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Journal of Wildlife Management, Vol. 64, No. 3 (Jul., 2000), pp. 752-758

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Abstract: We evaluated the accuracy and precision of tooth wear for aging gray wolves (*Canis lupus*) from Alaska, Minnesota, and Ontario based on 47 known-age or known-minimum-age skulls. Estimates of age using tooth wear and a commercial cementum annuli-aging service were useful for wolves up to 14 years old. The precision of estimates from cementum annuli was greater than estimates from tooth wear, but tooth wear estimates are more applicable in the field. We tended to overestimate age by 1–2 years and occasionally by 3 or 4 years. The commercial service aged young wolves with cementum annuli to within ±1 year of actual age, but under estimated ages of wolves ≥9 years old by 1–3 years. No differences were detected in tooth wear patterns for wild wolves from Alaska, Minnesota, and Ontario, nor between captive and wild wolves. Tooth wear was not appropriate for aging wolves with an underbite that prevented normal wear or severely broken and missing teeth.

JOURNAL OF WILDLIFE MANAGEMENT 64(3):752–758

Key words: Age estimation, *Canis lupus,* tooth wear, wolf.

Noninvasive techniques that are reliable and cost effective are needed to estimate ages of gray wolves. The most widely used technique is counting tooth cementum annuli (Ballard et al. 1995, Landon et al. 1998). This is the only method used to estimate age to the nearest year (Landon et al. 1998), except for marking pups that can later be identified (Mech 1988). To count cementum increments, teeth must be removed, sectioned, and stained. Alternative techniques (Dimmick and Pelton 1994) are needed to avoid injury and to comply with requirements of institutional animal care and use committees at universities, government organizations, and private foundations. Avoiding damage to specimens in museums and private collections is also important (Gipson and Ballard 1998, Gipson et al. 1998). Tooth wear may provide an alternative to cementum annuli aging, but not a replacement for the technique.

Tooth wear has been used to estimate wolf ages (Gipson et al. 1998, Fuller and Keith 1980), but the technique lacks precision and tooth abrasion might vary among regions (Ballard et al. 1995). Landon et al. (1998) examined 4 methods for determining wolf ages and concluded that tooth wear accurately aged pups and older wolves to within 4 years. They described tooth wear characteristics for 5 overlapping age classes and noted that additional study was needed to determine the precision of the technique.

Accurately placing wolves in age categories is important for studies of population dynamics, social organization, systematics, breeding, dispersal, relationships with prey including livestock depredations, and for determining suitability of individual wolves for restoration programs. These studies typically require accurate identification of pups <1 year old, yearlings and young adults 1–3 years old, mature wolves 3–9 years old, and individuals ≥10 years old, but seldom require precision ≤1 year. Our objectives were to determine the accuracy and precision achievable by using tooth wear to estimate wolf age, and to provide criteria for obtaining consistent results.

METHODS

We used skulls and teeth of 27 wolves from Alaska of known-minimum age, and for which estimates of actual age were available (Ballard

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Table 1. Skulls of wolves from Alaska used to define year age classes.

Assigned age class	Skull number	Basis for assigned age	Known-minimum age in yr
<1	122027	Killed as pup	<1
	122044	Killed as pup	<1
	122065	Killed as pup, cementum annuli	<1
	122127	Killed as pup, cementum annuli	<1
	122151	Killed as pup, cementum annuli	<1
	122421	Killed as pup	<1
	122456	Killed as pup	<1
	122559	Killed as pup	<1
1–2	122073	Cementum annuli	n.a.[a]
	122152	Tagged as pup, cementum annuli	1.8
	122252	Cementum annuli	n.a.
	122440	Tooth wear	n.a.
2–3	122148	Cementum annuli, tooth wear	n.a.
	122170	Cementum annuli, tooth wear	n.a.
3–4	122135	Tagged as adult, cementum annuli	1.8
	122143	Cementum annuli, tooth wear	n.a.
	122368	Tagged as adult, tooth wear	3.0
4–5	61977	Tooth wear	n.a.
5–6	122009	Tagged as adult, cementum annuli	3.8
	122018	Tooth wear	n.a.
	122038	Tagged as adult, cementum annuli	2.5
	122081	Cementum annuli	n.a.
	122251	Tagged as adult, cementum annuli	1.8
6–7	122255	Tooth wear	n. a
7–8	122136	Tagged as adult, cementum annuli	3.5
9–8	122174	Cementum annuli, tooth wear	n.a.
13–14	122094	Tagged as adult, tooth wear	8.0

