Journal of Mammalogy, 2026, **00**, 1–7
https://doi.org/10.1093/jmammal/gyag002
Research Article

Research Article

Evaluating the effect of tooth section thickness on cementum annuli analysis

Stacey L. Hannebaum[1,*], John B. Hopkins III[2], Katherine E. Rock[1], Arthur J. Stephens[1], Carolyn Nistler[1]

[1]Matson's Laboratory, 135 Wooden Shoe Lane, Manhattan, MT 59741, United States
[2]Center for Wildlife Studies, 36A High St, Camden, ME 04843, United States

[*]Corresponding author: Matson's Laboratory, 135 Wooden Shoe Lane, Manhattan, MT 59741, United States. Email: doscience@matsonslab.com

Associate Editor was Timothy Smyser

Abstract

Understanding the age-structure of mammal populations is important for understanding population dynamics and informing wildlife conservation and management. For decades, cementum annuli analysis (CAA), the process of estimating animal age by counting cementum annuli in teeth, has been a standard method used by wildlife biologists from around the globe. The process of histological preparation for CAA of demineralized teeth often involves multiple steps that can be achieved using a variety of techniques. One technical issue that has been largely unexplored is understanding the effect of tooth section thickness on the process of accurately aging mammals by CAA. In this study, we investigated the relationship between validation of 2 experts aging mammals identically by CAA and tooth section thickness, species, and animal age. Our purpose was to determine if cutting teeth thicker than our standard of 14 µm compromises the ability of experts to age teeth identically. To carry out our study, 2 experts used CAA to determine the age of 30 American Black Bear (*Ursus americanus*) from Alaska, 30 Elk (*Cervus canadensis*) from Colorado, and 30 White-tailed Deer (*Odocoileus virginianus*) from Maine using teeth cut to different section thicknesses: 14 µm (our standard), 25 µm, and 35 µm. Ages ranged from 1 to 8 yr for American Black Bear, 2 to 7 yr for Elk, and 1 to 17 yr for White-tailed Deer. We found that more teeth were aged identically by experts at 14 µm thickness (96%) compared to 25 µm (79%) and 35 µm thickness (82%). Age assignments from the experts agreed most frequently for Elk (93%), followed by American Black Bear (89%) and White-tailed Deer (74%). Animal age had no effect on experts aging teeth identically. Future studies interested in exploring an optimal tooth section thickness for CAA should strive to include individuals spanning the latitudinal range of the species and to use known-age animals whenever possible.

Keywords: American Black Bear, cementochronology, cementum aging, *Cervus canadensis*, Elk, *Odocoileus virginianus*, teeth, *Ursus americanus*, White-tailed Deer

Many key life history traits such as fecundity, dispersal, and survival are age-dependent (Vandermeer and Goldberg 2013). Age is therefore a crucial factor for understanding population dynamics and species distribution (Alexander 1958; Newman et al. 2014), both of which are used to inform conservation and management decisions that benefit wildlife and people (Leopold 1933; Morris 1972; Larson and Taber 1980). For example, wildlife managers use age-at-harvest data in statistical models to monitor population size trends of White-tailed Deer (*Odocoileus virginianus*)—a widespread species of economic importance in the United States (Hewitt 2015)—and set future harvest regulations to achieve management objectives (Collier and Krementz 2007; Brandell et al. 2022).

For decades, teeth have been useful for aging mammals (Laws 1952). Each year in the life of a mammal, the cementum—the outermost tissue of a tooth root—forms a new outer growth layer resulting in bands of cementum called annuli. When cross-sectioned, thick and light cementum bands are related to periods of fast growth (e.g., spring and summer foraging), whereas thin and dark cementum bands are related to periods of slow growth (e.g., low nutrition during winter) when mammals are in physiological stress (Grue and Jensen 1979; Lieberman and Meadow 1992; Colard et al. 2017; Fig. 1). Cementum growth layers are continuously synthesized in this fashion throughout the life of a mammal; thus, identification of annuli coupled with knowledge of tooth eruption timing can be used to estimate the age of an individual (Perrone et al. 2022). Cementum annuli analysis (CAA; also known as cementochronology), which involves identifying and counting these growth layers in teeth often under a transmitted light microscope (Fig. 1), can be a reliable method used by wildlife researchers and managers to determine age for a wide variety of mammals (Fancy 1980; Colard et al. 2018).

The steps of tooth preparation for CAA vary based on whether the tooth is demineralized or not (Fancy 1980). The procedure of histological preparation for CAA of demineralized teeth often involves the following steps: (i) the tooth is decalcified using a chemical treatment and processed (dehydration, clearing, and matrix infiltration); (ii) the tooth is then embedded in a matrix of paraffin wax, so the tooth can be cut into thin sections; and (iii) the tooth is stained to amplify the contrast between light and dark cementum annuli, which are then counted using the aid of a microscope (Fancy 1980; Matson et al. 1993). Although each of these steps can be achieved using a variety of techniques (Fancy 1980; Kvaal et al. 1996), one aspect of demineralized tooth preparation that has been largely unexplored is understanding the effect of tooth section thickness on the process of accurately aging mammals by CAA.

