An inter-site comparison of enamel hypoplasia in bison: implications for paleoecology and modeling Late Plains Archaic subsistence

By: Laura B. Niven, Charles P. Egeland, Lawrence C. Todd

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Abstract:
Bison bison mandibular molars from the Late Plains Archaic kill/butchery sites of Buffalo Creek (Wyoming) and Kaplan-Hoover (Colorado) exhibit significant frequencies of dental enamel hypoplasia (DEH), a defect believed to reflect information about physiological status of individual animals. This study provides a methodology to estimate the ontogenetic and seasonal timing of DEH formation in bison dentition. Integration of these estimates with data from bison life history and grassland ecology allows inferences on age- and season-specific factors exacerbating periodic physiological declines that were recorded in the form of enamel hypoplasias. Differences between assemblages indicate regional variability in grassland conditions, with data from Buffalo Creek pointing to recurrent drought that reduced forage capacity and contributed to physiological stress in bison over two consecutive years. Seasons of physiological stress reflected in the DEH correspond to each of the three kill events at the locality, suggesting that predictability of bison behavior in this location was a critical factor in influencing the seasonal timing and location of repeated hunting episodes. Unlike Buffalo Creek, timings of stress episodes are not consistent with season of death in the Kaplan-Hoover bison assemblage, suggesting that favorable grassland conditions were the primary factor influencing timing of this large single-kill event in order to provision for the upcoming winter. DEH analysis represents a developing approach in the construction of models addressing key aspects of local grassland and bison ecology as well as offers unique insights into the hunting strategies and subsistence decisions of Late Plains Archaic foragers.
Keywords: Enamel hypoplasia; Bison; Great Plains; Late Plains Archaic; Grassland ecology

Article:
1. Introduction
The isolation and quantification of key paleoecological variables and their potential impact on past human behavior is a major goal of current archaeological research [e.g., 4,32]. Modeling such interactions, however, requires appreciation of the ecology of human prey species. Because of their prominent role in subsistence economies of prehistoric foragers on the Great Plains of North America, bison (Bison bison) are ideal for ecologically focused investigations of this kind. This paper presents data on dental enamel hypoplasias (DEH) from mandibular dentitions of bison from two archaeological kill/butchery locales on the Northwestern Great Plains, United States. Estimation of the ontogenetic and seasonal timing of hypoplasia formation indicates that hypoplasias formed as a result of periodic physiological stress exacerbated by a range of age- and season-specific factors. The possible role of additional non-specific factors is also discussed. These data demonstrate that DEH is a powerful tool for understanding the physiological status of individual bison and paleoecological conditions on a local level. Moreover, they have implications for understanding and modeling the subsistence strategies of prehistoric groups during the Late Plains Archaic, ca. 2700–1500 radiocarbon years BP [23].

Enamel hypoplasias form as the result of physiological disturbances during amelogenesis, the secretory stage of enamel formation [27]. Research on human teeth shows that deficiency in enamel thickness is exhibited as abnormal topography in the form of lines, dents, or pits [18].

The exact origin of enamel defects is unclear, but a number of factors might be involved, including nutritional deficiency, psychological stress, infectious disease and ingestion of toxins [27,28,43,47]. Excessive amounts of fluoride can also lead to abnormal enamel formation in a number of domestic and wild ungulates [52,53]. Deficiencies of vital minerals such as iodine, selenium and sodium appear to have negatively affected the overall health of now extinct megaherbivores [34,41]. Although it is not clear whether these mineral deficiencies are manifested in tooth defects, the possibility merits further investigation [45].

Regardless of exact etiology, it is important to realize that enamel defects are often the result of "combinations of factors and physiological processes" [27, p. 74]. Goodman and Rose [27, pp. 73–74] propose that in order for defects like hypoplasias to form, disruption of enamel growth must surpass a "threshold level" brought on by these combined influences. For example, an individual affected by physiological stress is faced with an additional stressor, such as weaning, an outbreak of disease, or seasonal decline in environmental conditions, after which the threshold is surpassed and enamel defects form. In this paper, we refer to physiological stress as a cause, while additional factors are considered triggers.

Establishing the causes and triggers behind DEH in bison requires an evaluation of multiple themes. Physiological stressors specific to age are easier to discern, thanks to a rich body of knowledge on bison life history [e.g., 3,38]. However, factors relating to season or disease are more difficult to infer and directly associate with DEH formation due to a lack of research in these areas. Therefore we propose a set of working hypotheses based on bison biology and ethology, Great Plains paleoecology (past and present), and hypoplasia studies on other mammals.

Most of what is known about DEH comes from extensive research on modern and fossil human and non-human primate dentition [e.g., 26–28,35,37,46,54], though it has also been identified in suids [13,14], Miocene and Pleistocene rhinoceros [5,39] and Pliocene and modern giraffe [20,21]. While documented cases are rare in bison, notable amounts have been observed on a small number of archaeological bison assemblages from the Northwestern Plains region, including Casper, Wyoming [63], Ayers-Frazier, Montana [8] and Henry Smith, Montana [64]. Wilson's [64] pioneering work with the Henry Smith assemblage revealed a wealth of paleoenvironmental insights that could be gained by studying DEH in bison.