[a] n.a. = Not available.

et al. 1987, 1995), to develop criteria for assigning wolves to yearly age classes based on tooth wear. The known-minimum age of Alaska wolves differed by 0–7 years from estimated age. We evaluated the accuracy and precision of tooth wear by testing the ages of 20 wolves of known-age from Minnesota and Ontario. Ages were also estimated by Matson's Laboratory (Milltown, Montana, USA) by sectioning canine and–or premolar teeth and counting cementum annuli.

The Alaska skulls were arranged in 1-year age classes from youngest to oldest, <1–13 years old (Table 1). Progressive wear on canines, incisors, and carnassials was described for wolves of each age class. Three of the authors (Ballard, Gipson, and Nowak) then independently estimated the ages of 20 known-age wolves from Minnesota and Ontario by comparing wear on their incisors, canines, and carnassials to the Alaska collection. Next, we collectively compared tooth wear on the 20 wolf skulls and arrived at a consensus age estimate of each wolf. We were not aware of the actual ages or origins of the wolves, which included 12 wild wolves and 8 captives from Minnesota and Ontario.

Both accuracy (i.e., the proximity of the age estimates to the true ages) and precision (i.e., the repeatability of age estimates) of our age estimates and those of the commercial aging

Table 2. Linear regression analysis relating estimated age to known age wolves from Minnesota and Ontario. Values are comparison of known age to 3 individual readers, the consensus of readers, and counts of cementum annuli.

Independent variable	Intercept (α)	Slope (β)	*P*-value H_0: $\alpha = 0$	*P*-value H_0: $\beta = 0$	*P*-value H_0: $\beta = 1$
Reader 1	1.3	0.9	0.03	0.0001	0.31
Reader 2	0.9	1.0	0.12	0.0001	0.85
Reader 3	1.5	0.9	0.01	0.0001	0.40
Consensus	1.2	1.0	0.08	0.0001	0.66
Cementum annuli	0.4	0.8	0.12	0.0001	0.001

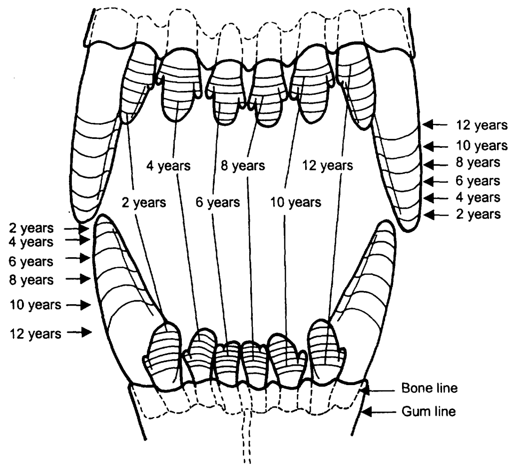

Fig. 1. Progressive wear on wolf incisors and canines in 2-year increments from ≤1—≥12 years of age. Wear on incisors typically progresses beyond the lobes on the first 2 upper and lower incisors at 8 years of age, leaving approximately 5 mm of enamel. At 10 years of age, 2–4 mm of enamel remain on the first and second incisors. Length of canines is reduced 30–50% with 10–16 mm of enamel remaining. Beyond 12 years of age, incisors may be worn to the roots, with a few peg-like stumps projecting above the gum line, or the gums may cover the roots. Length of canines is reduced ≥50% with ≤10 mm of enamel remaining.

