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SHORT COMMUNICATION

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Comparing simple methods for ageing roe deer *Capreolus capreolus*: are any of them useful for management?

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The dynamics of ungulate populations depend not only on the size, but also on the sex- and age-structure of the population. Successful management therefore depends on obtaining estimates of the age composition. Variation in performance due to age can be fairly well described by stages, and simple, rough methods for ageing cervids can therefore be useful to management. We assessed the performance of three relatively simple and objective methods based on tooth wear (height of molar), weight of eye lenses and diameter of pedicles (males only) on a sample of 77 female and 81 male European roe deer *Capreolus capreolus* from Lier, Norway. The relationship between tooth wear and age was linear, whereas the relationship between weight of eye lenses and diameter of pedicles was curvilinear with age, likely making them unreliable for old age classes. However, as only three males and six females ≥ 6 years old were included, we were unable to assess the uncertainty in age estimation for older age classes precisely. No simple method could precisely age roe deer, even up to five years of age. Our results do suggest that tooth wear, i.e. height of molar, can serve as a very simple and objective measure of age in roe deer, given that moderate precision (an error rate of ± 1 year and a success rate of 70% up to four years of age) is sufficient to reach management aims. As residuals between age estimates based on tooth wear and diameter of pedicle were not correlated, combining these methods improved the fit slightly. Since tooth wear may differ between areas, the scales presented here may perform less well in other areas, and a calibration for each area is clearly recommended.

Key words: eye lense weights, pedicle diameter, tooth sectioning, tooth wear

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Ungulate populations are strongly structured according to age and sex (reviews in Tuljapurkar & Caswell 1997, Gaillard et al. 1998, 2000), so there are large individual differences in performance within populations that are related to sex and age. The dynamics of ungulate populations of similar sizes may subsequently vary according to the age and sex composition of the herd (Coulson et al. 2001). Therefore, a manager needs not only to obtain indices of abundance or density (as well as other relevant information regarding condition of the animals and habitat quality), but preferably also of the sex and age composition of the population in order to predict future dynamics, and simple methods to age animals remain a central challenge in wildlife management. Fortunately, as performance can be fairly well described by age stages (i.e. juvenile, subadult, prime-aged and senescent stages; Gaillard et al. 1998), relatively coarse methods may be suitable for management.

Tooth sectioning is clearly the most widely used ageing method in ungulate research in Scandinavia and North America, as it has proven a highly reliable ageing technique in a number of ungulates inhabiting the strongly seasonal environments at northern latitudes (see e.g. Reimers & Nordby (1968) for reindeer *Rangifer tarandus*, Mitchell & Youngson (1969) and Hamlin et al. (2000) for red deer and elk *Cervus elaphus*, and Aitken (1975) for roe deer *Capreolus capreolus*). Tooth sectioning is based on counting annuli in the tooth cementum, which arise due to seasonally retarded growth during winter and increased growth during summer. However, to be able to read these lines it is necessary to have quite sophisticated laboratory equipment, or to send the samples to laboratories charging ~10€ per individual. In contrast, alternative methods either utilise the continuous wear with age (e.g. molar wear; Hewison et al. 1999), growth in the size of the eye lenses (Maringgele 1979, Ashby & Henry 1979, Angibault et al. 1993) or growth of the pedicles of male antlers (Stubbe et al. 1987, Stubbe 1997). However, the relative performance of these methods for ageing roe deer is largely unknown. Further, although the use of tooth wear has been subject to much research, several studies have assessed tooth wear based on a subjective scale (Szabik 1973, Hrabe & Koubek 1987, Cederlund et al. 1991). Studies that used an objective criteria (e.g. height of the molar) differ in their conclusions, reporting either limited (Cederlund et al. 1991), high (Ashby & Henry 1979) or variable (Hewison et al. 1999) success in predicting age.

In this paper, we compare three fairly simple methods for ageing roe deer using data on age obtained by tooth sectioning (as known-age material is unavailable). Our aim is to determine the success of these methods as viewed from a management perspective. However, such methods may also be useful for capture-mark-recapture studies, because a method for ageing live animals without the extraction of teeth would be valuable (Festa-Bianchet et al. 2002).