Fig. 1. Map of Great Plains area of the United States, showing location of the Buffalo Creek and Kaplan-Hoover sites.

2. Materials and methods

2.1. Archaeological sites and history of investigations

The sample in this study derives from two Late Plains Archaic bison kill/butchery locales from the Northwestern Plains (Fig. 1). The Buffalo Creek site is located on the western edge of the Powder River Basin, an area encompassing portions of southeastern Montana and northeastern Wyoming. Characterized by expanses of shortgrass prairie interspersed with buttes, escarpments and arroyos, the Powder River Basin region was excellent habitat for bison in the past, as reflected in an archaeological record rich with bison kill localities [23]. Excavations at Buffalo Creek were undertaken in two campaigns in 1962 and 1971–1972 [2,23]. Buffalo Creek is located in an arroyo near a spring. Bison were maneuvered into a nearby ravine, run into the head of the arroyo and subsequently killed. Evidence of post-holes in the bonebed indicates that the arroyo may have been modified by a corral structure, a common procurement tactic used at numerous bison kills in the region [23, pp. 195–197]. Charcoal yielded radiocarbon dates of 2460 ± 140 and 2600 ± 200 BP [23, p. 34].

The Kaplan-Hoover site is located near the town of Windsor, Colorado, and situated on the floodplain of the Cache la Poudre River, within an arroyo 0.8 km south of the current river channel. Modifications due to housing developments and gravel quarrying make characteristics of the paleo-landscape difficult to infer; however, like Buffalo Creek, Kaplan-Hoover is located within an area conducive to the movements of large migratory populations of bison. The site was discovered in 1997, and excavation and analysis are currently ongoing under the direction of the Department of Anthropology, Colorado State University [59]. Kaplan-Hoover also represents an arroyo trap into which animals were herded and subsequently dispatched. No evidence of postholes has yet been uncovered, although the use of this procurement tactic remains a possibility. Radiocarbon dates obtained from bone collagen and charcoal indicate an age of 2724 ± 35 BP [59, p. 133]. To date, Kaplan-Hoover is the largest single-event Late Plains Archaic bison kill on the northern Great Plains.

2.2. The bison dentitions

In addition to documentation of DEH, analysis of the Buffalo Creek and Kaplan-Hoover bison dentitions involved estimation of age and season of death. This information is critical for evaluating the causes and implications of DEH as well as the interpretation of Late Plains Archaic subsistence strategies. Determining age and season of death from bison molars is based on predictable and systematic tooth eruption schedules in addition to differential wear patterns, originally using modern samples of known ages [e.g., 24]. The methodology employed in analyzing the Buffalo Creek and Kaplan-Hoover bison molars follows Todd et al. [58]. Only mandibular dentitions were considered since the methodology is much less developed for maxillary molars. Although the Kaplan-Hoover assemblage contained several articulated or nearly articulated crania with both sets of mandibular and maxillary teeth, these specimens have not yet been examined for DEH since they were recovered during excavations after this study was completed. Examination of these molar sets would be worthwhile, as this assemblage offers a unique opportunity to further test the hypothesis that all simultaneously forming teeth similarly record metabolic stress in the form of DEH [13]. In support of this hypothesis thus far is a set of five associated mandibular teeth in the Henry Smith bison assemblage, all exhibiting DEH [64, p. 207].

For Buffalo Creek, a total of 290 mandibular molars representing a minimum number of 85 individual bison were analyzed for season of death [44]. Most specimens were complete tooth rows, in some cases with bilateral mates, although isolated molars were also included in the study. Tooth eruption and wear indicate that a minimum of three kill events took place at the site: (1) spring–early summer, (2) late fall–winter, and (3) mid-late winter. It is not clear whether these kills occurred during one year or over multiple years.

The Kaplan-Hoover season of death study involved a total of 249 molars. The majority of specimens were in complete or nearly complete tooth rows; isolated molars were also included. Based on crania, the site contains a minimum of 44 animals. However, because the site is currently under excavation, this number should be viewed as a gross underestimate; there may be as many as 200 animals present [59]. Dental evidence suggests the site represents a single-kill event that occurred in late summer/early fall.

2.3. Methods

Estimating the age and season in which each hypoplasia developed requires the developmental sequence of enamel for each tooth be known. A schedule of monthly incremental enamel growth until formation of the CEJ (cemento-enamel junction) was established using a sample of 75 modern bison mandibles of known age from different sexes and body sizes (Fig. 2). Most of the comparative B. bison sample used here is housed in the University of Wyoming, Department of Anthropology Zooarchaeological collection and includes individuals ranging from a fetal specimen that died two months prior to birth (Fig. 2: B0358), five individuals that died approximately one month prior to calving, 11 individuals that died at calving (e.g., Fig. 2: 8206B), and a series of additional older, dentally immature specimens (e.g., Fig. 2: B0357). A group of 40 individuals from a commercial bison herd which were all slaughtered at 19.5 months of age was also examined (e.g., Fig. 2: BP4L). Radiographs were made of each specimen used in this study, and measurements of dental development taken directly from the image. As illustrated by Fig. 3, although the range in crown heights for the 40, 19.5 month old individuals is nearly 20 mm, the standard deviation is 4.5 mm. The rate of dental development in this group of bison very closely approximates that reported by Brown et al. [6] for a much larger sample (n = 869) of domestic cattle.

