Taphonomy, pathology, and paleoecology of the terminal Pleistocene Marmes Rockshelter (45FR50) “big elk” (Cervus elaphus), southeastern Washington State, USA

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Abstract: In 1968, remains of what were reported to be a larger-than-modern elk (Cervus elaphus) were recovered from terminal Pleistocene sediments associated with the Marmes Rockshelter archaeological site in southeastern Washington State. Originally thought to have been butchered by humans, it is associated with radiocarbon dates suggesting an age of about 9800 14C years B.P. Taphonomic analysis in 2009 indicates the elk likely died of natural causes during winter months; it was lightly scavenged by carnivores prior to burial from silt-rich spring runoff. The elk suffered from two pathological conditions: one resulting in fusion of the fourth and fifth cervical vertebrae, and the other resulting in excessive bone tissue on the proximal ends of the first ribs, seventh cervical, and first and second thoracic vertebrae. The Marmes elk is larger than modern Rocky Mountain elk (C. e. nelsoni) and is on the large end of the size range of modern Roosevelt elk (C. e. roosevelti). It is also larger than the similarly aged elk skeleton from Three Hills, Alberta. A single elk bone from the Sentinel Gap archaeological site in central Washington State, dated to about 10 200 14C years BP and located 130 km west of Marmes Rockshelter, is the same size as the same bone of the Marmes elk. Terminal Pleistocene elk in eastern Washington likely grew to exceptionally large size as a result of abundant grass at the time, forage that decreased in abundance as Holocene climatic conditions developed.

Introduction

Initially excavated in 1962–64, the archaeological site known as Marmes Rockshelter (official state site number: 45FR50) in southeastern Washington State came to national attention in 1968 when some of the then oldest known hu-
The attention was because the human bones were, at the time, among the (if not the) oldest human remains known in the Americas, and initial interpretations were that the several represented individuals had been the subject of cannibalism (Anonymous 1968b).

The partial skeleton of a North American elk or wapiti (Cervus elaphus) associated with the human remains received less attention and publicity, and apparently raised only a bit of interest from the profession at the time. It was, however, noted almost immediately on discovery, in both the popular literature (Kirk 1968) and the professional literature, that the elk was “larger than those of living representatives in the area today” (Fryxell et al. 1968a, p. 514) and, hence, it came to be known in field notes as the “big elk”. At the time it was reported that “this animal may have been from 10% to 20% taller at the shoulder than the modern elk” (Kirk 1968, p. 57). Later, it was noted in an unpublished report that “the Marmes [big elk] bones averaged some 4% to 5% greater in length and nearly 8% greater in diameter [than a large modern bull elk...]. The Marmes wapiti apparently was about 15% larger than this very large modern specimen” (Gustafson 1983, p. 24). No comparative metric data have ever been presented to substantiate statements about the size of the Marmes big elk.

The elk bones were also originally reported as having been “clearly butchered” by the terminal Pleistocene human occupants of the site (Fryxell et al. 1968b, p. 177). Subsequently, Gustafson and Wegener (2004, p. 314) reported that the elk bones did not appear to represent butchered remains because they “differ from the [local] ‘typical’ pattern” in terms of fragmentation, plus “carnivore activity is clearly indicated.” None of the published and unpublished reports included detailed descriptions of carnivore damage, fragmentation, or morphometry, making it difficult to evaluate any of the interpretations previously offered or to perform comparative analyses with other, similarly aged elk remains from North America (Shackleton and Hills 1977). Further, the remains display pathologies that have not previously been noticed and hence have not been described in the literature. In this paper, the Marmes big elk remains are described in terms of their taphonomic, pathologic, and metric attributes and some of these observations are compared with those made on other like-aged elk remains. Together, attributes of the Marmes-site big elk suggest aspects of local paleoecology at the end of the Pleistocene.

Geological context and age of the elk remains

The majority of the big elk remains lay on a fluviually de-
posed silt layer approximately 4 m beneath the modern ground surface. This silt layer was interpreted by project geoarchaeologist Roald Fryxell to represent an incipient A pedogenic horizon (Hicks 2004). Some of the elk remains were found in sediment excavated by a bulldozer or backhoe such that their precise stratigraphic context is unclear; others were found lying relatively close together, but maps and photographs of the bones in situ indicate only that two thoracic vertebrae were in anatomical (articulated) position relative to one another. The author has determined that these articulated vertebrae were T6 and T7. Some of the specimens from the backhoe trench that lack provenience data clearly articulate with others for which precise information on recovery location is available, suggesting that many of the specimens were stratigraphically associated. The author assumes this was indeed the case for all remains of large elk recovered from the floodplain, even though several remains were recorded as coming from (within?) the incipient A horizon upon which many of the other bones of the big elk reportedly lay. Supposedly, a direct accelerator mass spectrometry radiocarbon date on an astragalus of the big elk was obtained (Gustafson and Wegener 2004, p. 313), but close study of laboratory notes and records indicates that none of the reported radiocarbon dates from the excavations (Hicks 2004, p. 390) can be unequivocally attributed to that astragalus. Catalog, inventory, and specimen numbers either do not align across multiple printed records, or provenience information cannot be aligned across multiple written records.

