an obvious dividing line between vertebrate paleontologists and zooarcheologists, with their training in identifying bones and species from fragmentary fossils, and ecologists, who know the living organisms but may have limited expertise in recognizing their internal hard parts. Identification of most vertebrate species using bones and teeth is not difficult, given appropriate training and comparative osteological collections. More problematic is distinguishing species that have very similar skeletal or dental morphology, such as many types of micromammals. Paleobiologists are used to dealing with genera rather than species in assessing diversity, but most ecologists would consider that a serious limitation in building a record of richness for a living community. Bird, reptile, and fish species can also be difficult to distinguish based on isolated bones, although higher taxonomic levels usually are identifiable, depending on the skeletal part.

5.4.2 Species Abundance

Determining species abundances allows many useful characterizations of diversity that are important in population ecology, community structure, and measures of environmental and human impact on vertebrate faunas. Again, ecologists rely on various methods of censusing to assess absolute or relative abundance within particular groups, such as large or small mammals, birds, etc. Taphonomists gather information on the number of individuals of all animals represented in their surveys – referred to as MNI (Minimum Number of Individuals). This number is an estimate rather than a direct count because of the dispersed and taphonomically altered nature of carcass remains on a land surface. There are various approaches to calculating MNI (e.g., Behrensmeyer 1991; Lyman 1994). Also, the relative numbers of MNIs for different species do not provide a snapshot sample comparable to an ecological census, but rather a time-averaged accumulation of dead animals over a period of years to decades. Nevertheless, MNI counts have proved to be a reliable indicator of relative population abundances for small mammals in the Great Basin ecosystem, USA (Terry 2010a, b), and for large mammals in the ecosystems of Amboseli National Park, Kenya (Western and Behrensmeyer 2009) (Fig. 5.5) and Yellowstone National Park, USA (Miller 2011a).

5.4.3 Causes of Mortality

Taphonomic methods could contribute to ecological studies of animal mortality. While ecologists can observe predation and other types of death in their field studies, these events are relatively rare and hard to document. Taphonomists have access to a much larger sample of mortality events and have developed various criteria to determine probable cause of death. Admittedly, this must be inferred from what