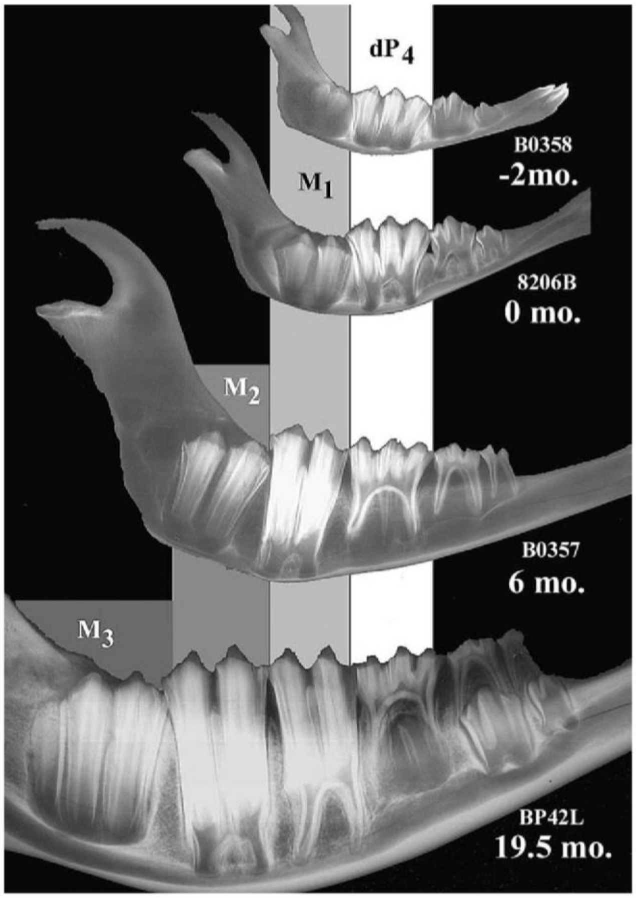

Fig. 2. Radiographs of *Bison bison* mandibles showing dental development from late term fetal (B0358 at two months short of term) to nearly two years of age (BP42L).

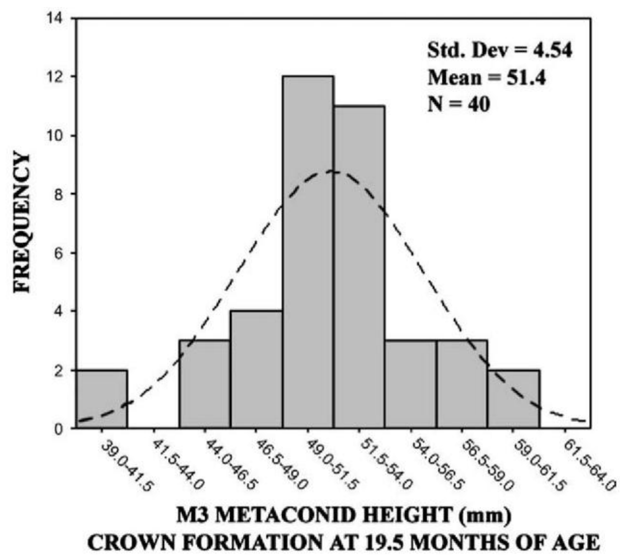

Fig. 3. Developing crown heights (measured from radiographs) of 40 known age-at-death *Bison bison* mandibular third molars.

The pattern of dental development for bison permanent mandibular teeth is summarized in Table 1. About half the M_1 forms in utero, with formation of the CEJ occurring approximately three months after birth. The M_2 bud is visible in radiographs beginning around two months of age and the CEJ forms at 13 months. The crown of M_3 begins forming at nine and is completed at 24 months.

In the majority of cases during examination, DEH was clearly visible on the Buffalo Creek and Kaplan-Hoover bison molars without the aid of magnification. When necessary, 10× magnification was used. Each hypoplasia was measured from its lowest point to the CEJ, to the nearest 10th of a millimeter. A similar technique was applied to suid molars [13] and by anthropologists on human teeth [18,26]. In the case of dents or pitting, the center of the hypoplastic area was used as a measuring point. A number of specimens exhibited multiple defects and in such cases, each was considered independently.

Dividing the monthly amount of enamel growth by the distance between hypoplasia and CEJ provides an estimate of how many months prior to CEJ formation the DEH developed. These estimates are then correlated with the nearest month, providing age of the individual and season in which the defect formed. Once an analyst is familiar with the morphology of DEH in bison molars, this technique is easy to apply to the assemblage under study and can be duplicated by multiple analysts.

