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## EVALUATING THE ACCURACY OF AGES OBTAINED BY TWO METHODS FOR MONTANA UNGULATES

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**Abstract:** We evaluated the accuracy of ages assigned by Matson's Laboratory from examination of annuli in the cementum of incisor root tips of 111 known-age Rocky Mountain elk (*Cervus elaphus*), 108 known-age mule deer (*Odocoileus hemionus*), and 74 known-age white-tailed deer (*Odocoileus virginianus*). Accuracy rates were 97.3% for elk through age 14, 92.6% for mule deer through age 14, and 85.1 % for white-tailed deer through 9 years old. There was no pattern of error relative to age. Accuracy for a sample of known-age mandibles aged by eruption–wear criteria was lower for mule deer (62.3%) and white-tailed deer (42.9%) than accuracy of ages in subsequent samples determined from cementum analysis of incisors. Accuracy of ages of elk assigned at check stations by eruption–wear criteria was >50% only for age classes 3 and 4, and averaged 16% for elk ≥5 years old. Ages assigned by eruption–wear criteria were not reliable for comparing physical measurements and population parameters by age among populations. Further, errors in ages assigned by eruption–wear in one age class were not equally balanced by offsetting errors in assigned ages among other age classes. This resulted in inaccurate estimates of population age structure when ages were assigned by eruption–wear criteria. The accuracy provided by the cementum annuli method is necessary to determine whether various physical and population parameters change significantly with age of the animal.

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**Key words:** aging, annuli, *Cervus elaphus*, dental cementum, eruption–wear, incisor, Montana, mule deer, *Odocoileus hemionus*, *Odocoileus virginianus*, Rocky Mountain elk, white-tailed deer.

Wildlife scientists have long required knowledge of the age of wild ungulates to answer research questions and improve management. Early advances included assignment of age based on tooth replacement and wear for white-

tailed deer (Severinghaus 1949), mule deer (Robinette et al. 1957), and elk (Quimby and Gaab 1957). Tooth replacement patterns appeared to accurately age these species through 2 years of age, and wear patterns seemed generally correlated with age. However, all authors cautioned that reduced accuracy might be expected for older animals because of individual variation

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in wear pattern, and variation in experience and interest of biologists. Some believed that compensation among individual errors might result in valid distributions of age estimates for an entire sample, especially if only broad age categories were necessary. An example of compensation is when the number of 3-year olds erroneously assigned to other ages is exactly matched by the number of other age animals erroneously assigned an age of 3 years. Thus, although some individual age assignments are in error, the total number of 3-year olds estimated exactly matches the true total for the sample. However, subsequent studies indicated that compensation might not occur because of a tendency to consistently over age young animals and under age older animals by the wear technique (Ryel et al. 1961, Lockard 1972, Cook and Hart 1979, DeYoung 1989). For some purposes, use of broad age categories was not acceptable, and more reliable aging of older ungulates was desired.

Following the pioneering work of Scheffer (1950) and Laws (1952) on aging marine mammals, Low and Cowan (1963) and Gilbert (1966) established that annual rings in the cementum of root tips of incisors of mule deer and white-tailed deer were related to age, at least for deer in northern North America. Evaluation of this technique generally confirmed the accuracy of counting annuli in dental cementum of incisor root tips to age ungulates (Reimers and Nordby 1968, Erickson and Seliger 1969, Keiss 1969, Lockard 1972, and Thomas and Bandy 1973). However, some investigators found the technique inaccurate south of 36°N latitude (Brox 1972, Hackett et al. 1979) in other geographic areas where distinct annuli were not found (Connelly et al. 1969), or for some species such as moose (*Alces alces*; Gasaway et al. 1978). Lockard (1972) found that incisors from states in the southern United States were more difficult to prepare to properly show annuli, but all known-age deer were aged correctly. Jacobsen and Reiner (1989) found that 71% of 76 known-age Mississippi white-tailed deer were aged correctly.

There were common problems with these early evaluations. Sample sizes of known-age animals were small, generally <75, with most <25. When data were presented for which we could determine composition of the known-age samples, the majority of these small samples were fawns, yearlings, and 2-year olds, those

most likely to be aged correctly by sequence of tooth eruption. Although these investigators were experienced in the technique relative to the time, experience with known-age material was limited to the small samples reported and usually to <200 incisors. An effort was probably made to avoid bias, but with such small samples, investigators who assigned ages to their own samples would have been aware of the range and general composition of the known-age sample. This could, at least subconsciously, bias error toward a lesser magnitude (e.g., the investigator might know that all samples were between 1 and 5 yr old). Also, preparation and processing techniques varied among researchers, possibly affecting results.

