Incisor wear and age in Yellowstone bison

David A. Christianson, Peter J. P. Gogan, Kevin M. Podruzny, and Edward M. Olexa

Abstract Biologists commonly use tooth eruption and wear patterns or cementum annuli techniques to estimate age of ungulates. However, in some situations the accuracy or sampling procedures of either approach are undesirable. We investigated the progression of several quantitative measures of wear with age, using permanent first incisors from Yellowstone bison (*Bison bison*), and tested for differences between sexes and herds. We further investigated the relationship of wear and age to explore an age-estimation method. Labial-lingual width (LLW) correlated best with assigned age (r^2=0.66, males; r^2=0.76 females). Labial-lingual width differed between sexes, with females showing ~0.2 mm more wear than males. Additionally, differences in rate of wear existed between bison of the northern and central Yellowstone herds (1.2 and 0.9 mm/year, respectively). We developed a regression formula to test the power of LLW as an estimator of Yellowstone bison age. Our method provided estimated ages within 1 year of the assigned age 73% and 82% of the time for female and male bison, respectively.

Key words age estimation, annuli, *Bison bison,* cementum, eruption-wear, incisor, Yellowstone

Biologists have sought effective age-estimation methods for ungulates to assess demographic processes. Because deciduous teeth evanesce and permanent teeth develop and erode predictably, patterns in tooth eruption, wear, and dental annuli provide age estimates (Servinghaus 1949). Fuller (1954, 1959), Winchell (1963), Frison and Reher (1970), and Larson and Taber (1980) recorded dental development in North American bison (*Bison bison*) for use in estimating age of individuals. Aging ungulates by counting dental annuli, a more accurate and less subjective method, became established when Sergeant and Pimlott (1959) examined the incisors of moose (*Alces alces*). Novakowski (1965) was first to use dental annuli to estimate the age of bison, and Moffitt (1998) confirmed that counts of cementum annuli in bison teeth are a reliable predictor of true age in this species.

In some situations age determination of live animals by eruption-wear patterns or cementum annuli may not be feasible (Cain et al. 2001). Although relatively reliable for young animals, the eruption-wear method presents problems in estimating age of adults, including high variability, subjectivity, and inconsistency of application by field personnel (Hewison et al. 1999, Hamlin et al. 2000, Van Deelen et al. 2000). Cementum aging is impractical where restraint methods are not amenable to extraction of teeth from live animals (Cain et al. 2001). Objective measures of teeth provide an alternative to eruption-wear and dental annuli methods of estimating age when neither of these methods is preferred (Spinage 1973).

Objective measures of wear are more consistent in application and require less experience than traditional subjective wear methods (Spinage 1973, Haynes 1984). Novakowski (1965) first measured the width of the permanent first incisor's (I_1) wear surface in bison and determined that this method showed promise for aging large samples. Wolfe et

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al. (1999) also found strong correlation between true age and I_1 width and used this connection to estimate age in live bison, while Berger and Cunningham (1994) found similar utility with I_1 height.

Several factors could confound the relationship between incisor wear and age. Dental anomalies (e.g., fluoride toxicosis and aberrant tooth wear) plague ungulates inhabiting geothermal areas such as Yellowstone National Park (YNP) due to high levels of fluoride and silica in the water, soils, and plants (Shupe et al. 1984, Garrott et al. 2002). Additionally, ungulates sometimes display differences in tooth wear between sexes and populations (Wasilewski 1967, Van Deelen et al. 2000). We undertook this study to model permanent I_1 wear in YNP bison, considering sex and geographic location of individuals, and to explore alternatives to dental annuli counts or traditional eruption-wear schedules for aging restrained bison.

Study area

Yellowstone bison occur in 2 distinct herds within YNP, Montana, Wyoming, and Idaho. Some 75–85% occurred in a central herd, comprised of the previously identified Mary Mountain and Pelican herds (Meagher 1973, Thorne et al. 1991), while the remaining 15–25% were found in a northern herd. Previous observations (Meagher 1971, 1973, 1989) suggested, and tracking of instrumented bison from November 1997–April 2000 (E. M. Olexa, United States Geological Survey, unpublished data) confirmed, little interchange of animals between the 2 herds.

