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Research Article

Evaluating Precision of Cementum Annuli Analysis for Aging Mule Deer from Southern California

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ABSTRACT We evaluated the precision of age estimates produced by cementum annuli analysis (CAA) of blind-duplicate specimens taken from 994 southern mule deer (*Odocoileus hemionus*) collected over 15 years. We found that the mean annual proportion of unreliably aged incisor pairs was greater for females (0.48, SD = 0.13) than for males (0.22, SD = 0.07). Most of the 308 unreliably aged tooth pairs disagreed by only 1 year. Sex, precipitation, and certainty codes assigned by Matson's Lab to the age estimates were the best predictors for agreement of estimated ages within incisor pairs. Our estimated overall age error rate of CAA (17%) was >2 times as large as estimated error rates from Montana and South Dakota, but less than half of error rates estimated for Mississippi and south Texas. Knowing the error rate of age estimates from a specific deer population allows wildlife managers to perform tasks requiring specific age class information such as monitoring the harvest rate of older female deer in a hunted population or performing population reconstruction. © 2011 The Wildlife Society.

KEY WORDS accuracy, cementum annuli analysis, mule deer, *Odocoileus hemionus*, precision, southern California.

Leopold (1933) and Caughley (1977) noted the value of age structure information for managing wildlife populations. Age data pooled into broad categories will suffice for many management decisions; however, some population analysis techniques require more specific age data. For example, population reconstruction using maximum-likelihood estimation allows managers to estimate herd abundance using harvest information, but the method requires year-specific age data (Gove et al. 2002, Skalski et al. 2007). Additionally, biologists can monitor the proportional harvest of older female deer (e.g., >3.5 yr) to prevent overexploitation (Caughley 1976).

Biologists most often estimate the age of deer by using tooth eruption, tooth wear, or cementum annuli analysis (CAA). Yet, reliably measuring age estimates using dentition is challenging (Caughley 1977). Previous investigations showed that tooth eruption can accurately age deer ≤1.5 years and that tooth wear was inaccurate for estimating ages of adult deer (>1.5 yr, Hamlin et al. 2000, Gee et al. 2002). Biologists use CAA for estimating year-specific ages of adult deer (Low and Cowan 1963, Hamlin et al. 2000). In deer teeth cementum annuli develop in the root tip with wide, light colored bands corresponding to fast growth and narrow, dark bands indicating slowed growth (Low and Cowan 1963). Formation of an annulus results from metabolic stressors that start and stop throughout the year. Metabolic stressors include seasonal changes in forage nutrition, changes in forage from deer density, and life history events such as the rut, late gestation, and lactation (Low and Cowan 1963, Lockard 1972, Hackett et al. 1979, DeYoung 1989, McCullough 1996).

The timing of the rut and parturition synchronize well with seasonal patterns of food abundance and quality for deer in northern parts of their geographic ranges (Bowyer 1991). In northern climates, CAA accurately estimates year-specific ages of adult deer (Low and Cowan 1963, Hamlin et al. 2000); however, CAA likely performs worse on deer in southern regions because rutting and parturition do not synchronize well to environmental conditions (Marchinton and Miller 1994). Environmental conditions in southern regions should cause increased variation in the timing of metabolic stressors among individual deer, and in turn, produce more variation in annuli patterns. Sectioned teeth of white-tailed deer (*Odocoileus virginianus*) from Venezuela and other populations in the southeastern United States contained cementum annuli that were difficult to interpret because the annuli often merged together and were poorly defined (Brokx 1972, Lockard 1972, Hackett et al. 1979, DeYoung 1989). Jacobson and Reiner (1989) noted that deer in Mississippi endure 2 nutritional stress periods (summer and winter) that could cause added variation in the annuli patterns.

Van Deelen et al. (2000) found a difference in tooth wear between white-tailed males and females while evaluating the

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tooth wear-replacement aging technique. Those authors also noted a previous lack of effort to evaluate sex-specific differences for the wear-replacement aging technique in deer. Given the differences in behavior and foraging between males and females, sex-specific stresses may produce different rates of cementum deposition that will in turn produce a sex bias in age estimates (Weckerly 1993).

The method of evaluation used to assess inaccuracies in age estimates can affect results (Brokx 1972, Lockard 1972, Hackett et al. 1979, Hamlin et al. 2000, Gee et al. 2002). Evaluations of observers who know about the evaluation can produce biased results. Age estimation using cementum analysis requires careful observation and subjective interpretation; therefore, age estimates may differ when observers know someone is evaluating them.

