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Calving seasonality at Pool, Orkney during the first millennium AD: an investigation using intra-tooth isotope ratio analysis of cattle molar enamel

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Abstract – The identification of dairying is essential if we are to understand economies of the past, particularly in northwest Europe, where a high degree of lactose tolerance suggests that fresh milk has long been a significant food product. This paper explores a possible link between economic focus and seasonality of calving. Although cattle (*Bos taurus*) can breed throughout the year, animals living in temperate regions with minimal or no human management tend to breed seasonally, their breeding behaviour being strongly influenced by the availability of food. In order to achieve a year-round supply of fresh milk in the past, it is likely that multiple-season calving was necessary, which would have required additional husbandry effort. Alternatively, for meat-focussed economies or those based on storable dairy products, a strategy of single-season calving in spring may have been favoured to maximise the utilization of spring and summer vegetation. Cattle birth seasonality is investigated through isotope ratio analysis ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$) of tooth enamel. Results for cattle from Pool, Orkney dating to the latter part of the first millennium A.D suggest that calving occurred during at least three seasons implying that the continuous provision of fresh milk was of economic importance.

Key words – Cattle; Birth Seasonality; Dairying; Fresh Milk; Carbon and Oxygen Stable Isotopes; Tooth Enamel; Orkney

Introduction

In order to gain an understanding of the economic basis of prehistoric communities, the identification of dairying is essential, particularly in northwest Europe, where a high degree of lactose tolerance suggests that fresh milk has long been a significant dietary component. Currently, prehistoric dairying is investigated using a variety of techniques. The two techniques that have been most widely applied are the examination of faunal remains and compound-specific stable isotope analysis of lipids in pottery residues. Examination of faunal remains to determine age-at-death slaughter patterns (mortality profiles) and female to male ratios (Higham 1968; Payne 1973) allows the economic role of a particular species (e.g. for meat, wool, milk or traction) to be inferred (e.g. Legge 1981), whilst lipid analysis is effective at identifying the presence of milk products in the archaeological record (e.g. Dudd and Evershed 1998; Copley *et al.* 2005a). Recent developments in the detection of archaeological proteins have allowed the identification of milk proteins to species in both organic residues and human dental calculus (e.g. Hong *et al.* 2012; Buckley *et al.* 2013; Warinner *et al.* 2014).

An additional approach to identify cattle (*Bos taurus*) dairying in prehistoric communities is explored in this paper: a possible relationship between calving seasonality, i.e. the distribution of births throughout the year, and economic focus. For economies focussed on the year-round production of fresh milk as a staple food product, it has been postulated that multiple-season calving would have been necessary (Towers *et al.* 2011; Balasse *et al.* 2012a; Gron *et al.* 2015). In contrast, a strategy of single-season calving, probably in spring, may have been favoured for meat-based economies or economies focussed on storable milk products. Increasingly, birth seasonality of domestic herbivores has been investigated using intra-tooth isotope ratio analysis of molar enamel (e.g. Balasse *et al.* 2003; Balasse and Tresset 2007; Blaise and Balasse 2011; Towers *et al.* 2011; Balasse *et al.* 2012a; Balasse *et al.* 2012b; Tornero *et al.* 2013; Towers *et al.* 2014; Buchan *et al.* 2015; Gron *et al.* 2015).

Each of the aforementioned techniques to identify prehistoric dairying has its limitations: faunal remains may be misinterpreted due to equifinality (Halstead 1998), potentially relevant to both mortality profiles and birth seasonality estimations, whilst neither lipid nor protein analyses provide information on the intensity of milk production and, consequently, its significance to ancient economies. However, a multi-proxy approach that combines evidence from a range of different techniques has the

potential to produce a more accurate and nuanced understanding of the economic basis of a prehistoric site or, at the very least, will act to generate a fresh series of archaeological questions, thus contributing to the debate on dairying in the past.

In this paper, we estimate calving seasonality at Pool, Orkney (Fig. 1), during the Iron Age/Scandinavian Interface period (c. AD 800 – c. AD 950) by analysing both oxygen and carbon isotope ratio data collected from cattle molars. Three different methods have been applied in order to interpret the data. Two of the methods use the positioning of the seasonally varying $\delta^{18}\text{O}$ signal recorded in molar enamel (Balasse *et al.* 2012a; Towers *et al.* 2014) whilst the third uses the timing of the onset of rumen functionality as evidenced in the $\delta^{13}\text{C}$ data (Towers *et al.* 2014). Our aims are twofold: to compare the calving seasonality results for Pool obtained using the three different methods, and to discuss the possible economic role of cattle at Pool with respect to both calving strategy and mortality profile. Although most of the isotopic data included in this study have been published previously (Towers *et al.* 2014), that particular publication did not estimate or discuss calving seasonality for any of the sites included. Instead, it focussed exclusively on method, combining data from a range of British sites to attempt to identify and quantify the principal sources of uncertainty involved in the estimation of calving seasonality.

Background

Manipulation of calving seasonality

The feasibility of manipulating the birth seasonality of sheep and cattle by prehistoric communities and the constraints on achieving this by various physiological and environmental factors have been discussed previously (Balasse and Tresset 2007). Biologically it is certainly possible for domestic cattle to produce offspring throughout the whole year (King 1978, 124). Thus, theoretically, it would have been feasible for prehistoric cattle farmers to manipulate calving seasonality to achieve calving during a particular season, over an extended period or all year round. To determine whether these options would have been readily achievable in practice it is informative to consider the reproductive behaviour of feral or semi-feral cattle living in temperate regions. Several examples are summarised in Table 1. All but one of these herds exhibit seasonal calving with the majority of births occurring during the season of spring, suggesting a strong relationship between calving and the spring flush of grass as temperatures rise after the winter (Reinhardt *et al.* 1986).

Only one herd included in Table 1, the Chillingham cattle, calve year-round. They are given hay in winter and have access to 130 ha of extremely well-managed mixed permanent grassland and open woodland, the number of individuals having risen from 13 in 1947 (Hall and Hall 1988) to approximately 100 strong at the beginning of 2012 (Chillingham Wild Cattle Association 2012). Most of the other herds, with more restricted calving periods (Table 1), do not receive supplementary food during the winter (Hall and Moore 1986; Berteaux and Micol 1992; Lazo 1995; Gómez et al. 1997) or, if they do, live in a region with harsh winters (Reinhardt et al. 1986).

The suggestion from this small number of feral and semi-feral herds is that nutrition and climate are important factors influencing calving seasonality. It is supported by studies of farmed cattle which have demonstrated the influence of nutrition on the oestrous cycling of cows (e.g. Joubert 1954; Durrell 1955; Wiltbank *et al.* 1962; Richards *et al.* 1986; Louw *et al.* 1988). Food energy tends to be prioritised for survival rather than reproductive functions, the order of priority from greatest to lowest being: 1) basal metabolism, 2) activity, 3) growth, 4) basic energy reserves, 5) pregnancy, 6) lactation, 7) additional energy reserves, 8) oestrous cycles and initiation of pregnancy and 9) excess reserves (Short and Adams 1988). Thus, when food becomes limited, the oestrous cycle will be one of the first physiological functions to become inactive (*ibid.*). Whether this happens depends on the quantity and quality of the available food (i.e. the energy input), the competing energy demands of other physiological functions such as lactation, how much activity is required to forage for food and water, whether the animal is growing and how much body fat is present as a stored energy supply (*ibid.*). In temperate winters under certain conditions, maintenance of body temperature may require heat production through shivering. Food energy would be prioritised for this vital body function (McDonald *et al.* 1988, 293-5).

The implication for prehistoric farmers is that spring-calving would have required the least amount of effort. Such a strategy, mimicking feral herd reproductive behaviour by maximising the use of spring and summer vegetation, has several advantages for meat production: a) calves are at least six months old before winter and therefore better able to withstand harsh conditions, b) milk yield is maximised for the calf, c) grass quality is at its highest as the calf begins to graze, d) fertility is maximised in time for summer mating, and e) cows are able to lay down body reserves during the latter part of the grazing season in time for winter (Younie 2001). Thus, spring calving effectively

maximises calf growth while minimising effort/cost. For a prehistoric dairy-based economy, calving strategy would have been influenced by both the duration of lactation and the shelf lives of the dairy products. If multiple-season calving was necessary, then, unless climatic conditions allowed plentiful natural grazing all year round, a high degree of effort and management would have been required to provide cattle feed of both sufficient quantity and quality throughout the year and perhaps shelter during the winter.