Central herd

The central bison herd wintered in the extensive geothermal areas at elevations of 2,000 to 2,250 m in the Madison-Firehole-Gibbon (MFG) river valleys and along the Duck and Cougar creek drainages toward Hebgen Lake, Montana. The bulk of the herd summered in the 2,500-m-elevation Hayden and Pelican valleys (Meagher 1973).

Most of this herd's range was within the Yellowstone caldera (Pierce and Morgan 1992, Good and Pierce 1996). Soils of the region are derived from rhyolitic rock or sedimentary deposits. Fluoride and silica exist in high concentrations in the soil, water, and plants throughout this area, causing dental tissue abnormalities in bison (Shupe et al. 1984).

Northern herd

The northern bison herd wintered on rolling topography at elevations of approximately 2,000 m from the Lamar and upper Yellowstone river valleys to approximately 1,500 m near YNP's northern boundary. In summer these bison shift their distribution to the upper Lamar Valley and the adjacent Mirror Plateau at approximately 2,745 m, although some animals range southward into the Pelican Valley. This herd's range was beyond the boundaries of the Yellowstone caldera, and geothermally influenced areas were uncommon and limited to the Mirror Plateau, Soda Butte, and Mammoth Hot Springs.

Methods

We recorded dental formulas and extracted I_1 teeth from YNP bison that died from anthropogenic or natural causes. We classified all bison with deciduous I_1s as calves or yearlings and restricted our analysis to animals with permanent I_1s ($\geq$ 2 years old) for this study. We assigned an age of 2 years to bison with permanent I_1s but deciduous I_2s, I_3s, and canines, and an age of 3 years to bison with permanent I_1s and I_2s but deciduous I_3s and canines. Matson's Laboratory, Milltown, Montana, supplied age estimates based on counts of dental annuli for all other bison with permanent I_1s. In this manuscript we refer to these age estimates of bison as assigned ages (i.e., an age based upon cementum analysis or eruption patterns).

We measured the following dimensions from each I_1. One individual collected all I_1 measurements to reduce variability.

Labial-lingual width (LLW)

Labial-lingual width is the width of the worn enamel and dentine occlusal surface at the crown of the I_1 measured between the labial and lingual sides, where the lingual, medial furrow terminates on the occlusal surface (Figure 1). We used a clear, plastic ruler (LLW-R) and metric caliper (LLW-C), measuring to the nearest 1 mm (Novakowski 1965) and 0.1 mm, respectively. The lingual boundary was difficult to determine in animals <5 years old due to a highly obtuse edge (i.e., a shallow chamfer occurs between the occlusal surface and the lingual side of the I_1, rather than a sharp angle). We used the middle point in this transition area as the lingual boundary for all width measures.

We considered the termination of the medial fur-

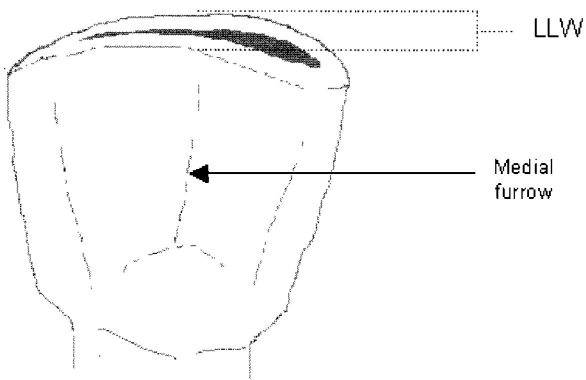

Figure 1. View of lingual side of permanent first incisor in ~4-year-old bison showing labial-lingual width (LLW) measurement. The medial furrow also is shown, revealing the location on the occlusal surface used to make the measurement.

row as a relatively unbiased location to secure consistent measurements of LLW. This enabled us to avoid inconsistencies in measurement location due to unusual tooth-wear patterns. For the same reason, we used the centerline of the tooth for the measurements below.

Exposed crown height (ECH)

We took this measurement on the labial side of the I_1 (Berger and Cunningham 1994) from the gum line to the tip of the incisor on the centerline of the tooth to the nearest 1 mm with a ruler. Because many I_1s were extracted prior to our analysis, actual measurements of ECH (i.e. in the mouth) were unavailable. Thus, we used the delineation formed by the accumulated residue and blood on the exposed crown as the former position of the gums on extracted teeth (Figure 2). In 2002 we used culled bison to test the accuracy of this approach by comparing measurements of ECH in situ with those obtained upon extraction.