Material and methods

Study area

The study area is located in the Lier valley near Sylling in the municipality of Lier in the county of Buskerud in southern Norway (between 59°45'-60°00'N and 10°05'-10°20'E). Most of the area is forested and situated within the boreonemoral region (Abrahamsen et al. 1977). Vegetation is varied and dominated by Norway spruce *Picea abies* mixed with Scots pine *Pinus sylvestris* on the drier and poorer locations. Along the valley bottom on richer soil, deciduous forest is dominant, fragmented by small, cultivated fields (Kjøstvedt et al. 1998). The topography is extremely hilly (see Mysterud & Østbye 1995, Mysterud 1999, Mysterud et al. 1999 for a further description of the study area).

Data

Jaw bones, eye lenses and skulls from 77 female and 81 male roe deer aged ≥ 1 year old were collected and processed by Eivind Østbye during 1985-2001. We excluded fawns, as these can be aged by their pattern of tooth eruption (only 4-5 cheek teeth in their first autumn; Cederlund & Liberg 1995). As tooth sectioning is regarded as a highly reliable method for age determination in strongly seasonal environments such as Norway (for roe deer, see Aitken 1975), we use 'tooth section age' as 'known age'. The Matson Laboratory in the USA did all the age determination by tooth sectioning. Any error in the ageing will most likely increase the error rates reported, and thus if the methods are successful, this would likely lead to a conservative result. The following three methods were compared:

Method 1: molar height

Tooth wear is a well-known method frequently used for ageing cervids including roe deer (e.g. Hewison et al. 1999). We used an objective measure, namely the height of the second molar (M_2) measured to the nearest 0.1 mm using a calibre.

Method 2: eye lens weight

The size of the eye lenses has also been used previously for ageing roe deer (e.g. Maringgele 1979, Ashby & Henry 1979). We extracted both eye lenses from fresh heads, and used the average weight (to the nearest 0.001 g) after fixation in 10% formalin for 10 days and subsequent drying at 80°C.

Method 3: diameter of the pedicles

For males, a method for ageing individuals based on the diameter of the pedicle has been described (Stubbe et al. 1987, Stubbe 1997). We used average length and width on both sides of the head as a measure of diameter.

We also tried to combine tooth wear and diameter of the pedicles (Stubbe et al. 1987, Stubbe 1997).

Statistical analyses

We used linear models to determine the relationship between our response variables (M_2 height, eye lense weight and pedicle size) and the predictor variables. We used model selection and assessed fit with the Akaike Information Criterion (AIC; Johnson & Omland 2004) or by comparing r^2, as the latter was used in previous studies. We tried adding sex, a sex*age interaction term and a second-order term for age (in addition to only age). We also tried an ln-transformation of the response variables. The most parsimonious model was subsequently used to derive predictions. We then established intervals for each age by interpolation from the predicted values of the best model, and then reclassified the data into age by using these intervals to check the success rate. All models were run in S-Plus version 6.2 (Crawley 2003).

Results

Height of the second molar was the only measure linearly related to age (Fig. 1A, Table 1). A second-order term for age entered both the model for the weight of the eye lenses and for the diameter of the pedicles (see Table 1). The weight of the eye lenses did not increase after seven years of age. The diameter of pedicles seemed not to increase after 4-6 years of age, but this was only based on two data points, and the relationship was linear up to five years of age (testing for age^2 below six years of age: $T = 0.128$, $P = 0.898$; see Fig. 1). The weight of the eye lenses was larger for females than for males. The fit was improved slightly by ln-transforming the height of the molar ($r^2 = 0.547$ vs 0.590), but this did not apply for the weight of the eye lenses ($r^2 = 0.713$ vs 0.698) or the diameter of the pedicles ($r^2 = 0.391$ vs 0.375). Excluding ages > 7 years decreased the performance of molar height slightly ($r^2 = 0.484$).

Except for 1-year-old roe deer, no method was able to determine 50% to the correct age. However, if allowing for ± one year, the success rate of the tooth-wear method was > 70% up to four years of age, but with a tendency to overestimate age (Table 2). Similarly, the success rate (± 1 year) of the eye-lense method was > 60% up to five years of age in both sexes, and up to four years for the size of the pedicle.