Three radiocarbon dates, two on bone and one on freshwater pearl mussel shell (*Margaritifera falcata*), are available for the incipient A horizon upon which many of the remains of the large elk lay. These dates are: 9710 ± 40 (Beta-156699, bone); 9820 ± 300 (W-2209, shell); and 9870 ± 50 (Beta-120802, bone). The simple average of these values is 9800 ¹⁴C years BP. Given that many of the bones that were found in place are readily attributed to a single individual, and that many of the bones have the same stratigraphic provenience, it is likely that all of the bones are of the same age. The author presumes that an accurate estimate of the chronometric age of the big elk is 9800 ¹⁴C years BP or a few years younger, given that many (but not all) of the elk remains lay just above, and directly on, the dated stratum.

Taphonomy

The remains of the big elk do not represent an entire skeleton despite the excavation of a surface area of approximately 9 m × 27 m. Within this area, many of the remains were concentrated in two clusters about 4.5 m apart from one another. One cluster was made up mostly of cervical and thoracic vertebrae and ribs; the other consisted of hind-limb elements. No remains of the skull, no teeth, and no parts of the pelvic girdle were recovered (Table 1). The vertebrae clearly articulate with one another in anatomical sequence (Fig. 2). Pathology (see later in the text) of the left and right first ribs matches that on the first and second thoracic vertebrae. The right tibia articulates with the lateral malleolus, naviculo cuboid, one of the calcanei, and the right metatarsal. According to field notes, the right astragalus also articulated with these elements, but it was apparently sacrificed for a radiocarbon date; thus, whether or not it articulates with the remainder of the ankle cannot be determined (these remains are incorrectly described as “left” elements in Gustafson and Wegener 2004, p. 313). The remaining right astragalus articulates with the other right calcaneum and represents a small individual relative to the more complete skeleton referred to as the “big elk” in field notes and publications. These small elk remains are insufficiently well preserved to be metrically compared with the big elk and their state of preservation is a bit different than that of the big elk. They are not considered in detail here, except when they shed light on aspects of the big elk.

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<th>Axial skeleton</th>
<th>Appendicular skeleton</th>
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<td>C1–C2, C4–C7</td>
<td>L femur, proximal and distal ends</td>
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<td>T1–T11</td>
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<td>10 R ribs (includes R1–R6)</td>
<td>L tibia, distal end</td>
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<td>8 L ribs (includes R1–R6)</td>
<td>R and L astragali</td>
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<td>Various rib fragments</td>
<td>R lateral malleolus (distal fibula)</td>
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<td>R calcanei</td>
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<td>R naviculo cuboid</td>
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<td>R metatarsal (proximal half)</td>
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<td>L metatarsal (distal half)</td>
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<td>2 first phalanges, 1 second phalanx</td>
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Note: R, right; L, left

Fragmentation

Gustafson and Wegener (2004, p. 312) indicate that the local “typical” pattern of fragmentation of artiodactyl long bones resulting from human butchering “results in intact joint ends where the shafts had been broken off directly above and below the joint. Carpals and tarsals often are complete and show no signs of cuts, scratches or other alterations. . . . Shattered shaft fragments, often exhibiting spiral fractures, and split or broken phalanges suggest further processing, perhaps for marrow extraction.” It was because of superficial resemblances of the Marmes big elk remains with this fragmentation pattern that it was originally thought the elk had been butchered by humans (Fryxell et al. 1968a; Fryxell and Keel 1969). Gustafson and Wegener (2004, p. 314) later concluded that the big elk had perhaps not been butchered by early human hunters because “most of the ribs are whole, rather than broken into several pieces and the vertebrae are intact. Most bones of the hind limb are broken near mid-shaft [and the] distal end of the right metatarsal and a first phalanx has been pierced from both sides by carnivore canines.” Apparently, differences in fragmentation between the remains of the Marmes big elk and the remains of ungulates clearly butchered by prehistoric people prompted the new interpretation.

My examination of the big elk remains confirms that most vertebrae and ribs are indeed intact and nearly complete, though a few transverse processes and dorsal spines of vertebrae are damaged or missing (see the following section, Carnivore damage) as are some distal rib ends. All old fracture surfaces on limb bones indicate fracture occurred when
the bones were fresh rather than dry (Johnson 1985; Lyman 1994). For example, the right and left tibiae both display spiral fractures, as do the distal femur and left metatarsal. Several ribs lack the proximal end and resemble archaeological specimens apparently butchered by prehistoric humans in the area (Lyman 1978, 1995), but the majority of ribs are not broken in this manner (Fig. 2). The degree and nature of fragmentation is similar to that displayed by large artiodactyl carcasses that have been lightly scavenged by carnivores (Haynes 1982). The carnivore-generated damage to the bones also suggests that light scavenging modified the skeleton.