Little evaluation has occurred since, possibly because there is a lack of known-age material (Dapson 1980). Today, without further experimental evaluation, aging of ungulates by counts of annuli in root tips of incisors seems to be an accepted technique that few question. Also, recent articles in scientific journals routinely refer to extracting teeth for aging but do not describe the process or mention who assigned ages. Thus, readers have no knowledge about the experience of the person assigning ages or the reliability of the results. Only articles that dealt specifically with technique, such as Harshyne et al. (1998), discussed process and mentioned who aged the teeth. Currently, few researchers report that they process and age incisors themselves or in-house. Based on the number of incisors processed, it appears that Matson's Laboratory, Milltown, Montana processes and ages most incisors collected in North America. Through October 1984, Matson's Laboratory had processed incisors from 10,600 mule deer, 20,333 white-tailed deer, and 13,552 elk. By May 1998 they had processed incisors from 51,838 mule deer, 84,859 white-tailed deer, and 74,420 elk (Matson's Laboratory website, <http://www.matsonslab.com/index.htm>). Clearly, the level of experience for this Laboratory is far beyond that of researchers reporting initial evaluations and of individual researchers today. Despite widespread use of this Laboratory, experimental evaluations of their accuracy for ungulate ages have not been attempted.

We captured and marked many deer and elk in Montana since 1972. As these animals died from hunter harvest or natural causes, mandibles of known age became available, and we accumulated substantial samples. Our objectives

were to (1) use our samples to evaluate accuracy of ages of Montana elk, mule deer, and white-tailed deer obtained from dental cementum annuli of incisors processed and aged by Matson's Laboratory; and (2) compare age structures generated by the cementum annuli method and eruption-wear criteria. These evaluations will establish reliability ratings or confidence levels for these methods of age determination. Some ecological analyses require accuracy to year for individual age assignments. Compensating errors in aging by any method, if they occur, may provide reliable sample age structures for some management purposes.

## METHODS

During 1972–97, we captured and marked for individual identification a total of 2,343 mule deer, 1,749 white-tailed deer, and 1,314 Rocky Mountain elk on research study areas in Montana. At capture, we aged these animals by both morphological characteristics and tooth eruption and wear patterns (Severinghaus 1949, Robinette *et al.* 1957, Quimby and Gaab 1957). We considered those captured as newborns, at 7–10 months old, and at 19–22 months old (yearlings) as known-age animals.

We collected mandibles and/or incisors (I1 or rarely I2) from most deer and elk (marked and unmarked) killed by hunters or found dead from various other causes during our studies. When we sent incisors to the Laboratory, we informed them when I2 was collected as the sample. We tried to obtain the entire mandible from marked animals >2 years old at check stations and during field checks. We extracted incisors from all animals >2 years old, assigned an identification (ID) number, and inserted the incisors into a small, labeled paper envelope. We assigned ID numbers in the order of collection; therefore specimens from known-age individuals were randomly scattered throughout collections from each study area. For some areas, all incisors from known-age animals were included in collections to be aged. For other areas, only a randomly-selected sample of incisors from known-age 1- and 2-year-old animals was included in collections. Once or twice per year each biologist sent these collections of incisors to Matson's Laboratory. Other information provided to the Laboratory included species and month or season of death.

Matson's Laboratory processed the incisors by decalcifying in a weak acid solution, rinsing

in water, dehydrating in isopropyl alcohol, clearing in toluene, and embedding in Paraplast (Oxford Division of Sherwood Medical, Saint Louis, Missouri, USA). They sectioned the embedded teeth at a 14- $\mu$ m thickness using a Leica Model SP9000 rotary microtome. They mounted these sections on microscope slides, stained them with Giemsa blood stain (Ricca Chemical Company, Arlington, Texas, USA), and applied a coverglass using Hypermount resin (Shandon, Pittsburgh, Pennsylvania, USA). G. M. Matson conducted all aging by examining the stained sections and counting annuli using a Leitz compound brightfield microscope at 50 $\times$  to 200 $\times$  magnifications. In addition to age, Matson's Laboratory reported a letter certainty code for each specimen: A = result nearly certain, B = error possible, and C = error probable.