In CAA studies, tooth section thickness ranges from 6 to 30 µm for decalcified teeth (Adams and Watkins 1967; Takken Beijersbergen

Received: March 4, 2025. Accepted: January 2, 2026

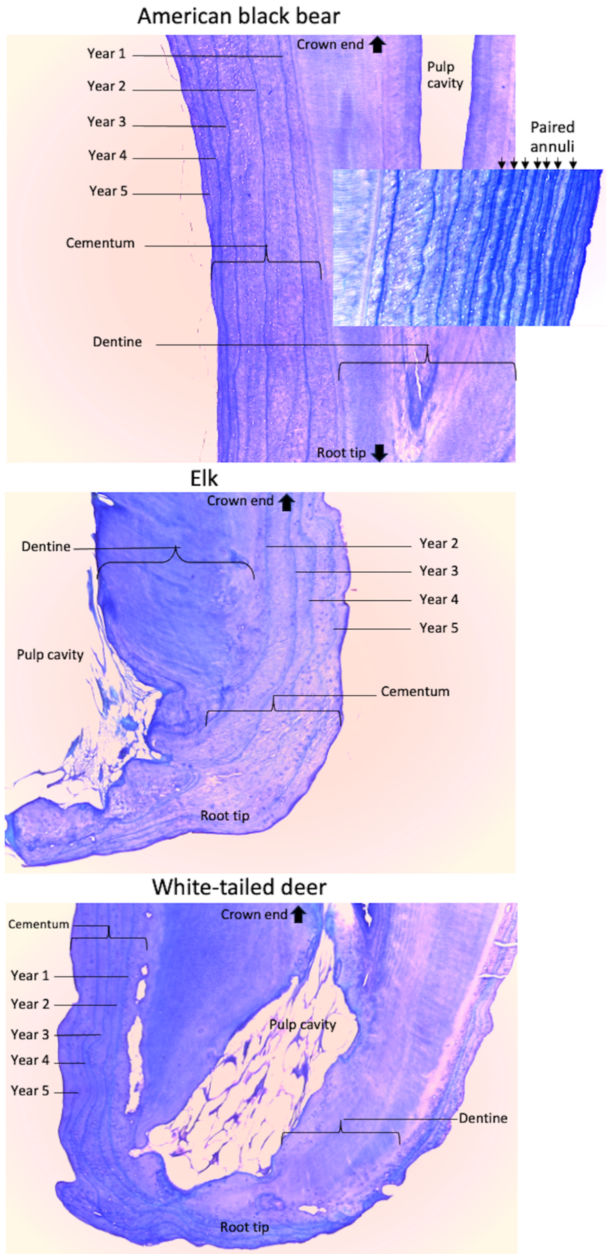

Fig. 1. Examples of cementum annuli (magnification = 40×) for American Black Bear (*Ursus americanus*), White-tailed Deer (*Odocoileus virginianus*), and Elk (*Cervus canadensis*). Numbers on annuli correspond to the age at which each was deposited and were therefore used to age each specimen. The inset for American Black Bear shows a pattern of paired annuli that is characteristic of a female during cub-rearing years (at least 7).

2019). Despite the range in section thickness used, there are no studies to our knowledge that have investigated an optimum thickness that achieves the most easily interpretable annulations. The purpose of this study was to determine if cutting teeth thicker than our standard of 14 µm compromises the ability of experts aging teeth identically. We therefore evaluated the relationship between the agreement of experts aging mammals by CAA and tooth section thickness, species, and animal age.

Methods

We performed all histological preparation and CAA at Matson's Laboratory (Manhattan, Montana, United States), a commercial lab that specializes in CAA. Since 1969, Matson's Lab has analyzed over 3 million teeth from over 200 different mammalian species submitted by biologists, researchers, and hunters from around the world (Matson's Laboratory 2024).

Tooth selection.

In this study, we focused on American Black Bear, White-tailed Deer, and Elk because of their environmental and economic importance (Ziegltrum and Nolte 2001; Koontz and Loomis 2005; Hewitt 2015), their availability for use in this study, and the Matson's Lab expertise in aging these species (e.g., Harshyne et al. 1998; Hamlin et al. 2000; Costello et al. 2004; Adams and Blanchong 2020). In 2024, these 3 species made up 57% (63,712 of 112,001) of the teeth processed and aged at Matson's Lab (American Black Bear = 38,458; White-tailed Deer = 17,093; Elk = 8,161).

We selected samples from teeth that were collected and stored dry in 2022, histologically processed at Matson's Lab (see Matson et al. 1993 for details of processing methods) in 2023, and stored at room temperature embedded in paraffin blocks for 6 mo or less after processing. Paraffin blocks have been shown to be a stable long-term storage option for tissues (Likhithaswamy et al. 2022). We are unaware of any studies assessing the deterioration rate of histological features in dry tooth specimens, but Matson's Lab has always processed tooth specimens stored in this manner and has had success correctly aging known-age specimens (Harshyne et al. 1998; Hamlin et al. 2000; Costello et al. 2004; Foley et al. 2022), suggesting that this manner of storage is not significantly deleterious.