Carnivore damage

Of 31 skeletal specimens representing vertebrae and limb bones, 23 display damage from gnawing carnivores (ribs not included in tallies). The damage is typical of that inflicted on artiodactyl carcasses consumed by North American Quaternary carnivores such as wolves (Canis lupus), coyotes (Canis latrans), bears (Ursus spp.), and cougars (Felis concolor) (Binford 1981; Burgett 1990; Haynes 1980a, 1980b, 1982, 1983). In particular, dorsal and transverse spines processes of most vertebrae and the distal ends of several ribs have been chewed, but none of them have been extensively or intensively chewed. Several vertebral neural spines display classic U-shaped ends diagnostic of carnivore gnawing, and the neural spine of one thoracic vertebra has several classic punctures (Fig. 3). The proximal femur and the distal femur both have punctures, the former around the neck on both anterior and posterior surfaces just distal to the femur head, and the latter on the medial surface of the medial patellar ridge. The anterior crest of the proximal right tibia has been bitten off. The distal metatarsal has punctures and tooth furrows on the anterior and posterior surfaces. One first phalanx also has furrows, and a hole has been bitten through the proximal end of its postero-ventral surface.

The right calcaneum of the big elk is complete and undamaged; a smaller right calcaneum of a different elk has been heavily chewed by carnivores and lacks the entire tuber calcis. The bones of the ankle that articulate with the large calcaneum display no damage from gnawing carnivores. The small calcaneum articulates with a small astragalus that is also gnawed. Given the high degree of gnawing damage to the small calcaneum and astragalus (the bones are approximately the size of a modern Rocky Mountain elk) and the light degree of gnawing damage to all specimens representing the big elk, the author suspects the former represents a different depositional episode independent of the deposition of the large elk. It is unclear whether the gnawed small elk ankle was deposited later than or earlier than the big elk carcass.

The low degree of carnivore-inflicted damage to the bones of the big elk suggests that there were very few hungry carnivores in the area, that there was little consumable soft tissue on the bones and minimal attractive grease and marrow in the bones when carnivores found the carcass, or that the carcass was buried shortly after deposition. The former possibility seems unlikely given that several carnivores are represented in the faunal remains from approximately contemporaneous strata at the site. These carnivores are coy-
ote (*Canis latrans*), noble marten (*Martes nobilis* (extinct)), long-tailed weasel (*Mustela frenata*), probable mink (*Mustela cf. vison*), badger (*Taxidea taxus*), arctic fox (*Alopex lagopus*), red fox (*Vulpes fulva*), and bobcat (*Lynx rufus*) (Gustafson and Wegener 2004; Lyman, unpublished data). This list is substantial given that only about 20% of the collection has been identified and it will likely grow longer once all remains are studied. For example, it would not be unexpected to find remains of wolf in the collection. Whether or not wolf remains are found, it is well documented that the smaller coyote can damage by gnawing as well as transport bones of elk (Burgett 1990).

Actualistic research indicates that during warm months in temperate latitudes ungulate carcasses the size of elk may be devoid of soft tissue sought by scavengers within four to six weeks of death (Miller 1975; Weigelt 1989). That the bones of the Marmes big elk had little consumable tissue of interest to scavenging carnivores is possible, but this cannot be determined with any confidence. The author suspects the animal died in late winter, froze shortly after death and light scavenging, and was subsequently buried by the fluvially deposited silts in which its remains were found. There are several lines of evidence that make this scenario probable. First, animals that are scavenged by wolves in winter tend not to be completely consumed but instead display levels of intensity and extent of gnawing damage and types and frequencies of surviving skeletal parts much like that displayed by the Marmes big elk (Haynes 1980a, 1980b, 1982). Some limb elements of the big elk, especially proximal elements, may have been carried away by scavengers to secluded areas where they would not be bothered by competitors (Burgett 1990). Second, the Marmes elk was a skeletally mature animal that was not at the peak of skeletal health (see the following section, Pathology), which may have placed the individual at a level of stress greater than that experienced by a healthy individual, especially if the winter was more severe than normal. When it died, the animal was in a relatively warm part of the region; the Snake River canyon bottom tends to be 5–8 °C warmer than the 250–300 m higher surrounding plateau areas throughout the year, making the canyon bottom unsavory in summer but a microclimatic haven in winter. Warmer temperatures translate to less metabolic cost of maintaining body temperature and more non-snow-covered forage. The elk was also near water in the Palouse River, a topographic feature often sought by winter-stressed male artiodactyls (Clutton-Brock et al. 1982). As noted later in the text, the large size of the big elk remains suggests that the individual was a male. Third, given that some elk migrate seasonally, occupying topographically lower (warmer, snow-free) areas in winter, it is not unreasonable to suppose that the Marmes elk died where it did in the winter. Cervid winter mortality tends to be greater among males than females (Coughenour and Singer 1996; Wisdom and Cook 2000). Males enter the winter with less fat reserves than females, having drained those resources during the rut. Males thus move to lower elevations where forage is likely to be more accessible, yet they tend to have higher winterkill mortality than females. Deeper snow results in higher mortality regardless of other variables (Cook 2002). If the animal died during a cold winter, its tissues would have frozen and, though accessible to scavengers (Guthrie 1990; Haynes 1982), bones would have been gnawed only with difficulty. If the animal died in late winter or early spring, its consumable tissues likely became quickly inaccessible thereby precluding extensive and intensive gnawing.