Our objective was to measure the precision of age estimation using CAA for incisors extracted from southern mule deer. We also investigated the relationships between that precision and the following variables: confidence of age estimates supplied by Matson's Lab, sex, and annual precipitation. Precipitation was our proxy of forage nutrition; in years with greater precipitation, nutritious forage should be more available than in years with less precipitation (Heffelfinger 2006).

STUDY AREA

Marine Corps Base Camp Pendleton (base) occupied 506 km^2 located in north-coastal San Diego County, California. The region had a Mediterranean climate characterized by hot dry summers and cool rainy winters with a historic average annual rainfall of 25.4 cm. Typical mean monthly temperatures ranged from 14° C in January to 22° C in August (Isla and Lee 2006). Vegetation communities frequently used by mule deer on base included coastal sage scrub, chaparral, oak (*Quercus* sp.) woodlands, riparian scrub, and riparian forest. Plants in those communities commonly eaten by deer included white sage (*Salvia apiana*), California sagebrush (*Artemisia californica*), laurel sumac (*Malosma laurina*), lemonade berry (*Rhus integrifolia*), chamise (*Adenostoma fasiculatum*), black sage (*S. melifera*), coast live oak (*Quercus agrifolia*), Engelman oak (*Q. engelmanii*), coyote brush (*Baccharis pilularis*), mule fat (*B. salicifolia*), poison oak (*Toxicodendron diversilobum*), arroyo willow (*Salix lasiolepis*), and black willow (*S. gooddingii*; Pious 1989). The Pacific Ocean formed the southwestern boundary of the base that transitioned through coastal terrace and then into coastal mountains on the northeastern edge of the property reaching approximately 800 m above sea level.

METHODS

Base biological staff collected incisor pairs from adult animals ($\geq$2.5 yr) taken through the base's deer hunting program between 1985 and 1999. During those years the deer hunting season on base extended from late August until December. Matson's Lab, Milltown, Montana provided age estimates for blind-duplicate samples of lower incisor (I1) pairs collected from harvested mule deer. For consistency we measured precision as the proportion of incisor pairs (i.e., 2 lower incisors from the same animal) with different age estimates and we measured the amount of that disagreement in years for each sex.

Matson estimated the age for all teeth in all years and he was not aware of the duplicate teeth submitted for processing. We assigned different sample identification numbers to duplicate incisors from the same animal so that laboratory technicians could not identify teeth from the same animal. A number key served to reunite age estimates from incisor pairs for comparison. We classified a deer as unreliably aged if its incisors received different age estimates. Certainty codes issued by Matson's Lab with each age estimate subjectively described the amount of confidence in the accuracy of the estimate. Matson's Lab defines the certainty codes as follows: (A) "Cementum characteristics very nearly match those of the standardized aging model for the species and tooth type;" (B) "Histological evidence supports the result and the correct age is expected to be within the range given;" (C) "The match between histological evidence and the standardized model is poor. Error is likely, and may occur within the range given" (G. Matson, Matson's Lab, unpublished report). We excluded tooth pairs if $\geq$1 age estimate was <2.5 years. The first incisor is the standard tooth for cementum age analysis in mule deer. Tooth pairs came less often from males with trophy antlers relative to their harvest frequency because hunters were more likely to deny tooth extraction from an animal worthy of taxidermy.

Marine Corps Air Station at Camp Pendleton provided monthly precipitation (cm) data. We measured cumulative precipitation for each year. We summed monthly precipitation for the 2 previous years because every deer in our data set was probably alive then. The precipitation year extended from October to September to accommodate when hunts occurred at Camp Pendleton.

For all analyses we used R (R version 2.11.1, www.r-project.org, accessed 20 Jan 2011). We first tested whether agreement in age estimates of incisor pairs varied across years and between sexes. A response variable code of zero indicated that the incisor pairs disagreed in age estimates and a code of 1 indicated the incisor pairs agreed in age estimates. The logistic regression analysis had categorical predictors for year, sex, and a year × sex interaction (Glantz and Slinker 1990). Likelihood ratio tests on the change in deviance determined whether there were effects due to predictors (Glantz and Slinker 1990).