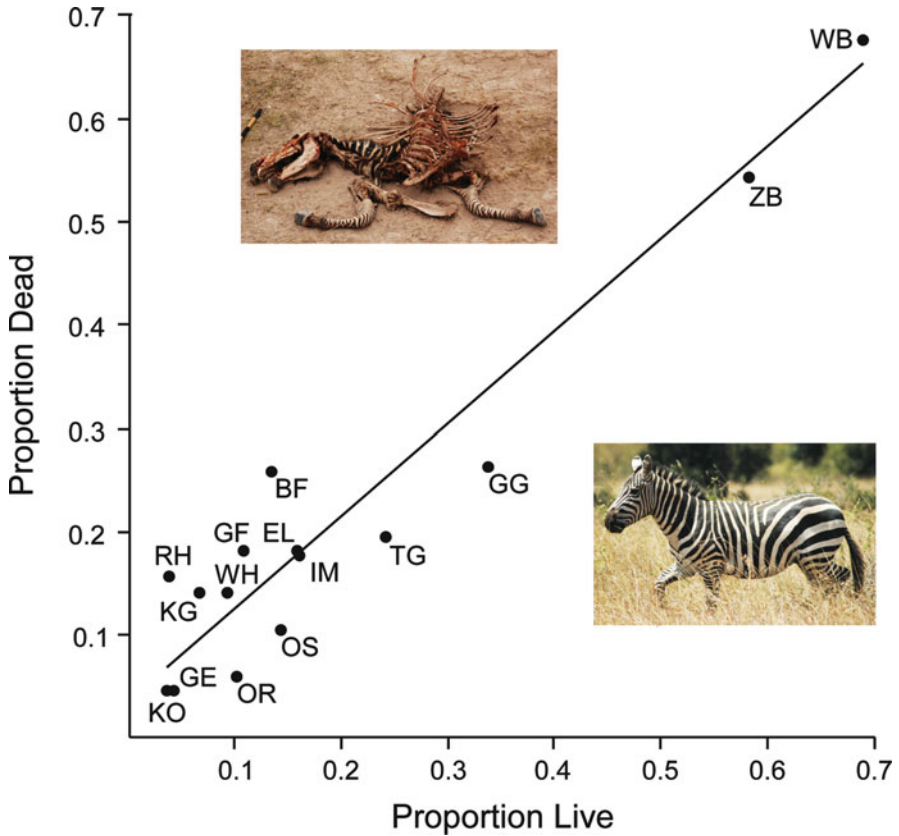


Fig. 5.5 Correlation between live population and carcass abundances for 15 ungulate species >15 kg body weight in Amboseli National Park, Kenya. Coefficient of reduced major axis correlation: $r = 0.9523$, $p < .05$. Totals were summed over the same sampling intervals, 1964–1975 and 1993–2004; $N(\text{live}) = 169,235$ total census counts, $N(\text{dead}) =$ total 1,502 carcass MNI. Key to species: *WB* wildebeest, *ZB* zebra, *GG* Grant's Gazelle, *TG* Thompson's Gazelle, *BF* buffalo, *IM* impala, *EL* elephant, *GF* giraffe, *WH* warthog, *KG* kongoni, *RH* Black rhino, *OS* ostrich, *OR* Oryx, *GE* + gerenuk, *KO* waterbuck. (Modified from Western and Behrensmeier 2009 Fig. 2)

could be termed forensic investigation, but there are clues that can allow a high level of certainty for many carcasses, especially if these are examined early in the post-mortem interval. Thus, in an ecosystem with diverse carnivores (e.g., lion, cheetah, spotted hyenas), a fresh intact carcass indicates death from disease or starvation, while a skeleton with soft tissues removed and intact limb bones is evidence for a felid predator rather than a hyena. When bone-consuming scavengers such as hyenas are abundant and have early access to a carcass, it is often impossible to determine the original predator, although tooth marks and skeletal part survival patterns can provide evidence for the sequence of carcass consumers (e.g., Cleghorn and Marean 2007). As predators, modern humans can leave distinctive marks on bones that are

easily interpreted by taphonomists (e.g., knife marks, bullet holes). Criteria have also been proposed to differentiate more subtle damage patterns inflicted by early stone-wielding hominins from those of other meat-eaters (Brain 1981; Blumenschine et al. 1996).

5.4.4 *Where Animals Live and Die*

There is a recurring story in the popular literature about “elephant graveyards” and other places where animals “go to die.” Darwin (1860) even mentions that this was proposed by locals to explain the massed guanaco remains, though he inferred that their deaths occurred during a winter storm. These stories likely originate from observations of real phenomena such as mass mortality events, or attritional bone accumulations around watering holes. Such obvious sites of localized mortality have their own taphonomic stories to tell about the circumstances and the animals involved. However, the spatial patterning of dispersed skeletal remains can provide more general ecological information about places and habitats where animals are dying, the role of predators, and seasonal behaviour patterns in the living populations. The study of surface bones in Amboseli National Park, Kenya, shows that resident species such as impala live and die in the same habitat, but migratory species such as wildebeest have carcass distributions that differ from the spatial patterns recorded in live censuses (Fig. 5.6) (Behrensmeyer et al. 1979; Behrensmeyer and Dechant Boaz 1980). During the dry season when wildebeest are abundant in the Park, they also move into the lush grazing of the swamp habitat by day and out to the plains at night, behaviour that is interpreted as a predator avoidance strategy (D. Western pers. comm.). Carcasses of wildebeest occur in all habitats but are abundant in the swamp edge and the plains, indicating that the bone distribution is skewed toward areas of greater vulnerability to predation (Behrensmeyer et al. 1979). In another actualistic study, bone distributions tracked changes in seasonal landscape use by live elk in Yellowstone National Park, including correctly identifying calving areas and bull elk wintering grounds from concentrations of neonatal skeletons and shed antlers respectively (Miller 2008).