For each species, we first identified a northern population with teeth from >50 different individuals. We limited sampling to northern populations because teeth from latitudinal regions that experience discrete seasons exhibit annuli that are more distinct due to sharp seasonal changes in metabolic rates and hormones (Asmus and Weckerly 2011; Kohler et al. 2012). We used a random number generator to select 30 teeth from 895 American Black Bear from Alaska, 1,001 White-tailed Deer from Maine, and 53 Elk from Colorado. We used the first premolar for American Black Bear (Willey 1974) and the first incisor for White-tailed Deer and Elk (Gilbert 1966; Keiss 1969). We removed teeth that were damaged, either from extraction or original sectioning, to avoid known negative effects on CAA accuracy (Grue and Jensen 1979; Costello et al. 2004), and a new random tooth was selected as a replacement. We did not stratify our sampling by sex because past studies of mammals with known-ages suggest that sex does not have an effect on the accuracy of CAA for American Black Bear, White-tailed Deer, or Elk (Hamlin et al. 2000; Costello et al. 2004).

The presence of known-age animals within a submission is rarely revealed to Matson's Lab because such animals are intended to act as a blind test of CAA accuracy. Due to this and the general paucity of known-age wild animals, we were unable to use known-age samples in this study; therefore, we were unable to directly analyze how tooth section thickness affects CAA accuracy. Nonetheless, our study provides insights to improve the performance of CAA by focusing on tooth section thickness, one of the few factors that can be controlled in such analyses.

Histological processing.

We embedded decalcified teeth in paraffin wax (Leica Surgipath Paraplast Plus) and sectioned teeth longitudinally using a Leica HistoCore Biocut microtome fitted with a C.L. Sturkey Permanent Microtome Knife. We chose 14 µm as the thinnest section because that is the standard thickness used by Matson's Lab and we were interested in examining the relationship between this and greater section thicknesses and CAA repeatability for subsequent isotope ratio mass spectrometry (IRMS) experimental studies. Tooth sections thicker than 35 µm have proven to not adhere adequately to microscope slides following Matson's Lab standard protocol. We did not include section thicknesses less than 14 µm because they are increasingly less likely to provide enough material for IRMS. A total of 6 sections were taken from each tooth at the following thickness in the following order: 14 µm, 25 µm, 35 µm, 14 µm, 25 µm, and 35 µm. We sectioned teeth in this order to ensure that at least 1 section of each thickness was obtained before optimal tooth tissue was exhausted. We collected 2 sections of each thickness to further increase the chances of obtaining sections suitable for analysis, which is standard practice at Matson's Lab.

We mounted sections in pairs by thickness on petrographic microscope slides (Ward's Natural Science 27 × 46 × 1.2 mm), resulting in 3 slides for each animal (14, 25, and 35 µm). The slides were deparaffinized and Giemsa-stained using standard Matson's Lab protocol (Matson et al. 1993). We did not place coverslips on the slides because of the nature in which they were to be used in subsequent IRMS studies.

Cementum age analysis.

All 90 teeth were analyzed by 2 experts trained using Matson's Lab species-specific aging models (Matson 1981). Experts aged each tooth independently. Both experts analyzed each 14 µm tooth section, waited at least 1 wk to analyze each 25 µm tooth section, and then waited at least 1 more week to analyze each 35 µm tooth section. Experts viewed duplicate sections of each tooth and assessed the collective evidence presented in both sections to determine a single age (Matson et al. 1993), yielding a total of 540 age measurements.

We applied a drop of reverse osmosis water (imitates a coverslip) over the sections immediately before viewing under a Leica DME or Leica DM750 compound light microscope (40× to 100× magnification). We removed reverse osmosis water and analyzed dry sections in cases when the water caused too much lighting of the sample, which was typical for the 14 µm sections.

For purposes of aging, we used 1 February for the birthdate of American Black Bear and 1 June for White-tailed Deer and Elk (Severinghaus 1949; Marks and Erickson 1966; Keiss 1969). If a tooth was extracted soon after those dates, the annulus denoting the most recent winter may or may not be visible along the periphery of the tooth section, especially for American Black Bear which have a birthdate during the non-growing season (Matson et al. 1993). In such cases, the outermost light cementum layer was included in the annuli count.

Statistical analysis.

We first used binomial regression to calculate the log odds that 2 experts will age a tooth identically depending on the age of the animal, tooth section thickness (14, 25, and 35 µm), and species (American Black Bear, White-tailed Deer, and Elk). We reported the estimated regression coefficient, SE, 95% CI, z-score, and *P*-value for each predictor in our logit model. Because these regression coefficients correspond to the change in log odds, we exponentiated each coefficient and reported the odds ratios (with 95% CIs) for easier interpretation. We then used a Wald's test to determine the overall effect of tooth section thickness and species on the uncertainty in aging and if both tooth section thickness coefficients and species coefficients were statistically different from one another. Lastly, we compared the relationships among the predicted probability of 2 experts aging an animal identically by tooth section thickness to determine the optimal tooth section thickness for aging the species in this study.

We conducted all analyses in R and reported statistical differences between groups using a standard significance level (α) of 0.05 (R Core Team 2023).

