Tooth Wear Age Estimation of Ruminants from Archaeological Sites

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ABSTRACT

The teeth of ruminants (cud-chewing herbivores) can be used to estimate age. Tooth wear age estimation is an especially valuable method in archaeological research because it is non-destructive, efficient, and is adaptable to multiple species, which provides effective results. The objective of this paper is to review tooth wear age estimation approaches taken with a focus on cervid (deer) and caprine (sheep and goat) mandibles. I discuss the process of dental attrition involving ruminant chewing, digestion, and feeding behaviour, as well as factors that affect the rate of wear including individual and population variance. The approaches to tooth wear age estimation have been divided into three overarching categories: the Crown Height Method, the Visual Wear Pattern Method, and the Wear Trait Scoring Method. These approaches are all non-destructive and require similar assumptions about the regularities of tooth wear. Each involves different levels of accuracy, ease of use, efficiency, and applicability to archaeological mandibles. This paper highlights the strengths and weaknesses for these approaches and explains that these various methods reviewed are each better suited to different research situations. Taken together, tooth wear age estimation is a valuable tool that zooarchaeologists employ to reconstruct age-based demographic profiles of animal remains recovered from archaeological sites, illustrating how people interacted with and used them.

Keywords: zooarchaeology, tooth wear, dental attrition, age estimation, ageing, Cervidae, Caprine

INTRODUCTION

Estimating ages of animals from archaeological sites using dental remains has proven essential to understanding how people and animals interacted in the past (Klein and Cruz-Uribe 1983; Gifford-Gonzalez 2018; Reitz and Wing 2008; Russell 2012; Stiner 1990). These age estimations can be used to reconstruct demographic profiles that can inform on past hunting strategies, domestication practices, and other aspects of human-animal interactions (Klein and Cruz-Uribe 1983; Gifford-Gonzalez 2018; Reitz and Wing 2008; Russell 2012; Stiner 1990). Tooth wear age estimation is one of the three most frequently applied ageing techniques in zooarchaeology because this method is efficient, non-destructive, and works for age adult individuals of many species (Twiss 2008).

The other two often-employed ageing methods are tooth eruption sequences and cementum annulation. Tooth eruption sequences are used to estimate the age of younger individuals and requires knowing the timing and order of deciduous and permeant dentition eruption (Hillson 2005, 229–37). The age at which deciduous teeth erupt, are lost, and the eruption of permanent teeth follow a biologically determined schedule specific to a given species or population (Hillson 2005). Variation of normal development and eruption

sequences must be considered between different individuals, populations, sexes, environments, and with biological stress (Miller 1972; Spiess 1979, 77; Tomé and Vigne 2003, 172).

While tooth eruption ageing is limited to animals that died before their permanent dentition came into place, cementum annulation can be applied to older individuals. Cementum annulation examines annually deposited bands of cementum on tooth roots, which are microscopically observed and counted in cross-section (Aitken 1975; McEwan 1963; Gifford-Gonzalez 2018, 127-29). More accurate than tooth wear age estimation, this method is applied as a close substitute for known-aged specimens (Pérez-Barbería, Carranza, and Sánchez-Prieto 2015; Miller 1972). Partial or complete destruction of one tooth is necessary to prepare a cross-section for this method (Pérez-Barbería, Carranza, and Sánchez-Prieto 2015; Miller 1972). Irreversible destructive methods like this are often avoided or not permitted when others exist that produce similar results, especially in museum curated collections that work to preserve these remains (Gifford-Gonzalez 2018, 129). Biological processes that lead to inaccurate results when using cementum annulation include missing or extra annuli lines that manifest during irregular times of bodily stress and resorption of cementum during life (Pérez-Barbería et al. 2014, 186; Reitz and Wing 2008, 76-77; Spinage 1973). At older ages, deposited layers are thinner, making the cementum annuli bands narrower and harder to read (Dudley Furniss-Roe 2008; Spiess 1979, 68-69; Turner 1977). This age varies between species. For example, narrower bands of cementum deposited in bighorn sheep (Ovis canadensis canadensis) teeth older than eight years lead to a significant discrepancy between cementum age and known age (Dudley Furniss-Roe 2008; Turner 1977).

Although tooth wear ageing methods are not as accurate as the two described above, they are especially useful for mandibles with

fully erupted dentition while also being a nondestructive form of analysis (Reitz and Wing 2008, 174; Steele and Weaver 2012, 2329). Compared to cementum annulation, tooth wear ageing is easy to learn, takes considerably less time to complete, does not require destruction of irreplaceable specimens, is inexpensive, and does not require specialized equipment (Reitz and Wing 2008, 174; Steele and Weaver 2012, 2329). The premise of this method is that as animals get older their teeth get progressively worn on the occlusal surface (DeMiguel et al. 2016; Spinage 1973). Chewing causes this occlusal wear which begins as each tooth erupts past through the gum and meets an opposing occlusal tooth (Hillson 2005, 214). Thus, correlating the degree of occlusal wear on teeth to the amount of time an individual was alive and eating is possible (Hillson 2005).

Tooth wear age estimation is more efficient and easier to learn than cementum annulation and can be adapted to additional species with some work and access to knownage specimens (Gifford-Gonzalez 2018; Lyman 2017; Miller 1974; Spinage 1973). This method has been developed for and applied to age a variety of mammals in zooarchaeology (Bowen et al. 2016; Dudley Furniss-Roe 2008; Grant 1982; Greenfield and Arnold 2008; Halstead 1985; Hambleton 1998; Klein and Cruz-Uribe 1983; Lubinski 2001; Morrison and Whitridge 1997; Mutze et al. 2021; Pasda 2009; Payne 1973; 1987; Pike-Tay, Morcomb, and O'Farrell 2001; Steele and Weaver 2012; Tomé and Vigne 2003; Twiss 2008; van den Berg, Loonen, and Cakırlar 2021), in wildlife management (Brown and Chapman 1990; 1991; Høye 2006; Lowe 1967; Miller 1972; 1974; Pérez-Barbería et al. 2014), and in veterinary studies (Aitken 1975). For mammals, mandibles and teeth survive well against taphonomic processes, and are therefore more likely available for archaeological research compared with fragile maxillae (Gifford-Gonzalez 2018, 125; Pasda 2009; Spiess 1979, 77; Winkler and Kaiser 2015).

Mandibles are often considered over maxillae because they are easier to work with, more robust to damage, and mandibular teeth are more likely to remain socketed (Hillson 2005, 231). Most ruminant tooth wear studies are made for lower (mandibular) dentition (Hillson 2005).

