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AGING BISON TEETH WITH A GIS: A NEW TOOTH AGE PREDICTION

METHODOLOGY AND ITS ARCHAEOLOGICAL

AND ECOLOGICAL IMPLICATIONS

by

Andrew Edward Owens

A thesis submitted in partial fulfillment of the requirements for the degree

of

MASTER OF SCIENCE

in

Anthropology and Cultural Resource Management

Approved:

David A. Byers, Ph.D. Major Professor Jacob Freeman, Ph.D. Committee Member

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UTAH STATE UNIVERSITY Logan, UT

2022

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ABSTRACT

Aging Bison Teeth with a GIS: A New Tooth Age Prediction Methodology and its Archaeological and Ecological Implications

by

Andrew Edward Owens, Master of Science

Utah State University, 2022

Major Professor: Dr. David Byers Department: Sociology and Anthropology

Archaeologists seek to understand site seasonality, frequency, and underlying human behaviors. Zooarchaeologists use bison teeth to infer occupation seasonality and frequency, as well as specific hunting behaviors based on tooth eruption, growth, and attrition. However, to date, no concise and repeatable methodology exists to age bison teeth. Current age estimation is based on comparisons made from past age estimation attempts and sparse comparative tooth collections. Therefore, we propose a new bison tooth age estimation methodology. This new Bison Tooth Transition (BTT) model uses 146 known-age comparative bison tooth rows, and "maps" tooth occlusal surface wear with a GIS, to produce probabilistic and replicable tooth age prediction models. Though the newly proposed BTT is not without problems, it is shown to be a functioning proofof-concept bison tooth age estimation technique that offers additional insights such as minimum animal counts and underlying bison mastication physiology. Archaeological BTT applications are illustrated using the Folsom (29CX1) site bison mandibular tooth assemblage.

(82 pages)

PUBLIC ABSTRACT

Aging Bison Teeth with a GIS: A New Tooth Age Prediction Methodology and its Archaeological and Ecological Implications Andrew Edward Owens

Archaeologists use teeth to estimate the age an animal died based on tooth eruption, growth, and wear. Animal age estimations then inform archaeologists about when and why archaeological sites were occupied. However, to date, no concise and repeatable practice exists to age estimate teeth. Therefore, we propose a new tooth age estimation methodology, in this case using bison teeth. The new tooth aging method uses GIS mapping software to draw tooth surfaces and then calculate tooth surface areas of knownage bison teeth. Then, this known-age tooth sample is used to derive algebraic equations that can estimate the age of prehistoric specimens. To test our age prediction models, we use the well-known Folsom, New Mexico bison tooth assemblage. Overall, the new method provides statistical insights to how often Folsom may have been occupied and which type of hunting behavior appears to have occurred. Most importantly, the new model has the potential to provide a wealth of information about past bison hunting behaviors and may greatly improve our understanding of prehistory.

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INTRODUCTION

How old was a zooarchaeological specimen when it died, and what can that tell us? Our study represents a novel approach to an old problem that has long been important to faunal analysts. This importance rests on the knowledge that prey age structures can answer a broad range of archaeological questions and increase our understanding of past hunting practices and prey demographics. Specifically, tooth morphology can indicate the age (Fuller 1959; Klein 1981; McCutchen 1969; Payne 1987; Robinson 1979; Steele and Weaver 2012; Todd et al. 1996; Winchell 1963), diet (Chisholm et al. 1986), health (Byerly 2007), and sex (Ruscillo 2003) of an individual, and provide opportunities for genetic sampling (Cannon 2007). Yet, the available tooth aging methods often rely on qualitative age assessments or quantitative methods that have not been tested for accuracy or precision. Subsequently, zooarchaeologists lack a method for capturing demographic information from teeth that is both demonstrably repeatable and has known confidence intervals.

Archaeologists employ various methods to understand site seasonality, occupation frequency, and human subsistence systems. Artiodactyl teeth, especially bison teeth, can provide important information within these archaeological contexts (Byers 2009; Byers and Hill 2009; Discamps and Costamagno 2015; Driver and Maxwell 2013; Fuller 1959; Frison 2013; Frison et al. 1996; Frison and Reher 1970; Frison and Stanford 2014; Hill 2010; Kornfeld et al. 2010; Larson et al. 2009; Lyman 1987; Moffitt 1998; Niven and Hill 1998; Rodriguez-Hildago et al. 2015; Todd et al. 1996). Zooarchaeologists often age bison teeth using tooth eruption and occlusal wear patterns (Todd et al. 1996). They then employ these data to construct demographic profiles of the bison. The resulting mortality profiles help address questions of age structure and season of kill. To do so, zooarchaeologists group specimens into age cohorts that are represented with simple bar graphs which describe the relative abundances of various age groups within a given population (Lyman 2001; Stiner 1994; Todd et al. 1996). Such mortality profiles provide generalized life cycle models that inform on prey demographics, predator-prey relationships, survivorship, and other factors (Lyman 2001; Stiner 1994).

Mortality profiles can provide two important pieces of information. First, site seasonality represents a standard zooarchaeological question pertinent to understanding settlement and subsistence systems. In such cases, archaeologists use incremental physiological wear and eruption-based age estimates to infer site or component seasonality (Monks 1981; Stiner 1994; Todd et al. 1996). Second, archaeologists also use tooth wear to construct mortality profiles to document subsistence strategies, because different hunting strategies can produce different age-structures (Stiner 1994). Given the importance of such information to subsistence adaptations, especially phenomena such as bison hunting, zooarchaeologists have invested considerable time into understanding the relationships between tooth morphology and physiology (Blitz et al. 2014; Byers and Hill 2009; Frison and Reher 1970; Frison and Stanford 2014; Kornfeld et al. 2010; Todd et al. 1996).

In this paper, we offer a new method for quantifying age-related tooth wear in bison teeth. Our method employs a GIS to quantify occlusal surface wear in a large sample of known-age bison mandibles. We then run a series of analyses to determine if tooth wear can predict age and do so in a way that allows us to understand the accuracy of our method. Finally, as an example, we use our regression models to age the mandibles from the well-known Folsom Site (Meltzer et al. 2006).