In 1985, we assembled 53 known-age mule deer mandibles and 21 known-age white-tailed deer mandibles, and assigned random numbers to each. Four biologists from Montana and 2 from Washington considered to be experienced in aging deer used eruption-wear criteria to age these mandibles, knowing species, but not known-age. They recorded their estimate of age on a form by assigned number of the mandible. We compared ages estimated by eruption-wear to known ages. Because each mandible was aged by each biologist, 318 and 126 ages were estimated for mule deer and white-tailed deer, respectively.

To reduce cost and because we believed that tooth eruption pattern and lack of wear on permanent teeth were adequate criteria to age elk  $\leq 2$  years old at hunter check stations, we obtained age by the cementum annuli method only for elk  $\geq 3$  years old. At least 1 of the 2 people who worked at each of 3 check stations was considered experienced in aging elk by the eruption-wear technique. Of the elk aged by check station personnel by eruption-wear criteria during 1989–96, we used the 556 female elk for which the cementum annuli age was determined to be  $\geq 3$  years old for comparisons. For our purposes, we assumed that ages assigned by cementum annuli analysis were correct. We compared those ages, both individually and as a sample age structure, to ages originally assigned under check station conditions based on the eruption-wear technique. We compared age distributions and proportions by use of chi-Square tests in STATISTICA (StatSoft 1997).

## RESULTS

### Accuracy of Ages Determined by Annuli

We did not find differences in accuracy rates for ages determined by counting annuli in root tips of incisors between geographic areas in Montana for elk ( $\chi^2_1 = 0.00$ ,  $P = 0.95$ ), mule deer ( $\chi^2_1 = 1.44$ ,  $P = 0.23$ ), or white-tailed deer ( $\chi^2_1 = 0.04$ ,  $P = 0.85$ ). Therefore, we combined samples by species (Table 1). Cementum annuli patterns of male elk and deer are often simpler and more distinct than those of females (G. M. Matson, personal communication). However, we did not find differences between the sexes in accuracy rate for ages determined by cementum annuli for elk ( $\chi^2_1 = 0.21$ ,  $P = 0.65$ ), mule deer ( $\chi^2_1 = 0.56$ ,  $P = 0.45$ ), or white-tailed deer ( $\chi^2_1 = 0.05$ ,  $P = 0.82$ ). We also combined the samples by sex for each species.

The 111 known-age elk ranged from 2–14 years old; individuals  $\geq 3$  years old made up 91.9% of the sample (Table 1). Accuracy of ages determined by counting annuli in root tips of incisors was 97.3% (Table 1). Additionally, second incisors from 2 elk, age 3 and 8, were correctly aged. All 3 errors were within 1 year of the known age. There was no pattern of increased error relative to age.

Known-age mule deer ranged from 1–14 years old; 73.2% of the sample of 108 was  $\geq 3$  years old (Table 1). Accuracy of ages determined by counting annuli was 92.6% for mule deer (Table 1). All 8 errors were within 1 year of the known-age (Table 1) and there was no pattern of increased error relative to age.

The 74 known-age white-tailed deer ranged from 1–9 years old; individuals  $\geq 3$  years old comprised 52.7% of the sample (Table 1). Accuracy of ages assigned by use of cementum annuli was 85.1% (Table 1). Two ages assigned were in error by 2 years. A 1-year-old deer was called 3B, and a 5-year-old deer was called 3A. Proportionately more errors may have occurred in white-tailed deer  $\geq 5$  years old (4 of 12) than those  $< 5$  years old (7 of 62), but the difference was not significant for this sample ( $\chi^2_1 = 2.54$ ,  $P = 0.11$ ).

Fewer errors were made for elk than white-tailed deer ( $\chi^2_1 = 9.39$ ,  $P = 0.002$ ). Error rates for elk and mule deer ( $\chi^2_1 = 2.54$ ,  $P = 0.11$ ) and mule deer and white-tailed deer ( $\chi^2_1 = 2.61$ ,  $P = 0.11$ ) were not significantly different.