The purpose of this paper is to explore how previous research has approached tooth wear to estimate ages of ruminants (large, cudchewing herbivores) while focusing on its utility in zooarchaeological contexts. The scope of this paper is on research surrounding the Cervidae family (deer) and Caprinae subfamily (sheep and goats), but concepts surrounding tooth wear studies apply generally to all ruminant teeth. This paper analyses three methods used to investigate ruminants. Before evaluating these methods, I first summarize the processes affecting the rate of wear and contributing to variation within individuals, between individuals in a population, and between populations. Second, I establish the assumptions about tooth wear that are necessary when attempting to apply this approach as a meaningful indicator of age. Third, this paper provides a comparison and discussion of several tooth wear ageing methodologies grouped into three overarching categories: the Crown Height Method, the Visual Wear Pattern Method, and the Wear Trait Scoring Method. This comparison demonstrates how each method works, their strengths and limitations, accuracy, ease of use, and how suitable they are for ruminant mandibular remains from archaeological contexts. This review conveys that there are a variety of tooth wear ageing techniques available to researchers, which here are divided into three overarching methodological categories. There is no 'one size fits all' approach; each of these approaches carries advantages and disadvantages rendering them useful in different situations

RATE OF WEARL VARIATIONS AND ASSUMPTIONS

Dental attrition is ultimately the product of food and other ingested matter chewed over a lifetime; the number of years an individual lived is only indirectly related (Spinage 1973, Reitz and Wing 2008, 174). Cervids and bovids (antelopes, bison, cattle, gazelles, goats, sheep, and relatives) have molar and premolar teeth that are adapted morphologically as two parallel, crescent-shaped rows for grinding plant matter in a side-to-side chewing motion (Hillson 2005; Pérez-Barbería, Carranza, and Sánchez-Prieto 2015: Winkler and Kaiser 2015). Figure 1 shows a reindeer (Rangifer tarandus) M₃ (third molar) that illustrates an example of this morphology. Ruminants depend on symbiotic microorganisms to break down and ferment vegetation as part of their digestion process (Hillson 2005; Pérez-Barbería, Carranza, and Sánchez-Prieto 2015; Winkler and Kaiser 2015). By regurgitating and re-chewing food, the particle size of vegetation is reduced, and the process of digestion works more effectively (DeMiguel et al. 2016; Loe et al. 2003; Hillson 2005, 132-35). Continual chewing causes the occlusal surface of ruminants' teeth to wear down where upper (maxillary) and lower (mandibular) occlusal surfaces contact. The

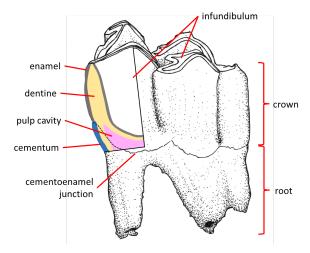


FIGURE 1–*Tooth morphology of a M*₃ showing dentine, enamel, cementum, pulp cavity, root, crown, cementoenamel junction, and infundibulum (Created by author)

enamel is then eroded, exposing the dentine and infundibula beneath (DeMiguel et al. 2016; Hillson 2005, 18; Janzen, Balasse, and Ambrose 2020; Winkler and Kaiser 2015). This process begins as soon as a tooth has erupted and continues until the tooth has been worn to the root or is lost (Hillson 2005, 212; Payne 1973, 285). Therefore, because teeth erupt at different times, each one has a different starting point (Hillson 2005, 212; Payne 1973, 285). For example, the M₁ (first molar) starts to wear and is exhausted sooner than the M₃, making the M₃ a better measure for older individuals (Spinage 1973).

Several factors affect the rate of tooth wear (see Figure 2). Differential diet is perhaps the greatest variable factor for ruminants. Simply put, the courser the food, the faster the wear on the occlusal surface (Pérez-Barbería, Carranza, and Sánchez-Prieto 2015; Skogland 1988). Softer plants like grass, lichen, and soft leaves cause slower wear than tougher leaves, twigs, and branches (Gifford-Gonzalez 2018, 131). Dirt or grit ingested along with grazed plants and lichens will also accelerate the rate of wear (Høye 2006, 206; Reitz and Wing 2008, 174). Increased grit is sometimes associated with overgrazing in which the animals are pulling up shorter vegetation closer to the ground (Spiess 1979, 75) with reindeer and caribou. Drier environmental conditions lead to more airborne sediment deposited on vegetation (Mutze et al. 2021). Mutze and colleagues

(2021) find that sheep (Ovis aries) and goats (Capra hircus) in Egypt exhibit extremely worn molariform teeth during dry conditions. Seasonal migration between pastures or extreme seasons affects the types and qualities of forage available (Mutze et al. 2021). In reindeer, the rate of wear significantly slows during the winter months because feeding behaviours change (Skogland 1984; 1988). When their diets are restricted to relatively course vegetation such as shrubs or overgrazed, low to the ground vegetation in which sediment is also ingested, occlusal attrition accelerates (Skogland 1984; 1988). Significant environmental change within an animal's lifetime or between generations could also cause a change in foraging behaviour increasing the rate of tooth wear variability over longer periods of time (Skogland 1984; 1988).

Differences in behaviour can affect the rate of tooth wear (Hillson 2005; Reitz and Wing 2008; Sten 2004). Discrepancies between tooth wear on right and left mandibles have been observed in cattle (Sten 2004, 134). However, in archaeological contexts assessing which side an animal preferred to chew with is rarely possible because mandibles from a single animal are rarely together in situ and each element may represent separate individuals (Reitz and Wing 2008, 117–25). Hillson (2005, 214) notes that animals, too,

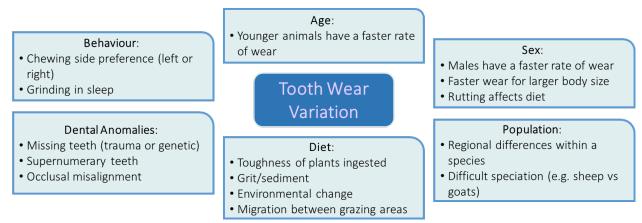


FIGURE 2-Summary of the sources of variation in ruminant tooth wear as outlined in this paper (Created by author)

grind their teeth while they sleep, which may be difficult to recognize osteologically.

The rate of wear also changes through various stages of an animal's lifetime (Høye 2006; Pérez-Barbería, Carranza, and Sánchez-Prieto 2015). Younger ruminants' teeth wear at a faster rate while their molariform cusps are only minimally worn and still relatively sharp (Høye 2006; Pérez-Barbería, Carranza, and Sánchez-Prieto 2015). Alternatively, the occlusal surfaces on teeth of older animals are worn flat and are made less effective at grinding food, requiring more energy to digest food (Høye 2006; Pérez-Barbería, Carranza, and Sánchez-Prieto 2015). As a result, older animals may experience a deterioration in health related to poor diet that Skogland (1988) observes in reindeer and that Pérez-Barbería, Carranza, and Sánchez-Prieto (2015) and Høye (2006) describe in red deer (Cervus elaphus).

Another source of variation on teeth within a population is the effects of sexual dimorphism on dentition and diet. Male ruminants' teeth typically wear down faster than females' (Twiss 2008, 343; van den Berg, Loonen, and Cakırlar 2021, 9; Høye 2006, 210). The contrast in rate of wear rate has been quantified for caribou (Morrison and Whitridge 1997) and red deer (Pérez-Barbería et al. 2014) using known-sex animals. Morrison and Whitridge (1997, 1097) find that while males initially wear teeth faster, by around two years of age females from the Qamanirjuaq (also known as Kaminuriak) caribou population caught up and exceed males later in life. Pérez-Barbería and collaborators (2014, 183) identify different sets of tooth wear traits and develop separate equations for whether the red deer is male, female, or indeterminate (Pérez-Barbería et al. 2014). This study finds that males' teeth are aged slightly more accurately because they wear faster (Pérez-Barbería et al. 2014). Loe colleagues (2003)explain and this phenomenon; males need greater amounts of food to fulfill greater energy expenditures

(larger body size and rutting) and so dental attrition is faster. This is confirmed by a greater measured reduction in crown height on average compared with females (Loe et al. 2003). In some instances, the sex of an animal can be determined using biometrics, for example, the length of reindeer and caribou mandibles have been used to indicate whether the animal is female or male (Morrison and Whitridge 1997; Spiess 1979, 82). However, differentiating tooth wear by sex is generally possible only for modern population datasets when there is access to the recently dead bodies or, though less reliable, entire skeletons (Pasda 2009).