Total crown height (TCH)

We defined TCH as the height of the enameled portion of the I_1 on the labial side measured to the nearest 1 mm with a ruler. Measured along the centerline, TCH's lower bound was the terminus of the enamel near the base of the crown where it meets the root on the labial side; the tip of the incisor demarcates the upper bound (Figure 2).

We regressed all wear measurements against assigned age, categorizing individual bison by sex and herd. We used analysis of covariance (ANCOVA) to compare regressions across techniques (LLW-R vs. LLW-C), herds (northern vs. central), and sexes using SYSTAT 10 (SPSS 2000).

To determine the utility of I_1 measurements as a predictor of age, we assumed our age assignments were correct. We randomly selected half the sample of central-herd bison, ≥ 3 years, to develop wear-age regressions using the I_1 measurement most correlated with assigned age. We used the remaining central herd I_1s to test the agreement of the regression formulas with the assigned ages.

We did not use bison with an assigned age of 2 years to develop the age-estimation regression because they could have negatively biased the regression line slope. That is, we assumed most of our age assignment errors to be ± 1 year (Moffitt 1998), and since permanent I_1s erupt at ~24 months, all animals assigned an age of 2 years based on eruption are at least this old and incorrect assignments are always underestimates, while incorrect assignments to all age classes >2 years are both under- and overestimates.

Results

We examined permanent I_1s from 244 Yellowstone bison, including 110 females, 98 males, and 4 sex unknown from the central herd and 26 females, 5 males, and 1 of unknown sex from the northern herd. Assigned ages for central-herd bison ranged from 2–16 years while northern-herd bison were

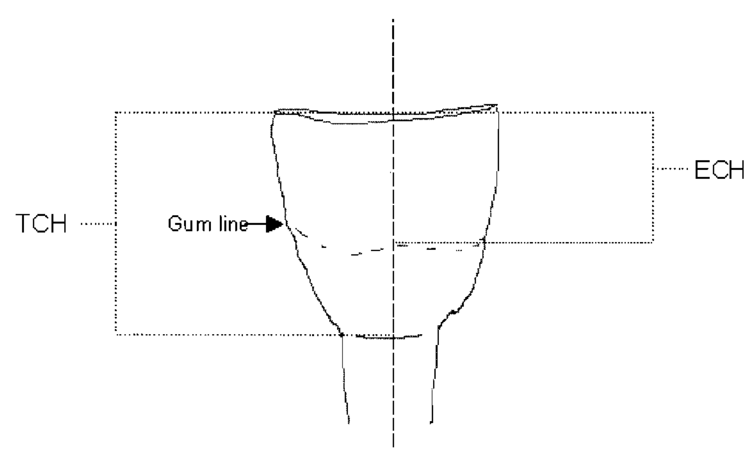

Figure 2. View of labial side of first incisor of ~4-year-old bison. Total crown height (TCH) and exposed crown height (ECH) measurements are shown located on the approximate centerline of tooth. The gum line also is indicated.

2–9 years old. The limited sample of northern-herd males forced us to characterize wear–age relationships and test for differences between sexes using central-herd bison only and test for differences between herds among female bison only.

A paired-sample t-test revealed no difference between measurements of LLW-C and LLW-R (t=1.46, n=212, P=0.144). However, we opted to focus on LLW-C measurements in our modeling and comparisons as variance in wear is age-specific, increasing with time (Spinage 1973) and coarser ruler measurements may not have revealed this. Additionally, we avoided the broad incremental categories created by ruler measurements (every 1 mm), which could have affected regression development and tests of significance. LLW-C ranged from 0.0–10.0 mm and increased with age in central-herd bison. The slope of the regression differed significantly from zero (slope=8.813, n=212, P<0.00001), and assigned age accounted for most of the variability in LLW-C measurements (r^2=0.72). No significant difference existed between male and female central-herd bison in the slopes of the regression of LLW-C and $\log_{10}$ (assigned age) (ANCOVA, $F_{1,204}$= 0.106, P=0.745). However, elevations of the regressions differed (t=2.472, n=208, P=0.014), with females showing, on average, ~0.2 mm greater LLW-C than males for all assigned ages (Figure 3). We detected significant differences in the relationships of female LLW-C and $\log_{10}$ (assigned age) between bison of the northern and central herds ($F_{1,133}$= 5.767, P=0.018), with northern-herd females exhibiting a more rapid rate of I_1 wear than central-herd females (Figure 4).