We conducted an information-theoretic model selection analysis to assess the influence of year, sex, certainty codes, and cumulative precipitation on agreement of age estimates in pairs of incisors (Burnham and Anderson 2002). For this analysis we excluded data from 1986 because the certainty codes for incisor pairs with agreeing age estimates were not available. This data set ($n = 896$) had 352 incisor pairs with certainty codes of AA, 272 incisor pairs with certainty codes of BB, 274 incisor pairs with certainty codes of AB (1 incisor assigned A, the other incisor assigned B), 22 incisor pairs with certainty codes of BC, and only 3 incisor pairs scored as AC or CC. We created categorical variables (0 or 1) for AA, BB, AB, and BC to assess the influence of these combinations of certainty codes on agreement of incisor pairs in age estimates. It was plausible that no distinction existed between AA and BB or AA and AB on agreement of age estimates because histological evidence supported the estimated age for samples that received either an A or B code. In contrast, the histological evidence did not support the age estimates well for tooth samples that received a C confidence code. Consequently, we created 2 additional categorical variables of AABB and AAAB. For AABB we coded an incisor pair as 1 if the certainty codes were AA or BB (0 otherwise) and for AAAB we coded an incisor pair as 1 if the certainty codes were AA or AB. For each logistic regression model considered we calculated Akaike Information Criterion corrected for small sample size (AIC_c) and Akaike weights. We selected the model with the highest Akaike weight. For the selected model we compared observed number of pairs of incisors that agreed in age estimates to the expected number of agreed pairs as predicted by the selected model via a chi-square goodness-of-fit test (Agresti 1996). For this test we used the residual degrees of freedom, the number of predicted values minus the number of parameters estimated by the selected model.

Table 2. Frequency of certainty codes assigned by Matson's Lab during cementum annuli analysis for estimated ages of individual lower incisors removed from 921 mule deer, Camp Pendleton, California, 1985–1999.

	Certainty codes[a] by sex					
	M			F		
Estimated age (yr)	A	B	C	A	B	C
2.5	321	188	2	156	166	2
3.5	148	113	2	61	115	4
4.5	42	47	2	41	76	3
5.5	27	21	2	23	42	2
6.5	23	13	1	22	46	5
7.5	5	6	0	10	28	2
8.5	3	1	0	10	15	0
9.5	3	1	0	8	2	0
10.5	3	0	0	17	0	0
11.5	0	0	0	4	1	0
≥12.5	0	0	0	7	0	0
Total	575	390	9	359	491	18

[a] Certainty codes of age estimates assigned during cementum annuli analysis defined by Matson's Lab as: A indicates Cementum characteristics very nearly match those of the standardized aging model for the species and tooth type. B indicates histological evidence supports the result and the correct age is expected to be within the range given. C indicates the match between histological evidence and the standardized model is poor. Error is likely (G. Matson, personal communication).

RESULTS

Base biological staff removed incisor pairs from 994 mule deer (545 M and 449 F) for age analysis between 1985 and 1999. Across all years, 308 incisor pairs (31%) had age estimates that disagreed. Of those pairs, 95% disagreed by ≤3 years; 240 differed by 1 year in age estimates, 38 differed by 2 years, and 15 differed by 3 years. The greatest disagreement in age estimates was 6 years in 4 incisor pairs. The mean annual proportions of incisor pairs that disagreed in age estimates were 0.22 (SD = 0.07) for males and 0.48 (SD = 0.13) for females (Table 1). Females received proportionally more age estimates with confidence codes of B or C than males (59% and 41% for females and males, respectively), indicating that Matson encountered more difficulty estimating ages of females in the sample (Table 2). The logistic regression analysis did not indicate a substantial drop in deviance from year ($\chi_{14}^2 = 17.26$, $P = 0.243$); although, the analysis did show substantial drop in deviance due to sex ($\chi_1^2 = 67.1$, $P < 0.001$), and the difference between the sexes in proportion of incisor pairs that disagreed in age estimates was inconsistent across years ($\chi_{14}^2 = 23.0$, $P = 0.060$).

Table 1. Annual proportions of unreliably aged incisor pairs by sex for teeth collected from mule deer on Camp Pendleton, CA, 1985–1999.