Dental abnormalities and pathologies are known to create irregular wear patterns. For example, Miller and Tessier (1971) record a series of dental anomalies including missing and supernumerary teeth as well as misaligned occlusion found in caribou. If one tooth is lost, the opposing tooth will continue to wear at a much slower, less predictable rate (Miller and Tessier 1971). Alternatively, they find that if extra-numerary molars or premolars (P_2 to P_4) are present, this dental addition disturbs placement within the tooth row and causes reduced attrition on the left-out tooth (Miller and Tessier 1971). When P_1 (first premolar) is present, teeth placement is not affected (Miller and Tessier 1971). The P₁ is commonly absent in ruminants. Any abnormality that alters the occlusal alignment between mandibular and maxillary dentition may result in an absence of wear on the opposing tooth or unusual wear patterning (Miller and Tessier 1971; Miller 1974). In an extreme case, Bowen and coauthors (2016, 1090–94) find that populations of fallow deer (Dama dama) raised in French menageries frequently show dental abnormalities, hindering age estimation for those individuals. Grant (1982, 91) also notes overcrowded teeth in domestic sheep, goats, and pigs (Sus scrofa) causing abnormal wear. Thus, when conducting tooth wear studies, recognizing abnormal dentition is

critical which may result in those individuals being outliers within the dataset and excluded from analysis.

Even difficult species differentiation or divergent populations of a single species can be a source of inaccuracy in tooth wear analysis. Mandibles and teeth from goats and sheep are usually aged together since the two species are very challenging to differentiate visually, despite the difference in diet, behaviour, and biology (Payne 1973, 284; Twiss 2008, 333). Similarly, modern reference populations must be used for archaeological animals with caution as there may also be considerable differences between the two, even of the same species (Salvagno et al. 2021; Klein and Cruz-Uribe 1983, 71). For a single species that covers a large geographic area, such as reindeer and caribou, there may be enough genetic variation between populations that render shared tooth wear ageing methods unreliable (Salvagno et al. 2021; Klein and Cruz-Uribe 1983, 71). For example, in their recently developed method for estimating ages of Svalbard reindeer (Rangifer tarandus platyrhynchus), van den Berg and colleagues (2021) caution that their Svalbard ageing scheme should not be applied to all Rangifer populations and devised a second, uncalibrated scheme for wider application.

All these ageing methods require a set of assumptions about the regularity of dental attrition. Keeping in mind all aforementioned sources of variation in the rate of wear (see Figure 2 for summary), the variation in tooth wear will either be insignificant, resulting in an acceptable margin of error, or that variation must be accounted for (Spinage 1973; Twiss 2008, 330; Gifford-Gonzalez 2018, 138). analyzing archaeological When animal remains, identify sources of variation from a mandible including diet, behaviour, sex, or genetic differences is rarely possible in macroscopic analysis (Spinage 1973; Twiss 2008, 330; Gifford-Gonzalez 2018, 138). Assumptions that must be accepted to apply

tooth wear age estimation to a population of ruminants from archaeological sites include:

• The rate of wear happens at a predictable rate within an individual's lifespan. While possible to identify dental abnormalities and remove those as outliers, identifying changes to dental attrition such as a change in diet or behaviour by visual inspection alone is much more difficult (Twiss 2008).

• The rate of wear is assumed to be uniform across individuals within each age category within a population. One must assume there is not a significant difference between male or female, right and left chewing preference, access to different qualities of food, or differences in health and nutrition (Twiss 2008, 330–31).

• The rate of wear between populations must be approximately the same. This is especially true between the known-age reference population used to develop an ageing scheme and the population the ageing scheme is applied to (Twiss 2008).

TOOTH WEAR AGEING METHODS

This section outlines multiple approaches to tooth wear age estimation that have been developed for Cervidae and Caprinae, some of which are better suited to certain research scenarios. These methods are divided into three overarching categories: Crown Height, Visual Wear Pattern, and Wear Trait Scoring Methods. Usually, researchers can easily tell which animals are younger or older relative to one another using tooth wear (Aitken 1975; Gifford-Gonzalez 2018; Lowe 1967; Spinage 1973; van den Berg, Loonen, and Çakırlar 2021). The greatest challenge is to relate relative age to an estimation of age in years or months (Miller 1974). To do this, a collection of mandibles of the same species are needed for which the age at death is known, ideally from a comparable environment and diet (Gifford-Gonzalez 2018). Table 1 shows a summary of many tooth wear age estimation methods that have been developed including

their reference sample size, the use of knownage individuals or cementum annulation, and the age ranges represented in their reference sample. More robust results are achieved when large reference sample sizes can be obtained with a well-distributed variety of age categories present, from early stages of life to very old (Reitz and Wing 2008, 250). Known age animals are preferred instead of cementum annulation because, although cementum annulation does produce fairly accurate results, this method potentially introduces inaccuracies into the tooth wear ageing method (Aitken 1975; Lowe 1967; Pérez-Barbería et al. 2014; Spinage 1973)

The quality of known-age data is also worth considering. Most studies listed in Table 1 that make use of known-age reference collections acquired from wildlife management tracking projects that ear tag or otherwise identify individuals within their first year and have a known date of death (Bowen et al. 2016; Brown and Chapman 1990; 1991; Dudley Furniss-Roe 2008; Høye 2006; Lowe 1967; Lubinski 2001; Pérez-Barbería et al. 2014; Steele and Weaver 2012). These samples will have a known age accuracy within months, depending on the circumstances of monitoring and recording births and deaths (Bowen et al. 2016; Brown and Chapman 1990; 1991; Dudley Furniss-Roe 2008; Høye 2006; Lowe 1967; Lubinski 2001; Pérez-Barbería et al. 2014; Steele and Weaver 2012). Known-age data can also be found in farmed animals, sheep and goats for example (Greenfield and Arnold 2008; Mutze et al. 2021), or from zoos and other forms of captivity (Bowen et al. 2016). For non-domestic animals, recognising the limitations or complete unsuitability of using specimens raised in captivity is essential because those animals lived in unnatural conditions that may affect diet, behaviour, and lower genetic diversity (Bowen et al. 2016; Taylor et al. 2016). Bowen and colleagues (2016, 1090) find that fallow deer raised in historic menageries in France had greater dental attrition and more frequent pathological dental disease.

Crown Height Method

Lowe (1967) states that the first published Crown Height Method was likely developed by Eidmann in 1932 with a sample size of 58 red deer using the height of incisor crowns to estimate age (Lowe 1967). However, this early attempt shows a poor relationship between crown height and age once plotted (Lowe 1967). This method also utilizes an earlier, rudimentary Visual Wear Pattern Method in place of known-age (Lowe 1967). Modern Crown Height Methods have become much more refined with the availability of more reliable reference populations.

The Crown Height Method relies on the premise that the longer an animal lived, the shorter the dental crown will be (Klein and Cruz-Uribe 1983). Nevertheless, molariform (premolar and molar) teeth have a complex shape so a more specific instruction is required to ensure reliable measurements are taken and to mathematically relate that measurement to the length of time lived (Spinage 1976). Since each tooth is measured individually, the Crown Height Method works well with fragmented assemblages and loose teeth, potentially involving specimens in analysis otherwise excluded (Klein and Cruz-Uribe 1983, 73-76). Even so, fragmented teeth or chipped enamel cusps make a tooth unsuitable for measurement (Twiss 2008, 343). If the tooth is still in its socket, crown height may be unavailable for measurement without removing teeth and causing damage (Lyman 2017; Twiss 2008, 343). One way to avoid this is to measure using an X-Ray of the mandible as Pasda (2009, 35) does, however, this requires access to specialized equipment and a greater time commitment.