With the spring thaw, the Palouse River overflowed its bank and quickly covered much of the carcass with the fine silts in which the bones lay, leaving little exposed to attract scavengers. The orientation of the long axis of 15 ribs and seven thoracic vertebrae, plotted in a rose diagram (Fig. 4) using 30° bins because of the small sample size, is suggestive of a preferred orientation that implicates fluvial action, but the distribution of specimens across the orientation categories is not statistically different from a random pattern ($\chi^2 = 4.68, p > 0.25$). If some of the carcass was not immediately buried, loss of exposed soft tissue would have been rapid, much like the loss of soft tissue from carcasses of domestic cattle (Miller 1975) and elk on the landscape today (Lyman 1989). Exposed bones would have dried out quickly and begun to weather; most specimens display weathering stage 1 or 2, indicating minimal exposure duration (Behrensmeyer 1978; Lyman and Fox 1989). One rib displays damage attributable to rodent gnawing and a second rib displays
damage that likely is the result of rodent gnawing. Rodents do not gnaw greasy bone, but instead gnaw dry bone (Lyman 1994), something relatively unattractive to scavenging carnivores because of the lack of nutritional value. Minimal rodent gnawing damage, plus minimal carnivore damage and minimal weathering damage, indicates the elk remains were quickly buried by spring runoff and the deposition of overbank silts. The pathologically fused C4 and C5 (see later in the text) were collected with a block of sediment, indicating they were at least partially covered by overbank silts.

Taphonomic history

There is no evidence of human involvement with the carcass despite the apparent occupation of Marmes Rockshelter by humans at the time the elk carcass was deposited (Hicks 2004). There are no butchering marks in the form of hammerstone scars on long bones meant to gain access to marrow, and there are no cutmarks or striae made by stone tools during skinning, dismembering, and filleting (Blumenschine et al. 1996). The femur, tibiae, and metatarsal were likely all fractured by wolves or perhaps ursids. The inventory of skeletal parts and gnawing damage indicates that the big elk likely died of natural causes and was subsequently lightly scavenged. The low degree of carnivore damage in conjunction with rodent gnawing suggests a winter death and early burial from overbank sediments deposited by spring meltwater. For any of several reasons, the skull and many appendicular elements simply were not recovered by the excavation and may remain buried in nearby unexcavated sediments.

Pathology

All long bone epiphyses of the big elk are fully fused, indicating that a skeletally mature individual is represented. Features of the vertebral column and ribs indicate that the big elk suffered two afflictions. First, C4 and C5 are fused together and immobile relative to one another; the ventral surfaces of the centra display an abundance of abnormal bone tissue that effectively fuses the two vertebrae together (Fig. 5). Probing with a dental pick suggests the centra themselves and the zygapophyses are not fused together, and though this could not be established with certainty, the apparent lack of fusion suggests the affliction is not spondyloarthropathy (Rothschild and Martin 1993). The anterior transverse foramena of C5, especially the one on the left side, are partially blocked by extra bone tissue. C6 displays no unusual features; C3 was not recovered. The manner and location in which C4 and C5 are fused and the "flowing" (Olivieri et al. 2009) appearance of the extra bone tissue indicates diffuse idiopathic skeletal hyperostosis (DISH) (Rothschild and Martin 1993). The extra bone tissue seems to be the result of ligamentous ossification (Olivieri et al. 2009). DISH-like osteological features — “bony thickening of the ventral longitudinal ligament on two thoracic vertebrae” (Greer et al. 1977, p. 41) — have been reported among modern elk.