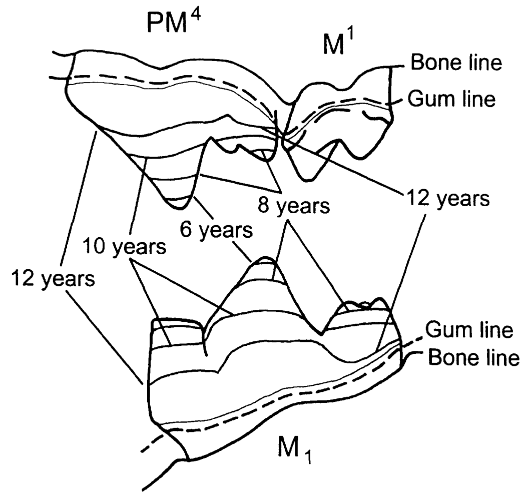

Fig. 2. Progressive wear on wolf carnassials (upper premolar 4 and lower molar 1) in 2-year increments from ≤6—≥12 years of age. Wear is visible on tips of major prominences at 5 years of age and profiles flatten slightly by 6 years. Deep wear on the posterior cusp of the lower carnassial after 10 years of age results from occlusion with the first upper molar, not the upper carnassial.

service were evaluated. We followed the recommendations of Campana et al. (1995), who examined the value of statistical and graphical methods for determining the consistency of fish age estimates. First, age-bias graphs were developed for diagnosing systematic differences between age determinations based on tooth wear and by the commercial aging service that counted cementum annuli. The age-bias graphs show known ages of the wolves along the horizontal axis and estimates of age by each reader on the vertical axis. Age estimates that are parallel but separate from the 1:1 equivalent line, or that diverge as the lower or upper age limit is approached, indicate systematic bias.

Next, to compare the precision of the 4 biologists, we estimated the coefficient of variation for their estimates relative to the known ages. We calculated individual coefficients of variation of the age estimate for each wolf, then averaged across wolves to produce a mean coefficient of variation for the reader (Campana et al. 1995). An estimate of the coefficient of variation was expressed as the ratio of the standard deviation to the mean (Campana et al. 1995). Higher coefficient of variation values indicate lower precision.

We used linear regression of known ages and estimated ages to test for significant differences from a slope of 1 and an intercept of zero. A slope other than 1 would reflect inconsistency in the age estimate compared to known age. An intercept other than zero would indicate a systematic bias between the estimate of age by a reader and known age. We then used the 20 wolves of known age to describe wear on incisors, canines, and carnassials characteristic of each yearly age class from ≤1–14 years of age. We also developed charts illustrating typical tooth wear in 2-year increments on incisors, canines, and carnassials that can be compared to the teeth of live wolves or museum specimens to estimate their age (Figs. 1, 2).

RESULTS

Precision and Accuracy

Readers 2 and 3 as a team, most accurately estimated ages of the known age wolves from tooth wear (Figs. 3, 4, Table 2). Estimates made independently by readers 1 and 3 were 1–2 years higher than known ages (Table 2, Fig. 3). Age estimates by reader 2 were more precise, as indicated by a relatively small coefficient of variation of 19.5 compared to 26.7, 23.7, and 24.0 for readers 1 and 3, and the consensus of readers, respectively. All readers experienced difficulty in estimating the age of a 7-year old wolf with an underbite and an 11-year old wolf