The Crown Height Method employs mathematical formulas to relate the crown height measured to an animal's age (Gifford-Gonzalez 1991; Klein et al. 1981; Pike-Tay, Morcomb, and O'Farrell 2001; Twiss 2008).

There have been several approaches that principally differ in what part of the tooth is measured and how the progression of wear over a lifetime is modelled. The Quadratic Crown Height Method (QCHM) and the Linear Crown Height Method (LCHM) differ both in the dental landmarks used in measurement (Figure 3) and in the mathematical relationship devised to estimate age (Gifford-Gonzalez 1991; Klein et al. 1981; Pike-Tay, Morcomb, and O'Farrell 2001; Twiss 2008). Moreover, researchers have developed different versions of the QCHM and LCHM and do not always measure teeth the same way or may adjust the equations. To ensure an individual is counted only once, different molars or premolars from each side must be counted separately (Pike-Tay, Morcomb, and O'Farrell 2001). For example, Lubinski (2001, 226-27) mitigates this risk by only including the first molar of pronghorn antelope (Antilocapra americana).

The QCHM measures crown height (CH) from the enamel-cementum junction to the tip of the cusp on the buccal side of the tooth on the mesial-most cusp (Figure 3a) (Twiss 2008). The estimated age for each tooth (AGE) is calculated using the quadratic formula below (Equation 1) from Klein and Cruz-Uribe (1983, 73-76; Twiss 2008, 331-32) as a function of the potential ecological longevity (AGE_{pel}) of the species, the age at which the tooth erupts and comes into wear (AGE_e) , and the initial crown height (CHo) before occlusal wear occurs (Klein and Cruz-Uribe 1983; Twiss 2008). Age can be calculated in years or months, so long as the units of time are consistent. Twiss (2008) assumes potential ecological longevity to be 10 years, and so age classes are each one year (one tenth of the AGE_{pel}). There are a couple of flaws. This approach requires an estimate of the full crown height before wear, which is not directly observable (wear begins before the tooth has fully erupted) and AGE_{pel} does not account for an animal living beyond the time one of its teeth wear to zero (Pike-Tay, Morcomb, and

O'Farrell 2001, 156; Steele and Weaver 2012, 2331; Twiss 2008, 333–34).

$$(1) \text{ QCHM:} \\ AGE = AGE_{pel} \\ -\frac{2(AGE_{pel} - AGE_e)CH_o}{CH} \\ +\frac{(AGE_{pel} - AGE_e)CH_o^2}{CH^2}$$

Steele and Weaver (2012) test and improve upon the QCHM finding that the original (see Equation 1) underestimates the ages of Montana elk (Cervus elaphus) using P4 (fourth premolar), M₂ (second molar) and M₃ when tested on 226 known-age individuals. Instead, they modify the equation (Equation 2) to better reflect the rate of wear at different life stages and performs significantly better (Steele and Weaver 2012, 2333). They replace AGE_{pel} with AGE_{tpl} , the age at which the crown height of the specific tooth type reaches zero and the exponent of two is replaced with variable m(Steele and Weaver 2012. 2333).

(2) Modified QCHM:

$$AGE = \left(AGE_{tpl} - AGE_e\right) \times \left(\frac{CH_0 - CH}{CH_0}\right)^m + AGE_e$$

The LCHM measures crown height (CH) differently, quantifying the distance between the bifurcation of the root to the tip of the cusp on the lingual side of the tooth's mesial-most cusp (Twiss 2008). A measurement for the basal crown breadth (CB) is also taken (Figure 3b) (Twiss 2008). While the enamel-cementum junction for the QCHM may be accessible above the socket, the LCHM requires access to the tooth root and the tooth to be fully removed from the mandible (Twiss 2008). The relationship between age, crown height, and basal crown breadth is expressed as a linear equation below (Equation 3) from Twiss (2008, 332). The estimation of age for a single tooth, AGE_i , is a function of the animals predicts maximum age $(AGEf_i)$, the age at which the tooth erupts and comes into wear $(AGEe_i)$, the crown height before wear begins (CH_{AGEmax}) and the basal crown breadth before wear begins (CH_{AGEmax}) (Twiss 2008).

(3) LCHM: AGE = $\frac{(AGEf_i - AGEe_i) \times CB \times CH_{AGEmax}}{CH \times CB_{AGEmax}}$ $+AGEf_i$

Morrison and Whitridge (1997) are also successful in applying a linear regression formula to crown height for caribou. In their study, Morrison and Whitridge include caribou that were cementum aged with known sex to determine the relationship between M₁ crown height and age for males and females, creating a linear regression formula for each (Morrison and Whitridge 1997). This method also measures crown height differently (Morrison and Whitridge 1997). Crown height is measured for both lobes of the tooth from the cementoenamel junction to the occlusal surface on the buccal side and the average between the two lobes is used (Figure 3c) (Morrison and Whitridge 1997).

The choice between using QCHM or LCHM in different research contexts depends largely on which better models the changing rate of tooth wear over a lifetime for the population and/or species in question. The variable degrees of success in applying each type of regression equation and measurement approach for different species implies that for researchers to confirm which equation is most applicable to their research is essential, especially concerning species. Twiss (2008) carries out a comparison of the two Crown Height Methods for sheep and goat teeth from Catalhöyük in Anatolia and finds better results using the OCHM. Although accuracy could not be directly tested without known-age data, the LCHM consistently does not produce any age estimates over four years old, in contrast to the results from the QCHM and Payne's (1973) method (described below) that went as high as more than ten years, suggesting a discrepancy results from the LCHM estimates.

Alternatively, Gifford-Gonzalez (1991; 2018, 136–37) finds that QCHM underestimates ages of eight-year-old bison (*Bison* bison) by up to 40 months compared with known-age individuals, and that the LQHM performs better for this species. The LCHM, as

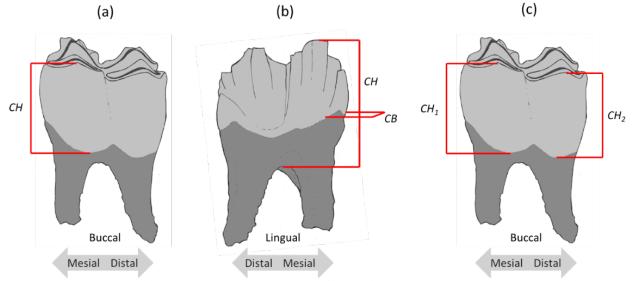


FIGURE 3–Three crown height measurements on M_1 tooth (Rangifer tarandus) using (a) QCHM (Klein and Cruz-Uribe 1983; Steele and Weaver 2012; Twiss 2008), (b) LCHM (Twiss 2008), and (c) QCHM or LCHM (Morrison and Whitridge 1997; Pike-Tay, Morcomb, and O'Farrell 2001 (Created by author)

defined by Twiss (2008) requires а measurement of the basal crown breadth instead of estimating the initial crown height. However, Gifford-Gonzalez (1991, 59; 2018, 137; see also Twiss 2008, 343) states that because basal crown breadth is not a useful proxy for the unworn crown height for bovids or reindeer, the QCHM is more suitable for these animals. For shorter-crowned animals like caribou and reindeer, the lesser annual decrease in height may make measurements less precise (Gifford-Gonzalez 1991, 59; 2018, 137; Morrison and Whitridge 1997; Twiss 2008). Qamanirjuaq caribou M_1 crowns shorten by less than 1mm per year, leaving little margin for error (Morrison and Whitridge 1997, 1098). In examining the same caribou collection, Pike-Tay, Morcomb, and O'Farrell (2001) caution that for older ages, when the slope of the quadratic regression formula is near horizontal, the QCHM for this shortcrowned species is less reliable as an ageing method. In contrast, high-crowned bovids will have a greater measurable loss of crown height per year (Hillson 1992; 2005). Thus, the performance of Crown Height Methods appears to be dependant on the species and/or population (Hillson 1992; 2005).

