

RESEARCH ARTICLE

Judging a reindeer by its teeth: A user-friendly tooth wear and eruption pattern recording scheme to estimate age-at-death in reindeer (*Rangifer tarandus*)

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Abstract

Reindeer (*Rangifer tarandus*) have shaped the cultures and provided livelihood to peoples of the Northern Hemisphere for thousands of years. They are still the socio-economic cornerstone of many northern cultures. Insight into reindeer mortality patterns is important for understanding past human–reindeer interactions and reindeer population fluctuations in relation to climatic and environmental change. Beyond archaeology, assessing the age structures of modern reindeer populations is important for developing wildlife management strategies. This paper presents a quick, non-destructive and cheap method to estimate age in reindeer in both modern and ancient populations based on tooth wear and eruption patterns of mandibular teeth. We devised the method using a large sample of Svalbard reindeer (*Rangifer tarandus platyrhynchus*) of known age. We blind-tested the method and tested its applicability on another known-age Svalbard reindeer mandible assemblage. The tests demonstrate our methods' user-friendliness and reliability to generate reproducible, reusable datasets and accuracy in estimating reindeer age-at-death.

KEYWORDS

Cervidae, dentition-based age estimation, mortality profile, reproducible datasets, Svalbard, zooarchaeological methods

1 | INTRODUCTION

Understanding the mortality patterns of mammals associated with humans is crucial to gain insights into past hunting, management, and husbandry practices. Mortality patterns also shed light on diachronic and regional population fluctuations induced by climate and environmental change. Most methods developed to reconstruct mortality patterns focus on teeth because tooth eruption patterns strongly correlate with age (e.g., De Bie, 1977; Silver, 1963) and teeth are commonly well preserved in the archaeological record (Lyman, 1994; Reitz & Wing, 2008, 195–196; Twiss, 2008). Teeth also allow for ageing beyond the range of epiphyseal fusion (Payne, 1973;

Hufthammer, 1995; Hambleton & Rowley-Conwy, 1997, 60), allowing distinctions between young, prime and older adults (Klein & Cruz-Uribe, 1984). Although the exact ages at which teeth are fully erupted and thus come into wear are variable (O'Connor, 2000; Payne, 1973), observing tooth wear and eruption (TWE) patterns is a commonly used method to age mammals.

Here we present an easy-to-use, non-destructive, high-accuracy method to record TWE and estimate age-at-death in reindeer (*Rangifer tarandus*) based on the visual examination of the senescence of the occlusal surfaces and eruption patterns of the lower molariform teeth of Svalbard reindeer (*Rangifer tarandus platyrhynchus*). The method entails two scoring schemes: One scheme is an absolute

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scheme (the Absolute Scheme) that is designed to estimate the age-at-death of the Svalbard deer pretty accurately. The second scheme is a relative scheme (the Relative Scheme) that is meant to estimate the relative age-at-death of any (archaeological) population of reindeer, which can be calibrated to estimate absolute age. Results of a blind test demonstrated the user-friendliness of both schemes and how they reduce inter-analyst bias.

Reindeer is one of the most common species in European zooarchaeological assemblages since the Palaeolithic (e.g., Napierala, 2009; Salmi et al., 2015; Takken Beijersbergen, 2017b). Methods that are currently in use to estimate age-at-death of archaeological, sub-modern and modern reindeer include measuring molar crown height (e.g., Enloe & Turner, 2002; Morrison & Whitridge, 1997; Pike-Tay et al., 2000), counting cementum annuli (e.g., De Bie, 1977; Loison et al., 2001; Miller, 1974a; Pasda, 2006; Reimers & Nordby, 1968; Takken Beijersbergen, 2017a) and, most commonly, observations on occlusal wear and eruption patterns (e.g., Bromée-Skuncke, 1953; Bouchud, 1966; Bergerud, 1970; Miller, 1972; Miller, 1974b; Pasda, 2009; Takken Beijersbergen, 2017b).

The molar crown height method has been tested for *Rangifer* several times (e.g., Enloe & Turner, 2002; Pasda, 2009; Pike-Tay et al., 2000) but proved quite inaccurate (also for *Capreolus capreolus*: e.g., Tomé & Vigne, 2003). The cementum annuli method is very accurate (Aitken, 1975; Baumgartner et al., 2004; De Bie, 1977; Miller, 1974a; Pérez-Barbería et al., 2014) but destructive, time consuming (Brown & Chapman, 1990) and relatively expensive. Ageing methods based on dental wear and eruption patterns are relatively quick, non-destructive and cheap and therefore often provide the largest datasets on animal mortality patterns available, including those for archaeological and modern Cervidae (e.g., Baumgartner et al., 2004; Bowen et al., 2016).

Tooth wear rates vary within and among populations, even change during an individual's lifetime, depending on diet, food availability, substrate, health, genetics and individual teeth's enamel mineralization characteristics (e.g., Hewison et al., 1999; Kojola et al., 1998; Miller, 1974b; Skogland, 1984; Skogland, 1988). Despite these limitations, several studies have shown that TWE is useful to estimate age-at-death for (archaeo)faunal populations (e.g., Lowe, 1967, in Grant, 1978, for red deer [*Cervus elaphus*]; Greenfield & Arnold, 2008, for sheep [*Ovis aries*] and goat [*Capra hircus*]; Payne, 1973, for sheep and goat; Høye, 2006, for roe deer; Bowen et al., 2016, for fallow deer [*Dama dama*]; Baumgartner et al., 2004, for red deer; Twiss, 2008).

TWE-based ageing schemes in use for reindeer (Banfield, 1954; Bergerud, 1970; Bouchud, 1966; Bromée-Skuncke, 1953; Miller, 1972, 1974b; Pasda, 2009; Skoog, 1968) have been criticized on various grounds, for example, high degree of subjectivity (Pasda, 2009, 33) and too narrow or too broad age classes (e.g., Spiess, 1979, 78–80; Grønnow et al., 1983, table 5; Takken Beijersbergen, 2017b). Some are not adapted for quick and easy (re-)use (e.g., Bromée-Skuncke, 1953). Probably for the same reasons, some studies on reindeer mortality have resorted to Payne's (1973) famous sheep/goat tooth wear diagrams (e.g., Hambleton & Rowley-Conwy, 1997, 59–60). More importantly, the age estimates previous schemes

offered have never been cross-checked with specimens of known age. The currency attempts to redress these shortcomings.

2 | MATERIALS

Two modern collections of mandibles of known-age Svalbard reindeer (*Rangifer tarandus platyrhynchus*), the northernmost living cervid and the only herbivore on Svalbard, were available for the study.

The first collection consists of mandibles from individuals from the Nordenskiöld region (Figures 1), where reindeer are subject to controlled hunting. It is curated by the Natural History Museum of the University of Oslo, Norway. The Nordenskiöld collection was aged based on tooth eruption patterns in young (between 0 and 2 to 3 years old) individuals and by counting the cementum annuli of the incisors in older individuals in a previous study (Hansen et al., 2012). For a detailed description of the cementum analysis used here, see Hansen et al. (2012). From here on we refer to the age determined through tooth eruption patterns and cementum analysis as “true age.” For this study, the teeth of 316 aged mandibles representing 163 individuals (a total of 316 left and right mandibles; for 10 individuals only the right or left mandible was present) were examined (Table S1 and Data S1) for tooth eruption and wear to build the Absolute and Relative Schemes, and blind-test the Absolute Scheme. Of the mandibles of 163 individuals, 12 individuals exhibited either unusual wear or eruption patterns, were pathological, broken or covered in left-over meat and/or mould. These were omitted from the analysis. Some individuals had either the right or left mandible present, so ultimately, we used 292 mandibles, representing 151 individuals. For more information on this collection, see Appendix S1.