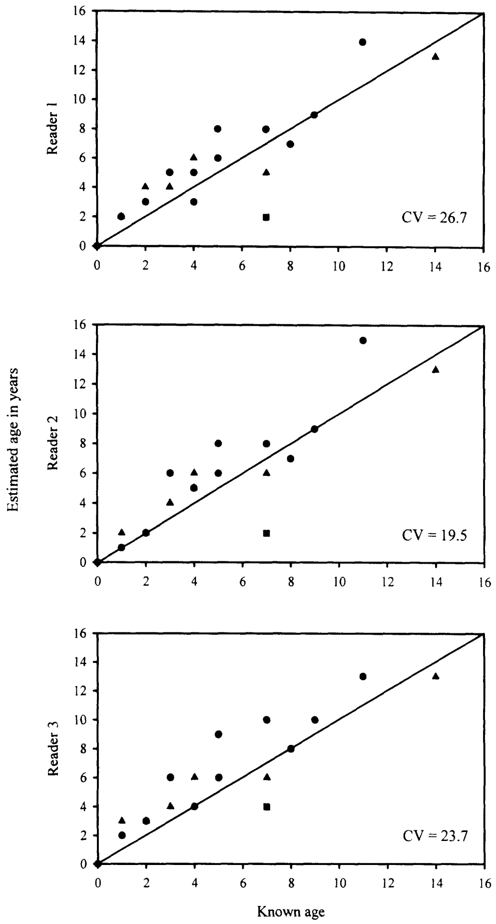

Fig. 3. Age bias graphs for 3 readers showing estimates of ages of 20 wolves from Minnesota and Ontario compared to known ages. On each graph age is show in years for known ages on the X axis and estimated ages on the Y axis. The solid line is the 1:1 equivalence line; solid square below the 1: 1 line represents the age estimate for a wolf with a severe underbite; solid circle on the upper right, above the 1:1 line, represents the age estimate for a wolf with broken and missing teeth from an old injury. Solid circles are age estimates for wild wolves; solid triangles are age estimates for captive wolves.

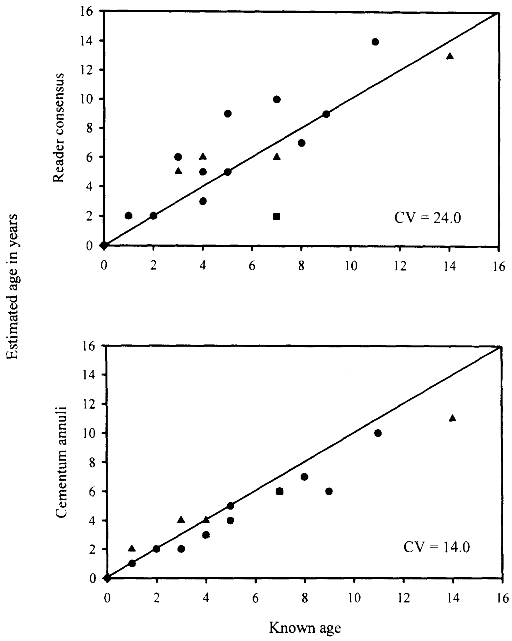

Fig. 4. Age bias graphs for a consensus of the 3 tooth-wear readers (upper graph) and a commercial aging service (Matson's Laboratory, Milltown, MT 59851) using counts of cementum annuli to estimate ages of 20 wolves from Minnesota and Ontario compared to known ages. On each graph age is shown in years for known ages on the X axis and estimated ages on the Y axis. The solid line is the 1:1 equivalence line; solid square below the 1:1 line represents the estimate of age of a wolf with a severe underbite; solid circle on the upper right represents the estimate of age for a wolf with broken and missing teeth from an old injury. Solid circles are age estimates for wild wolves; solid triangles are age estimates for captive wolves.

with broken and missing teeth (Figs. 3, 4). Estimates of age ranged from 3–5 years under actual age and 2–4 years over actual age for these 2 wolves, respectively.

The commercial aging service accurately aged young wolves, but older wolves were underaged (Fig. 4, Table 2). The precision of the aging service was ±1 year except for a 9-year-old wolf that they aged at 6 years and a 14-year-old wolf that they estimated to be 11 years old. The relatively low coefficient of variation of 14.0 for the aging service reflected less variation than among the 3 readers. Age estimates by the aging service may have been influenced by poor intensity of annulus staining because some specimens had been in storage for ≥20 years and some were boiled prior to tooth extraction.

Progressive Tooth Wear

There were no detectable differences in tooth wear patterns between wild and captive wolves (Figs. 3, 4). Adult incisor, canine, and carnassial teeth are fully erupted by 26 weeks of age (Mech 1970). During the first year of a wolf's life they are bright white, and incisors appear molded with sharp ridges that project slightly beyond the teeth. These small projecting ridges occur along the lobes of incisors and along the posterior and anterior-medial edges of canines. Between 1 and 2 years of age, incisors and canines begin to show detectable wear (Fig.1, Table 3).