Visual Wear Pattern Method

Unlike the Crown Height Method that considers wear to be the loss in dimensional height, the Visual Wear Pattern Method relies on the changing appearance of the occlusal surface as crown height diminishes. As teeth wear, enamel is removed exposing the dentine underneath (DeMiguel et al. 2016; Greaves 2012; Hillson 2005). A cross-sectional pattern of dentine and enamel is revealed and, because dentine is softer and erodes faster than enamel, the cusps take on a concave topography (Gifford-Gonzalez 2018, 131). As crown height is depleted, the wear pattern changes and can be applied to estimate age (Gifford-Gonzalez 2018, 131).

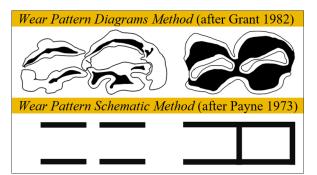


FIGURE 4–Comparative examples of M_2 from Rangifer tarandus at different stages of wear to illustrate the difference between Grant-style illustrations with Paynestyle schematic representations of wear patterns (Created by author)

There are several approaches that this paper classifies as Visual Wear Pattern Methods that are further categorized into photographic, illustrated, and schematic approaches. To visually record tooth wear patterns using photographs, a series of known-age mandibles are first chosen that adequately represent a full range of tooth wear patterns and eruption sequences (Aitken 1975; Lowe 1967; Miller 1974; 1972; Pasda 2009). Mandibles are ordered from least tooth wear, ideally including early eruption stages, to most wear with which one can estimate ages of animals relative to the reference photos (Aitken 1975; Lowe 1967; Miller 1974; 1972; Pasda 2009). Miller (1974) published a collection of mandibular wear photos from Qamanirjuaq caribou organized by view (occlusal and buccal), age in months, and sex for comparison. Pasda (2009) has produced a similar resource for Sisimiut reindeer (Rangifer tarandus groenlandicus) from Greenland, as well and Lowe (1967) for red deer from Rhum, Scotland, although neither is as extensive. The utility of this type of reference depends on the quality of the photos and how they are reproduced.

Aitken (1975) undergoes a similar project to age roe deer (*Capreolus capreolus*). Instead of photos, a 'jaw board', in which all mandibles are physically laid out in order from least to most amount of wear is used for reference (Aitken 1975). The reference mandibles

belonged to deer of known ages or aged using cementum annulation analysis (Aitken 1975). Using these as comparison, the remaining mandibles are assigned approximate ages according to tooth wear, then checked for accuracy using cementum annulation age estimation (Aitken 1975). The purpose of this study is to test the accuracy of relative age estimation based on tooth wear (Aitken 1975). This method is reportedly fairly accurate, 90-95% within a year of the cementum age (Aitken 1975, 24). While the author proves the validity of this technique, what became of the reference mandibles (the 'jaw board') is unclear (Aitken 1975). The author provides descriptions of tooth wear for one year age intervals up to eight years accompanied by oblique-angle sketches for some ages. Nevertheless, these descriptions are brief and suffer from vague and relative language (Aitken 1975).

One way to mitigate reproducibility issues and viewer subjectivity in reference material is with black and white, easily replicable wear pattern illustrations. Grant (1982) developed a method using tooth wear patterns for sheep/goats, cattle, and pigs which became one of the most frequently employed ageing techniques for domestic animals. This process is similar to that described above. Mandibular occlusal wear patterns representing a spectrum of wear stages from very young to very old are selected to be illustrated and ordered from minimum to maximum wear, including the eruption of deciduous dentition (see Figure 4 for example) (Grant 1982). Ideally, the mandibles have known age data, or otherwise accurately aged, animals (Grant 1982). However, because Grant (1982) did not have access to known-age data while developing this method, the age classes are relative only. Each tooth (dp₄, P₄, M₁, M₂, and M₃) is compared to the wear stages illustration and assigned an alphabetical value referred to as the tooth wear stage (TWS) (Grant 1982). The TWS corresponds to a numerical value found in a table (Grant 1982). The mandible wear stage (MWS) is the sum of the TWS values from M_1 , M_2 , and M_3 and is the value used to assess relative ages (Grant 1982). Although each tooth is assessed separately, this system does not handle fragmented mandibles well (Grant 1982). All three molars are needed to calculate MWS and if a tooth is absent Grant (1982, 96) proposes guessing the TWS of the missing tooth based on those present.

Efforts have been taken to adapt Grant's (1982) diagrams for other species. Bowen and colleagues (2016) follow a similar methodology to estimate ages of fallow deer using the same style of tooth wear pattern illustration while also incorporating tooth eruption sequences. Since their sample consists of fallow deer mandibles from a full range of known ages (0-16 years) they are able to convert their wear stages into estimated age ranges (Bowen et al. 2016). The degree of accuracy this method produces is adequate for archaeological purposes, achieving better accuracy with all three molars than for single tooth (79-96% in correct age category or 100% within one age category) rather than for single teeth (79-96% or 93%, respectively) (Bowen et al. 2016, 1095).

Similarly, van den Berg and colleagues (2021) adapt this approach for Svalbard reindeer. Using known-age individuals, they create two schemes: the 'absolute scheme', and the 'relative scheme' (van den Berg, Loonen, and Cakırlar 2021). The 'absolute scheme' is only for Svalbard reindeer mandibles (van den Berg, Loonen, and Çakırlar 2021). The 'relative scheme' could be applied to any reindeer or caribou population but requires the user to calibrate this scheme themselves using either known age or accurately ageing reindeer mandibles from the relevant region (van den Berg, Loonen, and Çakırlar 2021). There are also separate tooth wear illustrations for each scheme demonstrating the variation of wear between Svalbard reindeer and other Rangifer populations (van den Berg, Loonen, and

Çakırlar 2021, 4-6). Unfortunately, this method leaves the potential user outside the Svalbard region with three options: apply the 'absolute scheme' with the assumption that the accuracy will be close enough to be meaningful, apply the 'relative scheme' without assigning ages in their analysis, or calibrate the 'relative scheme' themselves (van den Berg, Loonen, and Çakırlar 2021). Not only would time be needed to calibrate this scheme, but if known-age specimens are unavailable, destructive and time-consuming cementum annulation may be required (van den Berg, Loonen, and Çakırlar 2021) and is not as reliable as true known-ages (Miller 1974).

Without a collection of appropriate known-age reference animals, approximating the rate of wear and estimating age is challenging. Salvagno and colleagues (2021) apply Grant's (1982) method for pigs (outliers in this article as they are not ruminants) to assess the rate of wear in archaeological populations. Assuming that tooth eruption is relatively regular and that molars erupt in the order of M₁, M₂, and then M₃, this approach considers the difference in wear in pairs (Salvagno et al. 2021). The difference between the M_1 and M_2 , and between the M_2 and M_3 , represents how much wear these teeth experience in the amount of time between each eruption and first comes into wear (Salvagno et al. 2021). The authors use this method to test the diets of ancient pigs at various times in the past, but such an approach may also be effective as an index of wear to calibrate ruminant ageing schemes between populations (Salvagno et al. 2021).