The archaeological site of Pool, Orkney

Located on the south-western peninsular of Sanday, Orkney, Pool is a multi-period settlement with evidence of occupation in the Neolithic period and from the Iron Age through to the Late Norse period (Bond 2003). The cattle molars analysed in this study are from deposits exhibiting the earliest signs of Scandinavian influence (Phase 7, the Iron Age/Scandinavian Interface period, c. AD 800 – c. AD 950). This influence is evident in new artefact types such as worked-bone implements and steatite vessels and a new sub-rectangular building style (Hunter 2007, 121). The mortality profile constructed from tooth eruption and wear data for Phase 7 shows a high level of juvenile mortality (Fig. 2, data from Serjeantson and Bond 2007a). The resemblance to Payne's (1973) milk model has led to the interpretation of a dairy-based economy (Serjeantson and Bond 2007a). An estimated female: male ratio of between 4:1 and 7:1, determined from measurements of metacarpal width, also supports a focus on dairying rather than meat (Bond 2007a). The number of older animals in the assemblage is lower than might be expected, possibly indicating that old milk cows ended their working lives elsewhere. Bond (2007a) has suggested that Pool may have been a producer settlement in a network of several interdependent settlements.

Oxygen and carbon stable isotope ratio analysis of cattle molar enamel

Cattle molars are high-crowned (hypsodont) teeth, the crowns forming sequentially over a period of several months from the cusp at the occlusal surface to the cervix, where the crown and root meet (Brown *et al.* 1960; Hillson 2005, 8-15). Enamel mineralization follows two phases: matrix formation and maturation, the organic matrix being deposited ahead of maturation (Suga 1982). Most of the mineralization occurs during the maturation stage and is a complex process both spatially and temporally (Suga *et al.* 1979; Suga 1982; Robinson *et al.* 1995; Hoppe *et al.* 2004; Tafforeau *et al.* 2007; see Towers *et al.* 2014 for a summary of the process). According to isotopic studies, cattle

molar enamel at any position on the crown takes at least 6-7 months to mineralize (Balasse 2002; Zazzo *et al.* 2005).

Isotope ratio mass spectrometry may be employed to measure the oxygen and carbon isotope ratios of the carbonate fraction of enamel bioapatite (the mineral component of enamel). Isotope ratios are expressed in the δ notation and units are per mil (‰) (Sharp 2007, 17-18). It is possible to obtain time-related isotopic data from enamel samples extracted at a number of positions along the length of a hypsodont crown (Fricke and O'Neil 1996). The intra-tooth $\delta^{18}\text{O}$ profiles recorded in cattle molar enamel generally follow a sinusoidal-like pattern, reflecting the seasonal variation in the $\delta^{18}\text{O}$ value of precipitation (Longinelli 1984; Luz *et al.* 1984; Fricke *et al.* 1998) with maxima corresponding to summer and minima to winter, due to a number of climatic variables including air temperature (Dansgaard 1964). Because of the lengthy mineralization process of cattle enamel, the intra-tooth $\delta^{18}\text{O}$ profile recorded along a molar crown is attenuated and temporarily shifted relative to the $\delta^{18}\text{O}$ of the drinking water (Passey and Cerling 2002; Kohn 2004). In addition, the $\delta^{18}\text{O}$ profile recorded in enamel forming early in life may be influenced by the ingestion of water via milk. $\delta^{18}\text{O}$ values of milk, derived from the mother's body water, tend to be more positive than those for drinking water by several per mil (Lin *et al.* 2003; Renou *et al.* 2004; Camin *et al.* 2008).

The $\delta^{13}\text{C}$ values measured in tooth enamel are influenced by both whole diet and digestive physiology (Sullivan and Krueger 1981; Hedges 2003; Passey *et al.* 2005). For cattle in first millennium AD Orkney, diet would have consisted of C_3 vegetation, possibly supplemented by seaweed, which has been used as cattle fodder in Orkney in the past (Fenton 1997, 428). The $\delta^{13}\text{C}$ value of C_3 vegetation is influenced by growing environment, species and plant part (Tieszen 1991; Heaton 1999) and tends to vary seasonally due to factors such as water availability, irradiance and the seasonally varying $\delta^{13}\text{C}$ value of atmospheric CO_2 (Farquhar *et al.* 1989; Ciais *et al.* 1995; Smedley *et al.* 1991; Dungait *et al.* 2010). If seaweed was a significant dietary component for the cattle at Pool, the $\delta^{13}\text{C}$ values measured in enamel would be elevated compared to a C_3 -only diet, as has been demonstrated for sheep from Orkney: modern seaweed-eating sheep from North Ronaldsay and prehistoric sheep from the Neolithic sites of Holm of Papa Westray and Point of Cott, and from Iron Age Mine Howe (Balasse *et al.* 2005; Balasse *et al.* 2006; Balasse *et al.* 2009).

Towers *et al.* (2014) have proposed that first molar enamel $\delta^{13}\text{C}$ patterning indicates the transition from non-ruminant (lower $\delta^{13}\text{C}$ values) to ruminant digestion (higher $\delta^{13}\text{C}$ values) that a calf undergoes within the first three months of life. At birth, a calf's rumen is undeveloped and digestion of milk takes place in its fourth stomach compartment, the abomasum, which digests food in a similar manner to the stomach of a non-ruminant (Davis and Drackley 1998, 13). However, by the age of two weeks, a calf will begin to consume dry food if available (Lengemann and Allen 1959; Godfrey 1961a), which stimulates the rumen to develop quickly, anatomically, microbially and physiologically, so that at 6-10 weeks of age, it is usually able to digest food like an adult ruminant (Bryant *et al.* 1958; Swanson and Harris 1958; Godfrey 1961b; Anderson *et al.* 1987). Rumen digestion involves the fermentation of food which produces methane, depleted in ^{13}C , and carbon dioxide, enriched in ^{13}C . Thus, any of this ^{13}C -enriched carbon dioxide entering the bloodstream and becoming incorporated in the mineralizing enamel of a ruminating calf will raise the $\delta^{13}\text{C}$ value of the enamel with respect to non-ruminant digestion (Cerling and Harris 1999; Passey *et al.* 2005).

Materials and Methods

First, second and third molars from five cattle mandibles and first and second molars from a sixth mandible, all different individuals, were selected for this study. For each molar, the crown was fully formed and the root either complete or still forming at death. Powdered intra-tooth enamel samples were obtained from the cusp to the cervix of a single lingual lobe from each molar. The distance from the cervix was measured for each sample. Mesial lobes were preferred, although distal lobes (for first and second molars) and central lobes (for third molars) were selected if mesial lobes were damaged or their enamel was of an inferior quality.

Sample preparation and analysis were carried out at the Stable Light Isotope Facility at the University of Bradford, following a protocol modified after Sponheimer (1999) and detailed elsewhere (Towers 2013, 107-9; Towers *et al.* 2014). Analytical precision was ± 0.2 ‰ for $\delta^{18}\text{O}_{\text{VSMOW}}$ (1σ) and ± 0.1 ‰ for $\delta^{13}\text{C}_{\text{VPDB}}$ (1σ), determined using an internal enamel laboratory standard (45 normalised measurements obtained over a 23 month period).

In this paper, three methods for estimating calving seasonality using intra-tooth isotope ratio analysis are applied to the Pool data-set. More than one method is used because it

is not currently known which method is the most accurate in estimating the distribution of births. Analysis of material from modern animals with known early-life histories would be hugely beneficial in this respect.

Method 1

The first method assesses how the timings of the second molar $\delta^{18}\text{O}$ minima relative to birth vary between the cattle and requires that the intra-tooth $\delta^{18}\text{O}$ data are plotted versus time rather than distance from the cervix as outlined below. The timing of each $\delta^{18}\text{O}$ minimum may be calculated through differentiation of a second-order polynomial fitted by Excel to the surrounding data points (Towers 2013, A32).

