A comparison of age estimation methods for the saiga antelope *Saiga tatarica*

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Age estimation is particularly crucial for the conservation of the saiga antelope *Saiga tatarica*, but modern laboratory methods for aging have not previously been applied to this species. There is an urgent need for evaluation of the techniques that could be used for age estimation in order that long-term ecological data sets can be correctly interpreted and conservation advice given. We evaluated the repeatability, practical feasibility and comparability of three techniques for age estimation of saiga antelopes; the tooth sectioning technique (TS), the tooth eruption and wear technique (TEW), and a visual aging technique routinely used in field studies. We found that TS and TEW gave repeatable results, and agreed well. The visual method underestimated the age of males compared to laboratory methods. It assigned animals consistently to the age class of at least one year old, but less consistently to the age class less than one year old. Although studies of known-age animals are needed to evaluate precision and accuracy of these methods, we suggest that either TS or TEW would be suitable for aging saiga antelopes, with the choice being determined by practicalities such as the availability of the necessary expertise and equipment.

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Until recently, the saiga antelope *Saiga tatarica* was an abundant and commercially important hunted species of the semi-arid rangelands of Central Asia (Bekenov, Grachev & Milner-Gulland 1998, Sokolov & Zhirnov 1998). However, it was heavily poached following the break-up of the Soviet Union, with hunters particularly targeting males for their horns, which are used in traditional Chinese medicine. The saiga was reassigned from Near-Threatened to Critically Endangered in the 2002 Red List of threatened plants and animals compiled by IUCN - the World Conservation Union (http://www.redlist.org/, see Hilton-Taylor 2000), because poaching has led to a ~90% reduction in the population size over the last 10 years (Milner-Gulland, Kholodova, Bekenov, Bukreeva, Grachev, Amgalan & Lushchekina 2001).

Age determination is a key component of ecological studies of wild animals and rigorous methods for aging saigas are urgently required. In particular, there is concern that reproductive collapse is occurring, with reports of the majority of one-year old females in the Kalmykian population failing to conceive apparently due to a lack of adult males (Milner-Gulland, Bukreeva, Coulson, Lushchekina, Kholodova, Bekenov & Grachev 2003). There is also concern about the vulnerability of saiga populations to epidemic disease transmitted from livestock, because of the collapse in veterinary services in Kazakhstan (Lundervold 2001). The age of individuals needs to be estimated for information on disease dynamics to be obtained from age-seroprevalence profiles. The age profile of the population and of poached individuals can give an indication of hunting selectivity and population structure (Fadeev & Sludskiy 1982).

A wealth of detailed long-term data on saiga ecology is available. For example, saiga pregnancy rates by age class were used in a comparative study of the effects of density dependent and independent factors on ungulate population dynamics (Coulson, Milner-Gulland & Clutton-Brock 2000). Long-term field studies over decades have produced published data sets on age class-specific fecundity rates and population structure (Bannikov, Zhirnov, Lebedeva & Fandeev 1961, Fadeev & Sludskiy 1982, Bekenov et al. 1998, Sokolov & Zhirnov 1998). These studies provide a valuable foundation for understanding the ecological factors involved in the saiga's current precarious position, and for making recommendations for the most effective forms of conservation action. The studies rely on visual estimation of age (using body size, condition and male horn characteristics), and if saigas are killed, a visual inspection of tooth eruption and wear also takes place (see below). The ability of these methods to provide good age estimates has not previously been tested, however; hence the reliability of the age data in these long-term data sets is unknown.

It is currently illegal to kill saigas in Kazakhstan, even under scientific licence. There are a few known-age animals in captivity in Kalmykia (Russian Federation) and in zoos, but the precarious status of the species means that culling these individuals for scientific purposes is unjustifiable. We carried out a study of the ecology and epidemiology of the saiga antelope in 1996-1997, before the catastrophic decline in population size. The study involved sampling a large number of individuals culled by commercial hunters (see Lundervold 2001 for details). Here we report on our use of the samples for an assessment of three methods for estimating saiga age; tooth sectioning, tooth eruption and wear, and the visual assessment technique that is currently used by saiga researchers.