Results

We found that the mean age assigned by experts was 3.7 for all species, but ages ranged from 2 to 7 ($\bar{x}$ = 4.8) yr for Elk, followed by 1to 8 ($\bar{x}$ = 3.4) yr for American Black Bear, and 1to 17 ($\bar{x}$ = 3.0) yr for White-tailed Deer (Table 1; Supplementary Data SD1). We found that the 14-µm section had the fewest misclassifications for all 3 species examined in this study (Table 1). Specifically, we found that the 2 experts assigned identical ages for far more teeth at 14 µm thickness (96%) compared to 25 µm (79%) and 35 µm thickness (82%; Table 1). Expert age agreement was 74% for White-tailed Deer, 89% for American Black Bear, and 93% for Elk (Table 1).

Using our 3-covariate (animal age, tooth section thickness, species) logit model, we found that animal age had no effect on experts aging teeth identically (i.e., the CI contained zero and $P>0.05$; Table 2). We did, however, find that both tooth section thickness (x^2 = 10.0, df = 2, $P = 0.007$) and species (x^2 = 14.7, df = 2, $P < 0.001$) had an overall effect on the uncertainty in aging. Unlike the coefficients for Elk (vs. American Black Bear) and White-tailed Deer (vs. American Black Bear), which were different from one another (x^2 = 12.4, df = 1, $P < 0.001$), we found no effect (x^2 = 0.32, df = 1, $P = 0.57$) of experts aging a tooth identically when comparing 25 µm versus 14 µm with 35 µm versus 14 µm. Regardless of animal age, the predicted probability of 2 experts aging a tooth identically is highest at 14 µm (Fig. 2).

Discussion

We made 2 important discoveries in this study. First, we found that experts were best at aging Elk followed by American Black Bear and White-tailed Deer when analyzing individuals from their northern ranges. We also learned that, regardless of animal age and species, our standard 14 µm sections yielded highest age agreement among experts and is therefore the tooth thickness we recommend for CAA analysis of decalcified teeth.

In order to produce histological samples with consistent visual properties, Matson's Lab follows a standard histological sample preparation protocol that employs tooth sections that are 14 µm thick. Matson's Lab also uses species-specific CAA aging models that describe detailed criteria for determining age. Matson's Lab produced these aging models using samples prepared following their standard

Table 1. Summary statistics of cementum annuli analysis age estimates recorded by 2 experts for each species, including tooth sections assigned different ages by experts (Misclass) and mean (with standard deviation, SD) of mean ages by species and tooth section thickness.

Section thickness	14 µm			25 µm			35 µm			
Species	Misclass	Mean	SD	Misclass	Mean	SD	Misclass	Mean	SD	Total Misclass
American Black Bear (*n* = 30)	1	3.35	0.02	3	3.35	0.07	6	3.13	0.14	10
Elk (*n* = 30)	0	4.77	0.00	3	4.75	0.40	3	4.75	0.07	6
White-tailed Deer (*n* = 30)	3	2.95	0.07	13	3.25	0.34	7	3.15	0.21	23
Total (*n* = 90)	4			19			16			
Mean	1.33	3.69	0.03	6.33	3.78	0.27	5.33	3.68	0.14	13.00

Table 2. Statistics used to interpret results from our binomial regression model, including the odds ratio (and 95% CI) that 2 experts will age a tooth identically by cementum age analysis depending on the estimated age of the animal: American Black Bear (*Ursus americanus*), White-tailed Deer (*Odocoileus virginianus*), and Elk (*Cervus canadensis*).
Model: $\text{logit}(p) = \log(p/(1-p)) = \beta0 + \beta1\times\text{Age} + \beta2\times\text{Thickness} + \beta3\times\text{Species}$.

	Coeff.	SE	Low CI (2.5%)	High CI (97.5%)	z	P	Odds ratio	Low CI (2.5%)	High CI (97.5%)
(Intercept)	3.778	0.656	2.493	5.063	5.762	<0.001	43.722	13.580	184.329
Age	−0.096	0.066	−0.225	0.334	−1.447	0.148	0.909	0.796	1.036
Thickness 25 µm	−1.840	0.588	−2.992	−0.688	−3.130	0.002	0.159	0.043	0.459
Thickness 35 µm	−1.618	0.595	−2.785	−0.451	−2.718	0.007	0.198	0.534	0.585
Elk	0.715	0.555	−0.374	1.803	1.287	0.198	2.043	0.702	6.426
White-tailed Deer	−1.071	0.427	−1.909	−0.234	−2.508	0.012	0.343	0.143	0.773