Method 2

The distribution of births may also be estimated using a method first developed by Balasse *et al.* (2012b) for sheep, and then applied to Neolithic cattle (Balasse *et al.* 2012a), which involves plotting the $\delta^{18}\text{O}$ data versus distance from the cervix, fitting a cosine curve to each $\delta^{18}\text{O}$ profile and normalising to period. Fitting the cosine function is carried out by the method of least squares through the adjustment of four parameters: X (period of the curve in mm), A (amplitude), x_0 (distance in mm between the cervix and the feature of the curve selected for inter-animal comparison) and M (mean $\delta^{18}\text{O}$ value) (Balasse *et al.* 2012a). For the Pool data, the feature selected for inter-animal comparison is the second molar $\delta^{18}\text{O}$ minimum. The method has been modified such that A and M are derived from the magnitudes of the second molar $\delta^{18}\text{O}$ minima and maxima. $\delta^{18}\text{O}$ minima and maxima magnitudes are calculated by fitting second-order polynomials in Excel to the surrounding data points in the plots of $\delta^{18}\text{O}$ versus time constructed for method 1 (Towers 2013, A32). Each cosine curve may then be fitted to the second molar data by the method of least squares through iterative adjustment of the remaining parameters, x_0 and X. Assuming that distance X represents 12 months, the number of months represented by x_0 may be calculated for each animal and the variation in x_0 will then produce an estimate of birth seasonality.

Method 3

The third method is based upon the changes in digestive physiology occurring during the first few months after birth, as reflected in the $\delta^{13}\text{C}$ profiles recorded in first molar enamel (Towers *et al.* 2014). First molar $\delta^{13}\text{C}$ values tend to be low in the earlier, cuspal part of the tooth, rise steeply and then, at a point in the cervical half of the tooth, display

a reduction in gradient. The reduction in gradient is believed to indicate the completion of rumen functionality 6-10 weeks after birth (Towers *et al.* 2014). If true, this inflection in the first molar $\delta^{13}\text{C}$ profile may serve as an indicator of an animal's birth, albeit displaced by several weeks. The relationship between the reduction in first molar $\delta^{13}\text{C}$ gradient and the seasonal cycle of the $\delta^{18}\text{O}$ profile, when considered for all the cattle included in the study, may then be used to estimate cattle birth seasonality. Plotting the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ data versus time is beneficial for this method.

Preliminary data handling: plotting intra-tooth data versus time

Conversion between distance from the cervix and time is achieved using a method detailed by Towers *et al.* (2014). Briefly, third molar unworn crown heights are predicted using incremental corrections calculated from plots of wear stage versus crown height for a collection of cattle third molars from Mine Howe, Orkney (data from Davis 2010, Appendix V). The unworn second and first molar crown heights are then assumed to be 97 % and 81 % of the predicted unworn third molar crown height respectively, based on measurements by Legge (1992, 21), Jones (2007) and Towers (2013, Appendix 1). For an animal with only first and second molars, the unworn second molar crown height may be predicted using the incremental correction obtained from the Mine Howe third molars since the size and morphology of the two molar types are similar. The timing of each intra-tooth sample relative to the cervix is calculated using the distance from the cervix measurement (as a proportion of unworn crown height) and the chronology of cattle molar crown formation published by Brown *et al.* (1960) (Table 2). Crown formation (i.e. matrix progression) is assumed to occur between -4.7 and 2.5 months (M1), 1 and 12.5 months (M2) and 10 and 23.5 months (M3) relative to birth (Brown *et al.* 1960; Soana *et al.* 1997). A uniform rate of formation is also assumed, which may be reasonable for second and third molars (Hillson 2005, 163) but unlikely to be true for first molars; according to Brown *et al.* (1960), only one third of the first molar crown is formed before birth (i.e. during the first 4.7 months of the 7.2 month period of formation).

Results

Intra-tooth oxygen and carbon isotope results for the cattle molars from Pool are presented in Table 3. The position along the tooth lobe (distance from the cervix) is given for each sample. Results for five of these animals (PL0278, PL0330, PL0339,

PL0344 and PL0386) have been published previously (Towers *et al.* 2014). The data are also shown in Figure 3, in which intra-tooth $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values from first, second and third molars are combined onto a single plot versus time. Although the first molar isotopic data are plotted in Figure 3, the x-axis time scale is removed for times earlier than 2 months because of the known non-uniformity of first molar matrix progression. The timing of each data point (x-axis value) relates to the initial deposition of the enamel matrix, whilst the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values (y-axis values) are for the completed enamel which would have taken at least 6-7 months to mineralize following matrix deposition (Balasse 2002; Zazzo *et al.* 2005).

Intra-tooth $\delta^{18}\text{O}$ values vary between 23.3 ‰ and 27.4 ‰ whilst intra-tooth $\delta^{13}\text{C}$ values vary between -16.2 ‰ and -11.0 ‰. All $\delta^{18}\text{O}$ profiles clearly show seasonal variation and the position of this sinusoidal pattern along the x-axis varies between cattle.

Estimating calving seasonality

Applying the three different methods to estimate calving seasonality leads to the following results:

Method 1

The timings of the second molar $\delta^{18}\text{O}$ minima relative to birth for the six Pool cattle, derived from the plots in Figure 3, are presented in Table 4. They range from 2.4 months for PL0386 to 10.3 months for PL0339. Thus, the distribution of births is calculated to be 7.9 months using this method.

Method 2

Figure 4 shows the fitted cosine and the magnitudes of the various parameters for each second molar. Value x_0/X varies from 0.16 for PL0444 to 0.94 for PL0386. If X represents 12 months, then the timings of the $\delta^{18}\text{O}$ minima relative to the second molar cervix vary between 1.9 and 11.3 months. The distribution of births is estimated to be 9.4 months using this method.

Method 3

For five of the six Pool cattle, first molar $\delta^{13}\text{C}$ values are very low in the cuspal part of the tooth, rise steeply and then display a reduction in gradient (indicated by the dashed lines in Figure 3). The profile of PL0444 is different to those of the other cattle: a reduction in first molar $\delta^{13}\text{C}$ gradient is not as clearly identifiable. There is a noticeable

change in gradient in the second molar data at approximately six months of age but, at that age, this is unlikely to represent the completion of rumen functionality (Fig. 3). In order to investigate calving seasonality, it is necessary to determine the relationship between the reduction in first molar $\delta^{13}\text{C}$ gradient and the seasonal cycle of $\delta^{18}\text{O}$. For PL0330, it appears to occur at a $\delta^{18}\text{O}$ maximum, for PL0344 just after a $\delta^{18}\text{O}$ maximum, for PL0278 midway between a $\delta^{18}\text{O}$ maximum and a $\delta^{18}\text{O}$ minimum, for PL0386 just before a $\delta^{18}\text{O}$ minimum and for PL0339 between a $\delta^{18}\text{O}$ minimum and a $\delta^{18}\text{O}$ maximum (Fig. 3). The seasonal cycle of $\delta^{18}\text{O}$ is shown schematically as a sinusoidal curve in Figure 5. The position on the $\delta^{18}\text{O}$ cycle at which the first molar $\delta^{13}\text{C}$ profile changes gradient is indicated for each Pool animal together with an equivalent data-point from a modern Dexter of known birth date (Towers *et al.* 2014). Assuming that one complete $\delta^{18}\text{O}$ cycle represents 12 months, it may be estimated that the difference between PL0339 and PL0386 is approximately $\frac{3}{4}$ of a cycle, i.e. approximately 9 months. If the reduction in $\delta^{13}\text{C}$ gradient indicates completion of rumen functionality then 9 months is also an estimate of the distribution of births. Comparison with the data-point of the modern Dexter (Fig. 5), which was born in late winter, suggests that calving occurred during spring, summer and autumn for the Pool cattle included in this study, although more modern comparison data are required to confirm this conclusion. PL0444 was probably born at a similar time of year to PL0339 given the similarity of their second molar $\delta^{18}\text{O}$ minima timings (Table 4) and x_o/X values (Fig. 4).