Methods for age estimation in ungulates

Among the techniques to estimate age in mammals (see Morris 1972 for a review), dentition (tooth eruption pattern, tooth wear and tooth sectioning) is particularly useful in ungulates (Klevezal & Kleinenberg 1967, Grue & Jensen 1979, Jacobson & Reiner 1989, Brown & Chapman 1991c, Langvatn & Meisingset 2001). Tooth eruption is accurate for aging sheep from the ages of 15 months (when the first, most central, permanent incisors erupt) to 33 months (when the fourth, most lateral, permanent incisors erupt; Williams 1988). In many wild ungulate species (e.g. Javan rusa deer *Cervus timorensis russa*, red deer *Cervus elaphus*, fallow deer *Dama dama* and roe deer *Capreolus capreolus*), eruption of permanent teeth is complete by 18-36 months, so aging beyond this limit is more difficult (Brown & Chapman 1991b, Brown & Chapman 1991a, Ratcliffe & Mayle 1992, Moore, Cahill, Kelly & Hayden 1995, Bianchi, Hurlin, Lebel & Chardonnet 1997, Langvatn & Meisingset 2001).

Tooth wear methods, usually based on the extent of wear of mandibular teeth, have been used for age estimation in moose *Alces alces* and roe deer (Passmore, Peterson & Cringan 1955, Brown & Chapman 1991c). However, the accuracy is poor (Hewison, Andersen, Gaillard, Linnell & Delorme 1999). Kierdorf & Becher (1997) showed that using enamel hardness to modify wear indices improved the accuracy of age estimation. In both moose and reindeer *Rangifer tarandus*, tooth sectioning (TS) has given more accurate results than tooth-wear (Sergeant & Pimlott 1959, Reimers & Nordby 1968, Grue & Jensen 1979). TS was pioneered by Laws (1952) for seals, and involves preparing thin sections of the canine teeth and examining the regular sequence of growth layers (annuli) in the dentine. Sergeant & Pimlott (1959) used TS to age moose. They suggested a seasonal sequence of deposition of the annuli, and considered accuracy to be plus or minus one year for younger animals, and two years for older animals. They therefore put animals into age classes, e.g. 5-6 years, 6-8 years, rather than attempting accurately to estimate their actual age. According to Ratcliffe & Mayle (1992), precise assessment of the age of adult ungulates is most reliable using TS. For example, roe deer can be aged to the nearest month if the collection date is known (Aitken 1975, Ratcliffe & Mayle 1992). However, Moore et al. (1995) compared different techniques for age estimation of fal-

low deer, and found that incisor height, molar height, molar wear and annuli in dental cementum were directly comparable techniques. Of these four methods, incisor height was most appropriate for the study population, accurately aging almost 90% of males.

Methods for age estimation in saigas

The primary reference for saiga age estimation is a detailed key by Bannikov, Zhirnov, Lebedeva & Fandeev (1961). However, no explanation is provided of the methods used to develop the key, and in particular there is no reference in that or later publications to the use of known-age animals. Hence the relationship between saiga age and the patterns of eruption and wear given in the key remains unclear, as does the variability in these patterns between individuals and locations.

For both sexes Bannikov et al. (1961) used tooth eruption up to the age of 19 months, and above 19 months they advocated tooth wear methods, using the molars. In this way, they grouped animals into age categories of 3, 4, 5-6, 7-8, and 9-10 years. Non-intrusive age estimation is suggested to be possible for male saigas ≤1.5 years old, using horn size and shape. After the age of 1.5 years, horns are thought only to be capable of giving a rough estimate. Young horns are shorter and straighter with black tips; the older the animal gets the more lyrate the horns become and the tips become less black. (Bannikov et al. 1961, Sokolov & Zhirnov 1998). For females, visual aging is more difficult, but intrusive methods can distinguish juvenile animals (≤1 year old) from other age classes because the last pair of molars has not yet erupted (Bekenov et al. 1998).