BACKGROUND

Aging Prehistoric Bison

Bison teeth represent an "information dense" portion of any so populated faunal assemblage (Hillson 2005, pp. 1–6; Lyman 2001). Moreover, bison teeth are common components of Plains and Intermountain bison assemblages in North America (Driver and Maxwell 2013), as these animals are common in local archaeofaunas, especially in regions where bison were dietary staples (Reher 1978; Hanson 1984). In fact, any time bison were present, they were likely pursued and taken as prey, as they provide a large caloric return relative to handling costs as well as numerous other valuable resource materials such as hide (Smith et al. 2008; Widga 2006).

Bison teeth are durable and consist of dentin and enamel which preserve well in many settings (Graves 2010). Bison have 32 teeth including 2 canines, 6 incisors, 12 premolars, and 12 molars. Each tooth is comprised of several features that include organic and inorganic components that grow to form a wide variety of species-dependent facets and features (*see* Frison et al. 1976, pp. 38; Hillson 2005, pp. 146–206; Rodriguez-Hidalgo 2015, pp. 4; Todd et al. 1996; Winchell 1963). For this study, tooth features include dentin, enamel, interfossettes, and ectostylids (*see* Figure 1, "GIS Tooth Surface Feature Classes").

Tooth aging techniques operate within the basic concept that measurable tooth eruption, growth, and occlusal surface attrition can be used to estimate a specimen's age at death (Hill 2010; Hillson 2005; Todd et al. 1996). Once an assemblage's teeth are "aged", zooarchaeologists use graphic representations of age distributions, often histograms or ternary plots (Stiner 1994), to understand seasonality and demographic composition. These methods, while informative, are not without their issues.

Archaeologists commonly age teeth using visual methods involving Payne's (1987) tooth wear codes and comparative tables and figures from references such as Todd et al. (1996). These methods and the results derived from them are subjective and lack methodological clarity and replicability, and, in our opinion, have not been adequately tested in controlled settings (see for example Todd et al.1996; pp. 151–154). Perhaps most important, is the observation that to date, we lack a method that directly, reliably, and quantitatively links tooth morphology, especially occlusal surface wear (or any other morphological tooth age-proxy), with an animal's age at death. Further, the traditional techniques often fall short of producing the high-resolution calendrical age estimates (i.e., seasons or months of death) that best inform on archaeological materials (Byers and Hill 2009; Driver and Maxwell 2013; Hill 2010; Meltzer 2006; Niven and Hill 1998). Finally, traditional methods lack the ability to place results within a confidence envelope. Given these concerns and the associated gaps in knowledge, we develop a new GIS based methodology that links quantitative measures of occlusal surface wear with animal age. Though available known age bison tooth data present biases that partly confound these attempts, this paper serves as a template for quantifying tooth age estimation and serves as a proof of concept for accurately, precisely, and replicably estimating tooth age(s).

The Bison Tooth Transition Model

Bison teeth erupt, grow, and wear differentially throughout a lifetime of grazing (Berger and Cunningham 1994). Here, we present a simple "bison tooth transition" (BTT) model that rests on the observation that tooth composition and morphology change with animal age (Fuller 1959; Todd et al. 1996). Available known-age bison tooth surface areas, which were field- and museum-collected for this study, inform our BTT model. These data suggest that surface areas of deciduous premolars, permanent premolars, and molars follow distinct, observable, and generally predictable age-related morphological change. Subsequently, our BTT model generalizes these patterns for conceptual, methodological, and inferential purposes.

We leverage our BTT model from known patterns in the wear trajectory of a bison's teeth across its lifetime (Frison and Reher 1970; Robinson 1979; Simon 2005). Deciduous second, third, and fourth premolars (P_2 – P_4) erupt first and provide chewing surfaces for juvenile animals. Premolars are also the first teeth replaced by their permanent counterparts. Molars, which lack deciduous counterparts, erupt shortly after deciduous teeth, beginning with the first molar (M_1). As the permanent premolar transition completes, molars begin erupting (M_1 – M_3 , respectively and in that order) until the animal has reached maturity. Molars are the last functional teeth present in old-age individuals, at which point premolars are often ground to the gumline. Permanent premolars never reach the mastication potential (surface areas) of their deciduous precursors, nor their molar counterparts. Eventually, teeth are "entirely worn" and the animal starves. Overall, deciduous surface areas peak during late adolescence, then

drastically dip during transitionary juvenile-adult periods. Permanent premolar and molar surface areas gradually increase through adulthood and then diminish with old age.

A GIS-Based Tooth Aging System

A GIS is "a spatial (geographic) information system used to import, edit, visualize, analyze, and output spatial and non-spatial information stored in a computer database" (Jensen and Jensen 2013, pp. 380). While designed for cartography and related analyses, innovative archaeologists have also explored ways that a GIS can aid in nongeographic research (Abe et al. 2002; Buchanan et al. 2007; Cambra-Moo et al. 2012; Charlin and Gonzalez-Jose 2012; Evin et al. 2016; Jalandoni and Kottermair 2017; Kaufman et al. 2015; Marean et al. 2001; Parkinson et al. 2014; Porter et al. 2016; Shott and Trail 2010). Operationalizing the BTT model within a GIS in a way that links tooth morphology with age requires understanding how researchers capture morphological data. Our research employs Photogrammetry, the use of photos to measure objects, as the foundation for our GIS-based method. In this study, we use scaled bison tooth surface photos (Appendix 1; Figure A) to document occlusal surfaces and changes to their morphologies. Our methodology includes three components. These include a known-age bison mandibular tooth sample with complete or nearly complete tooth rows containing undamaged teeth, 2) scaled, two-dimensional, representations (photos) of occlusal surfaces from our known-age sample, and, finally, 3) a simple GIS geodatabase for digitizing, measuring, and storing tooth surface data. We discuss this methodology in greater detail below.

METHODS

The Reference Sample

The known-age specimens derive from three sources. The University of Wyoming Archaeological Repository (UWAR) provided the bulk of our known-age sample. A smaller sample comes from the Idaho State Museum of Natural History (IMNH). The remainder were acquired by the authors from carcasses at the Terry Bison Ranch, Cheyenne, Wyoming and are now housed at Utah State University (USU) Zooarchaeology Laboratory.

The reference sample includes 142 aged mandibular tooth rows documenting 91 bison and include 51 paired sets from single individuals. UWAR specimens (N = 105) represent the greatest number of known-age mandibles, though not the sample with greatest age ranges. The IMNH provided the mandible sample (N = 21) that covers the widest age range. Field-collected USU specimens (N = 16) partly fill age gaps in the two museum collections. Together, the sample is dominated by bison roughly five years or younger.