Discussion

Comparison of the different methods for estimating calving seasonality

For each of the methods described above, there will be some uncertainty associated with the estimated distribution of births. The first method assumes that second molar crown formation occurs at a uniform rate and the ages at which formation starts and finishes are the same for all cattle. The second method assumes that second molar cervix formation occurs at the same age and that the period of the seasonal variation in precipitation $\delta^{18}\text{O}$ (the input signal) is always exactly 12 months. All of these assumptions are open to question. For example, start and finish times for cattle molar crown formation are given as ranges and described as “approximations” by Brown *et al.* (1960), although inter-animal differences in second molar formation do appear to be much less pronounced than for third molars (Towers *et al.* 2014). In addition,

precipitation $\delta^{18}\text{O}$ data can show varying periodicity from year to year (Towers 2013, 176-8).

The third method to determine birth seasonality eliminates sources of uncertainty due to inter-animal variability in molar formation through direct comparison of the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ profiles. However, it comes with its own uncertainties. Firstly, identification of the reduction in first molar $\delta^{13}\text{C}$ gradient is somewhat subjective. For PL0278, PL0339, PL0344 and PL0386 this feature is clearly identifiable (Fig. 3) and may be defined to within one data point, equivalent to a timing error of approximately ± 3 weeks (see Towers *et al.* 2014 for further discussion on sources of error). For PL0330, the feature is not as straightforward to pinpoint (Fig. 3). It is possible that it could occur later in the first molar profile, although this would not alter the conclusion that these Pool cattle were born during three seasons. Secondly, the age at which the rumen becomes fully functional is variable, occurring between 6 and 10 weeks (Bryant *et al.* 1958; Swanson and Harris 1958; Godfrey 1961b; Anderson *et al.* 1987). Thirdly, there may be unaccounted errors. For example, ingestion of water via milk is expected to raise the $\delta^{18}\text{O}$ values of enamel mineralizing during early life and, thus, distort the sinusoidal-like $\delta^{18}\text{O}$ profile, which could lead to misinterpretation regarding season of birth. It is also possible that, for some animals, completion of rumen functionality is wrongly identified or not visible in first molar $\delta^{13}\text{C}$ profiles because it is obscured or distorted by significant shifts in dietary $\delta^{13}\text{C}$ values. The likely severity of these effects is currently unknown.

Despite their different approaches and sources of uncertainty, all three methods applied to estimate calving seasonality for the Pool cattle have produced the same conclusion, that the animals were born during at least three seasons, which increases the level of confidence in that conclusion.

Possible indication of weaning strategy

For PL0278, PL0330, PL0344 and PL0386, the reduction in first molar $\delta^{13}\text{C}$ gradient occurs at a $\delta^{13}\text{C}$ value that is similar to the mean $\delta^{13}\text{C}$ value of third molar enamel, which would have mineralized after the animal was fully weaned. A possible explanation is that these cattle were weaned early through human intervention such that their diet included a high proportion of vegetation at 6-10 weeks of age. If they had still been drinking a significant amount of milk when their rumens became fully functional

and weaned several months later, the reduction in first molar $\delta^{13}\text{C}$ gradient might be expected to occur at a value lower than the mean third molar value because milk is digested in the abomasum rather than the rumen (McDonald *et al.* 1988, 142). The $\delta^{13}\text{C}$ profile might then have shown a further rise in $\delta^{13}\text{C}$ after completion of rumen functionality as the proportion of milk in the diet decreased (abomasum digestion, similar to non-ruminant digestion) and the proportion of vegetation increased (methanogenic rumen digestion). It is possible that such patterning is seen to some extent in the profile of PL0339 (Fig. 3), although any interpretation in terms of weaning age may be complicated by varying vegetation values. A reduction in first molar $\delta^{13}\text{C}$ gradient is not clearly identifiable in the profile of PL0444 but may occur at around the fifth intra-tooth sample (Fig. 3). The subsequent rise in $\delta^{13}\text{C}$ values until approximately six months of age perhaps implies an even greater reliance on milk at the age of rumen completion and becoming fully weaned later in life than PL0278, PL0330, PL0344 and PL0386. A more detailed discussion of the possible influence of weaning on cattle molar enamel $\delta^{13}\text{C}$ profiles is found elsewhere and includes profiles from maternally weaned modern Chillingham cattle that do show a subsequent rise in $\delta^{13}\text{C}$ after the reduction in first molar $\delta^{13}\text{C}$ gradient (Towers 2013, 158-62). More analysis of modern material from cattle with known early-life histories would be beneficial in the interpretation of such data.

The economic focus of cattle husbandry at Pool

A strategy of multiple-season calving at Pool during the Interface period is more likely to have been adopted for an economy focussed on dairying rather than meat production, for which spring-calving would have been more efficient. The possibility that some of the Pool cattle were weaned early through human intervention would also support the conclusion that the economy at Pool was dairy-focussed.

If the continuous provision of fresh milk was a principal goal of cattle husbandry at Pool, calving strategy would have been largely determined by the duration of lactation. Although it is not possible to predict the duration of lactation for Orcadian cattle during the first millennium AD with any degree of accuracy, an estimate may be made from historical sources. For example, Sinclair (1813, 115) wrote that Ayrshire cows in Scotland produced 5 gallons per day for the first 90 days after calving, 3 gallons per day for the next 90 days and finally 1½ gallons per day for 120 days. Petty (1719, 51) similarly observed that “in Ireland a Milch-Cow, if English breed, may be fed upon two

Acres of Pasture, and with as much Hay as will grow upon half an Acre of Meadow, will yield præter propter 3 Gallons of Milk for 90 days, one with another, and one Gallon at a Medium for 90 more, and for 90 more scarce 1 quarter of a Gallon one day with another, and for 90 more dry”. These rates of decline, whereby more than 80 % of the total yield is produced during the first six months, are similar to those for modern dual and beef breeds (Jenkins and Ferrell 1992). Since there is no reason to assume that the duration of lactation was shorter for prehistoric cattle given the evidence for a long tradition of dairying in Britain from the Neolithic period (Copley *et al.* 2005b), it is likely that two calving seasons, in spring and autumn, or an extended period of calving through spring, summer and autumn would have been required to achieve an adequate supply of fresh milk throughout the year.

The advantage of an extended calving period was acknowledged by 18th century scholar Richard Bradley (1732, 132), who recommended that “so as that they may have Plenty of Milk, let your Kine go to Bull from the Spring to Winter, whereby you may always milk some”. Similarly, the French agronomist Olivier de Serres (1617, 251) suggested that farmers should choose the time of year for breeding their cattle according to factors such as climate, quality of grass and the continuation of milking in winter. Even in the early to mid-20th century, Scottish farmers producing milk on a small scale for home use staggered the calving of their milk cows throughout the year to ensure a continuous milk supply (James Foubister and John Mainland, Orkney farmers, pers. comm.). In a description of her childhood on the island of Eilean nan Ròn, lying off the north coast of Scotland, Mina MacKay Stevens recalled that “Most families had two cows. One cow would calve in the spring, for milk through the summer, and one would calve in the autumn, to give milk through the winter” (Neat 2000, 67). A prehistoric community that manipulated its calving strategy for the continuous provision of fresh milk may have valued it for immediate use in porridge or broth, or as a drink; early Irish texts contain numerous references to the drinking of fresh milk (Kelly 1997, 324). Alternatively, fresh milk may have been converted to products with a shelf life of a few days such as curds or soft cheese (Fenton 2007, 245).