Aging is made easier by the saiga's life cycle, which is strongly influenced by the highly seasonal and harsh climate in which the species lives. Births take place over a short period (about 10 days) in May, hence animals can be reliably placed into non-overlapping age classes. This strong seasonality suggests that pronounced annuli in the tooth cementum are likely to be present. However, Pronyaev, Fandeev & Gruzdev (1998) used the tooth sectioning technique (TS) and found that the annuli were often not precisely defined. In their study, only 24% of incisors showed clearly visible annuli (N = 68). A further 33% were good enough for analysis, 37% were analysed with difficulty, and in 6% the annuli were not differentiable. Therefore, they recommended that Bannikov et al.'s (1961) technique should be used until further research had been carried out on TS.

Material and methods

We collected data from saiga antelopes culled in the course of a wider ecological survey (see Lundervold 2001 for details). Animals were shot under permit either by professional hunters or by scientific personnel of the Institute of Zoology of the Kazakhstan Academy of Sciences. Sampling took place during the hunting seasons in November-December 1996 and 1997 (117 males and 239 females), with a further eight males sampled in May 1997. As all saigas are born in May, animals culled in November are 0.5 years, 1.5 years, 2.5 years old, and so forth. To provide supplementary information on sex- and age-specific growth, the anterior and posterior parts of the mandible and the total mandible length were measured in specimens with complete lower mandibles (N = 57), following Langvatn (1977).

All animals were aged using visual assessment. Age estimates for specimens with mandibles were initially based on TEW, following the criteria described by Bannikov et al. (1961). Two incisors were then removed for TS. Another 180 animals for which only incisors were available resulted in a total sample size of 237 for TS. There were no known-age animals in the sample.

Age estimation by the tooth sectioning technique (TS)

The first incisor (I_1) is the largest and the first to erupt, at the age of 13-14 months (Bannikov et al. 1961). It was therefore chosen for age estimation. In young animals, the first incisor of the milk teeth (dI_1) was used. Incisor roots are easier to process than roots from molars, and they usually have a well defined dental cementum layer (Reimers & Nordby 1968, Grue & Jensen 1979). First incisors were available from 180 saigas. We also removed a further 57 I_1 incisor pairs from the saiga mandibles that had been used for the TEW analysis. Microscope slides were produced from decalcified, sagital sections of the incisor roots, following Reimers & Nordby (1968). Annuli in the dental cementum were counted and the age was estimated based on the time of eruption of the permanent first incisor (Bannikov et al. 1961, Gruzdev & Pronyaev 1994). The procedure was repeated using a different section from the same tooth, providing two age estimates for each individual.

Age estimation by analysis of tooth eruption and tooth wear (TEW)

Age estimation by TEW was performed on 57 mandibles. We scored eruption and development patterns in specific teeth using a four-stage assessment. Incisors (I_3) and canines (C) are the last permanent teeth, erupting

at the age of 19-26 months (Bannikov et al. 1961). This enabled us to allocate individuals to three age classes, rather than the two that can be distinguished based on molars alone (M_3 is fully developed at approximately 12-14 months). We classified individuals as calves (approximately 0.5-1 years old), subadults (approximately 1-2 years old) or adults (fully developed dentition with permanent teeth). Considering the timing of the birth season and culling, young animals could then be tentatively assigned an age in months (see Bannikov et al. 1961). This presumption is further supported because narrow, dark annuli are deposited in late winter or spring, whereas broader, light cementum zones are grown in summer and autumn (Grue & Jensen 1979, Langvatn 1995). However, variation in the progress of tooth eruption in some cervids (Langvatn & Meisingset 2001), suggest that age classifications of young animals should be interpreted with caution.

We estimated the age of individuals with fully developed permanent dentition from the degree of wear, primarily on premolars and molars. Crown height, oclusal surface, and the shape of crests and cusps on specific teeth were used as criteria, combined with general experience on lifespan-wear patterns in other bovids and cervids. We did not attempt to sex individuals based on tooth characteristics, although in some cervids male teeth wear faster than those of females (Grue & Jensen 1979, Peterson, Schwartz & Ballard 1983). Based on TS, adult cervid males can sometimes be distinguished from females by narrow dark lines between annuli in the cementum. Such lines may be related to rutting activity (Grue & Jensen 1979, Bartos, Malik, Hyanek, Vavrunek & Bytesnik 1984). No information about individual samples (e.g. sex, body condition and date of sampling) was available prior to analysis. TEW was repeated twice without cross-referencing, providing two independent age estimates.