Table 1
Schedule of crown and root formation on bison teeth (based on sample of 35 modern bison (*Bison bison*) mandibles of known age)

Tooth	Formation (age in months)		Enamel growth per month (mm)
	Crown	Root	
P_2	12–23	23–40	nd
P_3	9–20	20–40	nd
P_4	12–30.5	30.5–40	nd
M_1	Utero[a]–3	3–13	7.8
M_2	2–13	13–25	5.1
M_3	8–24	24–38	4.1

[a] In utero, from ca. two months prior to birth.

Table 2
Number of bison molars examined for DEH, affected by DEH, and minimum number of individuals (MNI) affected by DEH from Buffalo Creek and Kaplan-Hoover (expressed as number and percent)

	Buffalo Creek	Kaplan-Hoover
Molars examined	127	249
Affected molars (%)	41 (32.3)	35 (14.1)
Affected MNI	31	20

Fig. 4. Example of linear form of dental enamel hypoplasia (DEH) on bison left M_2 from Buffalo Creek. Affected area marked by white frame; two well-defined, horizontal hypoplasias are clearly visible. Right: close-up of affected area.

3. Results

3.1. Buffalo Creek

A total of 127 molars were examined[1] with 41 (32.3%) exhibiting DEH in some form. A minimum of 31 individuals were affected (Table 2). Linear DEH is the most common form on the Buffalo Creek molars, appearing as one or more lines across one or both cusps (Fig. 4). Dented, pitted and “patchy” hypoplasias are also present. All affected Buffalo Creek molars exhibit hypoplasias on the buccal aspect, several occur in combination with the lingual aspect (Table 3). Location of DEH is consistent among all teeth regardless of their ontogenetic development, supporting arguments by dental anthropologists that DEH is not randomly distributed among areas of molars [26, p. 487]. The presence of DEH is also quantified by molar, indicating that M_1s and M_2s were clearly more affected than M_3s (Table 4). DEH formed on the M_1 when individuals were two to three month old (summer), M_2 at 10–13 months (late winter–early spring), and M_3 at 21–23 months of age (late winter–early spring). Several sets of M_2–M_3 reflect DEH formation occurring over two consecutive years, during the same season.

3.2. Kaplan-Hoover

Of the 249 molars examined, 35 (14.1 %) exhibit one or more hypoplasias, representing a minimum of 20 affected individuals (Table 2). In contrast to Buffalo Creek, the most common manifestation of DEH at Kaplan-Hoover is dented enamel, although a linear form is also present in a few specimens. In addition, DEH is distributed more equally on the buccal and lingual aspects (Table 3). Similar to Buffalo Creek, M_1s were affected with the highest frequency, followed by M_2s and M_3s (Table 4). Kaplan-Hoover DEH developed in four peaks: M_1 from two months prior to birth to around the time of birth (late winter–early spring), two to three months (summer), M_2 at 10–13 months (late winter–early spring), and M_3 at 20–23 months of age (late winter–early spring). Age and seasonality estimates of DEH formation for both samples are presented in Table 5 and Fig. 5. In conjunction with information drawn from bison life history and grassland ecology, these estimates provide the basis for inferring specific stressors contributing to DEH formation.

Table 3
Number of DEH on bison molars quantified by crown aspect for Buffalo Creek and Kaplan-Hoover

Crown aspect	Buffalo Creek	Kaplan-Hoover
	n (%)	*n* (%)
Buccal	41 (100)	19 (54.3)
Lingual	0 (0.0)	12 (34.3)
Buccal + lingual	5 (12.2)	4 (11.4)
Total affected molars	41	35

Table 4
Quantification by tooth of DEH on bison molars from Buffalo Creek (n = 41) and Kaplan-Hoover (n = 35)

	M_1	M_2	M_3
	n (%)	*n* (%)	*n* (%)
Buffalo Creek	13 (31.7)	21 (51.2)	7 (17.1)
Kaplan-Hoover	18 (51.4)	13 (37.1)	4 (11.4)

4. Inferences of physiological stress

We hypothesize that an interplay of factors was behind DEH formation in the Buffalo Creek and Kaplan-Hoover bison molars. If the underlying cause of DEH was physiological stress, then a variety of triggers might have been responsible for surpassing the threshold level when tooth defects developed. We propose a series of age-, season-, and non-specific factors that might have acted as triggers.

4.1. Age-specific physiological stress

A large portion of DEH developed on M_1s from Kaplan-Hoover just before or coincident with the birthing pulse in late April–early May [3]. These defects may be linked to reproductive costs on the mother or the trauma of birth on the calf. Generally, female ungulates with suitable fat stores have higher reproductive success: pregnancy is less costly to them, calves have higher birth weight, and survival rate of calves to weaning age increases [10,19]. Since female bison are often nutritionally stressed in late spring [56], reproductive cost would be higher and presumably could affect a calf prenatally or neonatally.