The first step in our methodology focused on documenting our known-age sample. We photographed only mandibles with intact or nearly intact tooth rows. In all cases, only intact teeth were included in our study. Photographic equipment included a Canon® EOS Rebel T4I with an EX-Sigma; 30mm 1:1.4 DCHSM lens, a Nikon® D3200 with a standard 32mm lens, and an iPhone® 7 cellular phone. Bison tooth surface photos were (mostly) shot using ". raw" formatting, since this format captures maximum pixel information. Regardless of the camera used, our goal was acquiring high-resolution photos. To do so, each specimen was placed in a foam cradle. Before capturing an image, we placed a 10x2 cm photo scale next to and level with the specimen's occlusal surfaces. During photography, information from each specimen such as specimen number, side, condition, photo number (etc.), was entered in an Xcel® spreadsheet.

We note that the UWAR specimens contained only "age-group" level data (yearly increments; 1.6–4.6 decimal years), whereas the IMNH and personally collected data were aged by specific decimal years (continuous 0.1 decimal years). To narrow these age estimates to decimal years, each UWAR specimen was visually age-estimated (within the given year group of the specimen) using what we perceive as the best currently available age estimation comparative data sets, the Mill Iron (Todd et al. 1996) age estimation tables and the wear codes adapted from Payne (1987), so that these specimens were also associated with 0.1 decimal year data. We acknowledge that this method of known age sample correction introduces biases we are directly seeking to avoid, specifically that seasonal level data may be less accurate than preferred. Unfortunately, these biases are unavoidable given the current known age bison tooth sample. Therefore, we present how tooth age corrections were attempted while explicitly revealing how these attempts may bias age estimation in our current proof of concept bison tooth age estimation modeling.

Each specimen was age estimated by two different analysts. Assigning the UWAR sample to .01 decimal years involved three general steps. First, traditional measurements were taken for all known age UWAR teeth (Figure 1), and the resulting index information was cross referenced with aged Mill Iron tooth indexes. Second, the adaptation of the Payne (1987) tooth wear codes were visually compared with UWAR bison teeth. Third, UWAR bison teeth were visually compared with the available age estimated Mill Iron tooth surface illustrations. These three protocols were performed by both observers (independently) and the independent observer indexes and estimates were used to generate a decimal year age estimate of the UWAR bison tooth assemblage. Additionally, when left and right UWAR mandibular pairs were available, both specimens were aged and averaged. Five of the paired mandibles were missing a single premolar per individual. On these five occasions, missing premolar information was duplicated from paired (the opposing right or left) mandible in the assumption (evaluated quantitatively below) that tooth surfaces from left and right mandibles are similar. This procedure undoubtedly introduces some unknown level of bias into our comparative BTT sample. These potential biases are discussed further in the results and discussion sections.

We use the following age group classifications to define our experimental age structures: age decimals 0.1-0.9 fall into age group one, age decimals 1-1.9 are age group two, and so forth. Decimal ages are presented in tenths-years (0.1 decimal years) where the 0.0-0.1 birth event represents calving season. Note that calving seasonality is left to researcher discretion and can be manipulated freely. Neonatal and natal specimens (ages ≤ 0.0) are not considered in this study. Several additional morphometric indexes were captured once GIS tooth data were produced and include tooth length, tooth width, and tooth row length (Figure 1, bottom).

GIS Tooth Age Estimation Protocol

The BTT methodology employs a simple GIS to generate tooth surface data. First, we created an "undefined" geodatabase (GDB) projection with the ESRI ArcGIS® software package and this was designed to store, digitize, and quantify tooth surface feature classes (Figure 1). Next, each tooth row surface photograph was imported into ArcMap® and the photographed 10- by 2-cm photo scale was georeferenced (scaled) to

the corresponding 10- by 2-cm shapefile. Our digitization, or "tooth mapping" process began by creating shapefiles documenting each tooth surface feature and tracing the feature of interest over a digital projection of each scaled mandible photo. Since each feature was captured as a polygon, we were able to quantify areas for the various occlusal features contained by each tooth in our known-age sample. Once all the occlusal features belonging to our known-age specimens were mapped, we examined the dataset for mapping, naming, or other errors to ensure data quality and completeness. These data were then exported from the GIS attribute tables to Excel® spreadsheets.

We use our known-age dataset with the following caveat. We acknowledge the importance of capturing tooth row images in a repeatable and comparable manner since methodological errors run the risk of "inventing" non-realistic data (Jensen 2003). This is especially critical considering the photogrammetric "bend", or spatial distortion, which arises due to lens and object shape, lighting, camera angle, and distance-to-object. This study does not consider the bend created when 3D tooth surfaces are captured with 2D photography and georeferenced with GIS. Bends no doubt occur, as bison teeth have three dimensions, especially during adolescence; however, we consider the impact of these distortions acceptable given that this study is a proof-of-concept model which undoubtedly requires additional scrutiny to develop the models for archaeological interpretations.

Interobserver Replicability

Capturing shapefiles in an accurate, precise, and replicable way is fundamental to the efficacy of our methodology. To evaluate if our protocol would produce replicable results, we employed nine USU graduate students in an interobserver error study. This followed several hours of one-on-one methodological instruction and clarification. Participants were provided desktop computers with interobserver study folders that contained the same five mandibular tooth photos (.jpg), a prepared ArcGIS® geodatabase with simplified tooth-feature classes, a screenshot video tutorial of the tooth mapping process, a Microsoft Excel® spreadsheet with fields that captured participant GIS experience mapping times, and a Microsoft Word® document outlining tooth mapping procedures.

Interobserver ANOVA test results (Table 1; Figure 2) show that mandibular premolar and molar surfaces were similarly mapped between participants. No observers had previously aged bison teeth (or conducted any other zooarchaeological tooth research), and therefore represent a relatively "blind" subject-test. The few observed bison tooth identification errors serve as reminders that knowledge of tooth morphology and GIS experience are *a priori* considerations when mapping bison mandibular teeth.

RESULTS

Sex and Side Bias

Several aspects of bison physiology potentially bias the analysis that follows. Bison are dimorphic with males larger than females. This is important because the UWAR specimens that represent most of our sample (75.35%) also lack sex information. Known-sex specimens include 17 female and 18 male mandibular tooth rows (eight females and nine males; Appendix 1, Figure B, left). Moreover, except for the two-year and seven-year cohorts, the different sexes are found in non-overlapping age groups (Appendix 1, Figure B, right). Therefore, it is difficult to fully compare sexed specimens by age.