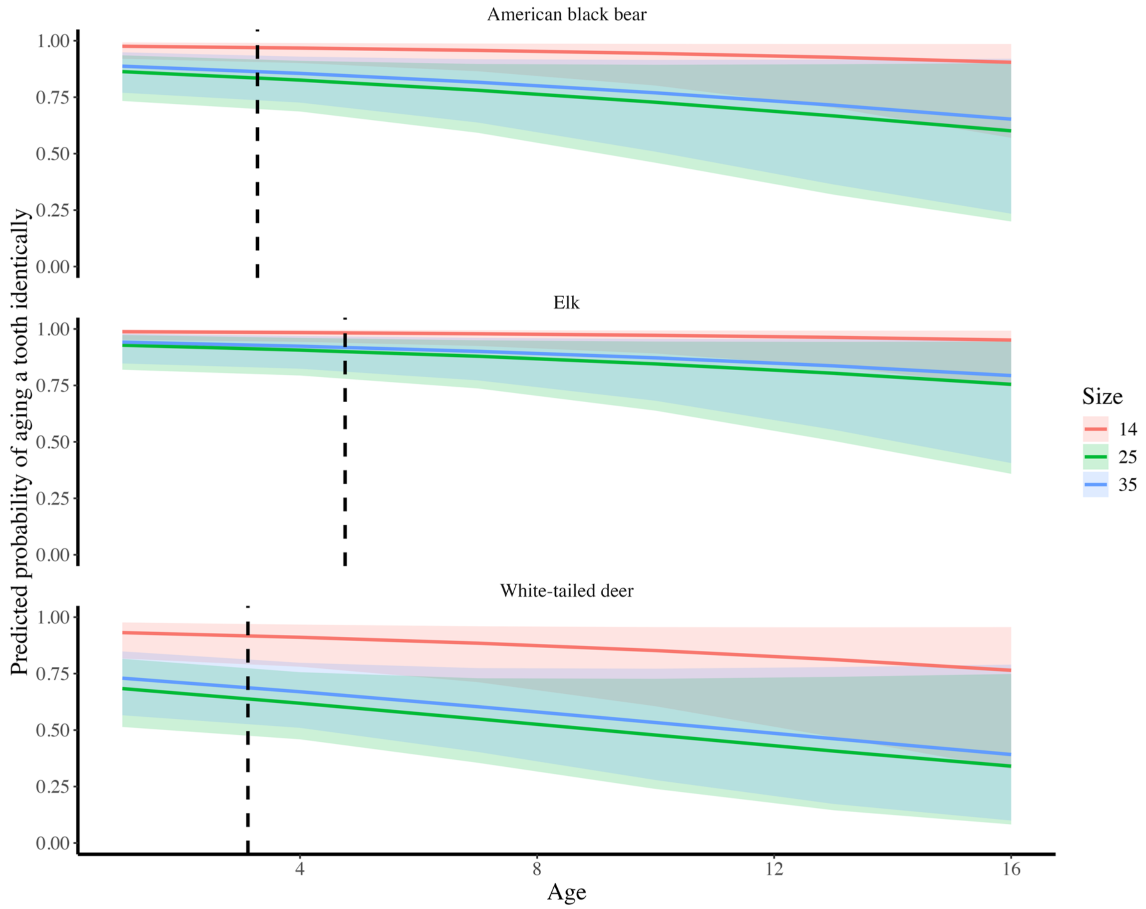

Fig. 2. The predicted probabilities of 2 experts aging a tooth identically by species (American Black Bear, *Ursus americanus*; Elk, *Cervus canadensis*; White-tailed Deer, *Odocoileus virginianus*), animal age (years), and tooth section thickness (µm). The dashed line denotes the average age measured by experts in this study for each species for all tooth section thicknesses combined.

histological sample preparation protocol; therefore, it is not surprising that our study revealed that experts aged animals most similarly using 14 µm sections, as experts are trained in CAA using this thickness. Interestingly, although an experts ability to age animals identically decreased as section thickness increased from 14 µm to larger section thicknesses, the number of misclassifications was similar when increasing section thickness from 14 to 25 µm and 14 to 35 µm. This may suggest that annuli of 25 and 35 µm sections are equally interpretable, leading us to wonder if experts could be trained according to nuances in the visual presentation of each. It is possible that the variable addition of reverse osmosis water during microscopy, which was most common for 25 and 35 µm sections, may have influenced the observed pattern, but we are unable to test this because water application was not recorded during analysis. Future studies interested in exploring an optimal tooth section thickness for CAA of decalcified teeth should utilize cover-slipped slides to eliminate this variable.

We did not find evidence that animal age influenced CAA. Our estimated ages ranged from 1 to 17 yr, but our dataset did not contain many older animals and did not span an age range wide enough to detect an effect of age on experts assigning identical ages for these species. Despite this result, our sample is likely representative of the actual age structure of the wild populations sampled (Robison and Bolen 1989). Other studies of White-tailed Deer incisor pairs from Iowa (Adams and Blanchong 2020) and known-age Elk, Mule Deer, and White-tailed Deer from Montana did not find a relationship between CAA consistency or accuracy and age (Hamlin et al. 2000). Adams and Blanchong (2020) attributed the lack in finding a relationship to deficiencies with their dataset (estimated ages ranged from 1 to 8 and 95% of their sample were aged 1 to 4). In contrast, other studies using known-age animals to investigate the effects of age on CAA accuracy found that accuracy declined with animal age and estimated animal ages were usually negatively biased (e.g., McLaughlin et al. 1990; Costello et al. 2004; Storm et al. 2014; Foley et al. 2022), except for 1 study that revealed mostly overestimates for American Black Bear in Pennsylvania (Harshyne et al. 1998). Loss of CAA accuracy with increasing animal age has been attributed to the decrease in cementum deposition with increased age, resulting in thinner and more compact annuli later in life that are more difficult to differentiate than earlier annuli (Sauer et al. 1966; Grue and Jensen 1979).