A correlation between birth or neonatal stress and hypoplasias has been proposed in humans [50,55] and might be applicable to other mammals; for example, in their early study of enamel hypoplasias Sarnat and Schour [50, pp. 67–68] noted that two-thirds of DEH in their sample formed during the weeks (up to 12) just after birth, as a result of “postnatal adjustment.” Formation of DEH at two to three months of age on the Buffalo Creek M_1s might be attributed to changes associated with infancy.

Bison calves wean at approximately nine months of age [38] and the associated dietary shift is likely responsible for DEH formation on some M_2s in both assemblages (Table 5 and Fig. 5). DEH has been frequently associated with weaning in humans [28,42,46; but see 51] as well as in pigs [14], giraffe [20,21], and fossil rhinoceros [39].

Table 5
Estimated age and season of formation of each hypoplasia on bison molars from Buffalo Creek and Kaplan-Hoover, expressed as number and percent

	Buffalo Creek hypoplasias	%	Kaplan-Hoover hypoplasias	%
M_1				
February	0	0.00	1	3.03
March	0	0.00	1	3.03
April	0	0.00	8	24.24
May	0	0.00	0	0.00
June	1	0.96	2	6.06
July	28	26.92	2	6.06
M_2				
August	0	0.00	0	0.00
September	0	0.00	0	0.00
October	0	0.00	0	0.00
November	0	0.00	0	0.00
December	0	0.00	0	0.00
January	0	0.00	0	0.00
February	2	1.92	2	6.06
March	13	12.50	2	6.06
April	25	24.04	7	21.21
May	20	19.23	2	6.06
M_3				
June	0	0.00	0	0.00
July	0	0.00	1	3.03
August	0	0.00	1	3.03
September	0	0.00	0	0.00
October	0	0.00	0	0.00
November	1	0.96	0	0.00
December	3	2.88	1	3.03
January	6	5.77	1	3.03
February	0	0.00	1	3.03
March	5	4.81	1	3.03
April	0	0.00	0	0.00
May	0	0.00	0	0.00
Total	104	100.00	33	100.00

Note: some molars exhibit more than one hypoplasia.

4.2. Season-specific physiological stress

All M1s from Buffalo Creek, three M_1s and one M_3 from Kaplan-Hoover developed DEH during the summer months (Table 5 and Fig. 5). Although the trigger or triggers are difficult to infer, it is possible that drought conditions were involved. Evidence shows that over the past 2000 years droughts on the Great Plains have ranged from five years to multidecadal in duration, in many cases surpassing the severity of those experienced during the 20th century [62,66]. Droughts of any significant length would impact productivity and quality of forage [11], reducing groundcover by as much as 65–90% [60] and thereby negatively affecting net primary forage production [33]. In addition, summer protein levels in many grasses decline beginning in late July, reaching a minimum in mid-August [48]. This in combination with drought may have exacerbated the conditions, since grasslands can undergo a lag-effect of several years in terms of drought recovery [33]. These conditions would have obvious dietary repercussions for local bison populations, especially for lactating cows, passing on nutritional stress to nursing calves that are less resistant to food stress [3]. In regard to the affected M1 s, below-average summer grazing in conjunction with stresses relating to infancy discussed above might have triggered DEH formation during newborn individuals' first summer.

While we believe there is a case for drought playing a role in physiological stress of the bison in question, additional lines of evidence would be ideal. For example, an unusual degree of polish or spalling of the teeth similar to what Wilson [64, pp. 217–218] noted on the Henry Smith sample. He attributed these traces to ingestion of grit with forage in drought conditions. The degree of spalling varied among samples, indicating fluctuations in aridity and poor forage. No such indications were documented on the Buffalo Creek or Kaplan-

Hoover teeth. Oxygen isotopic signatures have also shown a correlation between climate and hypoplasia formation in Miocene giraffe [21], demonstrating the potential of this avenue of research in hypoplasia studies. Late winter–early spring hypoplasia development seen on M_2s in both assemblages is likely associated with the normal decline in physical condition experienced by most ungulates at this time of year [56]. Winter severity during that specific year may have exacerbated the poor condition of bison, a trigger attributed to DEH in some of the Henry Smith bison [64,65].