This actualistic research provides vertebrate paleontologists with increased understanding of ecological information recorded by bone accumulations and how this information passes through the initial taphonomic filters leading to the fossil record – particularly for large, mobile animals. The benefit for ecologists is the realization that taphonomic data could provide important evidence for animal populations and their landscape use that may be unavailable from standard censusing methods. While GPS collars on animals provide the opportunity to examine geographic use on ultra-fine time-scales, deployment is often limited to a few individuals within a community, and establishing long-term variability takes many years or decades of study. Aerial surveys have a longer history of legacy data to draw upon, though such surveys primarily reveal diurnal behavior, and reactions to survey aircraft by target species may impact the data. A strength of bone survey

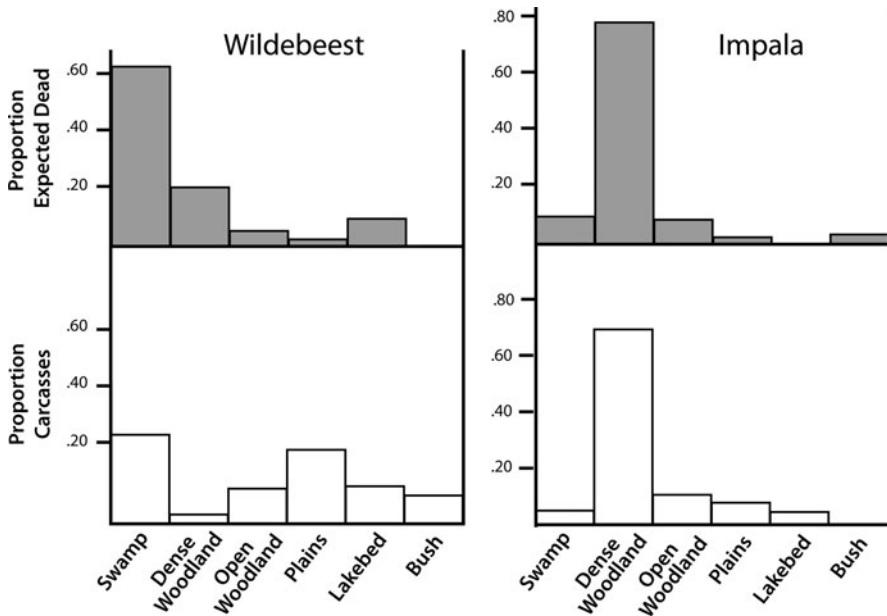


Fig. 5.6 Contrast between the habitat distribution of live populations and skeletal remains of two ungulate species in Amboseli National Park, Kenya. Proportion of expected dead is calculated based on the live population counts in each habitat and the species' annual turnover rate. Proportions of dead are based on MNI in each habitat. Wildebeest migrate out of the basin seasonally and also move between habitats diurnally. Live censuses record high wildebeest abundance in the swamp habitat where they feed during the day. Skeletal remains record relatively high abundance in both the swamp and plains habitats, where predation occurs during the day (swamp) and night (plains). Impala are resident species closely tied to the dense woodland habitat, and this is reflected in the spatial similarity of their live and dead abundances. (Modified from Behrensmeier et al. 1979 Fig. 5)

data is that it is averaged over many years to decades (or more) of biological input and, thus, may incorporate ecological variability over extended time-scales. Particularly for regions with limited historical data, bone surveys can provide readily accessible baselines on landscape use for comparisons to patterns of live populations.

5.4.5 *Carnivore Behavior and Impact on Prey Populations*

Bones record various aspects of the interaction of carnivores with prey populations and could be put to work by ecologists as a tool for assessing the impact of predators on their prey. In general, the more complete the utilization of carcasses – how disarticulated and damaged they are – the greater the predator pressure on the prey animals. This has been demonstrated in a long-term taphonomic study in Amboseli



Fig. 5.7 Examples of bone modification from Amboseli National Park, Kenya. *Top row* shows two distal wildebeest humeri with broken shafts; *right-most* has been chewed from the ends. The *lower image* shows a zebra mandible severely reduced by chewing; note scalloped edges and tooth scoring. Damage is attributed to spotted hyenas (*Crocuta crocuta*). These specimens were collected in 2002–2004 when hyena population levels were high and intraspecific competition for carcasses intense

National Park, Kenya, where a marked increase in the population of spotted hyenas (*Crocuta crocuta*) in the 1990s resulted in a ~75% decrease in the number of bones per individual in the surface assemblage (Behrensmeier 2007; Watts and Holekamp 2008). Many other taphonomic studies have documented the types of damage characteristic of different carnivores (e.g., Brain 1981; Hill and Behrensmeier 1984; Marean et al. 1992; Pickering et al. 2004), especially their ability to disarticulate, break and consume bones and leave distinctive tooth marks and other surface damage (Fig. 5.7). Bone-consuming specialists such as hyenas leave taphonomic evidence of fluctuations in predator vs. prey populations

(Faith and Behrensmeyer 2006), but this should also be detectable for other types of carnivores. In any given vertebrate community, the pressure for utilizing animal protein should be reflected in the degree of disarticulation and bone scatter from individual carcasses, the survival of more consumable (delicate) bones, and damage to the larger skeletal elements. Of course, this type of evidence also depends on the size ratio of predator to the prey; larger prey animals may suffer little damage, while smaller or juvenile individuals may be completely consumed (although their bones could occur in raptor pellets or mammalian faeces).