The second collection consists of mandibles collected from the reindeer's winter range on the island of Edgeøya during the Dutch Spitsbergen Expedition of 1968–1969 (Figure 1) (De Bie, 1977). The individuals represented by these mandibles may have been shot dead by hunters or died from natural causes from 1925 onward when the reindeer population became protected. Scientists picked them up from the ground. The collection is curated by the Arctic Centre of the University of Groningen, the Netherlands. The Edgeøya collection includes the mandibles of 244 individuals, 163 of which have been aged using tooth eruption and the cementum annuli method. The first molars (M1) were destroyed in the process (De Bie, 1977). For a detailed description of this method, see De Bie (1977). For this study, 60 of these aged mandibles from 60 different individuals from the Edgeøya collection were examined for TWE to test the Absolute and Relative Schemes.

For an overview of the mandibles used to construct the schemes, see Tables S2 and S3.

3 | METHODS AND RESULTS

To assess the tooth eruption patterns in the Nordenskiöld collection (Figure 2), the deciduous fourth premolar (Dp4), permanent fourth

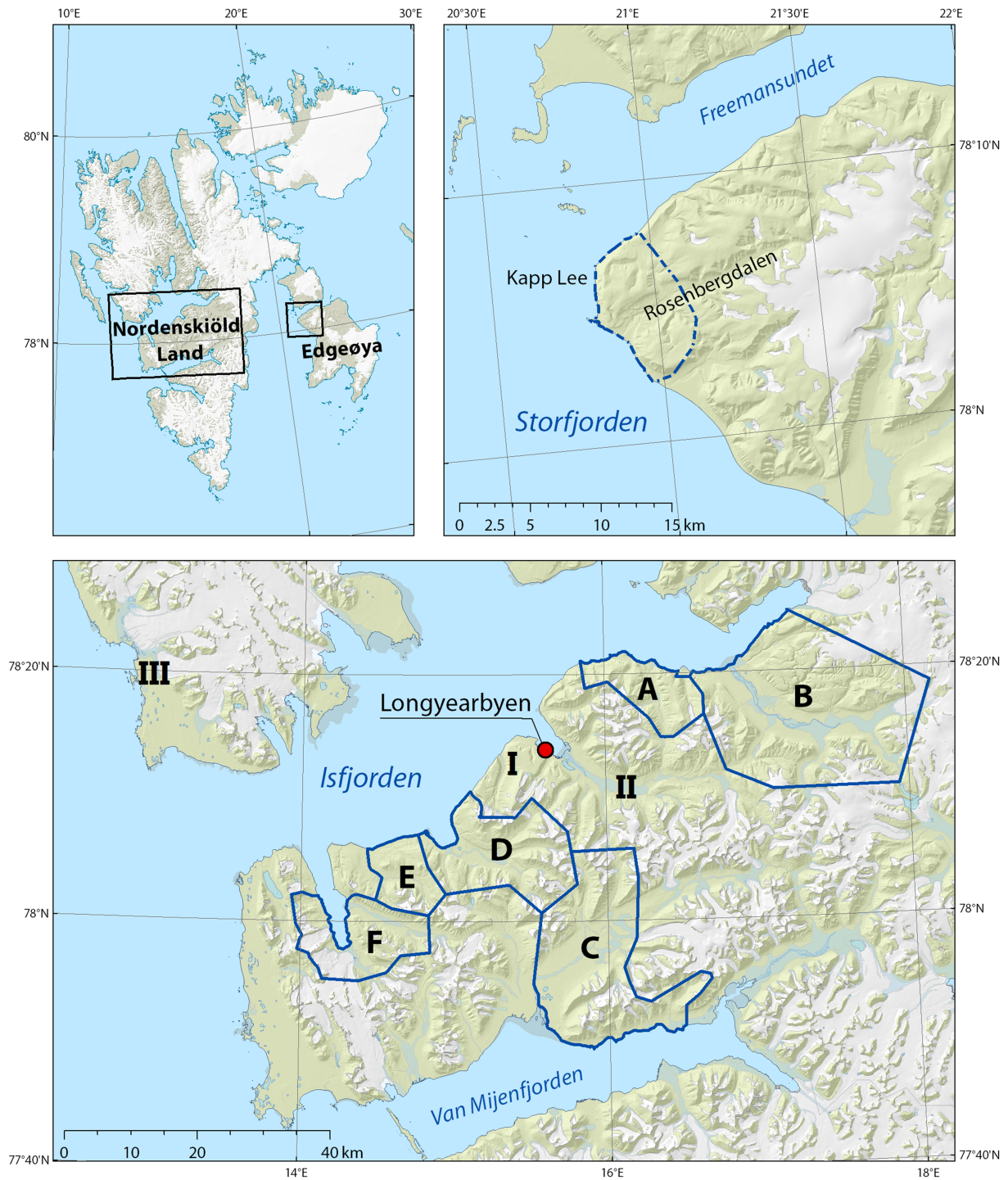


FIGURE 1 Upper left: The Svalbard Archipelago with the outlines of Nordenskiöld Land and Edgeøya. Upper right: The area of Edgeøya where the skulls and jaws were collected during the 1968–1969 Dutch Spitsbergen Expedition (after De Bie, 1977, fig. 1). Lower: the jaws of the Nordenskiöld collection mainly come from animals from the six hunting areas in Nordenskiöld (A, Diabas; B, Sassendalen; C, Reindalen; D, Colesdalen; E, Hollanderdalen; F, Grøndalen), and a minor portion comes from unknown or other areas (I, Platåberg Björndal; II, Adventdalen; III, Farmhamna) (after Governor of Svalbard, 2009, fig. 6) (maps by Frits Steenhuisen) [Colour figure can be viewed at wileyonlinelibrary.com]

premolar (P4), first molar (M1), second molar (M2) and third molar (M3) of the 0 to 3 years old (following De Bie, 1977) specimens from the buccal, lingual and occlusal views were examined. Of the 151 individuals that we ultimately used, 39 individuals exhibited tooth

eruption. State of eruption was recorded using the codes in Ewbank et al. (1964):

C: perforation in Crypt [=dental alveoli] visible

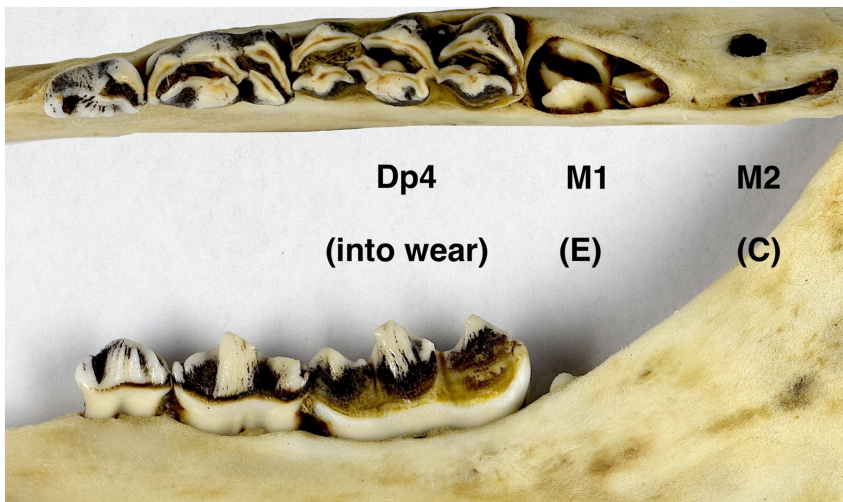


FIGURE 2 The occlusal surface and lingual view of the right mandible of a 0-year-old reindeer: an example of the assessment of state of eruption (Specimen 153/2009 from the Nordenskiöld collection). This particular specimen shows a deciduous premolar 4 (Dp4) that is into wear with exposed dentine, a first molar (M1) that is erupting through the bone (E), and a second molar (M2) for which the perforation in the Crypt (dental alveoli is visible (C)) [Colour figure can be viewed at wileyonlinelibrary.com]

V: tooth Visible in crypt

E: tooth Eruption through bone

H: tooth about Halfway between bone and full height

T: Tooth (almost) at full height but unworn

Reindeer have selenodont teeth; the dentine and enamel the teeth are composed of create complex patterns of enamel–dentine infoldings (Fortelius et al., 2002) that show on the tooth's occlusal surface when worn (Hillson, 1986, 214). The wear on the molariform teeth (Figure 3) proceeds from anterior to the posterior (Spiess, 1979, 70–71).