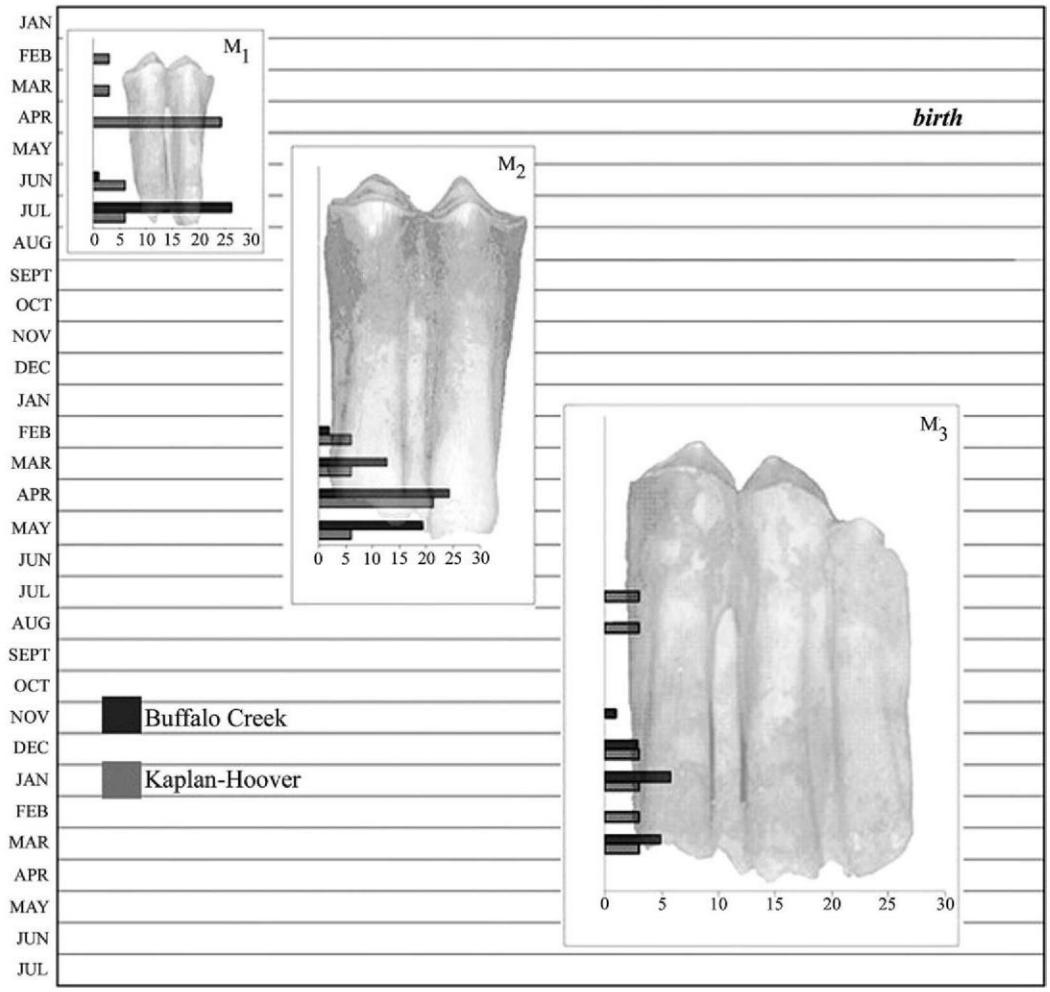

Fig. 5. Chart illustrating the months in which dental enamel hypoplasia (DEH) formed on M_1–M_3 from Buffalo Creek and Kaplan-Hoover. *X*-axis below each molar marks percent of hypoplasias occurring on that tooth.

Although most DEH on M_3s from both assemblages formed slightly earlier in the year (mid-winter) compared to the M_2s, stress recorded on M_3s continued into late winter–early spring, suggesting a yearly cycle in which bison herds underwent periodic nutritional stress in this season.

4.3. Non-specific stressors

Several additional stressors in combination with physiological stress could be involved in triggering hypoplasia formation. Whether their influence is age-specific is not clear, though correlation with season is possible.

Disease has been linked with some DEH formation in human teeth [27,50], suggesting a similar connection of the two in other mammals. A variety of diseases infect modern large ungulate populations, for example anthrax [15], brucellosis [3,7], tuberculosis [3,7], and others [e.g., 1] but less is known about their presence in fossil animals. To our knowledge, only tuberculosis has been confidently identified in Pleistocene bison [49], detected in erosive lesions in skeletal bone; however, its effects on bison tooth development are not yet known.

Parasites also infect bison and other large ungulates and have shown to trigger DEH formation in sheep [57]. The connection is logical, as infected ungulates will not absorb nutrients and protein effectively because their bodies must focus on fending off the parasites [12]. Some parasite infections occur seasonally [17], which is potentially relevant to seasonal peaks in physiological stress of animals as documented in this study. The role of parasites in DEH formation in bison remains speculative, though contemporary data demonstrating an interplay between nutrition, season and parasites are suggestive of one.

Lastly, human predation pressure could be a negative influence on feeding patterns of bison. Females with calves prefer to graze in open areas that allow better visibility of predators and will sacrifice nutritious forage for this advantage [3, pp. 86–87]. Bison tend to flee in response to predators [29], leading to interruptions in grazing. We propose that in times of poor grassland conditions, an additional negative variable such as human predation pressure could contribute to nutritional stress in some bison.