We found that species had a significant effect on CAA results. Specifically, using the 14 µm thickness, 2 experts aged 3 White-tailed Deer differently (90% assigned identical age; age difference of 1 yr in all misclassifications), 1 American Black Bear differently (97% assigned identical age; age difference of 1 yr in misclassification), and 0 Elk differently (100% assigned identical age; Supplementary Data SD1). Other studies from the United States that investigated CAA consistency conducted at Matson's Lab found matching CAA ages for 74% of American Black Bear ($n = 232$) analyzed from New Mexico and 81% of White-tailed Deer ($n = 473$) analyzed from Iowa (Costello et al. 2004; Adams and Blanchong 2020). In both studies, the majority of age misclassifications differed by 1 yr, though discrepancies up to 4 yr in White-tailed Deer and 6 yr in American Black Bear were reported. In contrast to our study, these studies compared age estimates of 2 different teeth (usually identical tooth type) from the same animal rather than age estimates of the same tooth by 2 different experts. Investigating the validity of CAA using 2 different teeth from the same animal could be problematic because different teeth from the same animal may be subjected to different biological factors (e.g., trauma, pathology) that affect cementum deposition and could lead to differential histological characteristics, resulting in different CAA ages. A study that evaluates CAA accuracy and consistency using the same expert analyzing different teeth from the same animal with a known age as well as different experts with similar training and experience analyzing the same tooth would be ideal.

Past studies using known-age animals revealed that the accuracy of CAA conducted by Matson's Lab ranges from 97% for Elk (Hamlin et al. 2000; Montana, USA, $n = 111$), 80% to 92% for American Black Bear (Costello et al. 2004; New Mexico, United States, $n = 30$: Harshyne et al. 1998; Pennsylvania, United States, $n = 671$), and 60% to 85% for White-tailed Deer (Foley et al. 2022; Texas, United States, $n = 264$: Hamlin et al. 2000; Montana, United States, $n = 74$). Past results combined with the findings of this study, which focuses on northern populations and therefore likely reports liberal estimates of age agreement, suggest that the reliability of CAA is not consistent across species or populations within the same species. Complexity or irregularity in the appearance of cementum annuli (i.e., split annuli, false annuli, resorption) and indistinct annulations prevalent in southern populations are often the greatest cause for uncertainty and error in CAA (Harshyne et al. 1998; Naji et al. 2022) and such characteristics are found in at least some individuals of all species (Grue and Jensen 1979). Ungulates, in particular, commonly exhibit irregularities in annuli appearance due to resorption resulting from reparative processes in response to pathology or trauma (Grue and Jensen 1979; Bosshardt and Selvig 1997). In our experience, White-tailed Deer show annuli complexity to a much greater extent than Elk, though we have not quantified these differences (Hamlin et al. 2000). Reproductive history also complicates CAA of American Black Bear, which is not observed in ungulates. In particular, cub-rearing years are evident by proportionally less light cementum deposition during that time (Coy and Garshelis 1992), resulting in the appearance of paired annuli that may be mistaken as annuli complexity (Fig. 1), especially if the sex of the bear is unknown. Ultimately, quantification of the histological characteristics (i.e., annuli complexities and irregularities) that accompany known-age animals across the latitudinal gradient of their range can help elucidate whether misclassifications during CAA are due to human errors or are species-related and/or regionally related. Future studies interested in exploring optimal tooth section thickness for CAA should strive to use known-age animals and animals from multiple latitudes to evaluate the accuracy and repeatability of CAA.

Acknowledgments

We thank Maine Department of Inland Fisheries and Wildlife (Nathan Bieber, White-tailed Deer), Alaska Department of Fish and Game (Jackie Empleo, American Black Bear), and Banded Peak Ranch (David Kelley, Elk) for permitting us to use remnants of their tooth samples for this study. We thank Matson's Laboratory staff members Jesse White, Eryn Foreman, Eric Elkins, Nicole Evec, and Traci Johnston for assistance with tooth processing. Lastly, we thank Jeff Stetz, Timothy Smyser, and 3 anonymous reviewers for their review of this manuscript.

Author contributions

Stacey Hannebaum (Conceptualization, Data curation, Investigation, Methodology, Project administration, Validation, Visualization, Writing—original draft, Writing—review & editing), Jack Hopkins (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Software, Visualization, Writing—original draft, Writing—review & editing), Katherine Rock (Data curation, Investigation, Methodology, Writing—review & editing), Arthur Stephens (Investigation, Methodology, Resources, Writing—review & editing), and Carolyn Nissler (Conceptualization, Funding acquisition, Investigation, Supervision, Writing—review & editing)

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1. Age assignments (years) determined by 2 experts (Ager 1 and Ager 2) using tooth sections of 3 thicknesses taken from 30 individuals of each studied species (American Black Bear, *Ursus americanus*; Elk, *Cervus canadensis*; and White-tailed Deer, *Odocoileus virginianus*). The absolute value of the difference in age assignments (Diff), mean age (Mean), and standard deviation (SD) are included for each individual at each tooth section thickness. For each tooth section thickness, the overall mean age and standard deviation and the total number of expert age differences (Misclass) are included at the bottom of each species table.