The second affliction is perhaps mechanically related to the first. The first and second thoracic vertebrae have an abundance of extra bone tissue around and ventral to the centra and also on and around the rib demi facets (Fig. 6). These osteophytes — a primary criterion of osteoarthritis in human knees and hips (Rothschild 1997) — are only around the vertebral centra and not on the zygapophyses, indicating that although the pathology is similar to osteoarthritis, the affliction is best referred to spondylosis deformans (Rothschild and Martin 1993, p. 83) or spinal osteoarthritis (Ortner 2003, p. 549). There is also an abundance of osteophyte tissue around the heads of the left and right first ribs (Fig. 7). As well, C7 shows osteophytes around the postero-ventral portion of the centrum, but not to the extent of T1 and T2. The centra of T1 and T2 display unusual porosity, an unlikely sign of osteoarthritis (Rothschild 1997). There is no clear evidence of eburnation, a marker of arthritis severity (Rothschild 1997). Finally, there are shallow dorso-ventral oriented erosive grooves in the conjoining centra of T1 and T2, signifying total loss of joint cartilage, a sign of osteoarthritis (Rothschild and Martin 1993).

Osteoarthritis is relatively uncommon in modern elk and tends to mostly affect limb joints (Thorne et al. 2002). It occurs in modern elk where populations are dense and unsanitary conditions occur on feed grounds where several bacteria have been identified as causal and can be introduced through wounds in feet (Thorne et al. 2002). There is no evidence of antemortem injury among any of the remains of the Marmes big elk. Osteoarthritis can result secondarily from brucellosis (Brucella abortus) infection among modern elk (Thorne et al. 2002). It is unlikely that unsanitary conditions were the cause of the spinal osteoarthritis in the Marmes big elk. Age is often strongly correlated with the onset and severity of osteoarthritis in humans (Weiss and Juran 2007). None of the other thoracic vertebrae (T3–T11) of the Marmes big elk displays any pathological features.

The spinal osteoarthritides of C7–T2 is likely related to the DISH of C4–C5 since the two conditions commonly are found together in humans (Ortner 2003, p. 549). Spinal osteoarthritides occurs among non-elk cervid taxa and increases in frequency and intensity with increased age of individual animals (Peterson 1988; Peterson et al. 1982; Wobeser and Runge 1975). It also occurs with relatively higher frequency...
among South American camelids that were used as beasts of burden than among those not used as pack animals (DeFrance 2010). Some evidence suggests that weight burdens might exacerbate osteoarthritis symptoms (Weiss and Jurmain 2007). If the Marmes big elk was in fact a male, perhaps large antlers placed load-bearing stress on the neck and anterior-most back, thereby exacerbating susceptibility to degenerative joint disease (Sokoloff 1969) of the spine such as osteoarthritis (see also Wobeser and Runge 1975). The skulls of male elk are disproportionately larger than those of females, presumably because of the necessity of bearing the weight of antlers (Schonewald 1994). The DISH could have also resulted from heavy antlers contributing to ossification of neck ligaments. Whatever the cause, additional documentation of prehistoric occurrences of arthritis and other pathologies among North American elk may eventually reveal much about disease history in this large cervid.

**Morphometry**

As noted earlier in the text, the elk remains from the floodplain in front of Marmes Rockshelter were originally reported to be larger than modern elk in the Pacific Northwest of North America (Fryxell et al. 1968a). This observation became part of the received wisdom regarding the Pleistocene–Holocene transition-era mammalian fauna of the Pacific Northwest, and it was reported in the literature many times that local late Pleistocene elk were large relative to modern elk (Chatters 2001; Kirk and Daugherty 2007; Leonhardt and Rice 1970; Lyman 2004a). Descriptive data on the size of the bones of the Marmes big elk have, however, never been reported, so comparison with size data for modern elk or other prehistoric elk has been impossible. The author measured several dimensions of the skeletal elements of the Marmes big elk (von den Driesch 1976). The same dimensions were measured in samples of the two subspecies of elk that today are found in Washington State. The Rocky Mountain elk (C. e. nelsoni) occurs in eastern Washington, and is said to be smaller than the Roosevelt elk (C. e. roosevelti) that is found today in western Washington (Bryant and Maser 1982; O’Gara 2002). This size differences between the two subspecies was observed among the modern skeletons that were measured (Lyman 2006).

The Marmes big elk is indeed larger in several dimensions than modern Rocky Mountain elk, the subspecies that occurs in the eastern Washington today (Figs. 8, 9). It is a bit larger than the modern size range of Roosevelt elk in three dimensions (astragalus distal width, distal metatarsal width of condyles, distal metatarsal condyle posterior breadth), and in three other dimensions the Marmes big elk is within the range of modern Roosevelt elk, but on the large end of that range (astragalus lateral length, distal metapodial condyle antero-posterior diameter, proximal first phalanx width). This should not, however, be taken to mean that the Marmes big elk was of the Roosevelt subspecies because it has not been robustly established that size of bones can be used to distinguish prehistoric remains of the two taxa (Lyman 2006).