Payne's (1973; 1987) system for ageing sheep and goats is like Grant's (1982) except that this method further develops this strategy to evaluate and simplify the characteristics of the occlusal wear pattern. This method has also been frequently applied, often in comparison with Grant's (Bowen et al. 2016; Greenfield and Arnold 2008; Hillson 2005; Lubinski 2001;

Twiss 2008; Reitz and Wing 2008) and has been adapted to other species including cattle (Bos taurus) (Halstead 1985), pigs, and wild boar (Bull and Payne 1982). Occlusal wear patterns are represented with rectangular schematic depictions that record worn and unworn enamel cusps, shapes and connections between exposed dentine, and the presence and size of infundibula (Payne 1973, 288). The schematic patterns are then translated to one of nine stages (from A-I) which provides an age range for each (Payne 1973, 288). Over a decade later, Payne (1987) improved this approach by assigning alphanumeric codes to each possible wear pattern to facilitate description in writing and be simpler for publishing.

Attempts have been made to reconcile the illustrative (Grant 1982) and schematic (Payne 1973; 1987) ageing schemes so that ages estimated using one method for a zooarchaeological assemblage can be meaningfully compared with others (Greenfield and Arnold 2008; Halstead's 1985; Hambleton 1998; Payne 1987). Payne (1987, Table 1) correlates the later coding scheme to Grant's (1982) MWS and TWS so that datasets could be translated from one to the other. Hambleton (1998) also converts between Grant's wear classes and both Payne's and Halstead's (1985) age stages. By applying the schematic method directly to Grant's illustrations, Hambleton (1998) converts them to Payne's age classes. While the conversion system developed by Payne (1987) includes a version for each tooth type so that every tooth would be converted individually, Hambleton's (1998) conversion is less flexible, looking at a whole mandible at a time. While the accuracy of each conversion has not been compared, converting the age classes of individual teeth and then assessing the MWS having better results seems likely. Following Hambleton (1998), Greenfield and Arnold (2008) suggest revisions to this conversion based on their own study of domestic sheep and goats from Manitoba. However, this study has limitations. Most of their sample size is

less than 18 months old and their revisions include only age classes when tooth eruption sequences are still more valuable than tooth wear patterns. They recommend that Grant's illustration method be used because only a one-way conversion from Grant's to Payne's methods is possible since this method had a greater number of MWSs, although neither Hambleton (1998) nor Payne (1987) mention such a restriction.

The popularity of the Visual Wear Pattern Method suggests that this approach is relatively easy to use while providing meaningful results. This method is straightforward to adapt to new ruminant species (Bowen et al. 2016; van den Berg, Loonen, and Çakırlar 2021; Lubinski 2001). Although Visual Wear Pattern Methods work for loose teeth or incomplete mandibles, the accuracy is severely reduced (Twiss 2008, 349). Twiss (2008, 346) abandons both Grant's (1982) and Payne's (1973) methods because the sheep and goat remains from Çatalhöyük are too fragmented and do not produce meaningful demographic profiles. Due to a lack of instruction or morphological Grant-style description in illustrations important details in the tooth wear pattern may be overlooked or misinterpreted (Hambleton 1998, 114

Wear Trait Scoring Method

Instead of visually or schematically analyzing wear patterns, another approach is to

observe and count scores of the presence or absence of predetermined traits caused by tooth wear. Brown and Chapman (1990; 1991) were first to develop a mandibular wear scoring system for fallow deer followed by red deer. Each of the variations below seek to minimize subjectivity and observer error by allowing for only two options – either a trait is present, scoring a value, or absent, with a value of zero. They also intend to improve the accuracy of age estimation by increasing the resolution of wear stages, especially for older animals

Payne's (1987) revised method includes reference codes that could arguably be considered to evaluate present or absent traits, especially connections between dentine shapes and loss of infundibula, however, the result is evaluated as wear stages. Brown and Chapman (1991; 1990) take this further by using similar criteria for evaluating wear and adding a value for each occurrence in their methods for fallow deer and red deer. Observable traits are identified for all molars including enamel wear, dentine wear, ovals or 'eyes' that appear within the dentine, links between dentine, loss of infundibula, and dark staining of dentine (see Figure 5) (Brown and Chapman 1990; 1991). Those traits are scored between 0-2 and the total score for that tooth is summed (Brown and Chapman 1990; 1991). Premolars can also be scored, but the authors find them unreliable and, thus, are excluded (Brown and Chapman 1990; 1991). The authors include known-age

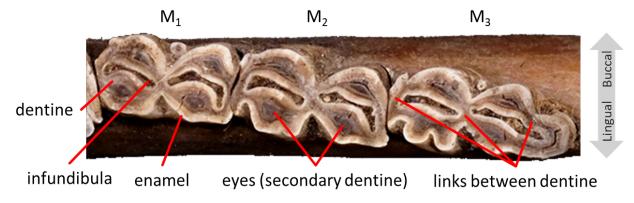


FIGURE 5–Occlusal view of reindeer mandibular molars showing locations of tooth wear traits used for scoring estimating age (not exhaustive) (Created by author)

animals to create a table where the estimated age class is determined using the total score for the mandible (Brown and Chapman 1990; 1991). A similar table exists for single molars, but singular teeth are considered less precise (Brown and Chapman 1990, 672). The systems for both species suffer from a lack of older individuals, likely contributing to the overlap in score values between older age classes (Brown and Chapman 1990; 1991).

Since published, multiple researchers have made efforts to improve upon this approach drawing directly from Brown and Chapman's (1990; 1991) work. For red deer, Dudley Furniss-Roe (2008) follows a similar workflow but generates new criteria using statistical analysis to weight the scores associated with each one. The full method includes 16-17 initial scoring elements for each molar and are applied to a known-age collection of red deer to statistically derive a weight for each scoring element between zero and three. After removing those with a score of zero, only eight traits remain, speeding up the process (Dudley Furniss-Roe 2008, 82-84). This is a relative scheme in which the final summed score could be calibrated for any population of red deer (Dudley Furniss-Roe 2008).

Other simplified versions have been developed. Clearly, the Wear Trait Scoring Method needed to be made more efficient and userfriendly (Lubinski 2001; Pérez-Barbería et al. 2014). Pérez-Barbería et al. (2014) simplify both Brown and Chapman (1990; 1991) and Dudley Furnace-Roe (2008) methods for red deer by seeking to eliminate redundancy and reduce the bias of traits while maintaining accuracy. The 'Simplified Brown and Chapman' and 'Simplified Dudley' schemes are both created by removing approximately 70% of the traits calculated to be statistically redundant. They also develop models that account for differing rates of wear between females and males. Likewise, Lubinski (2001) carries out a comparison of methods including counting exposed infundibula and a modified version

drawing from Brown and Chapman (1990). This study looks at 3-4 traits of occlusal wear with reference to a schematic diagram and scoring each tooth (including molars and adult or deciduous premolars) in the mandible. Wear scores are calibrated using known-age (and established-age) pronghorn mandibles so that the score can be referenced to age classes (Lubinski 2001, 226). Pérez-Barbería et al. (2014) finds that their 'Simplified Dudley' method is the more accurate of the two. According to Lubinski (2001, 223), the tooth wear scoring system performs better than Payne's (1973) for younger individuals because ridges and facets are counted independently. Lubinski (2001, 226) dismisses using counts of exposed infundibula per mandible as an ageing technique finding this method too inaccurate for archaeological purposes.