It may be possible to combine methods to improve accuracy in ageing if the same individuals are not over- or underestimated by both methods, i.e. if the residuals are not correlated. There was no correlation between

Table 1. Results from model selection and parameter values from the most parsimonious models. Model selection was done starting with age only, then adding (age)^2, sex and sex*age, including or excluding factors depending on whether fit was improved or not. AIC = Akaike Information Criterion, ΔAIC = difference in AIC value between the AIC for the model given in that row and the most parsimonious model (lowest AIC), l.s. mean = least square mean, SE = standard error, T = Student's T test statistic, P = significance probability.

Parameter	AIC	ΔAIC	l.s. mean	SE	T	P
A. ln(molar height)						
Intercept			2.1362	0.0135	157.944	0.000
Age	-237.151	0.000	-0.0641	0.0046	-13.950	0.000
(Age)^2	-236.053	1.099				
Sex	-235.466	1.686				
Age*sex	-234.097	3.054				
B. Eye lense weight						
Intercept			0.2184	0.0050	43.914	0.000
Age	-681.193	42.292	0.0379	0.0029	12.999	0.000
(Age)^2	-716.754	6.731	-0.0021	0.0003	-6.890	0.000
Sex	-723.485	0.000	-0.0119	0.0040	-2.958	0.004
Age*sex	-721.629	1.856				
C. Pedicle diameter						
Intercept			15.3328	0.7397	20.729	0.000
Age	315.399	2.051	1.9410	0.4918	3.946	0.000
(Age)^2	313.348	0.000	-0.1255	0.0628	-1.997	0.050

Table 2. Predicted values for the relationship between age and height of the second molar (in mm), weight of the eye lenses (in g) and diameter of the pedicles (in mm). The intervals used to estimate age in roe deer were based on the most parsimonious models given in Table 1, and the success rate (proportion correct and proportion within ± 1 year) is given relative to age estimated based on tooth sectioning.

				Age - based on tooth sectioning													
Estimated age	Predicted	Lower limit	Upper limit	1	2	3	4	5	6	7	8	9	10	12	N	Prop. correct	Prop. ± 1 year
A. Molar height															137		
1	7.941	>7.695		47	9	3	4								63	0.75	0.89
2	7.448	7.217	7.695	14	9	2	2								27	0.33	0.93
3	6.986	6.769	7.217	4	6	3	3								16	0.19	0.75
4	6.552	6.349	6.769	2	1	7	1	2				1			14	0.07	0.71
5	6.145	5.955	6.349		1	2	1	2							6	0.33	0.50
6	5.764	5.585	5.955				2	2							4		
7	5.406	5.238	5.585				1		1	1					3		
8	5.070	4.913	5.238												0		
9	4.755	4.608	4.913												0		
10	4.460	4.322	4.608				1							1	2		
11	4.183	4.053	4.322								1		1		2		
12	3.924		<4.053												0		
B. Eye lense - females															77		
1	0.263		<0.277	37	5										42	0.88	1.00
2	0.291	0.277	0.303	2	6	2	1								11	0.55	0.91
3	0.315	0.303	0.325	2	3	3	2								10	0.30	0.80
4	0.335	0.325	0.344			3	2								5	0.40	1.00
5	0.352	0.344	0.359			1	2	1	1						5	0.20	0.80
6	0.366	0.359	0.371			1		1					1		3		
≥7	0.376	>0.371												1	1		
B. Eye lense - males															81		
1	0.251		<0.265	36	5	1									42	0.86	0.98
2	0.278	0.265	0.290	3	4	2		1							10	0.40	0.90
3	0.302	0.290	0.313	1	3	3	3								10	0.30	0.90
4	0.323	0.313	0.331			4	2	3							9	0.22	1.00
5	0.340	0.331	0.347			1	4					1			6	0.00	0.67
6	0.354	0.347	0.359														
≥7	0.364	>0.359			1			2	1						4		
C. Pedicle diameter															68		
1	17.148		<17.931	21	6	2									29	0.72	0.93
2	18.713	17.931	19.370	6	3	2	2								13	0.23	0.85
3	20.026	19.370	20.558	2	2	1	2	1							8	0.13	0.63
4	21.089	20.558	21.495			2	2	2				1			7	0.29	0.86
5	21.900	21.495	22.461	2		1									3	0.00	0.00
≥6	22.461	>22.461			1		4	2			1				8		
D. Tooth wear and pedicle diameter															67		
1				22	9	1	1								33	0.67	0.94
2				7	1	3	1								12	0.08	0.92
3				2	2	1	2								7	0.14	0.71
4						3	3	3				1			10	0.30	0.90
5							1	1							2	0.50	1.00
≥6							2	1			1				3		