High quality photos of each mandible from the buccal, lingual and occlusal views were produced. Photos of the occlusal surfaces were examined, and the mandibles were arranged according to state of wear, just as Grant (1982) did for domesticated mammals. The schemes display right-side teeth in which left-side teeth were mirrored vertically to fit the schemes.

3.1 | Constructing two schemes: An Absolute Scheme and a Relative Scheme

Two TWE schemes were designed: An Absolute Scheme for the reindeer of Svalbard of all different valleys to estimate their

absolute age and a Relative Scheme for *Rangifer* and all of its subspecies (Figures 4 and 5) to estimate relative age. The Absolute Scheme displays a less linear tooth wear progression with more individual variation and is less precise than the Relative Scheme, because the tooth wear stages (TWS) of different ages overlap. The Relative Scheme exhibits an idealized pattern of tooth wear progression.

The reason for constructing two schemes is to highlight the large range of variation in TWE among individuals representing different subpopulations. The reindeer mandibles examined exhibited great variation in tooth wear progression within the same age classes (known from cementum annuli work). Overlap in wear between bordering age classes is quite normal for a given population, especially in older age categories (e.g., Bowen et al., 2016; Grant, 1982). The Nordenskiöld collection, on the other hand, comes from at least six different hunting grounds, and although these regions are adjacent to each other and less than 30 km apart, the Svalbard reindeer is site-bound (Governor of Svalbard, 2009, 8–9), mostly residing in their home valley year round (R.W.J. Visser, personal communication, 2018). Lower food availability leads to higher rates of tooth wear because reindeer forage on shorter vegetation, take more substrate into their mouth (Loison et al., 2001; Skogland, 1988) and

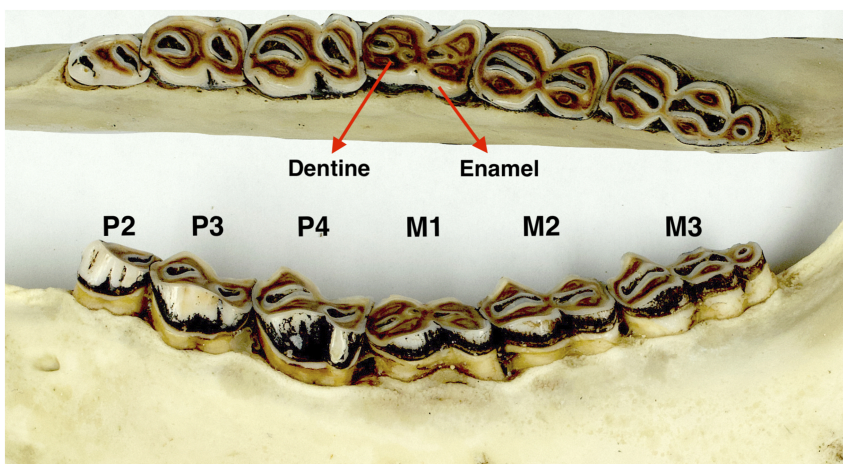


FIGURE 3 Molariform (M1, first molar; M2, second molar; M3, third molar; P2, premolar 2; P3, premolar 3; P4, premolar 4) reindeer teeth, showing the light-coloured enamel and dark-coloured dentine patterns as a consequence of tooth wear in this 8-year-old individual (Specimen 127/2008 from the Nordenskiöld collection) [Colour figure can be viewed at wileyonlinelibrary.com]

Tooth wear stages of reindeer teeth: the Absolute scheme

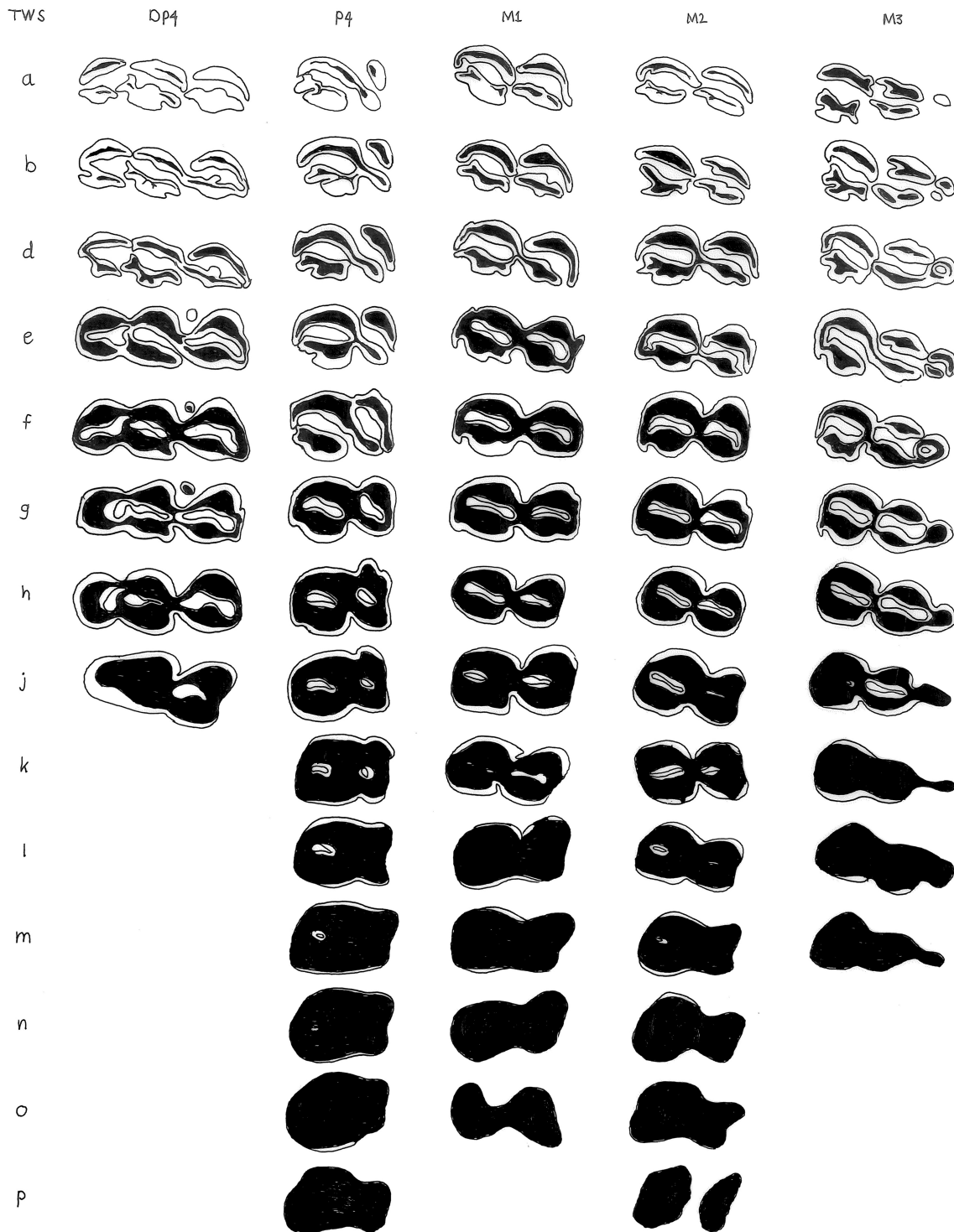


FIGURE 4 Absolute enamel-dentine pattern progression for the molariform teeth from the left mandible. See Figure S1 and Table S2 in the Supplementary material file for the original photos and exact specimens used for this scheme. TWS, Tooth Wear Stage for the tooth wear stages “a” to “p,” for the deciduous premolar 4 (Dp4), first molar (M1), second molar (M2), and third molar (M3)

graze on coarser, less preferred foods (Kojola et al., 1998). Variation in food availability between these valleys have probably affected subpopulations' tooth wear rates differently. To construct a scheme,

ideally the TWSs of the scheme and the absolute ages of the source population are linked in a linear manner, but reality is more complex.