Funding

This research was supported by Matson's Laboratory.

Conflict of interest

None declared.

Data availability

All data are available in the Supplementary Data SD1 file.

References

Adams DM, Blanchong JA. 2020. Precision of cementum annuli method for aging male white-tailed deer. PLOS One 15(5):e0233421. https://doi.org/10.1371/journal.pone.0233421

Adams L, Watkins SG. 1967. Annuli in tooth cementum indicate age in California ground squirrels. The Journal of Wildlife Management 31(4):836–839. https://doi.org/10.2307/3797994

Alexander MM. 1958. The place of aging in wildlife management. American Scientist 46(2):123–137. https://www.jstor.org/stable/27827106

Asmus J, Weckerly F. 2011. Evaluating precision of cementum annuli analysis for aging mule deer from southern California. The Journal of Wildlife Management 75(5):1194–1199 https://doi.org/10.1002/jwmg.133.

Bosshardt DD, Selvig KA. 1997. Dental cementum: the dynamic tissue covering of the root. Periodontology 2000 13(1):41–75. https://doi.org/10.1111/j.1600-0757.1997.tb00095.x

Brandell EE, Storm DJ, Van Deelen TR, Walsh DP, Turner WC. 2022. A call to action: standardizing white-tailed deer harvest data in the midwestern United States and implications for quantitative analysis and disease management. Frontiers in Ecology and Evolution 10:943411. https://doi.org/10.3389/fevo.2022.943411.

Colard T, Bertrand B, Naji S, Delannoy Y, Bécart A. 2018. Toward the adoption of cementochronology in forensic context. International Journal of Legal Medicine 132(4):1117–1124. https://pubmed.ncbi.nlm.nih.gov/25773917/.

Colard T, Falgayrac G, Bertrand B, Naji S, Devos O, Balsack C, Delannoy Y, Penel G. 2017. New insights on the composition and the structure of the acellular extrinsic fiber cementum by Raman analysis. PLOS One 12(3):e0174080. https://doi.org/10.1371/journal.pone.0167316

Collier BA, Krementz DG. 2007. Uncertainty in age-specific harvest estimates and consequences for white-tailed deer management. Ecological Modelling 201(2):194–204. https://doi.org/10.1016/j.ecolmodel.2006.09.017

Costello CM, Inman KH, Jones DE, Inman RM, Thompson BC, Quigley HB. 2004. Reliability of the cementum annuli technique for estimating age of black bears in New Mexico. Wildlife Society Bulletin 32(1):169–176. https://doi.org/10.2193/0091-7648(2004)32[169: ROTCAT]2.0.CO; 2

Coy PL, Garshelis DL. 1992. Reconstructing reproductive histories of black bears from the incremental layering in dental cementum. Canadian Journal of Zoology 70(11):2150–2160. https://doi.org/10.1139/z92-290

Fancy SG. 1980. Preparation of mammalian teeth for age determination by cementum layers: a review. Wildlife Society Bulletin 8(3):242–248. https://www.jstor.org/stable/3781696

Foley AM, Lewis JS, Cortez O, Hellickson MW, Hewitt DG, DeYoung RW, DeYoung CA, Schnupp MJ. 2022. Accuracies and biases of ageing white-tailed deer in semiarid environments. Wildlife Research 49(3):237–249. https://doi.org/10.1071/WR21050.

Gilbert FF. 1966. Aging white-tailed deer by annuli in the cementum of the first incisor. The Journal of Wildlife Management 30(1):200–202. https://doi.org/10.2307/3797906

Grue H, Jensen B. 1979. Review of the formation of incremental lines in tooth cementum of terrestrial mammals. Danish Review of Game Biology 11(3):1–48

Hamlin KL, Pac DF, Sime CA, DeSimone RM, Dusek GL. 2000. Evaluating the accuracy of ages obtained by two methods for Montana ungulates. The Journal of Wildlife Management 64(2):441–449. https://doi.org/10.2307/3803242

Harshyne WA, Diefenbach DR, Alt GL, Matson GM. 1998. Analysis of error from cementum-annuli age estimates of known-age Pennsylvania black bears. The Journal of Wildlife Management 62(4):1281–1291. https://doi.org/10.2307/3801992

Hewitt DG. 2015. Hunters and the conservation and management of white-tailed deer (*Odocoileus virginianus*). International Journal of Environmental Studies 72(5):839–849. http://dx.doi.org/10.1080/00207233.2015.1073473

Keiss RE. 1969. Comparison of eruption-wear patterns and cementum annuli criteria in Elk. The Journal of Wildlife Management 33(1):175–180. https://doi.org/10.2307/3799668

Kohler M, Marin-Moratalla N, Jordana X, Aanes R. 2012. Seasonal bone growth and physiology in endotherms shed light on dinosaur physiology. Nature 487(7407):358–361. https://doi.org/10.1038/nature11264