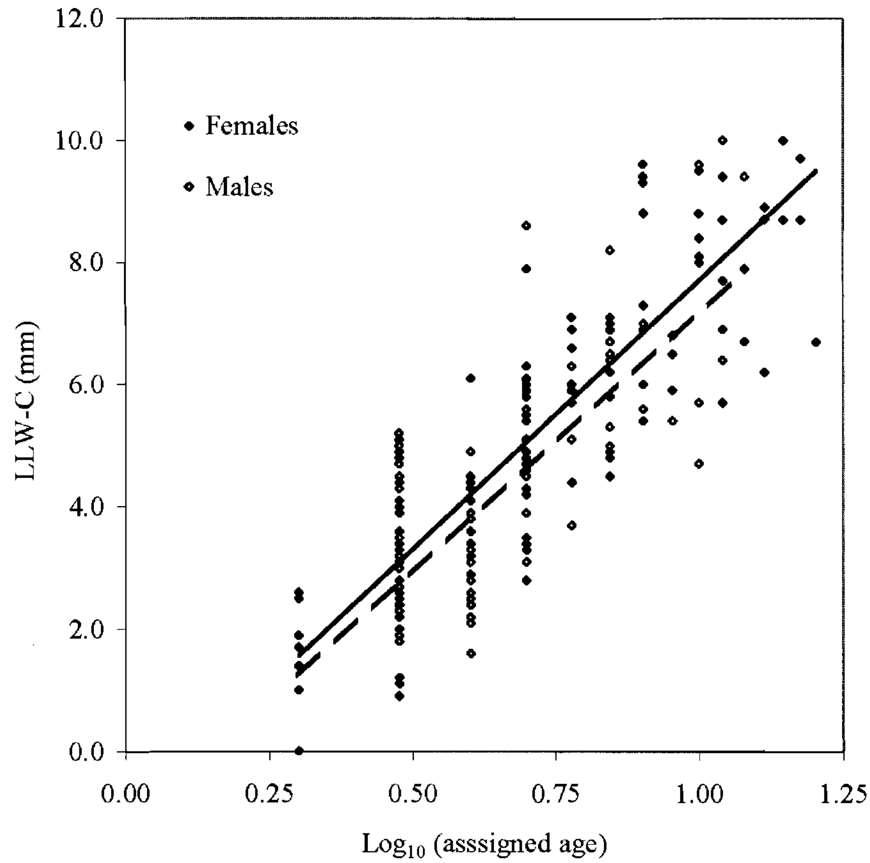

Figure 3. Relationship between I_1 LLW-C and $\log_{10}$ (assigned age) for Yellowstone central-herd bison with significantly different elevations in regressions between sexes. Males (dashed line, LLW-C = 8.5346 $\log_{10}$ (assigned age) −1.3299, r^2 = 0.6577, n = 98) show less wear (~0.2mm) than females (solid line, LLW-C = 8.7925 $\log_{10}$ (assigned age) −1.0888, r^2 = 0.7559, n = 110) across all ages.

We tested the accuracy of using the assumed gum line as the proximal bound for ECH in 2002 with 59 culled bison, comparing measurements of ECH in situ with those obtained upon extraction. We found no significant difference between the in situ ECH and the measured estimates once extracted (paired sample, t=-1.101, P=0.275). We found a significant linear relationship with a slope different from zero between ECH and assigned age (slope= -0.672, n=212, P<0.00001) among central-herd bison of both sexes, although these measurements were highly variable, producing a poor relationship (Figure 5). There was no significant difference in the regressions for ECH between sexes for central-herd bison (slopes $F_{1,204}$=0.222, P=0.638, elevations $F_{1,205}$=0.065, P=0.799).