Mandible side is a second variable that might introduce bias into our regression models, especially if bison experience side-dominant mastication. A visual comparison of the left (N = 73; 50.82%) and right (N = 69; 49.18%) mandibles indicates that bison teeth may wear differentially based on side and the greatest differences are observed in the lesser sampled old ages (Figure 5). This finding suggests that side dominant mastication can differentially condition tooth wear.

Does Tooth Wear Predict Age?

In the analyses that follow, we use our known-age sample (Figure 6) to generate a series of regression models designed to assign ages to archaeological specimens. As noted above, bison display sexual dimorphism, and some individuals may experience side-dominant wear patterns. Moreover, these animals have also shown diminution as a taxon across the Late Pleistocene and Holocene (Hill et al. 2008; Lyman 2003). In effect, these factors complicate the ability to use the regression models developed below from our recent, known-age sample on individuals of unknown sex, size, or species. For example, we suspect that using data derived from modern *Bison bison* to age larger *Bison antiquus* would result in ages older than those the animals reached in their lifetimes. To address this issue, before we ran our regression models, all tooth feature area data were first converted into Z-scores. Others have shown that using Z-scores can in such a way can alleviate body size sampling issues, as these scores examine deviations from a population mean regardless of the actual morphometric size of a specimen (Sedgwick 2014; Wilson 1978). That is, our independent variables are converted to areas measured

as deviations from a mean, instead of absolute values, so the overall size of an animal no longer drives the statistical comparisons. We next use the modified dataset to run a series of regression analyses.

Linear regression analyses perform best with normally distributed data. To evaluate how our data distributes, we first ran a Breush-Pagan test, which is used to identify heteroscedacity in linear regression models, to examine how a summary metric of tooth wear distributes around its mean. In this case, because our datasets contain seven different feature areas (Figure 1; note that polish was not included in the study). Here, we question the utility of evaluating each piecemeal, we summed all the feature areas from every tooth collected from each mandible and tested this value for normality. In effect, this gave us the total feature area at the mandible level. A Breush-Pagan test confirms that the aggregated sample displays some degree of heteroscedasticity (F = 0.007; df = 1, 142; p = 0.05). Splitting the dataset into young and old age groups lessens the degree of heteroscedasticity and provides distributions closer to normal (Figure 6). Importantly, however, homoscedasticity is not a requirement for ordinary least squared (OLS) modeling, and it rarely exists in real-world observations (Hutcheson 2011). Therefore, we move forward by using our known-age dataset to model animal age as a function of tooth feature wear.

To begin this analysis, we first use simple linear regression to examine how agemediated variability in the overall occlusal surface area of each tooth $(P_2 - M_3)$ explains changes in animal age within models defined by the overall (aggregate) dataset, as well as subsets of young, and old individuals (Figures 4 and 6; Table 2). Note that, at this initial stage of analysis we used the raw tooth surface areas and not the tooth surface zscore, because the raw data should support a surface area to age relationship without the need for additional z-score corrections. Z-scores are meant to increase modeling accuracy and precision; however, tooth surface and age data, if related, should show some degree of relationship without statistical correction. The young and old age groups were, once again, partitioned based on the presence or absence of deciduous teeth. In this instance, overall surface areas were the metrics of interests. These were calculated by adding the areas of all the various occlusal features recorded for each tooth in our comparative sample. We then ran models for each of the six teeth in a bison mandible. The regression models clearly show that tooth age and feature-area data correlate in predictable and statistically significant ways (Figure 4; Table 2).

The aggregate models, defined as all data from all individuals in our comparative sample and which include P₂, P₄, and/or M₃ tooth surfaces, demonstrate the greatest predictive power (Table 2). The split *young* and *old* models, though more normally distributed, predict less of the age variability than the larger aggregate sample model (Table 2). Deconstructing mandibles into their individual teeth shows that molars provide greater predictive power than premolars, with all aggregate model M₁, M₂ and M₃ displaying significant, positive relationships with age (Appendix 1, C1–C6). *Tooth Aging Models*

Having found course-grained relationships between tooth wear and animal age both at the individual tooth, and mandible levels, we next ran four stepwise linear regression models to determine which specific tooth features and from which teeth, if not all, comprise a best fit model for our dataset (Table 3.) The first model was run using all the data from all individuals in our sample regardless of age or sex (Equation 1; Table 3). Using this aggregate dataset results in a best fit model that employs eight variables and explains 80 percent of the variation in our known-age sample.

Equation 1:

$$y = 3.09 + 0.46(M2Dentin) - 0.2(P3Enamel) - 0.41(P4InterfossetteEnamel) + 0.2(P2Length) - 0.25(M1EctostylidDentinUnattached) + 0.19(P2Enamel) + 0.52(M3Length) - 0.28(M2InterfossetteDentin) + $\in$$$

As a point of comparison, we also ran a second analysis to produce a single-tooth, age estimate. This model is useful when a complete mandible is not available, but an intact M₃, which we identified above as the mandibular tooth with the greatest predictive power. We call this model the M_3 model (Equation 2). The M₃ model uses only the measured tooth features from third molars but does so from every individual regardless of sex or age. In this case, our M₃ model, which allows for the largest sampling, explains 85 percent of known-age variation.

Equation 2:

$$y = 3.09 + 0.94(M3Enamel) + 0.78(M3InterfossetteEnamel) + \in$$

We also derived models for old (\geq 4 years) and young (\leq 3.99 years) subsets of our sample (Figure 5 and Table 3) because we wanted to examine how tooth surface predicts age within a smaller and more normally distributed subset of the sample. The young model (Equation 3) includes three features that explain 87 percent of sample age/tooth surface variation. The old-age model (Equation 4) includes eight features that explain 80 percent of the variation in our sample.