Age estimation by visual assessment

Visual estimations of age were made by A. Grachev, a technician from the Institute of Zoology, Kazakhstan, with many years' experience working with saigas, using the eruption of the last molars and the general appearance of the animal as age criteria. The assessment was carried out on whole individuals in the field, rather than on mandibles as used for the TEW method. He distinguished 0.5 year-old females from those ≥1.5 years old based on whether the last molars were present or not. Males were aged using horn shape and size. This estimation technique is the one used routinely in previous and current studies of saiga ecology, hence it is important to compare it to the less subjective TS and TEW methods.

Results

Repeatability of the laboratory methods

Assigned ages ranged from 0.5 to 10.5 years (TEW) or 11.5 years (TS) for females, and from 0.5 to 7 (TEW) or 5 (TS) years for males. Consistency between the two iterations was high for both methods, but in both cases discrepancies were more likely to occur in older animals (Table 1). Previous studies have found that accurate age estimation by TEW is more difficult in older than in younger animals (Jacobson & Reiner 1989, Ratcliffe & Mayle 1992, Bianchi et al. 1997). In our study the animals with assigned ages that varied by two years using TEW were estimated to be 3-5 years old or older. TS gave estimated ages three years apart in three cases; the first was a mistake, the other two were in older animals, aged 4.5 or 7.5 years, and 8.5 or 11.5 years, respectively. The same animals tend to be problematic for both methods ($\chi^2 = 17.1$, df = 1, P < 0.001). These results are not surprising, as it would be expected that the level of discrepancy between the results might be greater for older animals, for which a broader range of potential ages

Table 1. Repeatability of the tooth eruption and wear technique (TEWT) and tooth sectioning technique (TST), and comparability between the mean ages assigned by the two techniques (TST vs TEWT). For the comparability test, differences of 0.5 and 1 are shown in the 1-year difference row, differences of 1.5 and 2 in the 2-year difference row. Columns show the number of samples (N) with a given difference between their assigned ages, the percentage of the total sample that N represents (%), and the mean age of animals with a given difference (Age). In all cases, the mean estimated age increases significantly with the amount of discrepancy between the two tests (ANOVA tests: TST - F = 12.5, df = 235, P < 0.001; TEWT - F = 38.1, df = 56, P < 0.001; TST vs TEWT - F = 32.5, df = 56, P < 0.001), however, when the young animals for which discrepancies do not occur are removed, the evidence for an increase in the discrepancy with age is less strong (ANOVA tests: TST - F = 5.62, df = 188, P = 0.001; TEWT - F = 3.46, df = 23, P = 0.05; TST vs TEWT - F = 0.97, df = 23, NS).

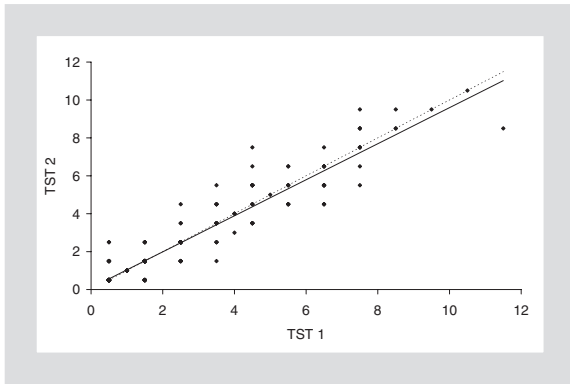| Difference	TEWT N	%	Age	TST N	%	Age	TST vs TEWT N	%	Age
None	38	67	1.5	145	61	2.1	39	68	1.5
1 year	10	18	4.3	78	33	3.2	15	26	5.0
2 years	9	16	6.7	11	5	4.6	3	5	6.3
3 years	0	0	-	3	1	8.0	0	0	-

Figure 1. Repeatability of the TS method for aging saigas. The age (in years) assigned on the first iteration is plotted on the x-axis, with the second iteration on the y-axis. The 1:1 line is shown in grey, regressions as a solid black line. Only one symbol is given at coordinates where more than one sample has the same result.

is available. Mean age increases with the amount of discrepancy between methods (see Table 1). Only animals aged ≥1 year had discrepancies between the two iterations using the TS. For TEW, there were no differences between iterations for animals aged ≤1.5 years. If these younger age groups are removed, the amount of discrepancy still increases significantly with age, but less markedly (see Table 1). There was no evidence that the amount of discrepancy varied by sex for either method.