Tooth wear stages of reindeer teeth: the Relative scheme

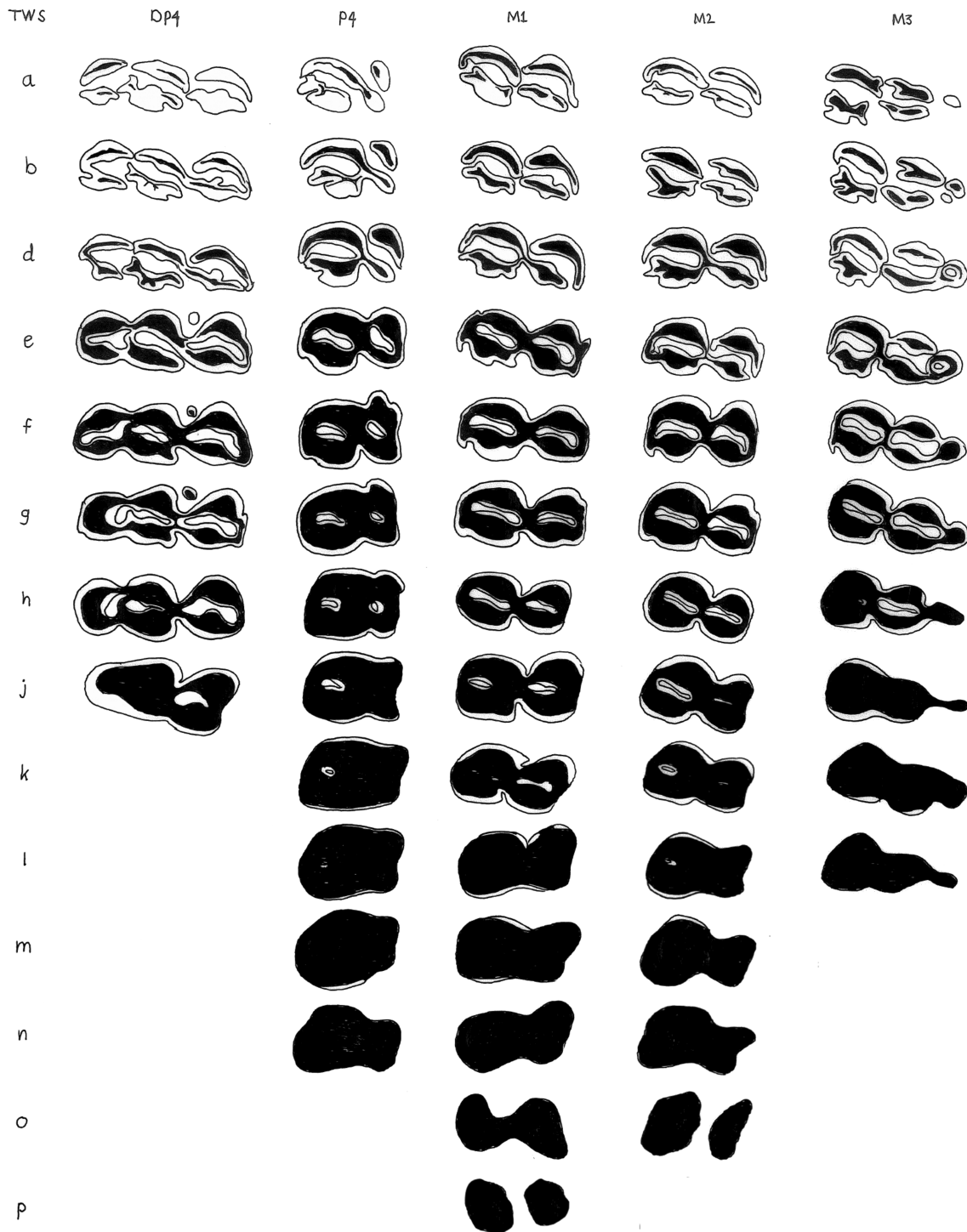


FIGURE 5 Relative enamel-dentine pattern progression for the molariform teeth from the left mandible. See Figure S2 and Table S3 in the Supplementary material file for the original photos and exact specimens used for this scheme. TWS, Tooth Wear Stage for the tooth wear stages “a” to “p,” for the deciduous premolar 4 (Dp4), first molar (M1), second molar (M2), and third molar (M3)

The final raw versions (Figures S1 and S2) of the Absolute and Relative Schemes were drawn with black ink and digitized. These illustrations are thought to be more useful than the photos, because

dentine and enamel (black and white in the illustrations, respectively) are easily recognizable in the drawings. In photos, colours can create confusion because the dentine and enamel can have different colours

in different mandibles, and sometimes the enamel or dentine is not clearly visible.

The state of eruption or the tooth wear progression of each tooth determines which TWS a tooth is assigned. For tooth eruption, five different Eruption Codes (C, E, V, H, and T) are used to describe the TWS, and for teeth displaying tooth wear, the TWS ranges alphabetically from “a” to “p,” excluding “c” and “i” because they could be confused with letters for other TWSs. Stage “a” was often confused with “T,” so we redefined TWS “a” to show the first stage of dentine wear. These TWS are linked to an Absolute Score for the Absolute Scheme (Table 1) and a Relative Score for the Relative Scheme (Table 2). These scores are numerical representations of the eruption pattern and tooth wear progression of a tooth: the further erupted or more worn a tooth, the higher the score. The Absolute Scores are the mean ages of the age range at which a particular tooth wear pattern is present. For example, the tooth wear pattern of the P4 of TWS “d: can be exhibited in 4- to 5-year-old individuals, so the mean age and score for TWS “d” is 4.5.

The Mandible Wear Stage (MWS) of each mandible was calculated by taking the mean of the individual tooth scores in a mandible. For example, when P4, M1, M2 and M3 are present in a mandible, the sum of all TWS scores is divided by four. When a mandible has the M2 and M3 present then the sum of the TWS scores is divided by 2. When a mandible has, for example, the Dp4, M1 and M2 present, but the M3 has not erupted yet, then the sum of all TWS scores

TABLE 1 Tooth Wear Stages linked to the Absolute Scores, for tooth eruption “C” to “T” (C, perforation in Crypt visible; V, tooth Visible in crypt; E, tooth Eruption through bone; H, tooth almost Halfway between bone and full height; and T, tooth [almost] at full height but unworn) and tooth wear stages “a” to “p”

T.W.S.	Dp4	P4	M1	M2	M3
C	0		0	0	0
V	0		0	0	1
E	0		0	0	1
H	0		0	0.5	1
T	0	2	0	1	1.5
a	0	2.5	1	2	3
b	0	3.5	1.5	2	3.5
d	0	4.5	2	3.5	4.5
e	1	6	3	4.5	6.5
f	1	7.5	3.5	5.5	7
g	1	8.5	5.5	6	8
h	1	9	8	8	11
j	1	10.5	8.5	9	11.5
k		12	8.5	11	11.5
l		12	11	11	12
m		11.5	10.5	11.5	13
n		13.5	11	12	
o		14.5	13	12	
p		14.5		14	

TABLE 2 Tooth Wear Stages linked to the Relative Scores, for tooth eruption “C” to “T” (C, perforation in Crypt visible; V, tooth Visible in crypt; E, tooth eruption through bone; H, tooth almost Halfway between bone and full height; T, tooth (almost) at full height but unworn) and tooth wear stages “a” to “p”

T.W.S.	Dp4	P4	M1	M2	M3
C	0	0	0	0	1
V	0	0	0	0	1
E	0	0	0	0	1
H	0	1	0	0.5	1.5
T	0	2	0	1	2
a	0	2.5	1	2	3
b	0	3.5	1.5	2	3.5
d	0	6	2	3.5	4.5
e	1	8.5	3	4.5	7
f	1	9	3.5	5.5	8
g	1	10.5	5.5	6	11
h	1	12	8	8	11.5
j	1	12	8.5	9	11.5
k		12	8.5	11	12
l		13.5	11	11.5	13
m		14.5	11	12	
n		14.5	11	12	
o			13	14	
p			13		

should still be divided by 4. The accuracy of the age estimation based on MWS increases with the number of TWS observations possible on a given mandible.