Equation 3:

 $y = 2.53 + 0.34(M3Length) + 0.65(M3Enamel) - 0.14(P3Surface) - 0.11(P4Enamel) + \in$

Equation 4:

$$y = 3.48 + 2.38(M3InterfossetteEnamel) - 0.71(P4InterfossetteDentin)$$

+ 0.73(M3EctostylidDentinUnattached) - 1.08(M1Dentin)
+ 0.46(M1EctostylidDentinUnattached)
- 1.75(M2InterfossetteEnamel) + 0.34(P4Length) + 0.3(P2Length)
+ \in

In our analysis, we derived four best-fit models each representing a different way of partitioning our data – 1) all tooth and all feature, 2) M₃ surface area and 3) young and old models. We note that using our dataset, a researcher could develop models for any combination of teeth to age partial mandibles or isolated teeth, with the recognition that different models will present different prediction intervals. Subsequently, each modeling option will also vary regarding its predictive power, and a larger known-age bison tooth sample would greatly improve tooth-wear/age prediction modeling regardless of the targeted population.

Cursory examination of the aggregate model and the segregated young- and oldage specimen models show that aggregate tooth surface data are most strongly correlated with age (Table 2; Figure 7). The M3 enamel model allows for a single tooth model that also may predict tooth age based on tooth surface area (Table 3). The aggregate data appears to currently provide the best modeling option as these models utilize all available known tooth-feature area data from the largest available sample size. Given a more complete known-age bison tooth sample, the split old- and young-age models may better reflect bison tooth morphology, since spitting these models appears to produce more normally distributed samples (Figures 7 and Appendix 1; D1–D6). However, this remains unexamined. For our current purposes, the aggregated data appear the most useful and easiest applied age predictors.

Old individuals are represented by the fewest mandibles and display the greatest tooth feature standard deviations within yearly cohorts (Figure 3 and Appendix 1, Figure B). This should not be surprising. Calve teeth are more closely related in size and shape then are those found in adults within a given population (Burger and Cunningham 1994; Lott 2002). This similarity results from the fact that teeth from older bison have been subjected to a lifetime of mastication and, subsequently, will better document variation in dietary and environmental impacts impact on tooth wear. Obviously, if we had available a larger sample of known-age mandibles our analysis would generate models with greater explanatory power. Nonetheless, we derived several different regression models from our data based on the number of tooth features included in each. Our results suggest that neither of the age specific models enjoy the same explanatory power as the aggregate models.

DISCUSSION

Bison Age and Kill-Event Seasonality at the Folsom Site: An Archaeological Application

To demonstrate the utility of our method within an archaeological context, we turn to an analysis of the mandibles from the well-known Folsom site (Cordell 1997, pp. 68–72; Cassells 1997, pp. 50–53; Figgins 1927; Meltzer et al. 2006; Thomas 2000, pp. 146–152). The sample used here includes all available mandibles and mandibular teeth from the Folsom Site we were able to locate, and these were housed in three

archaeological repositories. Curation facilities include the American Museum of Natural History (AMNH; New York, New York), Denver Museum of Nature and Science (DMNS; Denver, Colorado), and Southern Methodist University (SMU; Dallas, Texas). Each collection was similarly curated and overall, the materials were well preserved, and mandibular tooth rows were mostly complete (Table 4).

To age the Folsom collection, we focused on two of the models presented above, the all-tooth, all-feature model and the M₃ enamel model. We employ the latter as we acknowledge that single-tooth models may have some benefits because some archaeological bison mandibles will contain tooth rows of varying degrees of completeness or be represented by single, isolated teeth, namely the strong M₃ age predictor. Note that other models may suit aging, but these were chosen as they appear adequate given this sample and the exploratory nature of this study.

The aggregate model and the M₃ enamel model are used to age estimate Folsom bison teeth. Unfortunately, the Folsom mandible collecting includes both complete and incomplete specimens. Because of these requirements, we analyze only those Folsom specimens that are either complete (aggregate model; N = 25) or contain complete M₃ teeth (M₃ model; N = 46). Doing so resulted in the use of 38 and 71 percent of the overall 65 specimen bison tooth sample, respectively. For our Folsom case study, we do not attempt to pair left and right specimens, but instead assess each specimen separately. While we here focus on only those specimens relevant to the models in play, we do note that the remainder of the Folsom assemblage may be aged by creating equations specific to whichever combination of teeth are present in each specimen. Such models would subsequently have their own unique tooth-specific parameters and resulting predictive power(s).

The mortality profiles for each model illustrate some BTT modeling robusticity, seasonality profiles (though interesting) illustrate modeling and sampling issues and combined inform on modeling accuracy and precision (Figure 9). We begin by first comparing the mortality profiles generated from each model. As can be seen in Figure 9, both models produce statistically similar profiles dominated by prime age individuals (U=534.000; df=25, 46; p=0.624) which are often associated with selective hunting. Therefore, at the yearly cohort level, our regression approach appears robust between models. In contrast, seasonality level data (decimal years), derived from our methodology, resulted in significantly different age distributions (U = 302.500; df = 25, 46; p = 0.001). This difference can be clearly seen when comparing the distributions presented in Figure 9. Therefore, our regression approach appears to reliably describe age structures at the yearly cohort level, but finer grained analyses appear suspect. That is, the models appear relatively accurate at the yearly age estimate (Figure 9, mortality profiles) but less precise at the monthly seasonality level (Figure 9, seasonality profiles), and may well reflect poor fine-grained sampling or other sampling biases such as those introduced when attempting to narrow UWAR samples to the monthly level. Furthermore, this may indicate that using previous bison tooth age estimation materials may not produce accurate or replicable seasonal age estimates.

Bison ecology, and specifically birthing seasonality and cohort breadth, may also be marked based on seasonal clustering in the death assemblage (Figure 10, zero x-axis represents annual calving, which can be designated *ad hoc* per researcher discretion). If we assume the BTT at least partly predicts bison seasonality, and that animals grouped within a roughly 2-month period can be consider a birth cohort, then both the aggregate and the M₃ enamel models may show similar seasonal death markers (Figure 10). That is, both models indicate roughly three hypothetical kill event groupings (i.e., 2-month age cohorts). Further, both models show the largest groupings during mid to late summer (Figure 10; .1-.3 decimal years), observed also in Folsom seasonality histograms (Figure 9). Assuming the Figure 10 scatterplots are somewhat accurate, we might begin to see the age structure of each kill event; a truly fascinating, albeit not currently achieved, BTT model result.

It must be again noted that these bison tooth age modeling efforts are a proof of concept, and the current models fall short of precisely making well-founded claims and interpretations regarding the Folsom bison death assemblage, or bison ecology. Despite this, we see how the BTT approach might be applied when asking these specific research questions. We can also make some observations regarding the BTT Folsom tooth age estimates.