Carnivores are relatively rare, often nocturnal, and hard to observe, thus the taphonomic records they leave in the remains of their prey animals could be a valuable addition to ecological methods used for assessing modern carnivore populations. Comparisons of the spatial distribution of skeletal remains with habitat use by the living populations of the same species for the same time period is a potentially powerful tool for examining the role of predation in controlling resource utilization across an ecosystem.

5.4.6 Documenting Ecosystem Stability or Change

Given a sample of surface bones in different weathering stages, it is possible to divide this sample into subsets representing older and younger contributions to the death assemblage. This provides a potentially powerful tool for looking back in time for changes in community structure, species richness, habitat utilization, and predator–prey interactions. Ideally, the years represented by each weathering stage could be calibrated to establish six subsets corresponding to the weathering stages (Fig. 5.3) (Behrensmeyer 1978; Cutler et al. 1999). In reality, however, variability in the time bones spend in any given stage blurs temporal resolution, so that some bones from the same time of death are in WS 1 while others may be in WS 2. On the other hand, there is minimal overlap in years since death (at least for known examples) of WS 0–2 and WS 3–5. Thus, it is advisable to combine the samples into three (WS 0–1, 2–3, 4–5) or two (WS 0–2, 3–5) groups. The latter option provides the highest confidence for separation of older and younger components of the bone assemblage and permits comparisons of species abundances and habitat distributions from different times, usually across years to decades. For the Amboseli bone assemblage, this showed significant change over four decades in the proportions of browsers and mixed-feeders relative to grazers and also shifts in the composition of sub-communities in different habitats (Western and Behrensmeyer 2009).

Many land ecosystems lack reliable records for animal population shifts over the recent past. Ecologists in need of such historical data should consider adopting surveys of surface bones and their weathering stages as a way to “back-census” vertebrate communities. This approach is already being used to aid in conservation assessment in various areas of Kenya (Faith 2008; Odock 2011) and the Arctic National Wildlife Refuge (Miller 2011b, c).

5.4.7 Nutrient Recycling

Nutrient recycling provides a unifying concept for ecology and paleontology. What gets recycled in the early post-mortem environment doesn't become part of the fossil record, and what avoids immediate recycling at least has a chance at becoming fossilized. The effectiveness of the decomposer portion of the ecological cycle thus is critical in shaping the fossil record, from the scale of individual organisms to the fauna and flora of an entire biome. From the moment an animal dies, internal and external micro- and macro-organisms compete for the available nutrients, including both soft tissues and mineralized body parts. Ecologists see rapid and efficient recycling of nutrients from dead organisms as an indicator of a healthy, well-balanced ecosystem. Taphonomists see efficient recycling as fatal to any hope of a fossil record and look for circumstances that help organic remains escape the biological processes that have evolved to break down these remains. Such circumstances include mummification in arid environments, rapid permanent burial (e.g., the "Pompeii effect"), oversupply of remains relative to recycling capacity of the local biota, and even pre-burial mineralization (Trueman et al. 2004). Biotic recycling continues in the buried environment (e.g., soil) unless shut down by unfavourable chemical conditions (anoxia, water saturation, deep burial), or stymied by rapid mineralization of hard tissues.

The study of nutrient recycling from large vertebrate carcasses has attracted the interest of ecologists as well as forensic scientists. In one notable example, a study by Bump et al. (2009a, b) used 50 years of data on moose mortality on Isle Royale (Lake Superior, North America) to show how shifting focal areas of wolf predation helped to shape the island's vegetation structure over decades through the fertilizing and other effects of carcass decomposition.