This method of assigning MWSs to mandibles differs from the well-known and widely adopted method developed by Grant (1982). To create the MWS, Grant (1982) assigned each TWE stage to a number ranging from 1 to 20, in which the same number is always linked to the same TWS, independent of tooth. The first eruption stage is equal to 1, the second to 2, etc., and the first TWS “a” is equal to 6, the second TWS “b” is equal to 7, etc. In this method it does not matter whether the M1 or the M3 is linked to TWS “a”; they will both get the numerical value of 6.

However, M1, M2 and M3 erupt progressively, so assigning each molar the same TWS and number distorts the resulting age estimation. This problem is circumvented in, for example, Payne (1973) and Bowen et al. (2016) by defining several TWE stages, in which the degree of wear expected on individual teeth is specified. For example, for sheep and goat Payne defines MWS E as “M3 in wear, posterior cusp unworn,” and for fallow deer Bowen et al. define MWS E as “Dp4 has TWS between e-g; M1 has TWS between c-d; M2 has TWS between a-c; and M3 has TWS between C-H.”

Our method improves the TWE stages by assigning average age classes to the TWS linked to a particular tooth. Age classes derive from the true age of the individuals used to build the Absolute Scheme. The Relative Scheme applies a similar method; only that the scores are not

absolute but *relative*. This means that the Relative Scores are in no way meant to represent the *actual* ages of the individuals represented by the mandibles but meant only as *abstract* numbers.

The only problem with this way of assigning values to the Relative TWS is that when a MWS is created, the abstract number gives the impression of absolute age because it so closely resembles one. For example, when using the Relative Scheme, a MWS of 7–8 does not mean the actual age of between 7 and 8 years old, but it means a relative age stage of 7–8. Therefore, it is imperative that the person applying this method is aware of the manner in which the results of this method should be interpreted. It is impossible to predict the absolute age in years of an individual on the basis of TWE, if the tooth wear progression rate of that population is not well studied.

A TWS scoring and MWS calculation sheet is presented to aid users of our method with the procedure (Table S4).

3.2 | Blind tests

Available students and staff of the Groningen Institute of Archaeology (GIA) blind-tested the Absolute Scheme in order to assess ease of application, inter-observer bias, and the justification of age estimates. The Absolute Scheme granted an opportunity to test the accuracy of the age estimates as they are based on a population of known age. Both inexperienced ($n = 6$) and experienced ($n = 5$) observers participated in the test to evaluate the convenience of the method for individuals with different levels of experience. The inexperienced users applied the Grant (1982) TWE scheme on archaeological specimens for 6 to 8 h in a bachelor's level zooarchaeology 1 to 4 years prior to the blind test. They have not worked with such a scheme since. The experienced users are either specialized or specializing in

zooarchaeology, have worked with the Grant scheme independently and have more experience with ageing animals through their dentition.

Each observer was provided with a sub-sample of the Nordenskiöld collection containing photos of 20 to 25 randomly picked (left or right) mandibles representing all age classes (Table S5). Observers were instructed to look at the photos and score all molariform teeth in each pictured mandible for tooth eruption and wear using the Absolute Scheme and assigning a TWS to each tooth. There was no time restriction, but it took each observer between 1 and 2 h to complete the assignment. Each observer's TWS results were then transcribed to MWS scores of absolute age. Finally, the MWS was compared to the true age of the individual the mandible represented. Deviations of the estimated ages from the true age were calculated and classified into ranges of 0 to 0.5, 0.6 to 1, 1 to 1.5, 1.5 to 2, and more than 2 years. To test the scheme's accuracy when applied to mandibles from younger versus older reindeer individuals, the results were assessed in terms of three age categories (of 0 to 5, 6 to 10, and 11 to 15 years). The rare cases when participants noted a double TWS score for a tooth, for example, a “j/k” instead of a “j” or a “k,” were omitted, because double scores would have led to potentially erroneous statistical results, confusing the evaluations.

3.3 | Application of the Absolute and Relative Scheme on the Edgeøya collection

The Relative and the Absolute Schemes were tested on 60 mandibles from 60 individuals from the Edgeøya collection ranging from age class 0–1 to 16–17 years (Table S6). Age classes 0–1 to 7–8 each contained five different mandibles per class. Age classes 8–9 to 16–17

TABLE 3 Tooth eruption patterns observed on known-age individuals in this study compared with other studies of tooth eruption patterns in different reindeer subspecies and populations

Tooth	This study, $n = 39$	Bergerud (1970), $n = 48$	Bouchud (1966), $n = \text{unknown}$	Miller (1974b), $n = 374$	Pasda (2009), $n = 63$
Dp4	Into wear between 0 and 12, lost between 24 and 36	Erupting at 1.5			Erupting after birth, coming into wear at 3
P4	C-H between 0 and 12, T to into wear between 12 and 36	Fully erupted between 24 and 27.5	Erupting at 27, coming into wear between 30 and 33	Eruption at 21 months, halfway at 25, completed at 28	Erupting between 13 and 18, coming into wear between 36 and 42
M1	E-T between 0 and 12, into wear from 12 on	Fully erupted at 3, into wear at 4	Erupting at 3, coming into wear 5–11	Eruption at 3, halfway at 4, completed at 5	Erupting between 3 and 5, coming into wear between 6 and 18
M2	C-E between 0 and 12, T to into wear between 12 and 24	Erupting between 8 and 12, fully erupted at 13, into wear 15.5	Erupting at 13, coming into wear 15 and 21	Eruption at 10, halfway at 13, completed at 15	Erupting between 7 and 13 months, coming into wear between 12 and 35
M3	V-E between 12 and 24, T to into wear between 24 and 36	Erupting between 16.5 and 22, fully erupted at 25–27.5	Erupting at 24, coming into wear between 30 and 33	Eruption at 15, halfway at 26, completed at 28	Erupting between 13 and 18, coming into wear between 36 and 42

Note: All ages are in months.

contained one to four mandibles per class. Deviation from the true age was calculated in the same manner as it was for the blind tests.