Similarly, the regression between TCH and assigned age for central-herd bison was linear, with a slope significantly different from zero (slope= -1.025, n=212, P<0.00001). The association was stronger than that between ECH and assigned age (Figure 6). We found no significant difference in

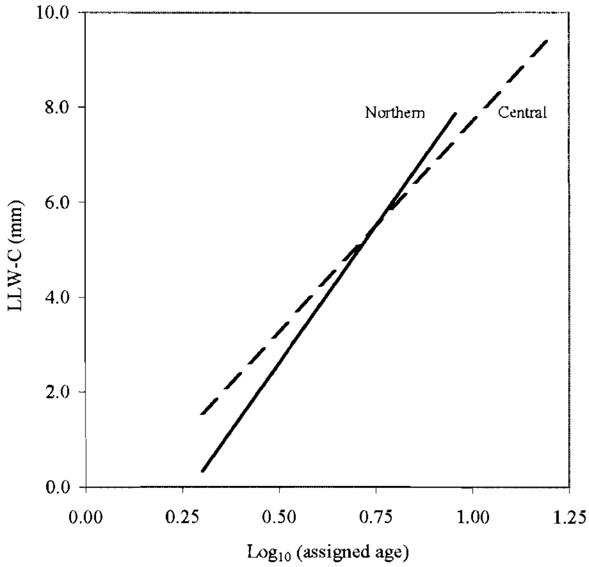

Figure 4. Significantly different regressions showing the relationship between I_1 labial-lingual width (LLW-C) and $\log_{10}$ (assigned age) of northern-herd female bison (solid line, LLW-C = 11.543 $\log_{10}$ (assigned age) −3.1454, r^2 = 0.9185, n = 26) and central-herd female bison (dashed line, LLW-C = 8.7925* $\log_{10}$ (assigned age) −1.0888, r^2 = 0.7559, n = 110).

TCH and assigned age between central herd bison sexes (slopes $F_{1,204}$=0.133, P=0.716, elevations $F_{1,205}$=2.351, P=0.127). Total crown height tended to drift toward ECH with age in central-herd animals (Figure 7). We found a significant difference

Table 1. Number of age estimates from I_1 labial-lingual wear measurements that were within 0, 1, 2, or ≥3 years of ages based on cementum-eruption analysis for 110 Yellowstone bison.

		Number of years difference			
Sex	n	0	1	2	≥3
Male	51	21	21	5	4
Female	59	17	26	11	5

between females of the northern and central herds in regressions of assigned age against ECH ($F_{1,132}$= 8.196, P=0.005) and TCH ($F_{1,132}$=5.451, P=0.021), with northern herd female bison showing higher rates of change than central-herd female bison (Figure 7).

In simulating the utility of LLW-R measurements for estimating age in the field, we used regressions of LLW-R against $\log_{10}$ (assigned age), for 51 female and 47 male central-herd bison with an assigned age of ≥3 years to estimate the ages of 59 female and 51 male central-herd bison ≥2 years of assigned age. The estimated ages agreed or were within ±1 year of the assigned ages (measured in one-year increments) in 73% and 82% of the cases for central-herd males and females, respectively (Table 1).

Discussion

As expected, bison I_1s wear steadily with age. Although assigned age correlated strongly with wear,

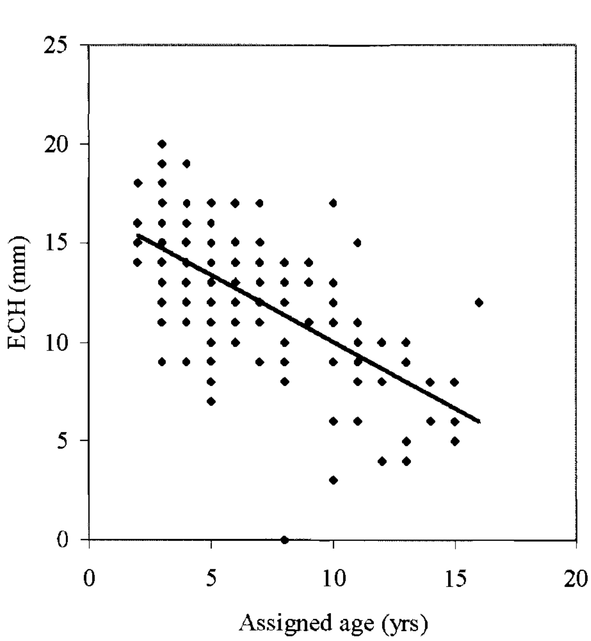

Figure 5. Relationship of I_1 exposed crown height (ECH) measurements and assigned ages for Yellowstone central-herd bison (ECH = -0.6719*assigned age + 16.739, r^2 = 0.408, n = 212).