Bias between the two iterations was checked for by linear regression. The two TS estimates were significantly correlated ($r^2 = 0.89$, P < 0.001), with a very slight tendency for the second estimate to be lower than the first (slope = 0.95, 95% confidence interval: 0.91-0.99; Fig. 1). The sex of the animal had no effect on this rela-
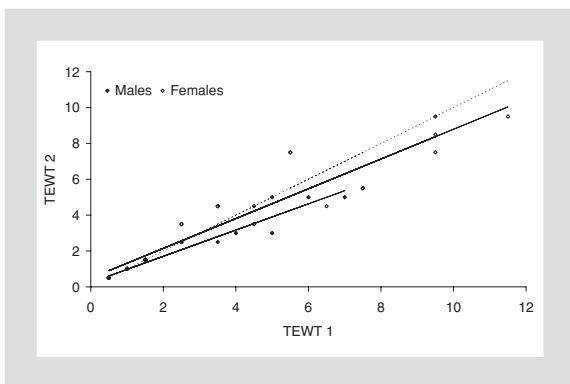
tionship. The TEW iterations were also significantly correlated ($r^2 = 0.91$, P < 0.001), with the estimated age slightly lower the second time than the first (slope = 0.81, 95% confidence interval: 0.73-0.88). Sequential bias was significantly related to sex (coefficients in the multiple regression have P < 0.05 for sex and P < 0.001 for the difference between tests). The reduction in the second estimate was greater for males than for females (slope for males = 0.73 and for females = 0.83; Fig. 2).

A comparison of the two laboratory methods

To compare the two methods, we first corrected for the lower sample size available for TEW. We sampled the TS data set randomly without replacement, to produce 1,000 subsets each of 57 TS samples (the same number used for TEW) and 95% of the slopes obtained lay between 0.86 and 1.04 (mean slope = 0.95; mean r^2 = 0.89). The probability that the TEW slope was drawn from the same distribution as the TS slopes was significantly low (P < 0.01). This confirms that the TEW method is significantly more affected by sequential bias than the TS method, but that the methods are very similar in their degree of correlation between the results of the two iterations.

We aged 57 saigas using both TS and TEW. The correlation between the ages assigned by two techniques was highly significant ($r^2 = 0.97$, P < 0.001, slope = 1.04; confidence interval: 0.99-1.10; Fig. 3). The slope was not significantly different from 1, showing that the estimated age (taken as the average of the two iterations) did not vary systematically between methods. There was no effect of sex, but mean age was a significant source of variation between the methods. This disappeared when animals aged ≤1.5 years (for all of which the two

Figure 2. Repeatability of the TEW method for aging saigas. The age (in years) assigned on the first iteration is plotted on the x-axis, with the second iteration on the y-axis. The 1:1 line is shown in grey, regressions as solid black lines. Separate lines show the regressions for males (♦) and females (◊). Only one symbol is given at coordinates where more than one sample has the same result.
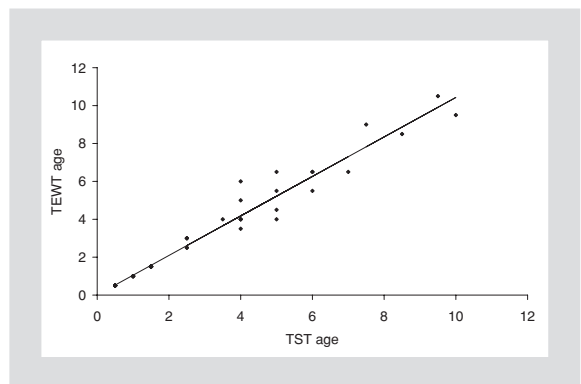

Figure 3. Comparison of the ages (in years) assigned by two different laboratory techniques for aging saigas; tooth eruption and wear (TEW) and tooth sectioning (TS). The assigned age for each technique was taken as the average of the two iterations. The data are shown as points, the linear regression as a line. Only one symbol is given at coordinates where more than one sample has the same result.