4 | RESULTS AND DISCUSSION

4.1 | Eruption patterns

The tooth eruption patterns observed in this study in the Nordenskiöld collection are compared (Table 3) with the studies of Pasda (2009, tab. 8), Bouchud (1966, tab. 21), Miller (1974b, tab. 6), and Bergerud (1970, tab. 2). Bergerud studied Newfoundland caribou (*Rangifer tarandus caribou*), Bouchud studied a Palaeolithic reindeer population from France, Miller studied individuals from the Kaminuriak population of barren-ground caribou (*Rangifer tarandus groenlandicus*), and Pasda studied the Sisimiut reindeer (*Rangifer tarandus groenlandicus*) population on Greenland. It seems that in our sample of the Nordenskiöld reindeer population teeth erupt slightly earlier than in other populations, but eruption times are generally consistent across distinct populations. The Palaeolithic reindeer of Bouchud erupted some of their teeth slightly later than other populations did, but these teeth did not come into wear later than the others. Observed variations likely reflect genetic, dietary and environmental factors that affected the populations observed, and differences in ageing method and recording of eruption stages. Most authors did not use a code system like the one of Ewbank et al. (1964) and used less well-defined stages such as “erupting,” “fully erupted,” and “coming into wear,” although Miller (1974b) also uses “halfway” to describe an eruption stage. Most authors use eruption times of “between month–month,” but Miller and in some cases also Bergerud seem to either have found little eruption time variation within the studied Kaminuriak and Newfoundland caribou populations or did not record it. The rough age classes (0–12, 12–24, and 24–36 months) of this study are due to the nature of the ageing method it is based on, that is, counting of the cementum annuli, which provides 1-year intervals.

4.2 | Tooth wear: Intra-individual and inter-sex variation

Several animals showed slight differences in tooth wear and/or eruption patterns between their left and right mandibles, the differences being more pronounced in older individuals (Figure S3 and S4). Slight differences in tooth wear progression between left and right mandibles of the same individual were expected and has been observed in earlier studies (e.g., Grant, 1978).

Tooth wear is also affected by sex. In several age classes females exhibited the least tooth wear and males displayed the most tooth wear (Data S1). Among 0- and 1-year-old animals the state of eruption was similar in males and females. Among 2-year-old individuals, females lagged slightly “behind” at the transition of the final stage of tooth eruption to “into wear.” Namely, 6 out of 10 females had a P4 or M3 that was at eruption stage T (tooth almost at full height but unworn), whereas 12 out of 12 males had all their teeth already

(slightly) worn. Among 0-, 1-, 3-, 6-, 7-, 9- and 10-year-old individuals, the molariform teeth were less worn in females than in males. For the 4-, 5-, and 8-year-old animals there is no clear difference in tooth wear progression between male and females. In the 2-, 11- and 12-year-old age groups both most and least tooth wear are displayed in the same sex (male, male and female, respectively) (Data S1). From the 12-year-old age group onward the number of female mandibles exceeded the number of male mandibles by far (12 females against 1 male; see Table S1), hindering the analysis of statistical differences between male and female cohorts. Loe et al. (2003) and Høyve (2006) found similar inter-sex variation in tooth wear in red deer and roe deer, respectively.

4.3 | Ease of applicability, age justification, and inter-observer bias

The ages of the younger mandibles (0 to 5-year-olds) were estimated with high accuracy (maximum 1-year age deviation from the true age) by both experienced and inexperienced observers with 87% and 93%, respectively (Table S7 and S8). The reliability of the Absolute Scheme decreased when age estimations involved older animals. Estimations falling into 1-year age deviation of the true age decreased down to approximately 41% (experienced) and 49% (inexperienced) for individuals between 6 and 10 years. The Absolute Scheme performed only moderately well for the next age group of 11- to 15-year-olds. Here, the experienced group estimated 50% of the mandibles within 1-year age deviation of the true age, and the inexperienced group around 59%.

Deviations of more than 2 years from estimated to expected age were uncommon, between 12% and 15%, among both experienced and inexperienced observers and mostly when observing mandibles older than 6 years old. The 0 to 5 age groups had no deviations larger than 1.6 years. To reverse the spotlight on this matter, that means that between 83% and 85% of the jaws were estimated within a 2-year deviation of the true age. Tooth wear becomes especially variable after 9 years of age. This observation is in agreement with the general understanding of the accuracy of tooth eruption and wear pattern schemes to assess age-at-death in older animals (Brown & Chapman, 1990).

4.4 | Applying the schemes on the Edgeøya collection

The Absolute Scheme works well (Table S9) for the two youngest age groups (0 to 5 and 5 to 10), and fairly well for the oldest age group (10 to 17). For the youngest age groups, 96% of the estimated ages are within a 1-year range from the true age. For the 5 to 10 age groups, 80% of the estimated ages are within a 1-year range, and for the oldest age groups about 60% of the estimations are within a 1-year range of the true age. Only 7% of all observations had an estimated to true age deviation of more than 2 years, and these all occurred in the oldest age category.

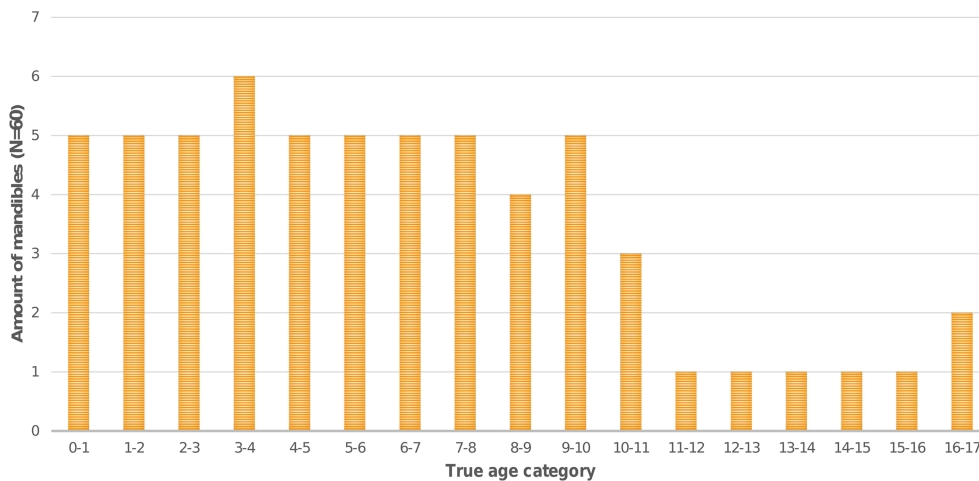


FIGURE 6 The true age composition of the sampled mandibles from the Edgeøya collection. The number of mandibles per true age category (based on cementum annuli analysis and tooth eruption) is presented per true age category [Colour figure can be viewed at wileyonlinelibrary.com]

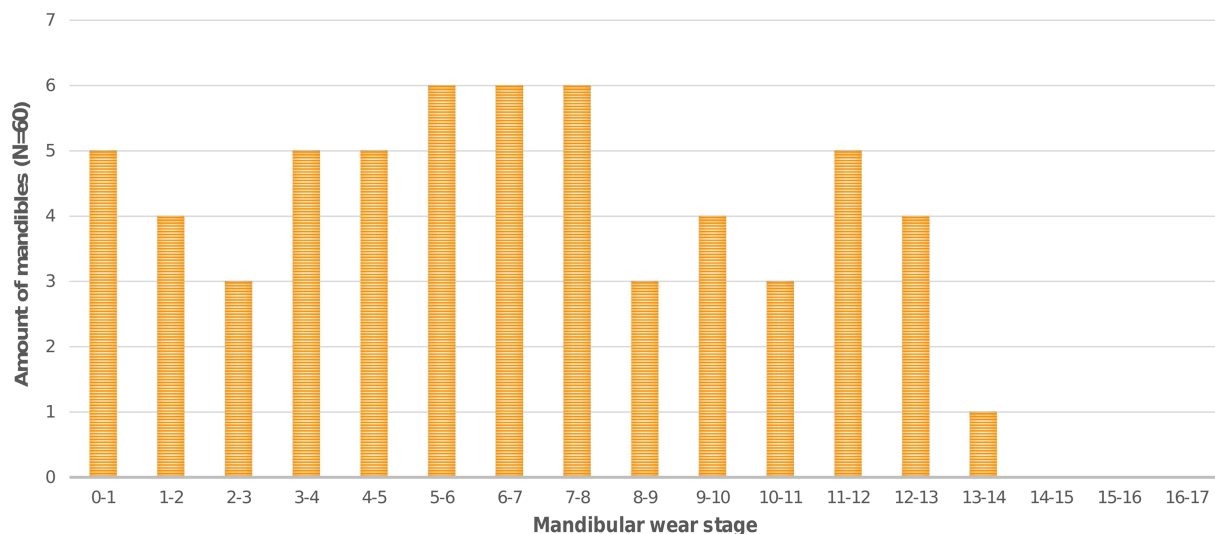


FIGURE 7 The estimated relative age composition of the studied mandibles from the Edgeøya collection by application of the Relative scheme. The number of mandibles that were scored and fit into a mandibular wear stage is presented per wear stage. Keep in mind that the mandibular wear stage does not represent true or reconstructed ages but only relative age categories [Colour figure can be viewed at wileyonlinelibrary.com]