Murie (1951, p.17) indicated the Pleistocene elk of Alaska were larger than their modern conspecifics, and on that basis Geist (1998, p. 214) stated that North American elk “have declined in body size postglacially”. Neither Guthrie (1966) nor Kurtén and Anderson (1980) comment on the size of late Pleistocene elk relative to modern elk, although postcranial remains of late Pleistocene elk from the Yukon are reported to be larger than modern specimens (Harington 1977, in O’Gara and Dundas 2002, p. 82). Some records of late Pleistocene to earliest Holocene elk provide mixed indications of the size of these animals. Burns (1986) reports that a 9500 14C year-old elk from northern Alberta was of
“comparable size” to modern individuals, but provides no metric data. Elk remains from the Dry Creek site in southeastern Alaska are 9000–10 000 $^{14}$C years old, and are said to represent individuals of larger than modern body size; available metric data are from teeth, precluding direct comparison with the Marmes big elk (Guthrie 1983; Hoffecker et al. 1996). Shackleton and Hills (1977) report that elk remains — what will be termed the “Three Hills elk” — from central Alberta dating to about 9650 $^{14}$C years BP are slightly larger in some dimensions than the bones of modern elk. Data they present bear this out; a comparison of their data with those for dimensions measured indicates that the Three Hills elk is indeed larger than an average Rocky Mountain elk and is about average in size compared with a Roosevelt elk (Fig. 9). Interestingly, the Marmes big elk is larger in most dimensions than the similarly aged Three Hills elk (Fig. 10).

Unpublished laboratory notes indicate that the Marmes big elk was thought to be exceptionally large because its bones are larger than a modern bull elk collected in the 1960s from the National Bison Range in northwestern Montana. The modern elk was said by rangers at the National Bison Range to be the largest they had seen (Gustafson 1983). The skeleton of this individual is curated in Washington State University (WSU) Connor Zoological Museum under accession number 65-68. Laboratory notes list the size of several bone dimensions for both the Marmes big elk and WSU 65-68, all of which were likely recorded by C. E. Gus-
Fig. 7. Anterior view of right (top) and left (bottom) first ribs.

Fig. 8. Metrics of four dimensions of Marmes big elk remains compared with modern Rocky Mountain elk (C. e. nelsoni) and modern Roosevelt elk (C. e. roosevelti) bones.
Fig. 9. Metrics of selected dimensions of early Holocene “Three Hills” Alberta elk (from Shackleton and Hills 1977) compared with modern Rocky Mountain elk (*C. e. nelsoni*) and modern Roosevelt elk (*C. e. roosevelti*) bones.

Fig. 10. Ratio diagram comparing the size of several dimensions of the early Holocene Three Hills Alberta elk (from Shackleton and Hills 1977) with the Marmes “big elk” and the modern WSU 65-68 elk. Points to the right of the Three Hills vertical line represent larger dimensions than the Three Hills elk.
tafson in 1968 or 1969. Those notes indicate that to determine the percent difference in size, Gustafson calculated the difference between the size of dimensions of bones of WSU 65-68 and dimensions of the bones of the Marmes big elk, and divided those differences by the size of the particular dimension in WSU 65-68. But whether WSU 65-68 is exceptionally large among elk, or just a large elk was not documented. Data the author has collected indicate that WSU 65-68 is indeed large, and it appears to be larger than the Three Hills, Alberta, elk (Fig. 10). Importantly, and as Gustafson observed, the Marmes big elk is considerably larger than WSU 65-68 (Fig. 10).

Several species of late Pleistocene mammal from North America consist of animals that were larger than their modern conspecifics (Edwards 1967; Kurtén and Anderson 1980). Such gigantism has been well documented for bison (*Bison* spp.) (Hill et al. 2008), and though some individuals are larger than modern conspecifics, available evidence is less clear for late Pleistocene bighorn sheep (*Ovis canadensis*) (Lawler 1996; Wang 1988) and pronghorn (*Antilocapra americana*) (Adams et al. 1999; Chorn et al. 1988). The author knows of no evidence that deer (*Odocoileus virginianus* and *O. hemionus*) were larger during the terminal Pleistocene than today, but there is evidence that middle Holocene white-tailed deer in the midwestern U.S. were smaller than modern deer, apparently as a result of differences in availability of high-quality forage (Purdue 1989, 1991). Given the reports cited earlier in this section, there is little evidence that all terminal Pleistocene elk were larger than their modern conspecifics. Is the Marmes Rockshelter “big elk” an anomaly, a singular exceptionally large individual that is not of more or less average size?