	Sample size		Proportion of unreliably aged incisor pairs	
Year	M	F	M	F
1985	86	24	0.23	0.42
1986	57	34	0.18	0.44
1987	64	31	0.23	0.35
1988	43	51	0.26	0.53
1989	43	54	0.21	0.48
1990	19	46	0.32	0.30
1991	29	31	0.21	0.48
1992	23	24	0.13	0.79
1993	16	18	0.13	0.50
1994	29	21	0.17	0.43
1995	14	19	0.36	0.32
1996	27	27	0.30	0.67
1997	26	25	0.31	0.44
1998	30	23	0.13	0.61
1999	28	25	0.21	0.44

We built 9 models for the data set that included age estimates for 896 incisor pairs collected from 1985 and 1987–1999. These models considered the influence on agreement in age estimates of incisor pairs from year and sex; certainty codes and sex; and certainty codes, sex, and cumulative precipitation (Table 3). The model with predictors of AA, BC, sex, and precipitation had the lowest AIC_c value. We selected that model because its Akaike weight indicated that it was 9.3 times more likely to fit the data than the model with the next highest Akaike weight. Moreover, the model provided a reasonable fit to the data ($\chi_{14}^2 = 8.8$, $P = 0.460$). Parameter estimates for the selected model indicated an increase in the log odds of age estimates agreeing when the certainty codes were AA and the incisor pairs were from males. Similarly, the log odds that age estimates would match declined for incisor pairs assigned certainty codes of BC and in years with higher precipitation (Table 4). To express these patterns intuitively we back transformed predicted values to proportions and plotted the relationships across the range of cumulative precipitations for males and females when certainty codes were AA and BC (Fig. 1). The annual proportion of incisor pairs with age estimates that agreed ranged from 0.92 to 0.84 for males with certainty codes of AA. Mean 2-year cumulative precipitation during the study period was 68.3 (SD = 23.2) cm. The proportion of incisor pairs from females with agreeing age estimates and certainty

Table 3. Logistic regression models we considered and findings from model selection analysis for agreement in age estimates of pairs of incisors extracted from mule deer, Camp Pendleton, California, 1985, 1987–1999. We report the Akaike Information Criterion corrected for small sample size (AIC_c), number of parameters estimated for each model (k), Akaike weight (w), and the deviance (−2 log likelihood).

Model covariates[a]	AIC_c	k	w	Deviance
AA, BC, sex, precipitation	1,023.9	5	0.84	1,013.8
AA, sex, precipitation	1,027.7	4	0.09	1,019.7
AA, BC, sex	1,028.9	4	0.06	1,020.9
AA, sex	1,032.3	3	<0.01	1,026.3
AABB, BC, sex, precipitation	1,048.3	5	<0.01	1,038.2
AAAB, BC, sex	1,052.7	4	<0.01	1,044.7
AABB, BC, sex	1,085.3	4	<0.01	1,077.3
AAAB, BC, sex, precipitation	1,086.6	5	<0.01	1,076.5
Year, sex, year × sex	1,112.9	28	<0.01	1,052.9

[a] AA indicates the certainty code assigned to each incisor was A. BC indicates the certainty code assigned was B to 1 incisor and C to the other incisor. AB indicates the certainty code assigned was A to 1 incisor and B to the other incisor. BB indicates the certainty code assigned to each incisor was B. AABB indicates incisor pairs were assigned AA or BB. AAAB indicates incisor pairs were assigned AA or AB. Precipitation refers to the combined, measured rainfall for the previous 2 years at Camp Pendleton.

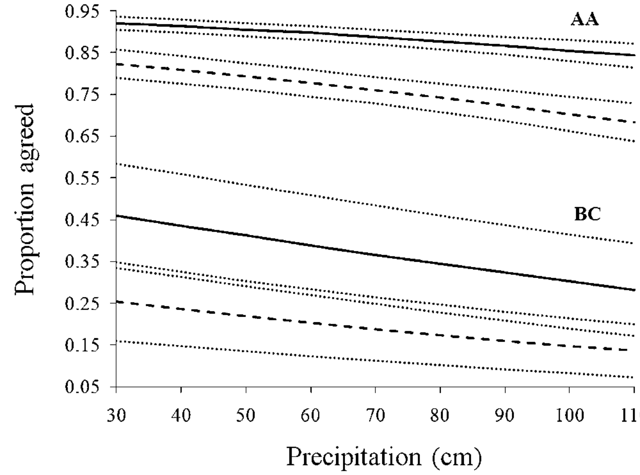

Figure 1. Relationships (in arithmetic scale) between cumulative precipitation for the previous 2 years (cm) and proportional agreement of age estimates for pairs of incisors extracted from the same mule deer, Camp Pendleton, California, 1985, 1987–1999. We report logistic regressions for males (solid lines) and females (dashed lines) when certainty codes assigned for both age estimates were A (AA) and when certainty codes assigned to 1 age estimate was B and C to the other estimate (BC). Dotted lines are 1 SE envelopes for each regression.