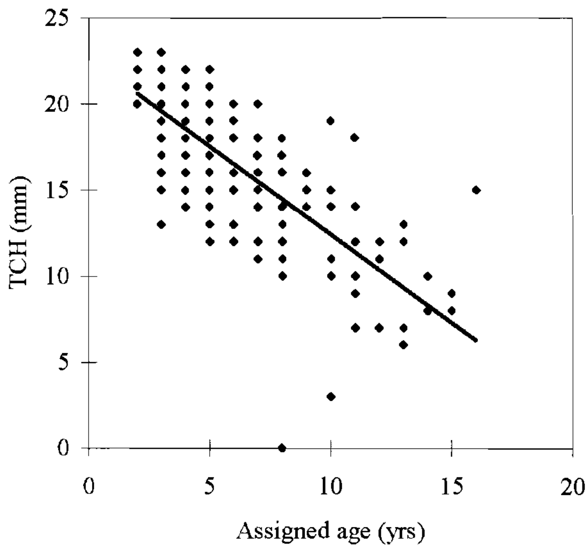

Figure 6. Relationship of I_1 total crown height (TCH) measurements and assigned age for Yellowstone central-herd bison (TCH = −1.0245*assigned age + 22.658, r^2 = 0.5806, n = 212).

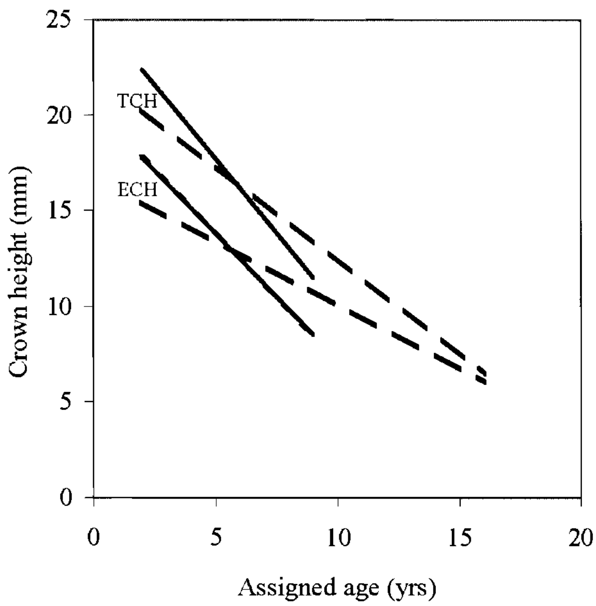

Figure 7. Relationships between assigned age and I_1 total crown height (TCH) and exposed crown height (ECH) for female bison of the Yellowstone northern herd (n = 26, upper solid line, TCH = –1.5599*assigned age + 25.513, r^2 = 0.7856; lower solid line, ECH = –1.3223*assigned age + 20.418, r^2 = 0.6439) and central herd (dashed line, n = 110). Central-herd regression formulas are presented in Figures 5 and 7.

there was significant residual variation. Undoubtedly, individual bison of the same age wear their teeth at significantly different rates or in dissimilar patterns. However, some of the residual variation in the regressions likely was due to inaccuracies in the techniques we used to assign ages to bison. Age estimates derived from eruption-wear criteria, which we used to estimate ages of 2 and 3 years old, are imperfect. In addition, age estimates derived from cementum have associated inconsistencies (Dapson 1980). Moffitt (1998) found an accuracy of 49% in dental annuli estimates of known-age bison. Application of our methodology to bison of known ages probably would have produced a tighter correlation between I_1 wear and age.