The author knows of but a single elk bone from eastern Washington that is similar in age to the Marmes big elk. This bone came from the archaeological site known as Sentinel Gap (45KT1362), located in southcentral Washington 130 km west of Marmes Rockshelter (Fig. 1). Five radiocarbon dates average about 10 200 14C years BP (Galm and Gough 2001, 2008; Gough and Galm 2003). This small site (~82 m2) is in a small drainage west of the Columbia River and represents a single, likely short-term occupation. The author identified all mammal remains recovered from Sentinel Gap, including bison (*Bison* spp.), elk, mountain sheep (*Ovis canadensis*), and badger (*Taxidea taxus*). A single left metatarsal of an elk, missing the distal condyles apparently as a result of carnivore gnawing, was sufficiently complete to provide size data. The author measured the lateral-medial width and anterior-posterior depth of the proximal end of the Sentinel Gap specimen, and also that of the right metatarsal of the Marmes big elk (anterior-posterior depth had to be estimated because of fragmentation). Relative to the Three Hills elk, two modern Rocky Mountain elk reported by Shackleton and Hills (1977) for which only lateral-medial width data are available, six modern Rocky Mountain elk from Wyoming, Washington, and British Columbia, and three modern Roosevelt elk from British Columbia that the author measured, the Marmes big elk and the Sentinel Gap elk are indeed large (Fig. 11).

It appears, in light of the Sentinel Gap elk, that the Marmes elk is not an exceptionally large individual given its calendric age. In light of the evidence for other North American ungulates — bison in eastern Washington State (Lyman 2004b) follow the pattern of temporal diminution apparent in the Great Plains of North America (Hill et al. 2008) — it seems reasonable to hypothesize that elk of terminal Pleistocene age were indeed larger than their modern conspecifics, and that this species will display the general Holocene-diminution pattern once remains of appropriate age are measured. Why might this hypothesis turn out to be correct?

A probable cause of Holocene diminution involves climatically driven decreases in quality and quantity of nutritious forage (Guthrie 1984a, 1984b; Hill et al. 2008; Purdue 1989, 1991). The argument can be summarized as follows. Adult body size (of ungulates in this case) is a function of food availability because the latter influences ontogenetic growth rate (Geist 1987a, 1987b, 1998; McNab 2010). Thus, net primary productivity (amount of plant biomass produced per unit of time and area) in general, and especially primary productivity that is ecologically relevant or available during the ungulate growing season (Huston and Wolverton 2009), influences final adult body size (Festa-Bianchet et al. 2004; Klein 1964; Wolverton et al. 2009), including the skeleton and excluding seasonal fluctuation in body mass. Climate, of course, influences plant productivity (Blackburn and Hawkins 2004; Huston and Wolverton 2009). The critical question with respect to the Marmes "big elk" therefore is—was ecologically relevant primary productivity greater 9800 14C years ago in southeastern Washington than it is today? Fortunately, data suggesting an answer to this question are available.

Palynological and other evidence indicates that grasslands spread and forests retreated upslope as the continental ice sheet shrank (Blinnikov et al. 2002; Takeuchi et al. 2009). Palynological data from two lakes in eastern Washington

![Fig. 11. Bivariate scatterplot of lateral-medial width and anterior-posterior depth of proximal metatarsals of the Marmes big elk, the Sentinel Gap elk, the Three Hills prehistoric elk (3 Hills), two modern Rocky Mountain elk (SH1, SH2) reported by Shackleton and Hills (1977), and six modern Rocky Mountain elk (RKM) and three modern Roosevelt elk (ROS) measured by Lyman. Anterior-posterior depth is unknown for 3 Hills, SH1, and SH2.](image-url)
Data from these lakes indicate that prior to about 10 200 14C BP, conifer pollen dominated over grass pollen. Relative abundances reverse abruptly after that time; then grass pollen makes up as much as 60% of the total pollen (Johnson et al. 1994; Mehringer 1996). This change in pollen rain at Williams Lake Fen has been said to be “perhaps the most striking change recorded in this region’s history of postglacial vegetation” (Mehringr 1996, p. 31). Climate is drying out and warming up, suggesting that at the time the Marmes big elk and the Sentinel Gap elk were deposited, ecologically relevant primary productivity in the form of grass was relatively high. Not only was there more forage available, it would have been available for a longer period of time each year as the glacial anticyclone weakened and the growing season increased in duration (Takeuchi et al. 2009). Given that elk tend to graze more than browse when habitats allow (Cook 2002), it appears that the Marmes and Sentinel Gap elk were big because they had access to abundant and nutritious forage in the form of grass. Continued warming and drying would eventually see reduced grasslands as sagebrush increased in abundance (Johnson et al. 1994; Mehringer 1996). Local elk likely became smaller for want of nutrition; bison seem to also have shrunk in size, plus they seem to have been unable to survive in the Columbia Basin of eastern Washington in any number during the warm dry middle Holocene (Lyman 2004b).