The multiple kill hypothesis at Folsom is not too farfetched considering what else we know about this site and others (Fenner 2009). For instance, numerous smaller hunting events may account for the paucity of occupational debris and formal features noted at the site (Meltzer et al. 2006, pp. 291–293), since small, short term hunting events typically leave less archaeological residue (Binford 1978). If Folsom was a single kill event, many hunters would be required to dispatch >30 *Bison antiquus*, whereas fewer hunters would be required for numerous smaller kills of prime age individuals. Geomorphology indicates that, if Folsom deposition occurred rather quickly (Meltzer et al. 2006, pp. 133 and 150–152), and numerous hunting events transpired, then perhaps the hunts belong to a narrow generation of Folsom hunters who knew the landscape (Zedeno et al. 2014). If so, this would not be the first Folsom kill site containing multiple hunting events. The Cooper site (Bement 2007), for example, also suggests multiple Folsom-age procurement events (also *see* Bement 2009; Bement et al. 2012).

Though these Folsom site interpretations remain untested, they exemplify some of the fascinating insights that might be answered given a more complete BTT model. A more informed BTT model could be used alongside other season(s)-of-occupation information, such as lithic and bonebed distributions (Andrews et al. 2008), to help determine if multiple kill events occurred at the site. Assuming bison hunting practices remained the same throughout prehistory, mortality, and seasonality profiles (if discernible) should also remain generally consistent in the archaeological record, though specimen counts might be expected to increase alongside hunter populations.

Minimum Mandible Units (MMU): Matching Mandibles and Deriving MNI Counts

Lastly, and in addition to all other BTT considerations, our methodology incidentally provides a way to use tooth wear to provide animal counts in large assemblages. We suspect that many of the Folsom specimens likely represent paired elements from the same individuals, because all but the least fortunate bison possess both left and right mandibles. We explore this observation using what we term minimum mandible units (MMU). The MMU is like the minimum number of individual methodology (MNI; Binford 2001; Dominguez-Rodrigo 2011; Grayson 1978; Lyman 1994; Marean and Spencer 1991; Marean et al. 2001; Marshall and Pilgrim 1993; Shotwell 1955) in that it uses left and right specimen side pairing to estimate minimum numbers of individuals in an assemblage. Like MNI, MMU pairs left and right mandibles, in this case visually (inductively), based on rights and lefts which appear to morphologically correspond. Once paired, individual side age estimates (within an MMU pairing) can be examined to help determine if the visual pairing is correct (Figure 11). The result is that, in the future, the MMU pairing methodology allows an observer to use quantitative data (right- and left-paired tooth age estimates) to statistically pair disarticulated mandibles. It is likely specimens 31 and 33 are perhaps not actual pairs (Figure 10) and are instead errors in our inductive visual pairing technique revealed when statistically exploring the pairings. Further, it remains unknown the degree mastication side dominance affects the MMU sample. However, many specimens appear closely aged (Figure 11, MMU 1, 3–7, 16, 18–19, 27), and it is clear left and right specimens are never identical. Once paired, the left and right age estimates were averaged to provide a single and (what we think to be) more accurate tooth age estimate.

Based on our MMU methodology, we estimate an MNI of at least 36 Folsom bison, and potentially more given the variability of several tooth pairing age estimates (above). This number includes 51 paired mandibular tooth specimens representing 22 individuals and an additional 14 unpaired specimens representing at least 14 more animals. If the MMU pairings are accurate, then they suggest four more animals at Folsom than previously identified (Meltzer and Todd 2002, pp. 17).

CONCLUSION

BTT age estimates, regardless of accuracy, illustrate several interesting bison physiological factors. For instance, MMU age estimates indicate animal-specific side dominant mastication (Figures 5 and 11). That is, age estimates for each side of the accurately paired MMU differ slightly because one side is more heavily worn. Another interesting insight is that, though the limited old age sample skews these results, BTT modeling shows that dimorphism increases greatly with age (Figures 4 and 5), which is expected (Berger and Cunningham 1994), but helps support that BTT modeling is at least somewhat accurate. BTT models also help document the tooth eruption, growth, and wear sequence (Figure 3), particularly that third year bison typically have shed all deciduous premolars. Deciduous tooth surfaces are smaller than their molar counterparts but grow similarly. The P4 has similar mastication surface as the M1, and the two teeth have roughly equal surface areas just prior to the P4 shed event, thus maintaining rear mouth mastication potential otherwise lost when the P4 is shed. Overall, BTT models offer greater insights into bison than simply a proxy to age.

Presently, the BTT methodology works towards a consolidation in bison (and other) tooth age estimation practices while producing traditional mortality and seasonality profiles (Figure 9) and tooth surface wear diagrams (Figure 1). That is, the BTT seeks a consistent and replicable tooth aging methodology. Previously, researchers used inductive/subjective wear codes and tooth surface diagrams (Payne 1987), and existing tooth index measurements and estimations (Todd et al. 1996) to make a best guess when aging bison teeth. Other times, teeth have been aged by experienced experts (Meltzer et al. 2006), which makes the process less-than-replicable.

The BTT builds on past tooth age estimation practices but seeks a more accurate, precise, and replicable technique that, importantly, is probabilistic. Further, the BTT is an inexpensive photogrammetric tool, and can be used to train basic GIS while performing
age estimation and building the known age tooth surface sample (Appendix 1, Figure G). Interestingly, the BTT also informs on more minute physiological nuances, which is important since no two bison are the same, habitat varies, and they are strongly dimorphic (especially with age).

The BTT, like all models, is imperfect (Bertalanffy 1950; Bokulich 2011; Kelly 2000). Current known age data are not as precise, especially regarding specific seasonality of death (year decimal ages) and older age specimens (also *see* Appendix 1, Figures F and G). Also, diet, diminution, and specimen sex require more specific examination and accountability. However, the BTT appears a statistically driven and replicable tooth aging tool that might be used (if improved) to derive better tooth aging models and predictions. It (as well as the MMU) provides unique insights and opportunities, like were there two (or more) occupations at Folsom, and will an improved BTT deliver surprisingly stark insights into past bison hunting and ecology?