Calving strategy for the production of storable dairy products would have depended on shelf life. Long term preservation would have necessitated the removal of liquid, the source of microbial activity. Columella, the Roman writer of the first century AD, described a method of making hard cheese suitable for export overseas that employed

both pressing and salting in order to dry and preserve the product (Millar 1745, 324-5). The early Irish diet included cheeses described variously as soft, hard, dry and pressed (Kelly 1997, 328-30). Descriptions from the 17th and 18th centuries suggest that cheese making changed little before the advent of refrigeration and mass production (e.g. Markham 1668, 149-53; Bradley 1736, 78-84) and that pressed cheeses were ready to eat after at least eight months or a year of storage (Bradley 1736, 81-3). It was also possible to preserve butter for several months: Markham (1668, 147-8) described the process of salting and storing butter in pots or barrels for consumption in the winter, recommending May as the best time of year to do this. Defoe (1742, 40) also commented that “ I have known a Firkin of Suffolk Butter sent to the West-Indies, and brought back to England again, perfectly good and sweet, as at first”. It is highly likely that shelf lives of more than six months were also achievable in prehistoric Britain. As a result, single-season calving would have been feasible assuming a lactation period of approximately six months. Spring calving would have maximised the quantity of milk and storable dairy product for the least amount of effort in terms of both fodder provision and manpower, as explained by Markham (1668, 142): “The best time for a Cow to Calve in for the Dairy, is in the later end of March and all April: for then grass beginneth to spring to its perfect goodness, which will occasion the greatest increase of Milk that may be”.

The conclusion derived from isotope ratio analysis of cattle molar enamel, that calving occurred during at least three seasons at Pool, supports the interpretation by Serjeantson and Bond (2007a) of a dairy-focussed economy, as inferred from the mortality profile (Fig. 2). It also suggests an emphasis on the year-round provision of fresh milk or dairy products with short shelf lives rather than the manufacture of products for long term storage, which may be achieved by spring-only calving.

Multiple-season calving implies a high level of organisational competence in cattle husbandry at Pool, ensuring that feed of sufficient quantity and quality was available throughout the year. Further support for the idea of a plentiful supply of food, at least for the human population, comes from faunal evidence from Pictish and Norse Orkney that suggests an under-utilisation of wild resources such as birds and shellfish (Bond 1998), although under-utilisation of wild resources may also be indicative of a labour-intensive farming system.

As might be expected, it is not possible to identify particular C₃ dietary sources for the Pool cattle from their $\delta^{13}\text{C}$ profiles. There is no clear co-variation between the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ profiles that would suggest year-round grazing of vegetation in one location, as observed in the profiles of modern sheep from Rousay, Orkney (Balasse *et al.* 2009). The $\delta^{13}\text{C}$ profiles of the Pool cattle may therefore be reflecting changes in diet through fodder provision or movement between grazing areas. Cultivated oats, probably introduced to the Northern Isles during the first few centuries AD (Bond *et al.* 2004), were a major crop by the Interface period and would have provided a highly nutritious addition to other possible sources of cattle fodder such as barley stubble and straw, hay, weeds and seaweed (Serjeantson and Bond 2007b). Oats have the advantage that, unlike barley, they do not require much in the way of manuring and can be grown on poor land, which is particularly true for black oats (*Avena strigosa*) (Bond 2003), a variety grown in the Northern Isles in historical times up until today. Limited diagnostic evidence suggests that black oats were also grown at Interface period Pool (Bond 2007b). Hence, the production of oats could have been achieved with a relatively modest amount of effort. Third molar $\delta^{13}\text{C}$ values for the six Pool cattle (≤ -11 ‰) are comparable to those measured for cattle enamel from Neolithic Knap of Howar, Orkney, interpreted as consuming C₃ terrestrial vegetation all year round (Balasse *et al.* 2006), suggesting that seaweed was not a significant dietary component.

Conclusions

Calving seasonality for the archaeological site of Pool, Orkney, has been investigated through intra-tooth isotope ratio analysis of cattle molars from the latter half of the first millennium AD. The isotopic data-set was interpreted using three different methods of data analysis and all three methods produced the same conclusion, that the animals were born during at least three seasons, which increases the level of confidence in that conclusion and provides evidence that first molar $\delta^{13}\text{C}$ patterning may also be used to estimate calving seasonality.

Since multiple-season calving requires considerable effort, particularly in the provision of good quality grazing and fodder throughout the year, there must have been a significant benefit to the community to adopt such a strategy. Year-round availability of fresh milk would have been the consequence of multiple-season calving and the likely impetus. Thus, the distribution of births found for Pool not only supports the interpretation of a dairy-focussed economy, as suggested by a high level of juvenile

mortality, but also suggests an emphasis on the consumption of fresh milk or dairy products with short shelf lives.

During the Atlantic Iron Age, the Northern and Western Isles are characterised by cattle mortality profiles which, as at Pool, demonstrate high death rates in the earliest wear stages representing calves which died at or around birth (Mulville *et al.* 2005). Similar trends are evident in the subsequent Viking and Norse periods, both in the Northern and Western Isles (Mulville *et al.* 2005) and across the North Atlantic islands (Mainland and Halstead 2005). The interpretation of these assemblages has been the subject of considerable debate after McCormick (1998) argued that high infant mortality in these regions was a consequence of agricultural marginality (i.e. fodder shortages, poor grazing) and was not necessarily an outcome of economic practice, while suggesting that the culling of calves would have actually hindered milk production in the largely unimproved Iron age and Norse breeds of cattle because they would not let down milk in the absence of their calves. This debate has polarised opinion within zooarchaeology on the validity of Payne- (1973) and Legge- (1981) based models for identifying milking and/or specialised dairying in cattle and other species, and has highlighted in particular the difficulty of separating natural deaths, which will occur in most herds, from deliberate culling of infants (Halstead 1998; Mulville *et al.* 2005; Balasse and Tresset 2007; Davis 2010). The methodology presented here provides an alternative way to approach this question which overcomes some of these issues. Furthermore, in identifying year-round milking and the high nutritional input from fodder crops or good pasture management that this implies, these results demonstrate once again that farming in the North Atlantic region is not by definition ‘marginal’ and impoverished because of its latitude but can support specialised or intensive production with appropriate cultural management practices, such as foddering and manuring (Bond *et al.* 2004).

Finally, previous assumptions that prehistoric domestic cattle would have always calved seasonally in spring at northern latitudes (e.g. Serjeantson and Bond 2007b) appear not to be supported by the conclusions drawn in this study. This has implications for seasonality studies using tooth eruption and wear in this species, which rely on an assumed birth season in spring (Jones and Sadler 2012).

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Figure 1. Outline map of Orkney showing the location of Pool (outline images from <http://d-maps.com/m/europa/europemax/europemax32.pdf> and <http://d-maps.com/m/europa/uk/ecosse/ecosse12.pdf>, with additions).

Figure 2. Mortality profile for Pool cattle from the Iron Age/Scandinavian Interface period (Phase 7). Data source: Serjeantson and Bond (2007a), age stages defined by Halstead (1985).

Figure 3. Plots of $\delta^{18}\text{O}_{\text{VSMOW}}$ and $\delta^{13}\text{C}_{\text{VPDB}}$ versus time of matrix formation for first, second and third molar enamel for six cattle from Pool. Dashed lines indicate the change of gradient in $\delta^{13}\text{C}$ and the corresponding $\delta^{18}\text{O}$ data-point. Analytical precision is $\pm 0.2 \text{ ‰}$ for $\delta^{18}\text{O}_{\text{VSMOW}}$ (1σ) and $\pm 0.1 \text{ ‰}$ for $\delta^{13}\text{C}_{\text{VPDB}}$ (1σ).

Figure 4. Second molar intra-tooth $\delta^{18}\text{O}$ values with best fit cosine curves. Analytical precision is $\pm 0.2 \text{ ‰}$ for measured values of $\delta^{18}\text{O}_{\text{VSMOW}}$ (1σ). x_0 and $X/2$ are illustrated in the plot for PL0444. Amplitude $A = (\delta^{18}\text{O}_{\text{max}} - \delta^{18}\text{O}_{\text{min}})/2$ and mean $M = (\delta^{18}\text{O}_{\text{max}} + \delta^{18}\text{O}_{\text{min}})/2$.

Figure 5. A schematic diagram of the seasonal cycle of $\delta^{18}\text{O}$ showing the positions on the cycle that correspond to the change in gradient of $\delta^{13}\text{C}$ for PL0278, PL0330, PL0339, PL0344 and PL0386. Also included is an equivalent data-point for a modern Dexter of known birth date (data from Towers *et al.* 2014).