The Relative Scheme works (Table S10 and S11) better than the Absolute Scheme on the Edgeøya collection. Eighty-four per cent of the estimations fall within a 1-year range from true age, and 94% of the estimations fall within a deviation of 2 years from the true age. Deviations of more than 2 years from the true age only occurred 3 times (5%), and the majority of these were estimations of mandibles from the oldest age categories (15- to 16- and 16- to 17-year-olds). Comparing the true and reconstructed age compositions (Figures 6 and 7) reveals the differences. The Absolute Scheme cannot estimate the age of the oldest individuals, putting them into the 12- to 14-year-old group, and overestimates the ages of the slightly younger individuals between 9 and 11 years.

5 | CONCLUSIONS

Investigating reindeer–human interactions has been hindered by the absence of an affordable, user-friendly and reproducible standardized

dental ageing method specifically designed for reindeer. This study established two user-friendly TWE schemes and age estimation methods using molariform teeth of recent known-age reindeer from Svalbard. The Absolute Scheme can be used to estimate the real age-at-death in Svalbard reindeer from six different hunting grounds with high accuracy. The Relative Scheme can be used to assess *relative* age-at-death in all *Rangifer* subspecies. The Nordenskiöld collection, which the Absolute Scheme is based on, displays a high degree of individual variation in terms of tooth wear progression. To reconcile this, the Relative Scheme was designed, predicting less individual variation with more linear tooth wear progression. The Absolute Scheme can substitute the Relative Scheme, but the estimations will be less precise due to variation in TWSs across different ages. Blind tests showed that the schemes are useful in generating large datasets quickly and accurately and reduce inter-analyst bias in tooth eruption and wear scoring.

Datasets created using the schemes will enhance the understanding of hunting and management practices and their change through

time of both contemporary and prehistoric communities inhabiting the Northern Hemisphere. Like all non-destructive ageing schemes based on osteological material, the schemes have their pitfalls. For example, the estimations will not perfectly match actual age-at-death, especially if tooth wear is advanced. The schemes will become more accurate when additional specimens from more populations representing a wider geographic range are observed. Correlating the results with environmental and genetic factors will enhance the baseline function of the schemes to explain archaeological patterns. Finally, the schemes still await to be applied on archaeological assemblages.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to report.

AUTHOR CONTRIBUTIONS

M. van den Berg: Methodology, formal analysis, investigation, writing (original draft, review and editing), visualization, project administration and funding acquisition. M. Loonen: Conceptualization, resources, data curation, writing (review and editing), supervision and project administration. C. Çakırlar: Conceptualization, methodology, validation, writing (review and editing), supervision and project administration.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

- Aitken, R. J. (1975). Cementum layers and tooth wear as criteria for ageing roe deer (*Capreolus capreolus*). *Journal of Zoology*, 175(1), 15–28. <https://doi.org/10.1111/j.1469-7998.1975.tb01387.x>
- Banfield, A. W. F. (1954). *Preliminary investigation of the barren ground caribou*. Ottawa: Canada Department of Northern Affairs and National Resources, National Parks Branch, Canadian Wildlife Service.
- Baumgartner, S., Steineck, T., Willing, R., & Arnold, W. (2004). Zuverlässigere Methode zur Altersbestimmung beim Rotwild. *Österreichs Weidwerk*, 2, 8–11.
- Bergerud, A. T. (1970). Eruption of permanent premolars and molars for Newfoundland caribou. *Journal of Wildlife Management*, 34(4), 962–963. <https://doi.org/10.2307/3799172>
- Bouchud, J. (1966). *Essai sur le Renne et la Climatologie du Paléolithique Moyen et Supérieur*. Périgeux: Imprimerie Magne.
- Bowen, F., Carden, R. F., Daujat, J., Grouard, S., Miller, H., Perdikaris, S., & Sykes, N. (2016). *Dama* dentition: A new tooth eruption and wear method for assessing the age of fallow deer (*Dama dama*). *International Journal of Osteoarchaeology*, 26(6), 1089–1098. <https://doi.org/10.1002/oa.2523>
- Bromée-Skuncke, F. (1953). Über Zahnentwicklung und Zahnabnutzung beim Rentier, verglichen mit denen bei einigen anderen Cerviden. Studien an skandinavischen Zahn- und Wildreintieren. *Arkiv för Zoologi*, 4(1), 1–43.
- Brown, W. A. B., & Chapman, N. M. (1990). The dentition of fallow deer (*Dama dama*): A scoring scheme to assess age from wear of the permanent molariform teeth. *Journal of Zoology*, 221(4), 659–682. <https://doi.org/10.1111/j.1469-7998.1990.tb04023.x>
- De Bie, S. (1977). Survivorship in the Svalbard reindeer (*Rangifer tarandus platyrhynchus* Vrolik) on Edgeøya, Svalbard. Reprint from *Norsk Polarinstitutt Årbok* 1976, Oslo: 249–270.
- Enloe, J. G., & Turner, E. (2002). Methodological problems and biases in age determinations: A view from the Magdalenian. In D. Ruscillo (Ed.), *Recent advances in ageing and sexing animal bones* (pp. 129–143). Oxford: Oxbow Books. <https://doi.org/10.2307/j.ctvh1ds02.12>
- Ewbank, J. M., Phillipson, D. W., Whitehouse, R. D., & Higgs, E. S. (1964). Sheep in the Iron Age: A method of study. *Proceedings of the Prehistoric Society (New Series)*, 30, 423–426. <https://doi.org/10.1017/s0079497x0001519x>
- Fortelius, M., Eronen, J., Jernvall, J., Liu, L. P., Pushkina, D., Rinne, J., Tesakov, A., Vislobokova, I., Zhang, Z. Q., & Zhou, L. P. (2002). Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years. *Evolutionary Ecology Research*, 4, 1005–1016.
- Governor of Svalbard. (2009). Plan for forvaltning av svalbardrein. En beskrivelse av mål og status for reinen på Svalbard, og en veileder for forvaltningen og forskningen. *Rapport 1/2009*. Published in Norwegian.
- Grant, A. (1978). Variation in dental attrition in mammals and its relevance to age estimation. *Research problems in zooarchaeology*, 3, 103–106.
- Grant, A. (1982). The use of tooth wear as a guide to the age of domestic ungulates. *Ageing and Sexing Animal Bones from Archaeological Sites*, Wilson B, Grigson C, Payne S. (ed.). BAR British Series, 109, 91–108.
- Greenfield, H. J., & Arnold, E. R. (2008). Absolute age and tooth eruption and wear sequences in sheep and goat: Determining age-at-death in zooarchaeology using a modern control sample. *Journal of Archaeological Science*, 35(4), 836–849. <https://doi.org/10.1016/j.jas.2007.06.003>
- Grønnow, B., Meldgaard, M., & Nielsen, J. B. (1983). *Aasivissuit—The Great Summer Camp. Meddelelser om Grønland*, Meddelelser om Grønland, Man & Society (Vol. 5). Copenhagen: Museum Tusulanum.
- Hambleton, E., & Rowley-Conwy, P. (1997). The medieval reindeer economy at Gaeccevaj'njar'ga 244 B in the Varanger Fjord, North Norway. *Norwegian Archaeological Review*, 30(1), 55–70. <https://doi.org/10.1080/00293652.1997.9965609>
- Hansen, B. H., Veiberg, V., & Aanes, R. (2012). Material from harvested Svalbard reindeer. Evaluation of the material, the data and their areas of application for research and management. Norwegian Polar Institute. *Brief Report Series*, 24.
- Hewison, A. J. M., Vincent, J. P., Angibault, J. M., Delorme, D., Laere, G. V., & Gaillard, J. M. (1999). Tests of estimation of age from tooth wear on roe deer of known age: Variation within and among populations. *Canadian Journal of Zoology*, 77(1), 58–67. <https://doi.org/10.1139/z98-183>