This study serves as a proof of concept with unique challenges, and as such, remains short of a comprehensive GIS tooth aging methodology. Future studies should develop more rigid tooth feature mapping guidelines, and statistical procedures and outputs such as tables and figures should be standardized. It is clear the BTT would greatly benefit from a greater-known age sample. Such a sample would contain precise known ages at death and better consider sex, side, and environmental bison tooth constraints such as diet and range. Also note that previous tooth aging indexes were not closely examined. These provide additional future modeling indexes, especially ectostylid distance to wear, which has been demonstrated a strong age proxy (Todd et al 1996). Ideally, a large and more accurate and precise known age tooth assemblage, as well as previous tooth aging indexes, might be used alongside GIS tooth surfaces to provide more informed zooarchaeological age estimates.

Unsurprisingly, bison teeth continue to illustrate the tooth's tremendous potential to inform on the archaeological record. If we consider bison tooth age estimation as a metaphorical microscope, past methods are the base, stand, and lens which gave us our first tool to examine age-at-death. The BTT model presented here is an attempt to provide a new lens, to increase tooth age estimation accuracy, precision, and replicability using photogrammetric and statistical tools to help bring mortality data into focus. With a more refined technique, we may be surprised at how microscopic a view we might gain from past death assemblages. Specifically, a refined and improved BTT could help test Bamforth's (2011) bison hunting intensification hypothesis, and function as a proxy to theoretical components of human *intensification* (Bettinger et al. 2006; Bettinger 2015; Morgan 2012 and 2015). Though a perfect BTT model is impossible, additional research should codify the current results, build more accurate and precise models, and examine the many available bison tooth assemblages to test Bamforth's bison hunting intensification hypothesis. Models used in contemporary past population estimations, which employ Bayesian probability distributions (Price et al. 2021) might prove useful when building improved BTT models (see hypothetical figurative example; Appendix 1, Figure H). Assuming these BTT corrections were made, we might gain a much clearer understanding of diachronic bison hunting as well as the overarching tenants of the human intensification process.

FIGURES



Figure 1. Bison mandibular tooth index master illustration (also see Table 3).

*A = attached ectostylid on P_4 (counted as part of dentin and enamel); B = unattached ectostylid on P_4 (which is counted separately); DS = distal; E = entoconid; EC = ectostylid; L = length; M = metaconid; MS = mesial; W = width; GIS Tooth Surface Feature Classes are those generally identified by previous researchers (Lyman 2001 and Todd et al. 1996).



Figure 2. Interobserver boxplots for nine independent observers, by tooth.

The tooth surfaces from five tooth-row mandible specimens, which were mapped by nine independent observers, are represented in order from left to right in each tooth surface area box. These plots demonstrate that the tooth surface measurements can be reliably replicated, as the observer's marks closely align within each tooth box, though some slight intra-observer error was noted (i.e., Specimen 3, teeth P_4 and M_3).



Figure 3. BTT model tooth surface change over time derived from known-age samples used in this analysis.



Figure 4. Comparison of male and female bison tooth surface.

Figure 5. Surface area by aggregated specimen sides (left) and by sides by age group (right).



Sex-differentiated Surface Area by Tooth Tooth Tooth 3.50 1.0 ○ Female • Male • NA 3.00 : 2.50 P2 0 0 M10 2.00 1.50 .2 1.00 .0 10 10 6 8 Ó 2 6 8 ò 2.00 5.00-Surface Area 4.00-1.50 3.00 0 0 0 P3 1.00 M2 2.00 .50 1.00 .00 .00 10 8 8 10 Ó 4 2 4 6 0 2 6 4.00 5.00 4.00 3.00 00 3.00-P4 2.00 M3 2.00 0 1.00 1.00 .00 .00 10 10 8 8 6 Ó 2 à 6 Ó ż 4 Age Decimal





Figure 7. Model fitness showing variance from predicted and standardized values.



Figure 8. BTT Folsom Tooth Age Estimate averages by model.

BTT Age Models



Figure 9. Folsom Age Estimates using two different regression models.



Figure 10. Folsom assemblage bison teeth age estimate distributions.



Figure 11. Folsom MMU Examination, Aggregate Model Right and Left Mandible BTT Age Estimate Boxplots.

The more closely that left and right MMU pairings align the more likely the pairing is accurate, since left and right tooth surface areas and subsequent age estimates should be close. When averaged, the MMU pairings are thought to represent a single, more accurate BTT age estimate.

	Sum of		Mean		
Tooth	Squares	df	Square	F	Sig.
P2	.765	9	.096	1.040	.425
P3	.984	9	.123	1.637	.149
P4	3.428	9	.429	.979	.468
M1	1.240	9	.155	.431	.895
M2	.121	9	.015	.053	1.000
M3	1.217	9	.152	.224	.984

Table 1. Interobserver ANOVA scores by total tooth surface.

Considering a 0.05 confidence interval, the significance of all ANOVA test scores shows that there does not appear to be a significant difference between the observer's mapping of tooth surface areas, and that the molars approximate or equal a significance of 1 which indicates they are extremely similarly mapped.

	Sub- Model	Predictors	Adi D	Residual Sum of	Change Statistics			
Model			Adj. K Square	Squares (RSS)	R Square Change	F Change	DF	Sig. F Change
Aggregate	1	M3	0.791	98.837	0.793	535.089	140	0
	2	M3, P4	0.802	93.147	0.012	8.491	139	0.004
	3	M3, P4, P2	0.81	88.409	0.01	7.396	138	0.007
Young	4	M3	0.68	9.38	0.684	187.905	87	0
	5	M3, P3	0.771	6.626	0.093	35.749	86	0
	6	M3, P3, M2	0.803	5.645	0.033	14.775	85	0
Old	7	M3	0.276	79.064	0.290	20.869	51	0
	8	M3, M2	0.393	65.042	0.126	10.780	50	0.002
	9	M3, M2, P2	0.44	58.794	0.056	5.207	49	0.027

Table 2. Three OLS regression model categories: total tooth surfaces by age (decimal years).