Given the complexity and power of ecological recycling, it may seem surprising that anything survives to become fossilized, but the diversity and richness of the vertebrate fossil record attests to the fact that the recycling filters are imperfect and equilibrium is rarely, if ever, achieved in energy transfer through the natural cycle of life and death. A continuing question for taphonomy, and vertebrate paleontology, is how the record that escaped recycling represents the much greater numbers of organisms that didn't.

5.5 Enhancing Links Between Paleontology and Ecology

5.5.1 What Taphonomy Could Do for Ecology

Ecological models of the carbon, nitrogen, and sulfur cycles show "dead organic matter" as a waypoint for nutrients returning to the ecosystem. Through actualistic research on this part of the ecological cycle, taphonomists have learned about a

wide array of biological, chemical and physical processes that leave recognizable signatures on bone assemblages. Skeletal remains hold a wealth of information about the vertebrate species inhabiting an ecosystem, age and condition of the animals at death, mortality relative to habitats frequented by the living animals, the predators and scavengers that utilize the carcasses, and rates of return of nutrients to the soil through decomposition. Bones survive long enough on the landscape to provide years to centuries (or more) of historical information on changes in these variables through time. This source of ecological information has been largely unrecognized by ecologists up to now but has great potential as a tool for monitoring and conservation as well as enhanced understanding of the decomposer part of the ecological cycle.

Taphonomic survey methods are logistically easy and inexpensive ([Appendix A](#)). Assembling a species list from a taphonomic survey does require at least one team member to have the expertise to correctly identify species in the bone assemblage. This is not as daunting as it might first appear; many taphonomists have learned by doing rather than through formal training, with frequent use of museum osteological collections and reference guides to skeletal parts and species.

5.5.2 What Ecology Could Do for Taphonomy and Paleontology

Paleontologists and taphonomists could learn a great deal from ecologists about controls on nutrient recycling, both on land surfaces and in soils, and how these affect what escapes into the fossil record. Ecologists can also help expand our understanding of animal population movements, predator–prey interactions, and the ecogeographic data contained in bone accumulations. Recent growth in the availability of GIS databases containing information on both predator and prey species provides novel opportunities to examine patterns of multi-species landscape use across decadal timescales. Such data could be integrated with the locations of skeletons relative to habitat boundaries, water sources, etc. to build ecosystem-wide understanding of the spatial data contained in bone accumulations.

Ecologists are often expert modellers, extending their thinking from laboratory experiments and localized field samples to broader hypotheses about ecosystem dynamics. Why not turn this talent toward modelling what taphonomic samples of communities and ecosystems would look like over varying amounts of time, under different conditions of species richness, body size distribution, predator prey interactions, and nutrient recycling efficiency? We know enough about taphonomic processes to provide realistic starting conditions for such models, and paleontologists could then collaborate to test how such models match what they find in both modern bone surveys and the fossil record.

5.6 Conclusion

Paleontologists initiated taphonomic studies of modern ecosystems to better understand what we can and cannot know about extinct ecosystems. Through such research we have learned that ecological insights available in modern bone accumulations can also enhance knowledge of living communities and their recent histories. The growing field of conservation paleobiology will continue to work towards broadening this window in modern ecosystems and contribute to management and conservation goals. At the same time, it is clear that unlocking the full complement of ecological data in actualistic taphonomy will require collaboration with scientists working closely with the living communities.

This overview has highlighted some of the ways that taphonomy can contribute to ecology and conservation. It also has suggested how ecological research could provide unifying ideas and modelling expertise that would be very helpful to taphonomy. Clearly there is great potential for future exchange between these fields of study, which also could draw upon expertise and ideas that have been developing independently in zooarcheology, paleoanthropology, forensics, and even agricultural science and metagenomics. Forging links between ecology and paleontology is an ambitious and daunting task, one that has been slow to gather steam in spite of many good intentions over the past decades. Workshops, symposia, cross-disciplinary publishing, guest lectures, and joint teaching of university courses all could help increase interaction between ecologists and paleontologists. However, since most of us are challenged by excesses of information and limitations of time, we suggest that one of the best ways to synergize increased collaboration in the future would be to plan field projects that bring together paleontologists and ecologists to conduct taphonomic bone surveys, set up bone weathering experiments, or tackle other bone-related studies (e.g., relating to nutrient recycling). Based on our experience working at the intersection of paleontology and ecology, we can virtually guarantee that focusing initially on a joint field project would lead to novel insights, enhanced communication, and new research possibilities for all concerned.

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