codes of AA was about 0.10 less than males when cumulative precipitation in the previous 2 years was 30 cm. That disparity grew to 0.15 when cumulative precipitation was 110 cm. The proportion of incisor pairs with age estimates that agreed was markedly less (about 0.5 for each sex) when the uncertainty code was BC.

DISCUSSION

Marine Corps Base Camp Pendleton's analysis of blind-duplicate age data that spanned 15 years and included >900 animals was the most rigorous evaluation yet for the precision of a deer aging technique. We found that, on average, females of southern mule deer received incorrect age estimates twice as often as males and variation existed in the precision of age estimates among years. Previous assessments of precision for aging techniques either used observers who knew they were under evaluation or did not consider annual variation in the precision of age estimates (Brokx 1972, Lockard 1972, Hackett et al. 1979, DeYoung 1989).

Precision and bias determine the accuracy of a measurement or estimation (Garton et al. 2005). Because our data came from deer of unknown age, the most important source of bias that we could not control was the effect of a deer's true age on the estimated age. Hamlin et al. (2000), however, did not find a relationship between errors in CAA age estimates of mule deer and known ages of those animals. In contrast, Lockard (1972) found more age discrepancies for cementum annuli counts from older white-tailed deer. Matson stated that older deer are more difficult to age correctly because their incisors contain more indistinctly formed annuli and the widths of the annuli are irregular both among years and within the same year, although less so for animals from northern regions (G. Matson, personal communication).

Table 4. Parameter estimates and standard errors of the model we selected to estimate agreement in age estimates in pairs of incisors extracted from mule deer, Camp Pendleton, California, 1985, 1987–1999.

Parameter[a]	Estimate	SE
Intercept	0.413	0.244
AA	1.414	0.185
BC	−1.200	0.500
Sex	0.913	0.154
Precipitation	−0.010	0.003

[a] AA indicates the certainty code assigned to each incisor was A. BC indicates the certainty code assigned was B to 1 incisor and C to the other incisor. The reference sex was female. Precipitation refers to the combined, measured rainfall for the previous 2 years at Camp Pendleton.

Matson's Lab cites the accuracy of CAA for mule deer from northern regions as "high accuracy" at 95% and for mule deer from the southwestern United States as "moderate," at 80–90% (Matson 2010). Hamlin et al. (2000) estimated a 92.6% accuracy rate for CAA based on 108 known-aged mule deer collected from Montana. That data set adequately sampled both male and female deer [K. Hamlin, Montana Fish Wildlife and Parks (retired), personal communication].

Differences in research methods, deer physiology, and local climate conditions among study sites hampered direct comparisons of our results to those of other researchers that previously evaluated CAA in deer. However, by invoking a key assumption, that only 1 tooth in an incisor pair with differing age estimates was inaccurately aged, we could compare the effectiveness of CAA for aging deer among different methods and study areas. This assumption was justified by the findings of Hamlin et al. (2000) and Jacobson and Reiner (1989), which both found incorrect age estimates from CAA performed by Matson most often differed from the known age of the deer by only 1 year. This consistency occurred despite the differing climates and habitats of their study areas: Montana and Mississippi for Hamlin et al. (2000) and Jacobson and Reiner (1989), respectively. We similarly found that 78% of unreliably aged incisor pairs from Camp Pendleton disagreed by only 1 year.