Based on the appearance of the plotted data, a log-linear relationship describes the association between LLW and assigned age well (Figures 3 and 4). The angle of occlusion changes with age (i.e., the plane of the wear surface begins nearly parallel to the long axis of the tooth and becomes perpendicular with old age) (Wasilewski 1967). Although wear increases the measurement of LLW, age-related changes in the angle of occlusion simultaneously function to decrease the width, resulting in an ever-slowing rate of in increase in LLW of bison I_1s.

Exposed crown-height measurements are influenced by high variability in gum lines between individuals and a receding gum line with age. On extremely old bison, the gums either protrude above the occlusal surface or recede onto the root, rendering ECH measurements less reliable. In such cases, TCH decreases faster than ECH, and eventually the 2 become the same (i.e., the gum line is located at or near the base of the crown in old animals) (dashed lines, Figure 7). We found that a linear relationship best described the correlation of I_1 crown height and assigned age in Yellowstone bison, as Berger and Cunningham (1994) also found for Badlands National Park (BNP) bison.

The rate of I_1 wear in Yellowstone bison was comparable to that reported for bison elsewhere. The LLW development, from eruption through the ninth year, in Yellowstone central-herd and northern-herd bison (0.9 and 1.2 mm/year, respectively) included the value of 1.1 mm/year derived from Novakowski (1965), and exceeded the rate from Kimball and Wolfe (1989) for Antelope Island bison ages 3–10 (0.6 mm/year). Berger and Cunningham (1994) found a 1.3 mm/year decrease in ECH in BNP bison. The value we obtained for ECH progression in Yellowstone bison was -0.67 mm/year in the central herd and -1.27 mm/year in the northern herd.

We cannot explain our finding of greater wear, across all ages, in female bison. Sex-specific differences in tooth wear have been found in other ungulates (Van Deelen et al. 2000) but have not been reported in bison. Differences in rates of tooth wear among bison herds have been attributed to differences in diet, nutrition, or local substrate (Wasilewski 1967, Haynes 1984). We can offer no reason for our finding of greater I_1 wear rates in northern-herd bison than in central-herd bison (Figures 4 and 7). Shupe et al. (1984) found dental and skeletal abnormalities were more prevalent in central- than northern-herd Yellowstone bison and ascribed these differences to the fluoride content of the vegetation and water in central Yellowstone's geothermal areas. Furthermore, Garrott et al. (2002) suggested the spatial differences in geochemical properties of the Yellowstone landscape cause greater tooth wear rates in elk (*Cervus elaphus*) from the Madison–Firehole drainages than northern-range elk, which possibly results in earlier senescence of the former. Although these findings contrast with our results, our study was limited to permanent I_1s in bison, while the above studies examined premolars and molars of elk and bison.

The LLW-C measurement correlated best with assigned age in Yellowstone bison. We show that sex- and herd-specific differences in permanent I_1 wear rates exist, and these differences should be recognized when applying any aging method based on objective measures of incisor wear to a population (Van Deelen et al. 2000). In physically restrained bison, caliper measurements of I_1 LLW may not be possible; others have used rulers to measurer incisors on restrained bison successfully (Berger and Cunningham 1994, Wolfe et al. 1999, Cain et al. 2001). Fortunately, the regression of LLW and $\log_{10}$ (assigned age) was not sensitive to collection by ruler or calipers, supporting incisor measurement by ruler to age live bison.

Our development of aging criteria based upon I_1 width does not escape the warning of Dapson (1980) against using age estimates (in our case, cementum age and eruption-wear) to develop other age-estimation methods. Yet, for many free-ranging populations, known-age animals are unavailable, and the need exists for alternative methods of accurate age determination in restrained bison (Cain et al. 2001). The accuracy of the eruption-wear method is limited and decreases with each successive year in the animal's life (Winchell 1963, Spinage 1973). Current methods provide anywhere from 1-7 age classes for bison $\geq$ 2 years old based on subjective characters (Fuller 1959, Winchell 1963, Frison and Reher 1970, and Larson and Taber 1980). Our study shows that a method based on permanent I_1 measurements is more accurate and provides an assessment of age to the year rather than an age class. Given that our regression developed from LLW-C provides ages within 1 year of the assigned age 73% and 82% of the time (Table 1) for female and male central-herd bison, respectively, this method may provide a reasonable alternative to cementum aging, affording more accurate age estimates in the field than traditional eruption-wear criteria.

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