5. Paleoecological interpretations and implications for modeling Late Plains Archaic subsistence

Regional paleoclimatic data provide the necessary background for evaluating the influence of localized grassland conditions on DEH noted among the Buffalo Creek and Kaplan-Hoover bison molars. Several studies suggest arid to semi-arid conditions for a broad area of the northern Great Plains from approximately 4500–2000 BP [25,61] although studies closer to the Buffalo Creek and Kaplan-Hoover sites present a somewhat different picture. For example, macrofossil and pollen samples from packrat middens in the Bighorn Basin of Wyoming/Montana indicate moist conditions in the area until 2700 BP, with increased aridity thereafter [36]. Most applicable to Kaplan-Hoover are studies of dune fields in northeastern Colorado. Episodes of dune field accretion, occurring in times of low moisture, were not indicated in northeastern Colorado at or near the time of the Kaplan-Hoover bison kill [9].

Despite these paleoclimate studies generally being supportive of the scenarios outlined above for season-specific factors influencing formation of DEH, they are too broad to be very informative on specifics of the grazing mammals and human groups of interest here. Instead, we fully support Wilson's [64,65] proposition that DEH data from bison have the potential to provide an independent source of relatively fine-grained information on local paleoecological conditions beyond that currently provided by broader climate studies. Research on bison DEH is in its early stages, though the results to date appear promising.

5.1. Late Plains Archaic bison hunting

Grassland conditions affecting the health of the Buffalo Creek and Kaplan-Hoover bison would have influenced the organization of subsistence activities of Late Archaic foragers. Although the relationship between climate conditions and human subsistence on the prehistoric Great Plains is complex [40], bison DEH offers a powerful tool for examining one aspect of this important issue.

Location of bison herds is largely dependent on forage capacity, which in turn is impacted by a number of unpredictable environmental parameters including rainfall, fire, overgrazing, biting insects and perhaps human hunting pressure [30]. Under "normal" climatic conditions, grasslands can support ample forage year-round and throughout the herds' range [30]. As a result, bison inhabit large areas of grassland essentially year-round, following no precise seasonal migration route. However, under adverse grassland conditions, their movements may be restricted to areas of better forage, resulting in their location becoming more predictable for human hunters. DEH information from Buffalo Creek supports this argument.

Fig. 6 presents DEH frequency data pooled by month in addition to season of death estimates based on dental evidence for the Buffalo Creek and Kaplan-Hoover dentitions. Each of the three hunting events at Buffalo Creek corresponds with periods of physiological stress (excluding those relating to reproduction costs or weaning, such as M_1s, some M_2s), providing strong evidence that bison grazing behavior under severe ecological conditions was a primary factor influencing the seasonal timing and location of kill events here. Since arroyos trap moisture, they are attractive to grazing animals both in early spring and summer when shortgrass forage could be found in these isolated patches. In fact, during drought, arroyos may have offered some of the only patches of water and/or forage available. Construction of a corral structure in this arroyo by Late Archaic hunters offers another line of evidence suggesting that large groups of animals were repeatedly exploited here, requiring increased levels of labor and time investment [see 16,22]. This in turn suggests that herd behavior was highly predictable here, resulting in increased levels of hunting efficiency as well as food return rate [following 31].

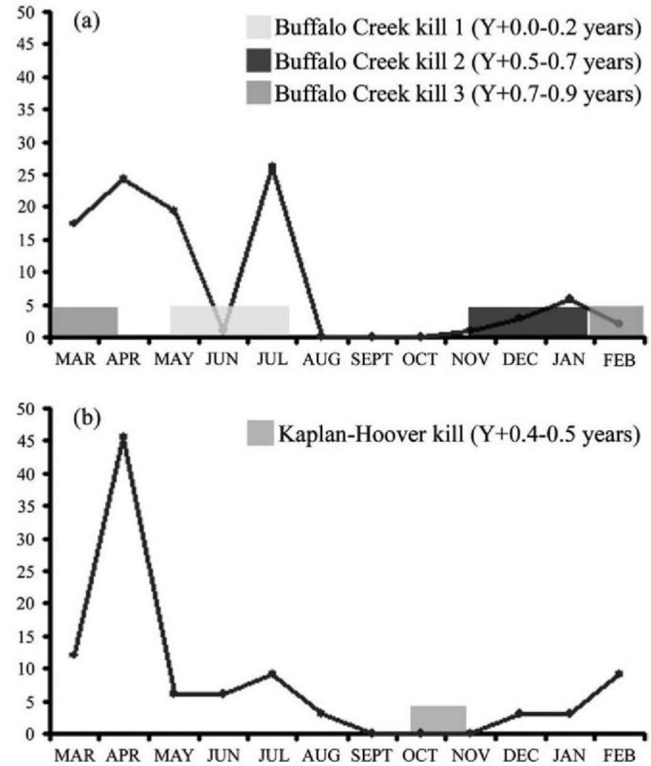

Fig. 6. Dental enamel hypoplasia (DEH) frequency (%) pooled by month in comparison with season of death for bison kill events for Buffalo Creek (a) and Kaplan-Hoover (b). The Buffalo Creek graph shows the correspondence between repeated, seasonal periods of physiological stress (and DEH formation) and timing of three bison hunting events, demonstrating that bison behavior during such periods influenced the timing and location of kills at the site. In contrast, the Kaplan-Hoover graph illustrates no correspondence between the seasonal period of physiological stress (and DEH formation) with timing of the single, large kill event at the site and hence, that normal or above-average grassland conditions were the primary influence behind the timing of the bison hunt.