Table 2. Comparison of the results of visual assessment (visual ages) and the average age (in years) assigned by laboratory methods (lab age) for the 50 male saigas assigned ages by both methods. The cells representing agreement between the two methods are shaded grey.

Lab age	Visual age							Total
	0.5	1	1.5	2	3	4	5	
0.5	32							32
1		8						8
1.5	5							5
2								0
3								0
4				1	1	2		4
5					1			1
Total	37	8	0	1	2	2	0	50

methods gave the same results) were removed from the analysis (see Table 1).

Comparing visual and laboratory methods

To compare the results of the laboratory aging methods with the visual method, we consolidated the laboratory age estimates into a single estimate for each animal. The age was taken as the mean of the four TS and TEW estimates, or as the TS estimate if TEW was not done. Visual assessment gave an actual age for males, but only an age class for females. Although the sample size was small, males were consistently aged younger by visual assessment than by laboratory analyses (Table 2).

Assignment to age classes

Since the visual assessment method is likely to perform best at distinguishing first year animals from older animals, and because of good agreement between the laboratory methods in younger animals, we compared the performance of all three methods at assigning individuals to two groups: first-year and older animals. This division is meaningful biologically and in terms of the long-term data sets, for example because first-year females are thought to have lower fecundity rates than older females (Bekenov et al. 1998).

Table 3. Comparison of the results of visual assessment and the average age (in years) assigned by laboratory methods for the whole sample. The animals are grouped into two age classes: Juvenile = first-year animals, Adult = older animals. Columns represent the age class assigned visually (visual age class). Rows indicate whether all methods agree on the age (agreed), the visual estimate differs from the laboratory estimates (visual differs, where both iterations of both laboratory methods agree), or the laboratory estimates disagree (labs disagree). Results are given as actual numbers, with the proportions of the total number of animals assessed that these numbers represent given in parentheses. The results differ significantly between the two age classes ($\chi^2 = 43.5$, df = 2, P < 0.001).

	Visual age class		
	Juvenile	Adult	Overall
Agreed	32 (0.43)	138 (0.85)	170 (0.72)
Visual differs	22 (0.30)	15 (0.09)	37 (0.16)
Labs disagree	20 (0.27)	10 (0.06)	30 (0.13)
Total	74	163	237

There was much more disagreement between the methods when animals had been visually aged as ≤1 year than when the visual assessment was >1 year old (Table 3). There were no differences in the age class assigned by the two iterations of TEW, but 12% of the TS samples were assigned differently in the two iterations (differences between iterations of the TS accounted for 29/30 of the cases where there were inconsistencies between the age classes assigned by laboratory methods). Hence, TEW was less repeatable than TS when actual ages were assigned, but was highly repeatable when assigning animals to age classes. There was also a high level of agreement between the visual assessment and TEW, with only 5% of assigned age classes differing, as opposed to 16% difference between TS (when both iterations agreed) and visual assessment. This agreement between TEW and visual methods is not surprising, given that both the visual assessment and TEW use tooth eruption to decide whether an animal is in its first year or older. The results were similar for both sexes.

Discussion

The laboratory-based methods we used for saigas are well-established for ungulates, and have proved successful for other species (Grue & Jensen 1979, Ratcliffe & Mayle 1992, Moore et al. 1995). There is a well-established protocol for using TEW in saigas, although the only previous study using TS for saigas was not successful because the annuli were not well-defined (Pronyaev et al. 1998). In this study we found that both TEW and TS gave repeatable results, and that the two techniques agreed well. Repeatability declined amongst animals estimated to be older, but the degree of agreement between the methods was not significantly related to estimated age in animals ≥1.5 years old. Higher ages tended to be assigned on the first iteration, which shows the importance of checking for bias by carrying out the test more than once. TEW was significantly more affected by bias between iterations than TS, although the degree of

bias was not great in either case (TEW had a 19% reduction in mean estimated age at the second iteration). Males were more prone to bias in TEW estimates, perhaps due to sex-specific differences in feeding ecology. Although repeatability was tested only for one person rather than between researchers, the two tests were carried out blind.