Høye (2006) takes a somewhat different approach for roe deer, also drawing from Brown and Chapman (1990; 1991), but instead a probability score table is used to estimate age. With a sample of known-age roe deer, 18 occlusal wear characteristics are chosen and the probability of each occurring within an age category determines the most probable age of an individual (Høye 2006). All permanent molars and premolars are required (Høye 2006, 212–14). The accuracy of this study is mixed – accuracy is sufficient for roe deer younger than four years old but drops off in older ones (Høye 2006, 212–14).

Wear Trait Scoring Methods are found challenging to execute (Pérez-Barbería et al. 2014). If presented in a user-friendly fashion, these methods can be understood and applied by other researchers. However, Pérez-Barbería and colleagues (2014) needed to first clarify details and fix ambiguities with the original authors (Brown and Chapman 1991; Dudley Furniss-Roe 2008) and published clarified versions of each as appendices in their publication. Although the Wear Trait Scoring Method has been claimed to be more objective than Visual Wear Pattern Methods (Lubinski 2001, 228), I do not wholly agree. Subjectivity certainly arises for 'close-calls', for example, a barely-there connection between shapes of dentine in which a characteristic must either be counted or not counted with no half measures. This score could easily be affected by the preference of the researcher and whether they are eager to count the trait as present or to be more conservative in their scoring.

As with Crown Height, Wear Trait Scoring Methods are quantitative and work well with statistical analyses, improving the accuracy of the age estimation. This approach also allows for slight variance in wear patterns as wear events may not occur in a regular order (Pérez-Barbería et al. 2014). Tooth wear traits do not correspond as well with tooth eruption sequences as other methods do (Brown and Chapman 1990). None include scores for tooth eruption, which is more accurate for ageing younger animals. A separate step of analysis would be required for younger-age mandibles. Additionally, these schemes are significantly more time consuming than the abovementioned tooth wear ageing methods with more features to observe and more recording needed.

	Source	Species	Sample Size	Sample Age Data	Geography/Population	Age Range (years)
Crown Height	Bowen et al. (2016)	fallow deer (Dama dama)	156	known age	France (n=10), England (n=8), Ireland (n=138) (modern and historical)	0–16
	Klein and Cruz-Uribe (1983)	eland (<i>Taurotragus</i> oryx) and Cape buffalo (<i>Syncerus caffer</i>)	80 (eland) + 36 (Cape buffalo)	unknown age	South Africa (archaeologi- cal)	_
	Lowe (1967)	red deer (<i>Cervus</i> elaphus)	33	known age	Scotland (modern)	0–8
	Lubinski (2001)	pronghorn (Antilocapra ameri- cana)	59	known age (55) and known date of mortality (228)	Montana (modern)	0>9
	Morrison and Whitridge (1997)	caribou (<i>Rangifer</i> tarandus groenland- icus)	74	cementum annuli	Qamanirjuaq herd, Canada (modern)	3–15
	Pasda	reindeer (Rangifer tarandus groenland- icus)	63	cementum annuli	Greenland (modern)	0–14
	Pike-Tay et al (2001)	caribou (<i>Rangifer</i> tarandus groenland- icus)	999	cementum annuli	Qamanirjuaq herd, Canada (modern)	0–16
	Steele and Weaver (2012)	elk (Cervus elaphus)	226	known age	Montana (modern)	0.5– 21.5
	Twiss (2008)	sheep (Ovis aries)/goats (Capra hircus)	267	unknown age	Turkey (archaeological)	0–10
Wear	Aitken (1975)	roe deer (Capreolus capreolus)	110	6 known age, 104 cementum annuli	Norfolk, England (modern)	2–7
Visual Wear	Bowen et al. (2016)	fallow deer (Dama dama)	156	known age	France (n=10), England (n=8), Ireland (n=138) (modern)	0–16

	Source	Species	Sample Size	Sample Age Data	Geography/Population	Age Range (years)
	Grant (1982)	sheep (Ovis aries)/goats (Capra hircus)	1301	unknown age	England (archaeological)	_
_	Greenfield and Arnold (2008)	sheep (Ovis aries)/goats (Capra hircus)	41	known age	Manitoba, Canada (modern)	0- 4.5yrs
	Halstead (1985)	sheep (<i>Ovis aries</i>), cattle (<i>Bos taurus</i>)	64 sheep, 20 cow	unknown age	England (archaeological)	_
_	Hambleton (1998)	sheep (Ovis aries), cattle (Bos taurus), pig (Sus scrofa)	164 sheep, 120 cattle, 128 pig	unknown age	England (archaeological)	_
_	Lubinski (2001)	pronghorn (Antilocapra ameri- cana)	284	known age (55) and known date of mortality (228)	Wyoming, Colorado, Montana (modern)	0 ->9
	Miller (1972)	caribou (<i>Rangifer</i> tarandus groenland- icus)	356	cementum annuli	Qamanirjuaq herd, Canada (modern)	0–3
ctd.	Miller (1974)	caribou (<i>Rangifer</i> tarandus groenland- icus)	999	cementum annuli	Qamanirjuaq herd, Canada (modern)	0–16
-	Mutze (2021)	sheep (Ovis aries)	1701	known age	UK and Germany (modern)	0–14
_	Payne (1973; 1987)	sheep (Ovis aries)/goats (Capra hircus)	147	unknown age	Turkey (archaeological)	0–10
-	Twiss (2008)	sheep (Ovis aries)/goats (Capra hircus)	47	unknown age	Turkey (archaeological)	0–10
-	van den Berg et al. (2021)	Svalbard reindeer (Rangifer tarandus platyrhynchus)	292	cementum annuli	Norway (modern)	0–17
	Brown and Chapman (1990)	fallow deer (Dama dama)	53	known age	England (modern)	0–8
ng	Brown and Chapman (1991)	red deer (<i>Cervus</i> elaphus)	111	known age	England (modern)	0–11.5
Wear Trait Scoring	Dudley Furniss- Roe (2008)	red deer (<i>Cervus</i> <i>elaphus</i>)	118	known age	Scotland (modern)	0–20
ear Tr	Høye (2006)	roe deer (<i>Cervus</i> elaphus)	471	known age	Denmark (modern)	0–14
We	Lubinski (2001)	pronghorn (Antilocapra ameri- cana)	59	known age (45) and known date of mortality (14)	Montana (modern)	0->9
	Pérez- Barbería et al. (2014)	red deer (<i>Cervus</i> elaphus)	694	known age	Scotland (modern)	0–16

TABLE 1-Sample sizes used in developing or improving age estimation techniques as outlined in this review paper (Created by
 author)

DISCUSSION

Age estimation methods are applicable between populations, including from different time periods, where no significant difference in tooth morphology and diet can be demonstrated (Spinage 1973). These methods largely rely on modern sample populations with known-ages (or accurately aged) to be calibrated and provide estimations in years (see Table 1). In the other direction, tooth wear data from archaeological populations are not useful for estimating the ages of modern animals because information for individual animal ages or life histories are not known. For example, reindeer in Greenland and North American caribou living in tundra environments (Pasda 2009) are more cross-comparable than Svalbard reindeer (van den Berg, Loonen, and Çakırlar 2021). This subspecies has been genetically isolated in a high arctic island environment for millennia and has a different mandibular morphology and diet (Reimers, Eftestøl, and Colman 2021; van den Berg, Loonen, and Çakırlar 2021). Similarly, Pérez-Barbería, Carranza, and Sánchez-Prieto (2015) demonstrate that red deer in Scotland have significantly slower dental attrition than red deer in Southern Spain, which is likely caused by the drier, courser diet available to the Spanish population. Although not the aim of this study, the authors provide different crown height regression equations for each sex of each population that could be applied in relevant zooarchaeological research contexts (Pérez-Barbería, Carranza, and Sánchez-Prieto 2015).