MMU	Side	Specimen	Age Group	Model (z- score)	BTT Age	Adj. R ²	Standard Estimate	Coefficients	Coefficient Values
							Error		
1	R	AMNH_ 130476	6	Aggregate All	5.16	0.80	0.82	Constant	3.088
1	L	AMNH_ 130477	5	Features All Teeth	4.73			M2 Dentin	0.463
3	R	AMNH_ 131244	5		4.78			P3 Enamel	-0.202
3	L	AMNH_ 130757	5		4.99			P4 Interfossette Enamel	-0.412
6	R	AMNH_ 131287	4		3.49			P2 Length	0.203
6	L	AMNH_ 131286	4		3.55			M1 Ectostylid Dentin Unattached	-0.247
36	L	AMNH_	3		2.18			P2 Enamel	0.193
		130265						M3 Length	0.515
								M2	-0.283
								Interfossette	
								Dentin	
1	R	AMNH_ 130476	6	Aggregate M3	4.13	0.85	0.72	Constant	3.088
1	L	AMNH_ 130477	5	Enamel	4.12			M3 Enamel	0.942
3	R	AMNH_ 131244	5		5.13			M3 Interfossette	0.779
3	L	AMNH_ 130757	5		5.3			Enamel	
6	R	AMNH_ 131287	4		3.21				
6	L	AMNH_ 131286	4		3.37				
36	L	AMNH_ 130265	3		0.37				

Table 3. BTT Folsom age estimation models and the seven specimens used to examine model robusticity.

Collection	Specimen	MMU#	Side	Folsom BTT Model Age Estimate	
	1			Aggregate	Aggregate M ₃
					Enamel
AMNH	AMNH 130012	8	R	3.70	1.32
AMNH	AMNH 130018	13	R	2.09	3.09
AMNH	AMNH 130019	21	R	2.31	1.57
AMNH	AMNH 130021	22	R	2.53	1.83
AMNH	AMNH 130022	20	R	2.87	1.60
AMNH	AMNH 130023	18	L	3.84	3.88
AMNH	AMNH_130028	12	L	3.24	5.90
AMNH	AMNH 130029	17	R	2.37	3.09
AMNH	AMNH 130036	23	R	2.30	3.09
AMNH	AMNH 130037	19	R	3.49	1.43
AMNH	AMNH 130038	16	L	2.42	3.09
AMNH	AMNH 130039	18	R	3.48	3.09
AMNH	AMNH 130040	18	R	2.62	3.09
AMNH	AMNH 130042	24	R	3.66	4.94
AMNH	AMNH 130265*	36	L	2.99	1.05
AMNH	AMNH 130266	27	L	3.01	3.09
AMNH	AMNH 130307	9	L	3.05	3.09
AMNH	AMNH 130338	16	L	3.11	3.09
AMNH	AMNH 130348	16	R	3.12	3.09
AMNH	AMNH 130416	15	R	3.06	0.67
AMNH	AMNH 130476*	1	R	2.18	0.37
AMNH	AMNH 130477*	1	L	4.88	4.07
AMNH	AMNH 130499	19	L	4.08	5.04
AMNH	AMNH 130616	5	L	3.37	3.09
AMNH	AMNH 130617	10	L	3.40	3.40
AMNH	AMNH 130695	5	R	3.16	3.09
AMNH	AMNH 130700	7	L	5.16	4.13
AMNH	AMNH 130701	7	R	4.73	4.12
AMNH	AMNH_130702	2	R	3.20	3.69
AMNH	AMNH 130703	2	R	1.27	3.09
AMNH	AMNH 130757*	3	L	0.33	3.09
AMNH	AMNH 130759	8	L	1.17	3.09
AMNH	AMNH 130760	16	R	2.76	2.65
AMNH	AMNH 130761	4	L	2.67	1.93
AMNH	AMNH 130762	4	R	3.89	4.30
AMNH	AMNH 130763	14	L	3.99	4.01
AMNH	AMNH 131244*	3	R	4.99	5.30
AMNH	AMNH 131286*	6	L	4.31	3.84
AMNH	AMNH 131287	6	R	3.35	3.09
AMNH	AMNH 131355	18	R	1.33	0.60

Table 4. BTT Folsom Age Estimates by model and MMU.

AMNH	AMNH_131356	18	L	1.16	0.55
AMNH	AMNH_131450	11	R	2.02	3.09
AMNH	AMNH_131577	9	R	4.78	5.13
AMNH	AMNH_131652	25	R	3.55	3.37
DMNS	DMNH_1236	33	R	3.49	3.21
DMNS	DMNH_1420	28	R	3.33	3.22
DMNS	DMNH_1420	28	L	3.23	3.14
DMNS	DMNH_3000	29	R	3.57	2.98
DMNS	DMNH_3001	29	L	3.83	4.69
DMNS	DMNH_3002	31	R	3.13	6.23
DMNS	DMNH_3003	31	L	4.46	3.75
DMNS	DMNH_3004	34	R	3.65	4.08
DMNS	DMNH_3004	34	L	4.08	3.49
DMNS	DMNH_3007	35	R	2.28	1.66
DMNS	DMNH_3008	32	L	1.79	3.09
DMNS	DMNH_3009	30	R	1.95	3.09
DMNS	DMNH_7121	30	R	-0.69	-0.61
DMNS	DMNH_7128	30	L	3.39	2.62
SMU	1	25	L	2.58	3.03
SMU	24	24	R	2.96	2.24
SMU	136	26	R	3.72	3.67
SMU	140	26	L	5.10	4.75
SMU	141*	25	R	4.17	3.09
SMU	146	23	R	3.17	3.01
SMU	ECK2006	27	R	2.55	3.09

*= these specimens were randomly selected for model comparison (see Table 3).

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APPENDIX

Figure A. Bison mandibular tooth photo example (specimen: USU_Known DSC_0022) showing 10- by 2-cm photo scale and photographed 2D bison mandibular tooth row.
















Figure C-3. Young model premolar surface area and age correlations.















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Figure E. Known bison tooth sample ages compared to BTT sample age estimates, by assemblage.



This figure illustrates how the aggregate predictive model predicts the known samples from which they were derived. We see here that predictions have lingering prediction issues caused by various confounding factors such as the UWAR known-age sample correction method, which sought to increase the sample's monthly precision, as well as sex and old age sample biases.



Figure F. Known bison tooth *sample ages* (hollow) and known sample *age estimates* (solid).

This figure shows an overlay of the known age sample and a prediction of that samples ages based on the known age predictive model. Essentially, this is an example of using the sample to predict the sample. An ideal model would show an exact overlay, where the known sample tooth surfaces would exactly predict their actual age. Again, this illustrates the need for a larger and more precise known age bison tooth sample to best predict archaeological tooth samples.





Figure H. Hypothetical BTT age estimate reporting borrowing from contemporary radiocarbon methods and perhaps involving a Bayesian methodology.

Age Decimal