Predictability and significant numbers of aggregated bison appear to be the factors behind corral construction and timing of hunting events at Buffalo Creek, while physical condition of the prey did not seem to be a deterrent. The assemblage reflects selective use of the carcasses, with numerous complete or nearly complete articulated skeletons and anatomical portions and little evidence for marrow exploitation. This suggests that while poor physical condition of some or all bison was not a factor in the hunt, it was an important factor in the degree of butchery and transport of meat packages and processing for within-bone nutrients [44; see 56].

Grassland conditions in northeastern Colorado may have been average or above-average during the period when Kaplan-Hoover was occupied, a scenario supported by the dune field paleoclimate data discussed above. Under such conditions, we might expect bison herds to be relatively small and dispersed after the rut [30]. Their unpredictability does not appear to have discouraged seasonal timing of the large hunting event at Kaplan-Hoover; in fact, site size indicates the hunt was a large undertaking, requiring the cooperation of numerous individuals. The season of death suggests it was designed to meet nutritional needs of a large group or groups well into the winter months. Discovery of at least two typologically distinct projectile points made from different raw materials [59] may indicate the involvement of different cultural groups in the kill event. Similar to Buffalo Creek, it appears that many carcass portions were not processed for meat and marrow at Kaplan-Hoover [59, p. 138], although it is not clear if this was related to physical condition of the adult cow and bull herd or other factors. In summary, grassland conditions (below-average or optimal) influenced the timing and location of bison hunting at Buffalo Creek and Kaplan-Hoover, though in quite different ways. Nonetheless, both examples are informative about regional paleoecology and the responses of bison as well as Late Archaic human groups to their environments.

6. Summary and conclusions

DEH offers indelible and relatively fine-grained records of physiological changes occurring during tooth development. These patterns can provide valuable insights into local paleoecological conditions as well as details of the relationship of individual animals to their environment. Based on the integration of ontogenetic and seasonal estimates of DEH formation in bison from two Late Plains Archaic kill/butchery locales with information on bison life history and grassland ecology, we propose that physiological stress was exacerbated by age-specific (birth, weaning) and season-specific (below-average forage capacity due to drought and/or winter severity) factors. In addition, non-specific factors such as disease, parasite infection, or human predation pressure may have been contributing stressors, though they are more difficult to link specifically with age or season. The combination of the physiological condition of bison and one or more stressors was significant enough to push disruption in tooth development over the “threshold level” and manifest in tooth defects in many individuals.

Differences between these two assemblages are most informative about local grassland conditions but especially intriguing are the responses of Late Plains Archaic foragers to them. DEH data from Buffalo Creek imply that bison predictability in the arroyo location was a critical factor in influencing the seasonal timing and location of repeated hunting events. In contrast, DEH information from Kaplan-Hoover indicates above-average forage capacity and favorable conditions for bison herds and in turn large-scale bison hunting by Late Plains Archaic groups. Both examples nicely illustrate how the dynamic relationship between humans and their local environment stimulated several unique events of communal hunting on the prehistoric Great Plains.

Based on the results of this study, it seems probable that observed DEH frequencies from Kaplan-Hoover are in fact quite normal, reflecting common patterns of stress within a bison population under average or above-average grassland conditions. Aside from a few cases with especially high DEH frequencies (e.g., Buffalo Creek, Henry Smith, Casper), we believe that enamel hypoplasia affected many Plains bison to some degree. Future comparative studies of bison DEH are needed in order to evaluate this possibility. The limited documentation of DEH in bison is likely due to two main factors: (1) the lower portion of the tooth crown where DEH is most likely to be visible is embedded in mandibular bone in assemblages consisting of complete mandibles; and (2) many researchers have not recognized DEH due to lack of familiarity with the defect.

Wilson’s [8,64] research was the first to demonstrate the exciting paleoecological and anthropological implications of tooth defects in bison. In this paper, we have built upon Wilson’s insightful work by presenting a practical method for estimating ontogenetic and seasonal timing of hypoplasia formation in bison molars. We have also sought to expand the comparative database of bison with DEH in order to further our understanding of northern Great Plains grassland conditions in the past as well as relating these to the organization of prehistoric human subsistence during the Late Plains Archaic.

Lastly, we hope this study instigates similar research in the Old World, where a number of outstanding fossil bison assemblages have been recovered. DEH information from such assemblages could provide an intriguing component to the study of Paleolithic human–bison interaction.

Notes:

[1] It should be noted that in the Buffalo Creek assemblage, molars in some complete mandibles could not be examined for defects since the relevant portion of tooth was under mandibular bone. Therefore, only in cases where the specimen would remain in good condition were complete mandibles subjected to the sawing of a small “window” on the lingual aspect to expose the lower tooth crown.

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