We calculated the mean proportion of unreliably aged incisor pairs (weighted by sex) as 34% for deer from Camp Pendleton. Assuming that only 1 of the incisors in an unreliably aged pair from our sample was inaccurately aged, then the overall error rate of age estimates was approximately half of the proportion of unreliably age incisor pairs. Hence, our results suggested an error rate of about 17% for CAA age estimates in mule deer from southern California. We calculated mean error rates weighted by age for deer ≥2.5 years from 2 other studies and found that the error rate of deer age estimates on Camp Pendleton was greater than the 7.9% error rate for mule deer from Montana (Hamlin et al. 2000), yet less than the 35.5% error rate for white-tailed deer from Mississippi (Jacobson and Reiner 1989). Both the Montana and Mississippi studies used known-aged, male and female deer collected from the wild. The sample of 76 deer in the Mississippi study included 29 animals that were pen-raised and given supplemental food [H. A. Jacobson, Department of Wildlife and Fisheries, Mississippi State University (retired), personal communication], however, those authors did not find a significant difference in the error rates of CAA age estimates between wild and captive animals.

Similar to our study methods, DeYoung (1989) and Rice (1980) also evaluated precision of CAA using duplicate incisors from wild deer. DeYoung (1989) submitted lateral incisors (I2, non-standard for CAA in deer) to Matson's Lab for age analysis using teeth collected from male white-tailed deer in south Texas. Age results showed that Matson provided unreliable age estimates for 68.4% of 19 incisors pairs from deer with estimated ages ≥2.2 years. Matson also provided correct age estimates of single incisors from 3 known-aged deer. Assuming that only 1 age estimate per incisor pair was erroneous, and including the results of the known-aged deer, then the weighted error rate for CAA age estimates was about 31%. In contrast, Rice (1980) personally performed cementum age analysis using teeth from both sexes of mule and white-tailed deer taken by hunters in South Dakota. Using 422 deer collected in 1975 and 1976, including 200 yearlings, Rice-produced age estimates that did not match for 8% of incisor pairs that translated to an assumed error rate of about 4% (not weighted).

Although a relationship between latitude and CAA accuracy is evident from the results of previous research (Brokx 1972, Rice 1980, DeYoung 1989, Jacobson and Reiner 1989, Hamlin et al. 2000), our results show stronger support for the conclusion that local weather and vegetation conditions are the primary factors affecting variation in the patterns of cementum annuli deposition in deer incisors. The Jacobson and Reiner (1989) evaluation of CAA for deer in Mississippi, where latitudes are similar to southern California, found an error rate for adult white-tailed deer that was more than twice the rate we estimated for mule deer in southern California. Connolly et al. (1969) used CAA to derive age estimates for 5 known-aged black-tailed deer (*Odocoileus hemionus*) collected from the Hopland Research and Extension Center in northern California and found that most of the estimates were in err by ≥1 year. The Hopland site is similar to Camp Pendleton because deer at both locations endure nutritional stress from lean browsing conditions in late summer due to a prevalence of summer-dormant plants adapted to survive droughts. However, the sample size was small and an unknown number of the animals were captive deer that received supplemental food, thus limiting comparisons to our results [G. Connolly, USDA Wildlife Services (retired), personal communication].

Differences in diet or physiology were likely causes for the elevated rate of unreliably aged tooth pairs that we found in females versus males from our sample. Based on 128 mule deer collected on Camp Pendleton in the fall of 1986, Pious (1989) found significant differences in diet selection, by forage category, between males and females. Males in all age classes ingested more browse and fewer forbs than females of the same sex and age classes. Researchers have reported that forbs provide nitrogen, calcium, phosphorous, potassium, carotene, and energy (Cook 1972, Longhurst et al. 1979). Males on base endured substantial metabolic stress during the rut that coincided with a nutritionally stressful period, which may have produced patterns of cementum annuli that formed more distinctly in contrast to the annuli patterns found in females on base.

MANAGEMENT IMPLICATIONS

Researchers have tested and found CAA to be more accurate than the commonly used tooth wear technique; however, tooth eruption is accurate and reliable for aging fawn and yearling deer (Hamlin et al. 2000, Gee et al. 2002). We recommend CAA for situations when managers need age-specific mortality data for unmarked adults classified as ≥2.5 years by tooth eruption.

Our research shows, the precision of CAA can vary substantially among years and between sexes for animals from the same population. Measuring the precision rate of CAA for a specific deer population gives the wildlife manager a more thorough understanding of age data collected from that population. For managers relying on CAA age estimates, submitting blind-duplicate samples is a cost effective way to evaluate the precision of the technique for animals in their region. Managers can use this information to decide if it is worthwhile to pursue the additional precision and accuracy provided by CAA for methods such as population reconstruction and monitoring the proportional harvest of older female deer.

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