residuals estimated from tooth wear and those estimated based on the diameter of the pedicle ($r_{Pe} = 0.127$, df = 66, P = 0.302), very weak correlation between residuals based on tooth wear and those from size of the eye lenses ($r_{Pe} = 0.217$, df = 117, P = 0.018), whereas the residuals from using the size of eye lenses and the diameter of pedicles to age roe deer were correlated ($r_{Pe} = 0.522$, df = 57, $P < 0.001$). This indicates that combining methods using measures of body size will not add much more predictability, whereas combining tooth wear and methods using size will improve success. Indeed, slightly improved precision was obtained when combining tooth wear with the diameter of the pedicles (see Table 2).

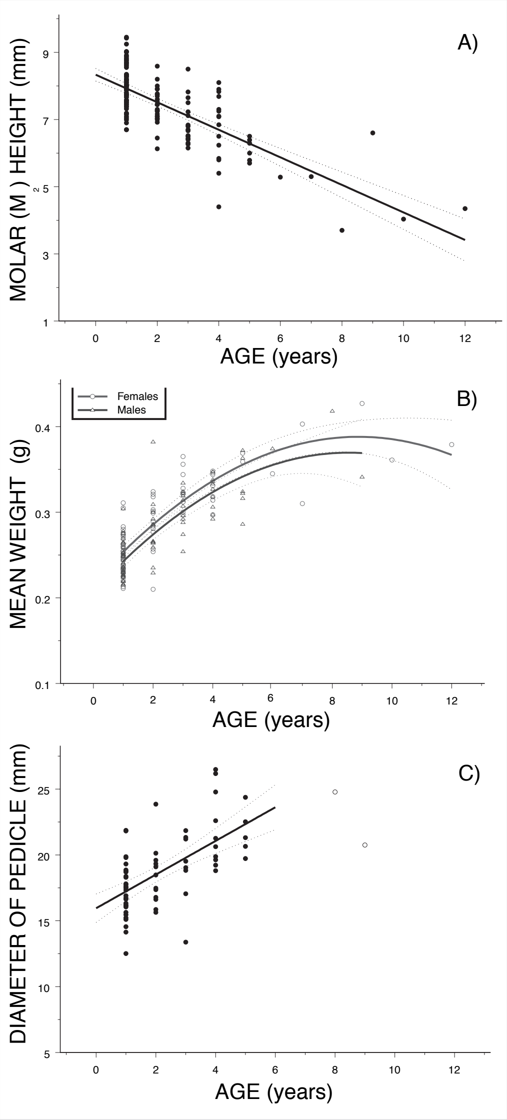

Figure 1. Relationship between age (as determined by tooth sectioning) and A) molar height, B) mean weight of the eye lenses and C) mean diameter of the pedicles. The lines indicate 95% confidence intervals.

Discussion

We compared the performance of three fairly simple methods for ageing roe deer based on: the relationship between age and tooth wear, the size of the eye lenses and the diameter of the pedicles. The main result is that none of these simple methods could age roe deer precisely. However, if a lower precision is sufficient, some of them may still be useful for management.

The general body size in roe deer males reaches a plateau at about 4-5 years of age (Andersen et al. 1998). Although based on only two data points, we found a pattern consistent with this. From around 4-6 years of age, the diameter of the pedicles does not seem to increase further (see Fig. 1). Any size measure will likely perform equally well, making this the least useful method. It is difficult to see any advantages of this method over for example tooth wear rates.