Koontz L, Loomis JB. 2005. Economic importance of Elk hunting in Jackson Hole, Wyoming. Reston (VA, USA): US Department of the Interior, US Geological Survey. Open-File Report 2005-1183. 10.3133/ofr20051183

Kvaal SI, Solheim T, Bjerketvedt D. 1996. Evaluation of preparation, staining and microscopic techniques for counting incremental lines in cementum of human teeth. Biotechnic & Histochemistry 71(4):165–172. https://doi.org/10.3109/10520299609117155

Larson JS, Taber RD. 1980. Criteria of sex and age. In: Schemnitz SD, editor. Wildlife management techniques manual. Washington, DC: The Wildlife Society; p. 143–202

Laws RM. 1952. A new method of age determination for mammals. Nature 169(4310):972–973. https://doi.org/10.1038/169972b0

Leopold A. 1933. Game management. New York (NY, USA): Charles Scribner's Sons

Lieberman DE, Meadow RH. 1992. The biology of cementum increments (with an archaeological application). Mammal Review 22(2):57–77. https://doi.org/10.1111/j.1365-2907.1992.tb00120.x

Likhithaswamy HR, Madhushankari GS, Selvamani M, Mohan Kumar KP, Kokila G, Mahalakshmi S. 2022. Assessing the quality of long-term stored tissues in formalin and in paraffin-embedded blocks for histopathological analysis. Journal of Microscopy and Ultrastructure 10(1):23–29. https://pubmed.ncbi.nlm.nih.gov/35433260/

McLaughlin CR, Matula GJ, Cross RA, Halteman WH, Caron MA, Morris KI. 1990. Precision and accuracy of estimating age of Maine black bears by cementum annuli. Bears: Their Biology and Management 8:415–419. https://doi.org/10.2307/3872945

Marks SA, Erickson AW. 1966. Age determination in black bear. The Journal of Wildlife Management 30(2):389–410. https://doi.org/10.2307/3797827

Matson GM. 1981. Workbook for cementum analysis. Milltown (MT, USA): Matson's Laboratory

Matson G, Van Daele L, Goodwin E, Aumiller L, Reynolds H, Hristienko H. 1993. A laboratory manual for cementum age determination of Alaska brown bear first premolar teeth. Anchorage (AK, USA): Alaska Department of Fish and Game, Division of Wildlife Conservation

Matson's Laboratory. 2024. This is Matson's laboratory. Manhattan (MT, USA): Matson's Laboratory. [accessed 22 October 2024]. https://matsonslab.com/

Morris P. 1972. A review of mammalian age determination methods. Mammal Review 2(3):69–104. https://doi.org/10.1111/j.1365-2907.1972.tb00160.x

Naji S, Rendu W, Gourichon L. eds. 2022. Dental cementum in anthropology. Cambridge (UK): Cambridge University Press

Newman KB, Buckland ST, Morgan BJT, King R, Borchers DL, Cole DJ, Besbeas P, Gimenez O, Thomas L. 2014. Modelling population dynamics: model formulation, fitting and assessment using state-space methods. New York (NY, USA): Springer

Perrone V, Gocha TP, Randolph-Quinney P, Procopio N. 2022. Tooth cementum annulation: a literature review. Forensic Sciences 2(3):516–550 https://doi.org/10.3390/forensicsci2030038.

Development Core Team R. 2023. R: a language and environment for statistical computing. Version 4.3.2. Vienna (Austria): R Foundation for Statistical Computing. www.R-project.org

Robison WL, Bolen EG. 1989. Wildlife ecology and management. 2nd ed. New York, (NY, USA): Macmillan Publishing Company

Sauer PR, Free S, Browne S. 1966. Age determination in black bears from canine tooth sections. New York Fish and Game Journal 13:125–139

Severinghaus CW. 1949. Tooth development and wear as criteria of age in white-tailed deer. The Journal of Wildlife Management 13(2):195–216. https://doi.org/10.2307/3796089

Storm DJ, Samuel MD, Rolley RE, Beissel T, Richards BJ, Van Deelen TR. 2014. Estimating ages of white-tailed deer: age and sex patterns of error using tooth-wear-and-replacement and consistency of cementum annuli. Wildlife Society Bulletin 38(4):849–856. https://doi.org/10.1002/wsb.457

Takken Beijersbergen LM. 2019. Determining age and season of death by use of incremental lines in Norwegian reindeer tooth cementum. Environmental Archaeology 24(1):49–60. https://doi.org/10.1080/14614103.2017.1394625

Vandermeer JH, Goldberg DE. 2013. Population ecology: first principles. 2nd ed. Princeton, (NJ, USA): Princeton University Press

Willey CH. 1974. Aging black bears from first premolar tooth sections. The Journal of Wildlife Management 38(1):97–100. https://doi.org/10.2307/3800203

Ziegltrum GJ, Nolte DL. 2001. Black bear forest damage in Washington state, USA: economic, ecological, social aspects. Ursus 12:169–172. https://www.jstor.org/stable/3873245.