### Comparison of Eruption–Wear and Cementum Annuli Methods

For the samples tested, 198 of 318 (62.3%) ages for mule deer and 54 of 126 (42.9%) ages for white-tailed deer were estimated correctly by eruption–wear criteria (Table 2). This accuracy was substantially lower than recorded for samples aged by the cementum annuli technique (Table 1). Accuracy of ages assigned by eruption–wear was significantly different between species ( $\chi^2_1 = 13.85$ ,  $P < 0.001$ ) and decreased with age for both mule and white-tailed deer (Table 2). For mule deer, 2- and 3-year olds tended to be over aged, and those  $\geq 4$  years old were under aged. All white-tailed deer except 5-year olds tended to be over aged. The accuracy for individual biologists ranged from 29–38 of 53 (54.7–71.7%) ages correct for mule deer, and 5–14 of 21 (23.8–66.7%) ages correct for white-tailed deer. Errors in ages assigned by eruption–wear were as much as 3 and 4 years for mule deer and white-tailed deer, respectively. An even greater opportunity for error with the eruption–wear technique may have occurred if known-age animals older than 7 years had been available at the time of this test.

Given the results presented earlier (Table 1), we assumed that ages assigned to elk by Matson's Laboratory were the correct ages for purposes of the following comparisons. When we combined all ages  $\geq 13$  years old into 1 age category, the distribution of ages that check station personnel assigned to elk by use of the eruption–wear technique was different ( $\chi^2_{10} = 59.84$ ,  $P < 0.001$ ) than the distribution of ages assigned by use of cementum annuli (Table 3). The percentage of ages assigned by eruption–wear criteria that was correct (the same as annuli ages) exceeded 50% only for 3- and 4-year-old elk (Table 4). None of 19 9-year-old and only 1 of 41 7-year-old elk was correctly aged by eruption–wear criteria at check stations (Table 3). On average, the eruption–wear technique over aged 3- and 4-year-old elk and under aged elk  $\geq 6$  years of age (Table 3 and 4). The distribution of ages assigned by eruption–wear criteria within any age class was wide, however. Ages assigned by eruption–wear criteria were in error by up to 3 years even for 3-year-old elk and by up to 8 years for 16- and 18-year-old elk (Table 3).

For some management purposes, grouping of ages into broader categories may be sufficient.

Table 1. Age assigned by use of cementum annuli of incisors for known-age Rocky Mountain elk, mule deer, and white-tailed deer in Montana.

Known age	Age assigned by annuli								
	Elk			Mule deer			White-tailed deer		
	Total no.	No. correct	No. errors <sup>a</sup>	Total no.	No. correct	No. errors	Total no.	No. correct	No. errors
1				7	7	0	1	0	1 <sup>b</sup>
2	9	9	0	22	20	2 <sup>c</sup>	34	31	3 <sup>d</sup>
3	26	24	2 <sup>e</sup>	32	30	2 <sup>f</sup>	18	16	2 <sup>g</sup>
4	25	25	0	16	16	0	9	8	1 <sup>h</sup>
5	13	13	0	14	12	2 <sup>i</sup>	4	2	2 <sup>j</sup>
6	14	13	1 <sup>k</sup>	9	7	2 <sup>l</sup>	5	5	0
7	13	13	0	3	3	0	1	0	1 <sup>m</sup>
8	5	5	0	1	1	0	1	1	0
9	1	1	0				1	0	1 <sup>n</sup>
10									
11	1	1	0						
12	1	1	0	2	2	0			
13	2	2	0	1	1	0			
14	1	1	0	1	1	0			
Total	111	108	3	108	100	8	74	63	11
% Correct		97.3			92.6			85.1	

<sup>a</sup> Errors footnoted as: annuli age and certainty level (A = result nearly certain, B = error possible, and C = error probable).

<sup>b</sup> 3B.

<sup>c</sup> 1B, 3C.

<sup>d</sup> 3B, 3B, 3B.

<sup>e</sup> 4A, 2A.

<sup>f</sup> 2A, 2A.

<sup>g</sup> 2A, 4A.

<sup>h</sup> 5A.

<sup>i</sup> 4A, 6A.

<sup>j</sup> 3A, 4A.

<sup>k</sup> 5A.

<sup>l</sup> 7B, 7B.

<sup>m</sup> 8B.

<sup>n</sup> 8A.