Two other possible causes for large late Pleistocene elk should be considered. First, Geist (1987b, 1998, 1999) proposed that individual ungulates in colonizing populations would grow to large sizes as a result of minimal intra-specific competition and relatively nutritious rich habitats. Elk were present south of the Pleistocene continental ice sheets at least 40 000 years ago but do not seem to have become abundant there until the terminal Pleistocene (Graham and Lundelius 1994; Guthrie 2006; O’Gara and Dundas 2002). It has been suggested that the similarities in morphology, behavior, and genetics of modern North American elk and related Asian subspecies suggest the U.S. were colonized mostly by elk from more northern latitudes (O’Gara and Dundas 2002). If elk were indeed rare in low latitudes prior to the end of the Pleistocene, they likely would have been larger bodied; males would have had larger antlers at younger ages, and females would have reproduced at younger ages, much like recent colonizing elk populations (McCrorquodale et al. 1988, 1989). Given the possibility that the record of radiocarbon-dated elk remains may be a function of specifically choosing what seem to be terminal Pleistocene and archaeological elk remains (Guthrie 2006; Meltzer and Mead 1983), whether or not the colonization process accounts for the size of the Marmes (and other) big elk remains to be robustly demonstrated. And even if colonization of low latitudes is determined to be responsible for the large size of terminal Pleistocene elk, they were large because of an abundant food supply.

The second possible cause for late Pleistocene elk being large relative to their modern congeners and conspecifics is Bergmann’s rule; that is, for reasons of thermoregulation (Millien et al. 2006). However, mounting evidence indicates that the correlation between body size and ambient temperature (typically measured as latitude) is imperfect and not universal, prompting the suggestion that body-size trends that seem to be the result of Bergmann’s rule may in fact be the result of other environmental variables, either singly or in combination (for a sampling of pertinent literature, see Allen et al. 2006; Blackburn et al. 1999; McNab 2010; Meiri et al. 2007; Millien et al. 2006; Watt et al. 2010). It is also becoming clear that populations seem to respond individually rather than taxonomically (Millien et al. 2006). Robust determination of the specific environmental variable(s) responsible for a particular, apparently Bergmannian response within species will require fine-resolution data for chronometric age of multiple specimens representing a temporal series, for paleoecological settings and changes therein, and numerous morphometric data points (Hill et al. 2008). These same data will provide an indication of the contribution of colonization variables to the large size of terminal Pleistocene elk (Geist 1987a).

Modern North American elk exhibit geographic size clines in both body mass and skeletal dimensions (Schovold 1994). Further, the closely related European red deer (Cervus elaphus) is sufficiently phenotypically plastic that improved forage conditions can result in larger skeletons within few generations (Geist 1998; Langvatn and Albon 1986; Post et al. 1999). Unfortunately, we have no data points from 10 000 to 15 000 14C years BP, or from 500 to 500 14C years BP from eastern Washington to plot against the Marmes big elk. Until such time as the steep data requirements identified above are met, the author prefers the hypothesis of abundant, highly nutritious forage that was available for long portions of each year.

**Discussion and conclusions**

When first discovered, the Marmes big elk seemed to confirm the then typical notion that the early Americans represented by human remains from the site were big-game hunters. Perhaps more remarkable at the time was the size of the bones that indicated the represented animal had been quite large by modern standards. It is now clear there is no evidence the Marmes big elk was preyed upon or even scavenged by early American hunters. Rather, the most parsimonious explanation is that the individual likely represents a winter-killed animal that underwent minimal scavenging by carnivores before being buried by silt carried by spring floodwaters of the Palouse River.

Although the possible implication of the Marmes big elk as signifying early big-game hunters has faded from local archaeological awareness with time, the observation that this elk was big has not. Thus archaeologist James Chatters (2001, p. 150) recently wrote that about 9500 years ago “oversized elk still roamed the grasslands of the Columbia Basin.” Not only were there no metric data at the time to back up statements of this sort, the paleoecological significance of what might be larger than modern elk has not previously been considered. The data on ancient elk bone size available in the literature, in conjunction with data on the size of modern elk bones summarized here, indicate that indeed the Marmes elk was quite large relative to modern individuals in the same area. And the Marmes elk was not
alone; at least one other elk of similar age that roamed eastern Washington, the Sentinel Gap elk, was also considerably larger than modern elk and apparently the same size as the Marmes big elk. Thus the Marmes big elk is not an anomaly. The paleoecological significance of these terminal Pleistocene elk is that they align with the greater abundance of grass as forage in the soon to be arid and shrub-steppe covered Columbia Basin indicated by the paleobotanical record. The terminal Pleistocene relative abundance of grass likely also contributed to the presence of larger than modern individual bison in eastern Washington (Lyman 2004b).

Finally, although skeletally large, the Marmes big elk was not skeletally healthy when it died. It suffered from two, perhaps related, afflictions. The skeletal disease status of late Pleistocene ungulates in North America is a seldom reported phenomenon (see Rothschild and Martin (2003) for an exception). The Marmes elk, afflicted with what likely represent diffuse idiopathic skeletal hyperostosis and spinal osteoarthritis, provides an initial glimpse of such among this large member of the deer family. For that alone the skeleton holds value as a data point in studies of disease history.

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References


Burgett, G.R. 1990. The bones of the beast: resolving questions of faunal assemblage formation processes through actualistic research. Ph.D. dissertation, Department of Anthropology, University of New Mexico, Albuquerque, N.M.


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