- Hillson, S. (1986). *Teeth*. Cambridge: Cambridge University Press.
- Høyte, T. T. (2006). Age determination in roe deer—A new approach to tooth wear evaluated on known age individuals. *Acta Theriologica*, 51 (2), 205–214. <https://doi.org/10.1007/bf03192672>
- Hufthammer, A. K. (1995). Age determination of reindeer (*Rangifer tarandus* L.). *Archaeozoologia*, VII(2), 33–42.
- Klein, R. G., & Cruz-Uribe, K. (1984). *The analysis of animal bones from archaeological sites*. Chicago: University of Chicago Press.
- Kojola, I., Helle, T., Huhta, E., & Niva, A. (1998). Foraging conditions, tooth wear and herbivore body reserves: A study of female reindeer. *Oecologia*, 117, 26–30. <https://doi.org/10.1007/s004420050627>
- Loe, L. E., Mysterud, A., Langvatn, R., & Stenseth, N. C. (2003). Decelerating and sex-dependent tooth wear in Norwegian red deer. *Oecologia*, 135(3), 346–353. <https://doi.org/10.1007/s00442-003-1192-9>
- Loison, A., Cuyler, L. C., Linnell, J. D. C., & Landa, A. (2001). Sex, age, and tooth wear of harvested caribou in west Greenland 1995–1998. *Wildlife Biology*, 7(4), 269–279. <https://doi.org/10.2981/wlb.2001.031>
- Lowe, V. P. W. (1967). Teeth as indicators of age with special reference to red deer (*Cervus elaphus*) of known age from Rhum. *Journal of Zoology*, 152(2), 137–153. <https://doi.org/10.1111/j.1469-7998.1967.tb01881.x>
- Lyman, R. L. (1994). *Vertebrate taphonomy*. Cambridge: Cambridge University Press. <https://doi.org/10.1017/cbo9781139878302>
- Miller, F. L. (1972). Eruption and attrition of mandibular teeth in barren-ground caribou. *The Journal of Wildlife Management*, 1972, 606–612. <https://doi.org/10.2307/3799093>
- Miller, F. L. (1974a). Age determination of caribou by annulations in dental cementum. *The Journal of Wildlife Management*, 38(1), 47–53. <https://doi.org/10.2307/3800199>
- Miller, F. L. (1974b). Biology of the Kaminuriak population of barren-ground caribou Part 2: Dentition as an indicator of sex and age; composition and socialization of the population. *Canadian Wildlife Service Report Series*, 31, 1–88.
- Morrison, D., & Whitridge, P. (1997). Estimating the age and sex of caribou from mandibular measurements. *Journal of Archaeological Science*, 24 (12), 1093–1106. <https://doi.org/10.1006/jasc.1996.0189>
- Napierala H. 2009. Reindeer and seasonality: An overview of methods and their applicability to archaeological materials, as exemplified by the Kesserloch Cave faunal assemblage. *Festschrift für Margarethe und Hans-Peter Uerpman, DeBeauclair R, Münzel S, Napierala H. (ed.)*. *BioArchaeologica* 5: 181–192.
- O'Connor, T. P. (2000). *The archaeology of animal bones*. London: Sutton Publishing.
- Pasda, K. (2006). Assessment of age and season of death of west Greenland reindeer by counting cementum increments in molars. *Documenta Archaeobiologia* 4. In G. Gruppe & J. Peters (Eds.), *Microscopic examinations of bioarchaeological remains. Keeping close eye on ancient tissues* (pp. 125–140). Rahden/Westfalen: Marie Leidorf GmbH.
- Pasda, K. (2009). *Osteometry, and osteological age and sex determination of the Sisimut reindeer population (Rangifer tarandus groenlandicus)*, British Archaeological Reports International Series (Vol. 1947). Oxford: John and Erica Hedges Ltd. <https://doi.org/10.30861/9781407304533>
- Payne, S. (1973). Kill-off patterns in sheep and goats: The mandibles from Asvan Kale. *Anatolian Studies*, 23, 281–303. <https://doi.org/10.2307/3642547>
- Pérez-Barbería, F. J., Duff, E. I., Brewer, M. J., & Guinness, F. E. (2014). Evaluation of methods to age Scottish red deer: The balance between accuracy and practicality. *Journal of Zoology*, 294, 180–189. <https://doi.org/10.1111/jzo.12166>
- Pike-Tay, A., Morcomb, A., & O'Farrell, M. (2000). Reconsidering the Quadratic Crown Height Method of age estimation for Rangifer from archaeological sites. *Archaeozoologia*, XI, 145–174.
- Reimers, E., & Nordby, Ø. (1968). Relationship between age and tooth cementum layers in Norwegian reindeer. *The Journal of Wildlife Management*, 1968, 957–961.
- Reitz, E. J., & Wing, E. S. (2008). *Zooarchaeology* (second ed.). Cambridge: Cambridge University Press. <https://doi.org/10.1017/cbo9780511841354>
- Salmi, A. K., Äikäs, T., Fjellström, M., & Spangen, M. (2015). Animal offerings at the Sámi offering site of Unna Saiva—Changing religious practices and human–animal relationships. *Journal of Anthropological Archaeology*, 40, 10–22. <https://doi.org/10.1016/j.jaa.2015.05.003>
- Silver, I. A. (1963). The ageing of domestic animals. In D. Brothwell, E. Higgs, & G. Clark (Eds.), *Science in archaeology: A comprehensive survey of progress and research* (pp. 250–268). New York: Basic Books.
- Skogland, T. (1984). Wild reindeer foraging-niche organization. *Ecography*, 7(4), 345–379. <https://doi.org/10.1111/j.1600-0587.1984.tb01138.x>
- Skogland, T. (1988). Tooth wear by food limitation and its life history consequences in wild reindeer. *Oikos*, 51, 238–242. <https://doi.org/10.2307/3565648>
- Skoog, R. O. (1968). Ecology of the caribou in Alaska. Doctoral dissertation, University of California.
- Spies, A. E. (1979). *Reindeer and caribou hunters: An archaeological study*. New York: Academic Press.
- Takken Beijersbergen, L. M. (2017a). Determining age and season of death by use of incremental lines in Norwegian reindeer tooth cementum. *Environmental archaeology. The Journal of Human Palaeoecology*, 24, 49–60. <https://doi.org/10.1080/14614103.2017.1394625>
- Takken Beijersbergen, L. M. (2017b). Heaps of fascinating fragments: Reconstructing a medieval reindeer population based on bone middens from the Hardangervidda high mountain plateau, Norway. *Acta Zoologica*, 98(4), 340–361. <https://doi.org/10.1111/azo.12175>
- Tomé, C., & Vigne, J. D. (2003). Roe deer (*Capreolus capreolus*) age at death estimates: New methods and modern reference data for tooth eruption and wear, and for epiphyseal fusion. *Archaeofauna*, 12, 157–173.
- Twiss, K. C. (2008). An assessment of the archaeological applicability of faunal ageing methods based on dental wear. *International Journal of Osteoarchaeology*, 18, 329–351. <https://doi.org/10.1002/oa.940>

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