In contrast, ageing methods for domestic animals such as sheep, goats, cattle and pigs, namely Grant's (1982) and Payne's (1973; 1987) methods, have been applied to assemblages from varying geographical and time period contexts with success (for examples: Brunson, He, and Dai 2016; Crabtree 1996; Greenfield et al. 1988; Greenfield and Arnold 2008; 2015; Groot 2016; Halstead 1985; Hambleton 1998; Janzen, Balasse, and Ambrose 2020; Landon 1996; Munson 2000; Pilaar Birch et al. 2019; Rabinovich and Hovers 2004; Stiner 1990; Twiss 2008). Although a geographical and temporal survey of cross-applicability of tooth wear ageing methods is beyond the current scope, this paper has demonstrated that a researcher using a method developed from one population for another population must have reasonable expectations for the accuracy and precision they will achieve.

An understanding of the accuracy inherent in each method is important to know what expectations are reasonable. Tooth wear is not accurate enough to predict seasonality (Spiess 1979, 70-71). In contrast, tooth eruption sequences may be used to estimate age with accuracy from several months to a year, depending which tooth is analyzed (Hillson 2005). Tooth eruption sequences must be well studied for a specific species. When birth times are seasonal and occur within a short time frame, the age of an animal can help estimate the season of death as well (Bergerud 1970; Bowen et al. 2016; Lubinski 2001; Miller 1972; Spiess 1979, 70). One of the greatest determining factors for accuracy and usefulness is the presence and quality of a known-age reference sample to draw from (Grant 1982, 105; Dudley Furniss-Roe 2008; Brown and Chapman 1990, 678; Lubinski 2001, 219). A lack of older animals in the sample will reduce the sensitivity of the model for those ages.

A similar level of accuracy is achieved for the two methods that rely on occlusal tooth surface observations, the Visual Wear Pattern and Wear Trait Scoring Methods. For younger adult individuals, these methods generally yield satisfactory accuracy within a year or two of known age. For example, Aitken's (1975, 24) 'jaw board' was fairly accurate; 90–95% were aged correctly within a year of the cementum age. Lubinski (2001, 223) finds that for younger stages or wear, their Wear Trait Scoring Method for pronghorn antelope

derived from Brown and Chapman (1990) performs better than the Visual Wear Pattern Method following Payne (1987). In contrast, Crown Height Methods generally do not yield results as accurately. Twiss (2008, 344) finds that LCHM is not meaningful over four years old, and Klein and Cruz-Uribe (1983, 76) realizes that QCHM is inadequate by both overestimating and underestimating ages; however, the positive and negative inaccuracy would balance out in a larger population. Additionally, Crown Height and Wear Trait Scoring Methods are quantitative and work well with statistical analyses, improving the accuracy of the age estimation (see Twiss 2008; Pérez-Barbería et al. 2014). This approach also allows for slight variance in wear patterns as wear events may not occur in a regular order (Brown and Chapman 1990, 678–79).

Each of these approaches involves distinct procedures that differ in user-friendliness and in efficiency. Crown Height and Visual Wear Pattern Methods would take significantly less time to complete than Wear Trait Scoring Methods because there are so many more features to examine per specimen. Lubinski (2001, 223) refers to Brown and Chapman (1990) as being more 'cumbersome'. Indeed, this issue is the purpose of Pérez-Barbería and associates' (2014) article that seeks to eliminate redundant traits and speed up the process. The traits in Wear Trait Scoring Methods do not coordinate as well with tooth eruption sequences as other methods since none include scores for tooth eruption. An additional step of analysis would be required for younger-age mandibles. In a general sense, this approach is more time consuming with more features to observe and more recording required.

An important factor in assessing usefulness also depends on the species and whether someone has created a calibrated method using known or precisely aged mandible collections for that species or population (Hillson 2005, 212). Some species, including reindeer and caribou, vary substantially in tooth eruption times and rate of wear between populations across the Circumpolar North (Miller 1974, 16; see also Bergerud 1970; Pasda 2009, 32; Spiess 1979, 76). The process of calibrating an existing relative ageing scheme would undoubtedly be difficult and require access to an adequately relevant sample of mandibles. This is true for any uncalibrated tooth wear ageing method.

Animal remains from archaeological sites may be recovered in varying degrees of fragmentation. Therefore, which tooth wear age estimation method will be most suitable is important to consider. For highly fragmented assemblages with loose (but intact) teeth, the Crown Height Method may be a strong choice (Klein and Cruz-Uribe 1983; Lyman 2017; Twiss 2008). The other tooth wear methods lose much of their accuracy when only one tooth is considered (Twiss 2008). However, if mandibles are fully or partially complete and teeth are socketed, crown height often cannot be measured if the cementoenamel junction is covered by the mandible (Twiss 2008, 343). Additionally, if preservation is too poor and cusps are damaged, this prevents measuring crown height as well (Twiss 2008, 343). Both other occlusal wear approaches have the ability to contend with individual teeth or incomplete dentition, the accuracy of the estimated age might just be less robust (Twiss 2008, 343).

CONCLUSION

Tooth wear age estimation is an effective method of inferring the age-at-death of animals from archaeological sites. Methods for ageing Cervidae and Caprinae have been considered in this review. This approach to age estimation is substantially more efficient, easier to learn, provides faster results, and does not require destruction of specimens as is the case with cementum increment analysis. Despite these positives this approach is an ageing method that is not without sources of inaccuracy. Tooth wear ageing methods can be employed in zooarchaeology to estimate ages of adult animals and cover all life stages when applied in conjunction with tooth eruption sequences. These estimated ages can be compiled to reconstruct demographic profiles of the population of animals recovered from an archaeological site. Age-based demographic profiles provide valuable insight into how people were interacting with animal populations, such as selection and strategy during hunting and livestock management (Klein and Cruz-Uribe 1983; Gifford-Gonzalez 2018; Reitz and Wing 2008; Russell 2012).

Dental attrition is ultimately the result of the amount of food and particulates chewed over a lifetime. The rate of attrition if affected by diet, behaviour, age, sex, population, and any dental anomalies or traumas. These variables need to be understood to recognize the limitations inherent in tooth wear ageing. Despite these sources of variation, the rate of wear must be assumed to be predictable within an individual's lifetime, between individuals within a population, and between populations that are used together in analysis. These assumptions are necessary for the three overarching approaches outlined in this paper, the Crown Height Method, the Visual Wear Pattern Method, and the Wear Trait Scoring Method.

Different research contexts call for different tooth wear ageing approaches to provide meaningful results. This paper shows that the various ways of quantifying tooth wear for cervids and caprines differ in accuracy, efficiency, and user-friendliness. Crown Height provides a statistically-friendly method that is well suited for loose, yet intact teeth. Visual Wear Patterns are efficient, intuitive, and can be carried out remotely or in the field; however, many of the specific approaches that have been developed are better suited to complete mandibles. Wear Trait Scoring Methods provide thorough results but need complete mandibles (at least all three molars) and are relatively time consuming. This article demonstrates that there is no one approach to tooth wear age

estimation for all zooarchaeological research projects.

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