Figure 1

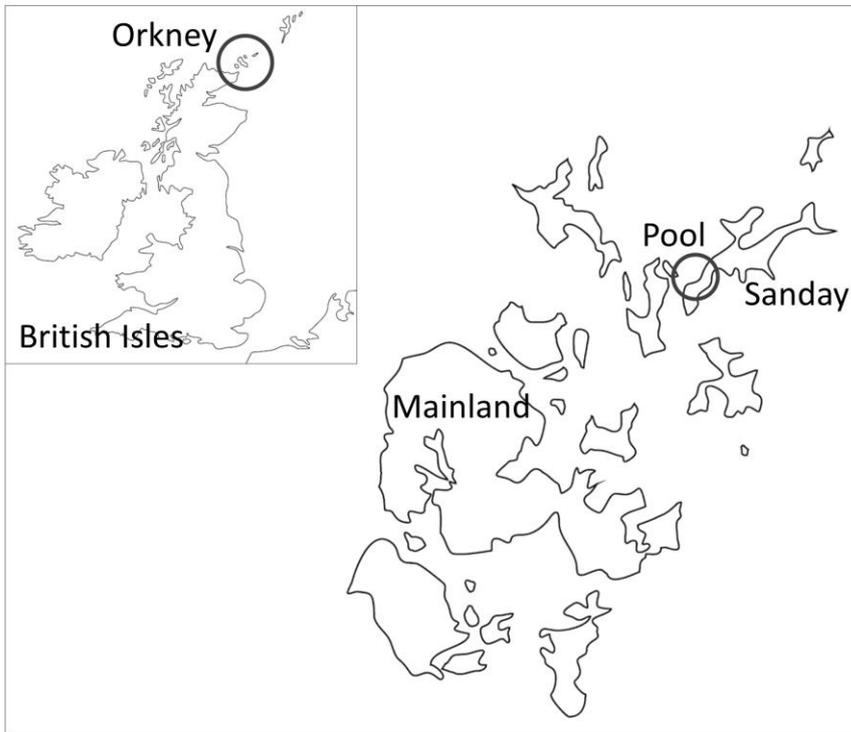


Figure 2

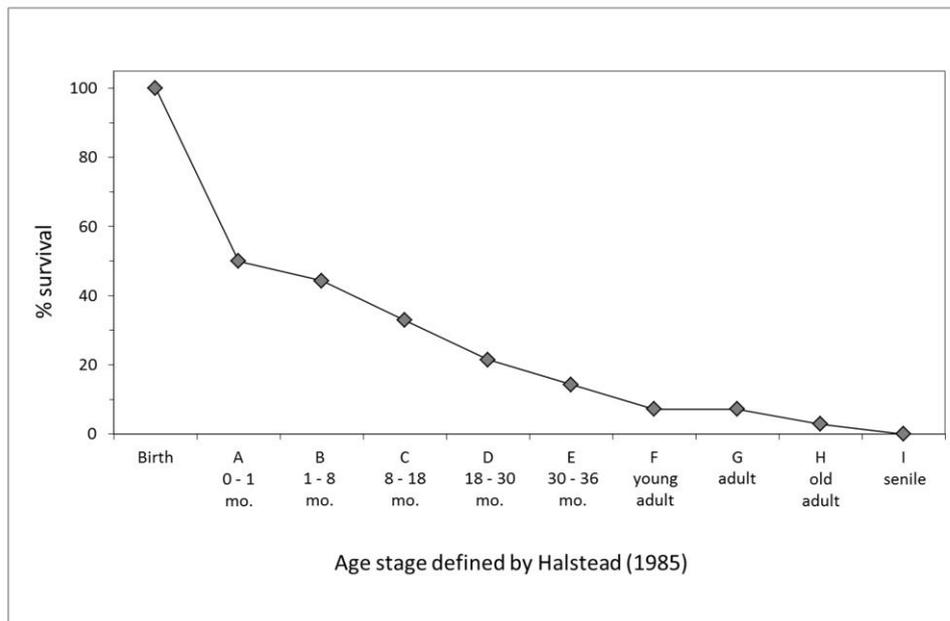


Figure 3

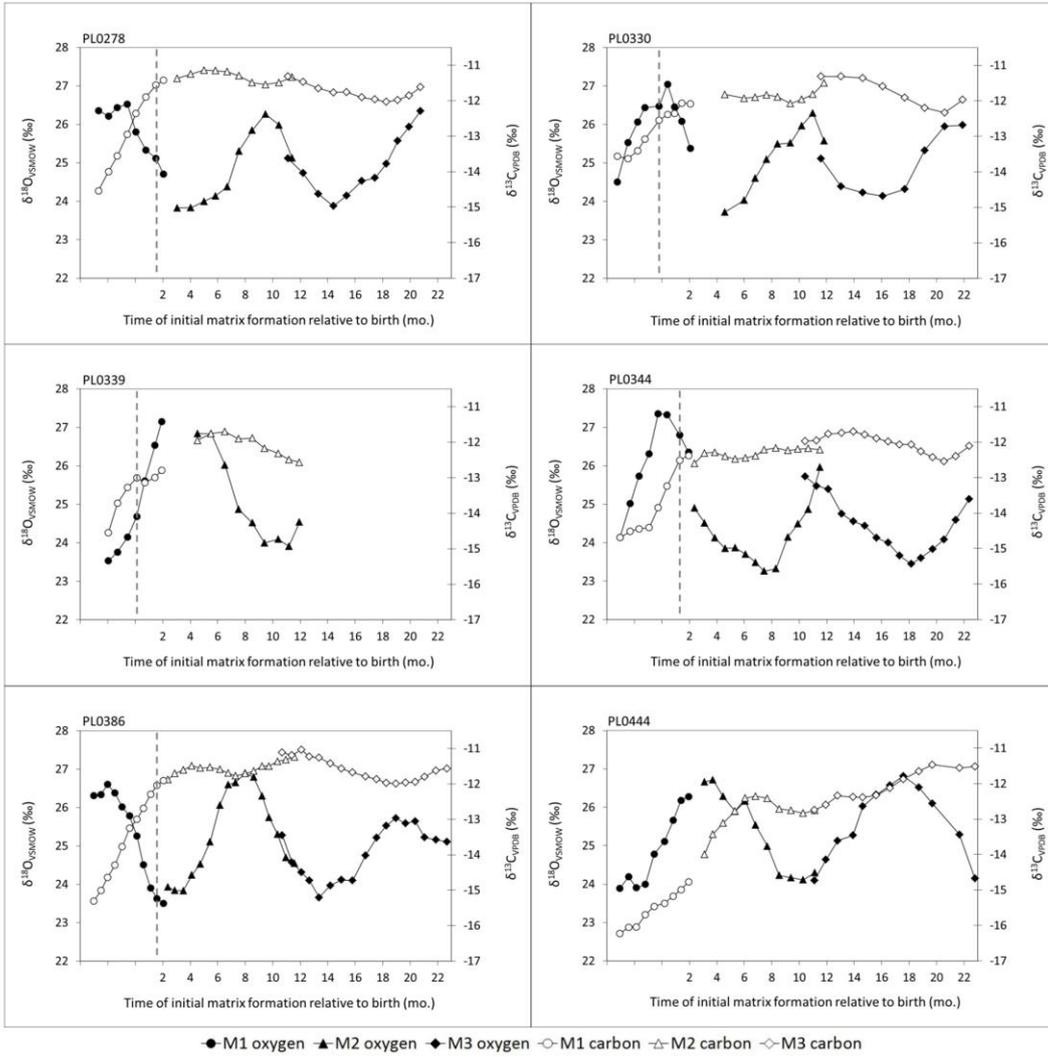


Figure 4

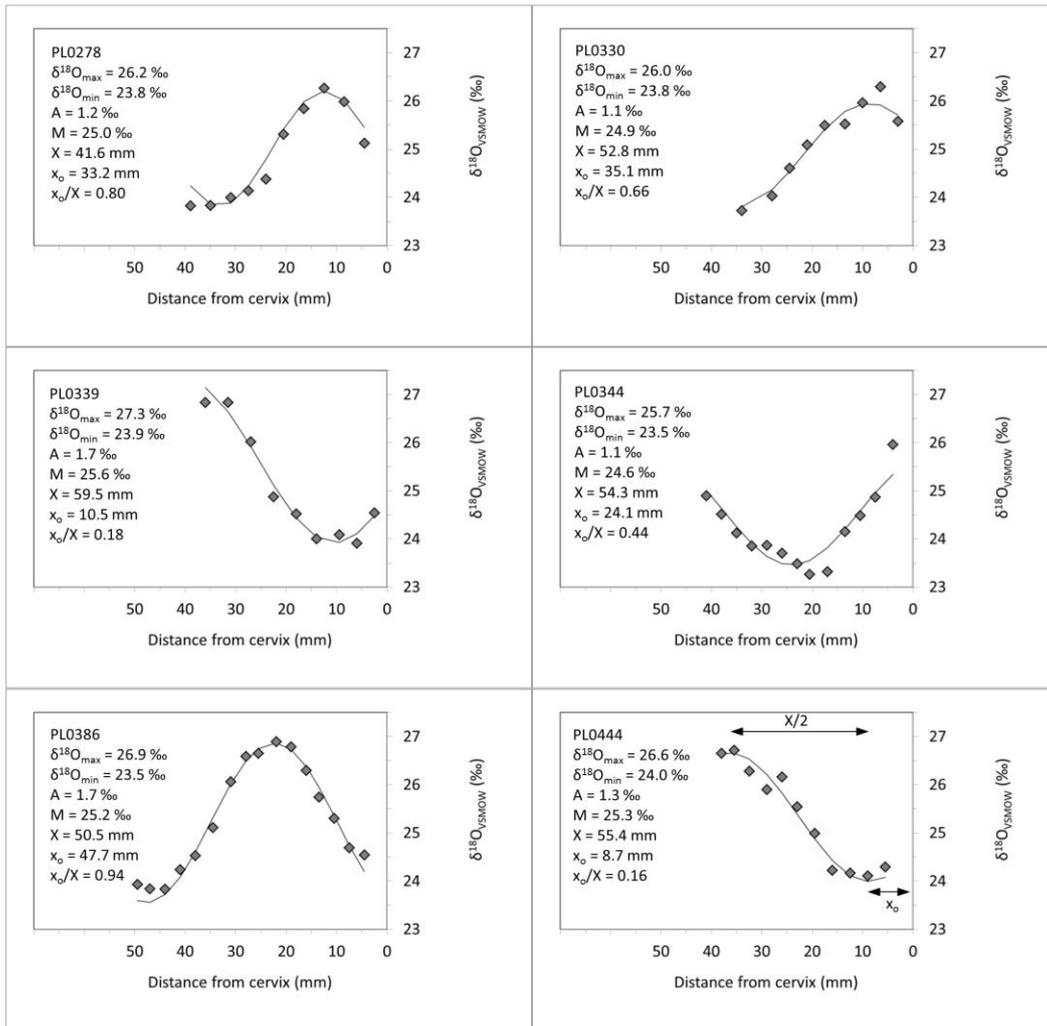


Figure 5

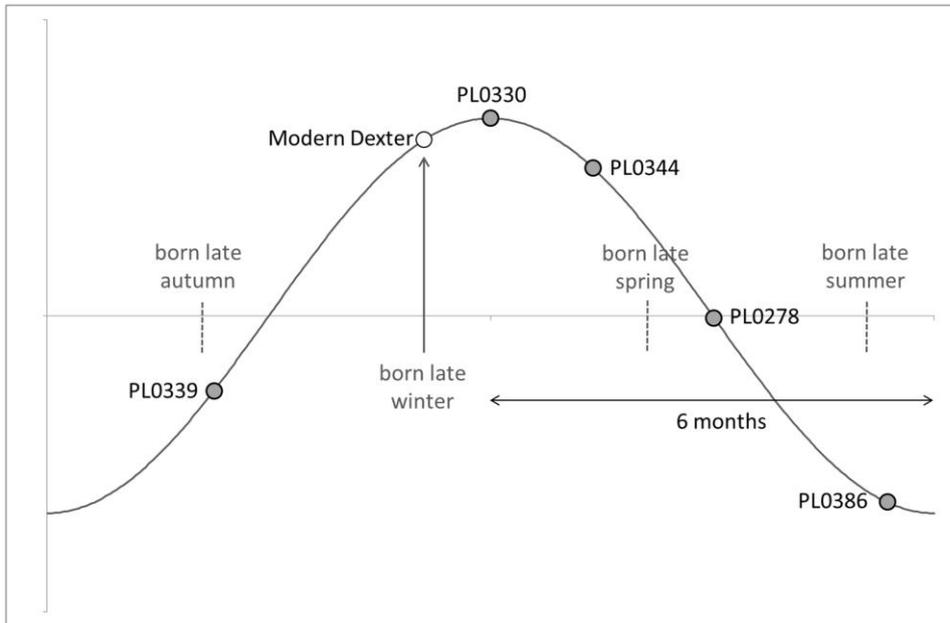


Table 1. Seasonality of calving for seven feral or semi-feral herds living in temperate regions. Information from Hall and Moore 1986 (Swona), Reinhardt *et al.* 1986 (Rhein-Taunus), Vitale *et al.* 1986 (Maremma), Hall and Hall 1988 (Chillingham), Berteaux and Micol 1992 (Amsterdam Island), Lazo 1995 (Doñana), Gómez *et al.* 1997 (Basque Country), Annal, pers comm (Swona).

Table 2. Development chronology of mandibular cattle molars. Data source: Brown *et al.* (1960). * A foetal age of 140 days according to Soana *et al.* (1997) (~4.7 months before birth).

Table 3. Oxygen and carbon isotope composition values from Pool cattle tooth enamel. Mandibular 1st and 2nd molars are designated M₁ and M₂. Wear stages after Grant (1982). Results for PL0278, PL0330, PL0339, PL0344 and PL0386 were first published in Towers *et al.* (2014).

Table 4. Timings of second molar $\delta^{18}\text{O}$ minima, calculated for each animal by differentiation of a second order polynomial fitted to the surrounding data points.

Table 1.

Herd location and breed	Supplementary food?	Seasonality of calving
Swona, Orkney, UK (mixed breeding)	No	March and April
Chillingham, Northumberland, UK (Chillingham cattle)	Hay in winter	Year round
Rhein-Taunus Naturpark, Hesse, Germany (Highland cattle)	Hay, straw and silage in winter	91 % births in March and April
Basque Country, Navarre and Pyrénées Atlantiques (Betizu cattle)	No	Around March
Doñana National Park, Andalusia, Spain (Mostrenca cattle)	No	February – August (60% births March – May)
Maremma National Park, Tuscany, Italy (Maremma cattle)	Not mentioned in publication	March – June
Amsterdam Island, southern Indian Ocean (mixed breeding)	No	90 % births between September and January

Table 2.

Development	First molar (age in months)	Second molar (age in months)	Third molar (age in months)
Crown formation starts	in utero*	1	9 - 10
Crown formation complete	2 - 3	12 - 13	23 - 24

Table 3.