Size of the eye lenses is a simpler method than tooth sectioning, and the method performs quite well. Indeed, for ages up to five years it performs better than tooth wear (see Table 2). Our results are roughly in accordance with previous studies also reporting that a plateau for eye-lense size was reached at about 6-7 years of age (Maringgele 1979, Ashby & Henry 1979). Ashby & Henry (1979) concluded that eye lense weights were useless as a method, since the relationship between age and eye-lense size was not linear. However, this can be overcome by fitting a curvilinear relationship for age (see Fig. 1), and does not mean that the method is useless, but rather that weight intervals for estimating age decrease with increasing age (see Table 2). The method seems unsuitable for age determination above a threshold age of around seven years. We also found a sex difference in eye-lense weight, which was not tested for previously. Sexing the animals can therefore increase performance relative to previous accounts (Maringgele 1979, Ashby & Henry 1979). However, drying and preparing the eye lenses still requires some equipment not available to most managers, and may therefore be less suited than tooth wear if larger samples should be processed each year in population monitoring.

Using either a subjective or objective assessment of tooth wear has been a common approach to age roe deer (Szabik 1973, Cederlund et al. 1991, Hewison et al. 1999). When comparing a subjective assessment of wear with an objective criteria (height of the molar), Cederlund et al. (1991) reported that the subjective assessment of wear seemed to perform slightly better. However, the persons performing the assessment in Cederlund et al. (1991) were skilled, possibly underestimating the error rates of the subjective assessment. A more serious problem is related to the fact that such subjective methods give biased results which depend on the experience of the observer, inexperienced persons typically being more likely to overestimate age of younger animals and underestimate age of older animals (Cederlund et al. 1991, Szabik 1973, Hewison et al. 1999). The studies that have used molar height to assess age differ in their conclusions, reporting either limited ($r^2 = 0.44$; Cederlund et al. 1991), high ($r^2 = 0.74$; Ashby & Henry 1979) or variable success depending on population (r^2 = 0.36-0.66; Hewison et al. 1999) in predicting age. Our study comes between this (r^2 = 0.59), while two other studies used molar height without giving an exact fit (Stoddart 1974, Aitken 1975). In our case, the fit was improved by an ln-transformation, which was not used in previous studies. Ashby & Henry (1979) excluded ages of 8-10 years, and indeed, the wear rate of very old age classes (in red deer) decreased more than predicted even from a log-linear relationship (Loe et al. 2003). Our fit was not improved by excluding the few very old animals, while animals of old age were not present in the study by Cederlund et al. (1991). At least some of the within-age variation in tooth wear may be due to reported individual variation in diet due to local-scale habitat variation (Mysterud et al. 1999).

Since measuring the height of the molar is an objective method, it is possible to estimate the likelihood of bias. Indeed, we seemed to overestimate age with the tooth-wear method (see Table 2). Also, since error rates are not much higher than for subjective criteria (Cederlund et al. 1991), this makes it a more appropriate method for long-term monitoring when changes in the personnel performing the procedure are common. Some caution is nevertheless required. Since the performance of the methods in our study is scaled with the same material, as was also done in previous studies (Ashby & Henry 1979, Cederlund et al. 1991), the intervals presented may not perform equally well in other areas. Tooth wear may vary somewhat between areas (Hewison et al. 1999), which may lead to biased estimates. This is not overcome by using an objective assessment of wear. Clearly, more sophisticated ways for measuring tooth wear than molar height may increase precision (Pérez-Barbería & Gordon 1998a, Pérez-Barbería & Gordon 1998b), but such measures cannot be easily obtained. As residuals for age estimates based on tooth wear and those based on the diameter of the size of the pedicle were not correlated, an increased fit was obtained by combining the two methods (Stubbe et al. 1987, Stubbe 1997), but this method can only be used with males.

Whether the precision reported for molar height in our study is good enough or not, depends on the objectives. For a manager, it is most important to be able to classify the proportion of juvenile, subadult, adult and senescent stages (see Gaillard et al. 1998). Harvested populations also have a low average age (Langvatn & Loison 1999), so it may not be important to have a very high precision for old age classes. Using the height of the molar provides a very easy method for ageing, and we argue that it is suitable for most routine studies. However, we clearly need more information to be able to predict spatially variable molar wear rates in ruminants in general, which is necessary in order to avoid biased estimates. Even though these methods are mainly aimed at management, such methods may also be useful for science when performing capture-mark-recapture studies, as the ability to age live animals without having to extract teeth would be valuable (Festa-Bianchet et al. 2002). This may be feasible for some species, but error rates will likely be higher due to measurement error, severely restricting the applicability in studies of life history variation.

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