Among the 3 prominences on upper incisors, the central 1 projects well beyond those on each side. Lower incisors have only 2 prominences;

Table 3. Wear on teeth of wolves associated with increasing age (yr).

Age	Diagnostic wear on teeth: Incisors	Canines	Carnassials
<1	Bright white, no visible wear, sharp edges project slightly beyond lobes.	Bright white, no visible wear, small ridges project slightly on posterior edge of C^1 and anterior-medial edges of C_1.	Bright white, no visible wear.
1–2	Slight wear on sharp edges of lobes.	Slight wear on distal end of posterior small ridge of C^1.	No visible wear.
2–3	Central lobes of I^1 and I^2 slightly flattened, median lobes of I_1–I_3 flatten slightly.	Tips slightly blunted, distal portion of C^1 and C_1 show wear on small ridges.	No visible wear.
3–4	Flat tip on central lobes of I^1–I^3, flat surface on I_1 extends into lateral lobe, and median lobe of I_2 and I_3 flatten.	Tips show distinct, but rounded blunting.	Visible wear on tip of most major prominences.
4–6	Flat surface of I^1 progresses into median lobe, flat surfaces progress beyond lateral lobe on I_1 and into lateral lobe on I_2.	Tips flattened.	Wear on tip of all prominences.
6–8	Wear progresses beyond median lobe of I^1 and I^2, and lateral lobe of I_2, reaches lateral lobe of I_3.	Tip clearly flattened, 1–2 mm of tip lost.	Tip of all prominences flattened.
8–10	Wear progresses beyond all lobes of I^1, I^2, and I_3, and reaches median lobe of I^3.	Visibly shortened profile with 3–5 mm of wear on tips.	Profile of prominences almost flat.
10–12	Length of incisors reduced ≥50%, 2–4 mm of enamel remain, flat profile.	Flat tip, length reduced 30–50%, 10–16 mm of enamel remain, distinct wear on anterior-posterior surfaces.	Height reduced by ≥30%, posterior cusp of M_1 worn almost to gum line.
≥13	Remaining incisors worn almost to gum line, some missing, and roots covered by gums.	Tips blunt, length reduced ≥50% with ≤10 mm enamel remaining, anterior-posterior width reduced ≥30%.	Prominences almost flat, posterior cusps of PM^4 and M_1 near gum line.

a relatively large median one projects beyond the lateral prominence. Incisors do not correspond to an opposing tooth, except for the first lower incisor that is opposed by the wider first upper incisor. Each of the 2 lateral lower incisors occludes with 2 upper incisors. Incisors wear at a relatively consistent rate throughout life.

Canines are large spike-like teeth that curve slightly to the posterior, and when normally alined, the lower canine fits into a gap between the upper canine and the third upper incisor. Because canines do not oppose each other when the mouth is closed, there is little wear from occlusion. Wear on canines becomes apparent when wolves are 3–4 years old, possibly due to lack of tooth occlusion and continuous eruption of cementum deposits on their roots as the points are worn down (Allen 1974).

The carnassial teeth (lower molar 1 and upper premolar 4) provide a convenient cross-check for wear patterns on incisors and canines, especially where wolves have broken incisors and–or canines and the damaged teeth make the wolf appear older. Wear is visible on the pointed prominences of carnassials by 5 years of age, but the profile has not yet been distorted. After 5 years of age, the prominences and cutting surfaces become progressively flattened (Fig. 2, Table 3). Wear is due to chewing bone and other hard objects, and occlusion of lower molar 1 with upper premolar 4 and upper molar 1. Wear on the carnassials is easy to observe in immobilized wolves by pulling back the lips along the sides of the mouth. The profile of carnassials may be observed from the side while overall wear is best estimated by opening the wolf's mouth wide and looking from the front directly into the mouth.