Sample number	Distance from cervix (mm)	$\delta^{18}\text{O}_{\text{VSMOW}}$ (‰) normalised	$\delta^{13}\text{C}_{\text{VPDB}}$ (‰) normalised
PL0278 (M ₃), from left mandible, wear stage a, lingual mesial lobe, cusp to cervix 49.0 mm			
1	45.0	25.1	-11.3
2	41.0	24.7	-11.5
3	37.0	24.2	-11.7
4	33.0	23.9	-11.8
5	29.5	24.1	-11.8
6	25.5	24.5	-11.9
7	22.0	24.6	-12.0
8	19.0	25.0	-12.0
9	16.0	25.6	-12.0
10	13.0	25.9	-11.9
11	10.0	26.3	-11.6
PL0278 (M ₂), from left mandible, wear stage e/f, lingual mesial lobe, cusp to cervix 43.0 mm			
1	39.0	23.8	-11.4
2	35.0	23.8	-11.2
3	31.0	24.0	-11.1
4	27.5	24.1	-11.2
5	24.0	24.4	-11.2
6	20.5	25.3	-11.3
7	16.5	25.8	-11.5
8	12.5	26.3	-11.5
9	8.5	26.0	-11.5
10	4.5	25.1	-11.3
PL0278 (M ₁), from left mandible, wear stage j, lingual mesial lobe, cusp to cervix 31.5 mm			
1	28.5	26.4	-14.5
2	24.5	26.2	-14.0
3	21.0	26.4	-13.6
4	17.0	26.5	-12.9
5	13.5	25.8	-12.4
6	9.5	25.3	-11.9
7	5.5	25.1	-11.6
8	2.5	24.7	-11.4
PL0330 (M ₃), from right mandible, wear stage a/b, lingual central lobe, cusp to cervix 51.0 mm			
1	45.0	25.1	-11.3
2	39.5	24.4	-11.3
3	33.5	24.2	-11.4
4	28.0	24.1	-11.6
5	22.0	24.3	-11.9
6	16.5	25.3	-12.2
7	11.0	26.0	-12.3
8	6.0	26.0	-12.0
PL0330 (M ₂), from right mandible, wear stage ?, lingual distal lobe, cusp damaged			
1	34.0	23.7	-11.8
2	28.0	24.0	-11.9
3	24.5	24.6	-11.9
4	21.0	25.1	-11.8
5	17.5	25.5	-11.9

6	13.5	25.5	-12.1
7	10.0	26.0	-12.0
8	6.5	26.3	-11.8
9	3.0	25.6	-11.5
PL0330 (M ₁), from right mandible, wear stage g, lingual mesial lobe, cusp to cervix 35.5 mm			
1	33.0	24.5	-13.6
2	28.5	25.5	-13.6
3	24.5	26.1	-13.4
4	21.5	26.4	-13.1
5	15.5	26.5	-12.5
6	12.0	27.0	-12.4
7	9.0	26.5	-12.4
8	6.0	26.1	-12.1
9	2.5	25.4	-12.1
PL0339 (M ₂), from left mandible, wear stage f, lingual mesial lobe, cusp to cervix 44.0 mm			
1	36.0	26.8	-12.0
2	31.5	26.8	-11.8
3	27.0	26.0	-11.7
4	22.5	24.9	-11.9
5	18.0	24.5	-11.9
6	14.0	24.0	-12.2
7	9.5	24.1	-12.3
8	6.0	23.9	-12.5
9	2.5	24.5	-12.6
PL0339 (M ₁), from left mandible, wear stage h, lingual mesial lobe, cusp to cervix 33.5 mm			
1	27.0	23.5	-14.5
2	23.0	23.8	-13.7
3	18.5	24.2	-13.3
4	14.5	24.7	-13.0
5	11.0	25.6	-13.1
6	6.5	26.5	-13.0
7	3.5	27.1	-12.8
PL0344 (M ₃), from right mandible, wear stage b, lingual central lobe, cusp to cervix 48.0 mm			
1	46.5	25.7	-12.0
2	43.5	25.5	-12.0
3	40.5	25.4	-11.8
4	37.0	24.8	-11.7
5	34.0	24.6	-11.7
6	31.0	24.4	-11.8
7	28.0	24.1	-11.9
8	25.0	24.0	-12.0
9	22.0	23.7	-12.1
10	19.0	23.4	-12.1
11	16.5	23.6	-12.3
12	13.5	23.8	-12.4
13	10.5	24.1	-12.5
14	7.5	24.6	-12.4
15	4.0	25.1	-12.1
PL0344 (M ₂), from right mandible, wear stage f, lingual distal lobe, cusp to cervix 44.0 mm			
1	41.0	24.9	-12.6
2	38.0	24.5	-12.3
3	35.0	24.1	-12.3
4	32.0	23.9	-12.4
5	29.0	23.9	-12.5
6	26.0	23.7	-12.4

7	23.0	23.5	-12.4
8	20.5	23.3	-12.2
9	17.0	23.3	-12.2
10	13.5	24.1	-12.2
11	10.5	24.5	-12.2
12	7.5	24.9	-12.2
13	4.0	26.0	-12.2
PL0344 (M ₁), from right mandible, wear stage g, lingual distal lobe, cusp to cervix 35.0 mm			
1	30.0	24.1	-14.7
2	26.0	25.0	-14.5
3	22.5	25.7	-14.4
4	18.5	26.3	-14.4
5	15.0	27.4	-13.9
6	11.5	27.3	-13.2
7	6.5	26.8	-12.5
8	3.0	26.4	-12.4
PL0386 (M ₃), from right mandible, wear stage a/b, lingual mesial lobe, cusp to cervix 57.5 mm			
1	55.0	25.3	-11.1
2	52.0	24.6	-11.2
3	49.0	24.3	-11.0
4	46.5	24.1	-11.2
5	43.5	23.7	-11.3
6	40.0	24.0	-11.4
7	36.5	24.1	-11.6
8	33.0	24.1	-11.7
9	29.0	24.7	-11.8
10	25.5	25.2	-11.9
11	22.5	25.5	-12.0
12	19.5	25.7	-12.0
13	16.5	25.6	-12.0
14	13.5	25.6	-11.9
15	10.5	25.2	-11.8
16	7.0	25.2	-11.6
17	3.5	25.1	-11.6
PL0386 (M ₂), from right mandible, wear stage f, lingual mesial lobe, cusp to cervix 51.5 mm			
1	49.5	23.9	-11.9
2	47.0	23.8	-11.7
3	44.0	23.8	-11.6
4	41.0	24.2	-11.5
5	38.0	24.5	-11.6
6	34.5	25.1	-11.5
7	31.0	26.1	-11.6
8	28.0	26.6	-11.7
9	25.5	26.7	-11.8
10	22.0	26.9	-11.7
11	19.0	26.8	-11.6
12	16.0	26.3	-11.5
13	13.5	25.7	-11.5
14	10.5	25.3	-11.4
15	7.5	24.7	-11.3
16	4.5	24.5	-11.2
PL0386 (M ₁), from right mandible, wear stage g, lingual mesial lobe, cusp to cervix 39.0 mm			
1	36.0	26.3	-15.3
2	32.5	26.3	-15.0
3	29.5	26.6	-14.6
4	26.0	26.4	-14.3

5	22.5	26.0	-13.8
6	19.0	25.8	-13.3
7	15.5	25.3	-13.0
8	12.5	24.5	-12.7
9	9.0	23.9	-12.3
10	6.0	23.6	-12.0
11	3.0	23.5	-11.9
PL0444 (M ₃), from left mandible, wear stage b, lingual mesial lobe, cusp to cervix 47.0 mm			
1	44.0	24.1	-12.7
2	41.0	24.6	-12.6
3	38.0	25.1	-12.3
4	34.0	25.3	-12.4
5	31.5	26.0	-12.4
6	28.0	26.3	-12.3
7	24.5	26.6	-12.1
8	21.0	26.8	-11.9
9	17.0	26.5	-11.6
10	13.5	26.1	-11.5
11	6.5	25.3	-11.6
12	2.5	24.1	-11.5
PL0444 (M ₂), from left mandible, wear stage f, lingual mesial lobe, cusp to cervix 41.0 mm			
1	38.0	26.7	-14.0
2	35.5	26.7	-13.4
3	32.5	26.3	-13.1
4	29.0	25.9	-12.8
5	26.0	26.2	-12.4
6	23.0	25.5	-12.4
7	19.5	25.0	-12.4
8	16.0	24.2	-12.7
9	12.5	24.2	-12.8
10	9.0	24.1	-12.8
11	5.5	24.3	-12.8
PL0444 (M ₁), from left mandible, wear stage j, lingual distal lobe, cusp to cervix 33.5 mm			
1	30.0	23.9	-16.2
2	26.5	24.2	-16.1
3	23.5	23.9	-16.0
4	20.0	24.0	-15.7
5	16.5	24.8	-15.5
6	12.5	25.1	-15.4
7	9.0	25.7	-15.2
8	6.0	26.2	-15.0
9	3.0	26.3	-14.8

Table 4.

Animal ID	Timing of M ₂ δ ¹⁸ O minimum (months after birth)
PL0278	4.5
PL0330	4.9
PL0339	10.3
PL0344	6.7
PL0386	2.4
PL0444	9.9