Our results suggest that either technique would be useful for future research in terms of repeatability, although TS performed rather better. Logistically, TS requires laboratory facilities for processing teeth, microscopes to read the annuli and trained technicians. However, the development of a consistent TS procedure for saigas could have major advantages for future investigation into saiga life histories (e.g. Coy & Garshelis 1992). TEW requires the collection and preparation of mandibles, which may be time consuming. Mandibles are also bulky to transport. TEW analysis is a relatively quick procedure, but requires training for reliable and consistent aging. Saigas aged in this study were from two populations in Kazakhstan; results might be different for populations living in other areas (where conditions influencing tooth wear may be different).

Visual methods for age estimation are potentially very useful, because they allow age estimation of live animals. Despite its advantages, however, the use of visual age estimation raises concerns about accuracy, particularly for older animals. Prior to our study, both horn shape and size (for males) and eruption of posterior molars (for both sexes) were felt to be reliable in distinguishing first-year animals from older animals. We found that horn shape and size underestimated age compared to the laboratory methods. Hence visual estimation is only useful in assigning animals to two age classes: first-year and older animals. Even then, the time of year at which the survey is undertaken affects the reliability and usefulness of visual methods. Our surveys were undertaken during the hunting season, when first-year animals are six months old. This is the time at which visual age estimation is most likely to be useful, because first-year animals are well-enough grown that it is not trivial to distinguish them from older animals, but are young enough that the back molars have not yet erupted. Distinguishing visually between one-year-old and older females in May (when births occur) would be more useful biologically, but may be less reliable. Only 13 animals were aged in May during our study (all male), all of which were placed consistently into age classes 0-1 year or >1 year by all three methods. We suggest that a full study of the reliability of methods for aging females in the spring would be worthwhile.

The strong agreement we found between TEW and the visual estimate in assigning animals to age classes confirms repeatability between researchers. This is to be expected because both methods used molar eruptions to age the animals (TEW used detailed analyses of clean mandibles, visual assessment used examination of the mouth under field conditions). We suggest that visual estimation is consistent at placing animals in the ≥1 year age class, when judged against laboratory methods, but less consistent at placing animals into the 0-1 year age class. This may be because it is easier under field conditions to miss erupted molars (hence to underage the animal) than it is to mistakenly see erupted molars when there are none. The smaller sample size for TEW means that this supposition cannot be tested, because differences between the laboratory and visual estimates are mostly due to TS, which does not involve looking for molars. The use of annuli rather than threshold-based diagnostic characters (molars) may also explain why dividing animals into age classes rather than actual ages did not improve the repeatability of TS, unlike TEW. Hence if TS is used to age animals, there is no advantage gained from repeatability by lumping animals into age classes to offset the loss of information that is incurred.

Although we considered internal repeatability and comparability between aging techniques for saiga antelopes, we cannot make judgements about the precision or accuracy of the methods. This can only be done with the use of known-age animals, which is clearly the next step in developing reliable aging techniques for saigas. Since captive herds exist in saiga breeding centres, this should be possible in the future, provided that tooth wear patterns in captive animals are representative of patterns found in the wild. However the herds are not large, and given the conservation status of the species, it is not currently justifiable to kill animals for age determination studies. Tagging studies offer opportunities for retrospective aging of dead animals, although these are limited by the saiga's nomadic lifestyle. Similar procedures to those used in our study have also been applied to other species, including known-age individuals. They have proved to be satisfactory in terms of both accuracy and precision (Clutton-Brock, Price, Albon & Jewell 1991), suggesting that our results are likely to be robust.

Our results suggest that the long-term data sets, which are such a valuable resource for researchers, are robust for the ≥1 year age class. This is the age class for which Coulson et al. (2000) found significant effects of population density and climate on fecundity. However, there is likely to be more uncertainty in the assignment of indi-

viduals to the 0-1 year age class. This is of concern because recent suggestions of sharp declines in fecundity suggest that it is this age class which is particularly suffering (Milner-Gulland et al. 2003). Visual assessment of females as being in the 0-1 year age class is not adequate for studies on which factors determine conception rates, and hence how best to target conservation action.

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