DISCUSSION

Limited research has been conducted on the validity of either cementum annuli or tooth wear as aging techniques for wolves and coyotes (*C. latrans*). Validation studies are expensive and few reference specimens of known-age wild specimens are available. Both techniques need more evaluation with known age specimens. The limited published evaluations suggest that accuracy of age estimates for wolves and coyotes from tooth wear are comparable to estimates from cementum annuli, but precision is generally believed to be lower for tooth wear. Linhart and Knowlton (1967) found a strong positive correlation between the 2 techniques when used on coyotes. Bowen (1982) found that coyote ages based on the 2 techniques agreed within 2 years for coyotes up to 9 years old. Goodwin and Ballard (1985) found cementum annuli to be an accurate technique for aging wolves, but it was impractical for use on live wolves because it required canine teeth. Ballard et al. (1995) compared estimates of ages based on cementum annuli from wolf canines and premolars using 2 types of stain and found significant differences between the 2 teeth in annuli counts with one of the stains. Landon et al. (1998) concluded that tooth wear was accurate for aging wolf pups and adults to within 4 years, but noted errors up to 6 years.

We were less precise in our estimates of age from tooth wear than cementum annuli for wolves ≤3 years old (Figs. 3, 4), but precision of the 2 techniques was comparable for wolves ≥9 years of age (Figs. 3, 4, Table 2). Our age estimates from tooth wear for wolves <3 years old were either correct to a single year class or were 1–2 years over actual age. For wolves ≥3 years old, 2 of our 3 readers tended to over estimate age by 1–2 years. Estimates from premolar cementum annuli were ±1 year of known age for wolves up to 3 years old, and 1–3 years under actual age for wolves up to 14 years old. The major advantage of using tooth wear as an estimator of age is that it is noninvasive, places a minimum of stress on living wolves, and requires no damage to museum specimens.

The lack of readers skilled in estimating age from tooth wear, and no written or illustrated guides to train readers, are valid concerns. All techniques available for estimating the age of wolves and other carnivores have elements of subjectivity that require training to produce consistent results. The only guide to estimating age from tooth wear for canids that we are aware of is for coyotes (Gier 1957). Linhart and Knowlton (1967) found a strong positive correlation between Gier's (1957) tooth wear and cementum annuli. Bowen (1982) found tooth wear to be accurate for 15 of 20 coyotes aged 1 and 2 years, but it tended to under-age coyotes ≥3 years old by 1 or 2 years. Landon et al. (1998) noted that variation among readers estimating wolf ages from cementum annuli was related to the experience of readers. Harshyne et al. (1998) in their evaluation of cementum annuli for aging black bears (*Ursus americanus*) found that a written and illustrated manual was a useful training tool.

We provide descriptions of progressive tooth wear and charts showing stages of wear typically found on incisors, canines, and carnassials of wolves that can be compared to teeth of living wolves or preserved specimens. We also have photographs (available from the first author) of wolf skulls showing wear on incisors and canines typical of age classes that can be used with the written descriptions and our charts. Our use of teeth from Alaska to age wolves from Minnesota and Ontario suggests that patterns of tooth wear may be similar among wolves from distant regions with different prey. Additional study of this issue is needed.

We estimated the age of 15 of 20 (75%) known-aged wolves to within 2 years of their actual age using tooth wear. The maximum error was 5 years for an atypical wolf with an underbite. When 2 wolves with atypical tooth wear were not considered, we aged 15 of 18 (83%) known-aged wolves to within 2 years of actual age, with a maximum error of 4 years.

MANAGEMENT IMPLICATIONS

Our descriptions of tooth wear should allow future wolf researchers to improve their accuracy and precision in estimating age. We recommend that 2 or more readers work together to reach a consensus on age estimates when possible. Estimates of age based on tooth wear, although not as precise as counts of cementum annuli, are suitable for most studies of population dynamics, social organization, systematics, dispersal, and interactions with prey, including livestock depredations. Age estimates from tooth wear may also be helpful for evaluating the suitability of individual wolves for restoration programs.

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Received 1 September 1999.
Accepted 18 February 2000.
Associate Editor: Maehr.