However, we also found significant differences in age distributions between eruption-wear and cementum annuli techniques when the sample of elk was grouped as 3-4, 5-6, 7-8, 9-10, 11-12, and ≥13-year-old categories ( $\chi^2_5 = 20.67, P < 0.001$ ). Similarly, differences were significant when the oldest category was grouped as ≥11 years old ( $\chi^2_4 = 20.65, P = 0.004$ ) and as ≥9 years old ( $\chi^2_3 = 19.75, P < 0.001$ ). The major contributions to differences for all combined age category tests were that the 5-6-year-old category was over represented, and the oldest category was under represented by eruption-wear ages compared to ages assigned by cementum annuli. Combination of the 3- and 4-year-old classes did result in compensation of errors such that the proportion of that combined category was the same for both aging techniques.

## DISCUSSION

We established accuracy levels for age of Montana elk, mule deer, and white-tailed deer

determined by Matson's Laboratory from examination of cementum annuli of incisor root tips. We believe the accuracy levels observed were sufficient to allow comparisons of physical measurements and population data among age classes. For example, we would be comfortable using cementum annuli based ages to compare reproductive and mortality rates, or antler length and weight by age among different elk populations in Montana. Similarly, the accuracy rate we observed would allow estimation of survival rates with age-structure data (Udevitz and Ballachey 1998). Accuracy of the level we observed is also necessary to compare effectiveness of different harvest strategies for producing older male elk and deer.

We did not find differences in accuracy within species for different areas in Montana. Based on literature cited earlier, however, differences likely occurred among broader geographic areas. A proportional increase in sample size of 65% would have resulted in differences in accuracy among all 3 species at  $P < 0.05$ . Thus,

Table 2. Eruption–wear (E-W) ages assigned by 6 biologists to known-age mule deer and white-tailed deer mandibles from Montana.

Species	E-W Age	Known age						
		1	2	3	4	5	6	7
Mule Deer	1	12	6					
	2		90	10	4			
	3		11	45	16	2		
	4		1	11	27	20	4	
	5				7	17	5	3
	6					12	6	2
	7					1	2	1
	8					2	1	
<i>n</i>		2	18	11	9	9	3	1
Total ages <sup>a</sup>		12	108	66	54	54	18	6
% correct		100.0	83.3	68.2	50.0	31.5	33.3	16.7
% ±1 year		100.0	99.1	100.0	92.6	90.7	72.2	50.0
Mean E-W age		1.00	2.06	3.02	3.69	4.93	5.50	5.67
White-tailed deer	1							
	2		28	4				
	3		22	19				
	4		4	11	2	2		
	5			5	4	4	1	1
	6			3	4		1	1
	7				2		2	
	8						1	2
	9							1
	10						1	1
<i>n</i>			9	7	2	1	1	1
Total ages <sup>a</sup>			54	42	12	6	6	6
% Correct			51.9	45.2	16.7	66.7	16.7	0.0
% ±1 year			92.6	81.0	50.0	100.0	66.7	50.0
Mean E-W age			2.56	3.62	5.50	4.67	7.17	7.67

<sup>a</sup> Total ages = number of individual mandibles × 6 (biologists).

accuracy of ages determined by cementum annuli may vary among the 3 species, but we have no explanation for that variation. Rocky Mountain elk apparently have the most distinct and least complex cementum annuli of the 3 species we studied in Montana. This was also true when Montana elk were compared to elk from other geographic areas (G. M. Matson, personal communication). Because the complexity of cementum annuli varies among species and locations (G. M. Matson, personal communication), we encourage others to publish their results to broaden the scope of accuracy parameters in the literature.

Our data indicated that ages determined by eruption–wear criteria tended to be overestimates for younger animals and underestimates for older animals. Thus, not only were ages determined by eruption–wear criteria unreliable for comparison of physical and population data among age classes ≥3 years old, they also did not provide an accurate estimate of age structure and relative cohort importance for popu-

lation modeling. For elk, the relative importance of 3- and 4-year-old cohorts was not the same for eruption–wear and cementum annuli (Table 3). If this were a single year sample, use of eruption–wear ages would lead to the erroneous conclusion that the 3-year-old cohort was smaller than the 4-year-old cohort. When the 3- and 4-year classes were combined, errors in aging did compensate for that category, but not for the 5- and 6-year-old and oldest categories. Errors in age were too few to speculate whether compensation might occur for the cementum annuli method.

The inaccuracy of ages assigned by eruption–wear criteria and the lack of compensation are important considerations for even relatively simple tests of management practices. For example, to accurately answer whether hunting season B resulted in a greater proportion of males ≥4 years old in the harvest than hunting season A would require that ages were determined by the cementum annuli method. However, the extra expense of obtaining age by the

Table 3. Distribution of ages for female Rocky Mountain elk determined by cementum annuli to be  $\geq 3$  years old compared with distribution of ages assigned by use of eruption-wear (E-W) criteria at check stations in the Gravelly-Snowcrest Mountains of Montana.

Age assigned by E-W	Age assigned by annuli																	Total	a (%)
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19		
3	90	15	5		1	1												112	(20.1)
4	50	63	28	11	6	1												159	(28.6)
5	14	22	23	21	10	5	2											97	(17.5)
6	1	10	15	10	16	7	4	2	2									67	(12.1)
7		3	7	9	1	1	4	4	1	1	1							32	(5.8)
8			1	2	6	6	7	2	6	2	1			1				34	(6.1)
9				1				3	1	4	1							10	(1.8)
10				1	1	2		2	3	2	2		1	1		1		16	(2.9)
11						1	2	2					1	1				6	(1.1)
12								1	1	3		1	1					9	(1.6)
13												1						2	
14														1				1	
15										1				3	1			5	
16														1				1	
17																			(2.5) <sup>b</sup>
18																1		1	
19													1		1			1	
20															1			2	
21																			
22														1				1	
Total <sup>c</sup>	155	113	79	55	41	24	19	16	14	13	5	2	5	6	3	4	2	556	(100)
% <sup>c</sup>	27.9	20.3	14.2	9.9	7.4	4.3	3.4	2.9	2.5	2.3				(4.9) <sup>d</sup>					

<sup>a</sup> Total number (%) of elk assigned to each age class by the eruption-wear technique.

<sup>b</sup> Percent of elk  $\geq 13$  years old as assigned by the eruption-wear technique.

<sup>c</sup> Total number and % of elk assigned to each age class by annuli of incisors.

<sup>d</sup> Percent of elk  $\geq 13$  years old as assigned by annuli of incisors.

Table 4. Eruption-wear (E-W) ages for female Rocky Mountain elk assigned at check stations in the Gravelly-Snowcrest Mountains compared to ages assigned by incisor annuli (assumed correct).

Age assigned by incisor annuli	% E-W ages same as incisor ages	% E-W ages within 1 year of incisor ages	Mean E-W age
3 <sup>a</sup>	58.1	90.3	3.52
4	55.8	88.5	4.32
5	29.1	83.5	4.92
6	18.2	72.7	5.58
7	2.4	56.1	5.80
8	25.0	29.2	6.67
9	0.0	36.8	7.37
10	12.5	43.8	8.56
11	0.0	28.6	8.43
12	23.1	23.1	10.00
13	0.0	0.0	8.80
14	0.0	0.0	11.00
15	0.0	0.0	13.20
16	16.7	66.7	15.17
17	0.0	0.0	16.00
18	25.0	50.0	14.75
19	0.0	0.0	13.00

<sup>a</sup> Sample sizes in Table 3.

cementum annuli method would not be warranted if a question concerned only fawn, yearling, 2-year-old, and  $\geq 3$ -year-old age categories.

Possible reasons for the degree of error observed in assignment of age to elk by eruption-wear criteria included: (1) the mandibles were examined under less than ideal conditions that included a variety of inclement weather and a sense of pressure from impatient hunters, (2) most check station personnel were volunteering their time and may not have been as conscientious as desirable, (3) individual differences among elk in wear patterns were evident and appeared to increase with age, and (4) training of personnel and example jawboards were based primarily on elk associated with Yellowstone National Park (Quimby and Gaab 1957) and those wear patterns may have differed from elk in other parts of Montana.

The error rate for ages of white-tailed deer determined by eruption-wear was higher than for mule deer, and white-tailed deer were consistently aged older than mule deer (Table 2). This may have occurred because the biologists participating in the experiment were most experienced at assigning ages to mule deer. A predominant mental visual model based on mule deer (Robinette et al. 1957) would tend to over age white-tailed deer (Severinghaus 1949) because most mandibular teeth erupt earlier in whitetails than mule deer.

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