Environmental constraints on the reproductive activity of domestic sheep and cattle: what latitude for the herder?

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ABSTRACT

In temperate climates, the sexual activity of sheep is synchronised by photoperiod. Cattle do not experience periodic infertility; however their reproductive strategy is related to seasonal food availability. The herder can modulate this system only to a certain extent. Restriction of the birth period is achieved by physically controlling the animals. Extension of the birth season for sheep cannot be achieved outside of the period defined by photoperiod without the intervention of artificial light and hormonal treatments. In cattle it requires supplying the mates with food on demand the whole year round. This suggests that physiological and environmental constraints might have been strong influences on reproduction management in early sheep and cattle husbandry. It is most likely that sheep and cattle reproduction were seasonal. Within this framework, how restricted in time the birth season was remains to be defined. Assessment of birth seasonality from stable isotope measurements ($\delta^{18}O$) of teeth was carried out on the north-western European Neolithic assemblages of the Knap of Howar (ca. 3600 BC), the Holm of Papa Westray (beginning of the 3rd millennium BC) and Er Yoh (second half of the 4th millennium BC). The results suggest a more restricted birth season both for cattle and sheep at the Knap of Howar than seen later in time at the Holm of Papa Westray and at Er Yoh. However it is not yet possible to disentangle climatic from biological and cultural factors responsible for this difference. These observations must be re-evaluated after widening of the data set.

KEY WORDS
Birth seasonality,
sheep,
cattle,
Neolithic,
north-western Europe,
oxygen stable isotope ratio,
tooth enamel.

RÉSUMÉ

Contraintes environnementales sur la reproduction des ovins et bovins domestiques : quelle latitude pour l'éleveur ?

Sous les climats tempérés, l'activité sexuelle des ovins est synchronisée par la photopériode. Quant aux bovins, s'ils ne connaissent pas de période d'infertilité, leur stratégie de reproduction est cependant liée à la disponibilité saisonnière des ressources alimentaires. L'éleveur n'a qu'une certaine marge de manœuvre pour moduler ce système. Il est possible de restreindre la période des naissances en contrôlant physiquement les animaux. Chez les ovins, l'extension de la période des naissances en dehors de celle définie par la photopériode requiert aujourd'hui la mise en œuvre de traitements hormonaux et lumineux artificiels. Chez les bovins, elle requiert le maintien d'une alimentation à volonté toute l'année. Ceci suggère que les contraintes physiologiques et environnementales ont pu être très fortes sur la gestion de la reproduction dans les élevages ovins et bovins primitifs. Selon toute probabilité, la reproduction des ovins et des bovins était saisonnée, mais il reste à définir plus précisément dans quelle mesure la saison des naissances était restreinte dans le temps. Par des analyses isotopiques dans l'émail dentaire ($\delta^{18}O$), nous avons examiné la saisonnalité des naissances des bovins et des ovins sur les sites néolithiques d'Europe nord-occidentale de Knap of Howar (~3600 BC), Holm of Papa Westray (début du 3^{e} millénaire BC) et Er Yoh (seconde moitié du 4^{e} millénaire BC). Les résultats suggèrent une saison des naissances plus restreinte, pour les bovins comme pour les ovins, à Knap of Howar que ce qui est observé plus tard à Holm of Papa Westray et à Er Yoh. Il n'est pas encore possible, cependant, de distinguer entre les facteurs climatiques, biologiques et culturels responsables de cette différence. Ces premières observations devront être réévaluées après élargissement du corpus de données.

MOTS CLÉS
Saisonnalité des naissances,
ovins,
bovins,
Néolithique,
Europe nord occidentale,
rapports isotopiques de l'oxygène,
émail dentaire.

RESUMEN

Restricciones ambientales sobre la actividad reproductive de la oveja y Ganado doméstico : ¿qué latitud para el pastor ?

En climas templados la actividad sexual de las ovejas está sincronizada con el fotoperíodo. El ganado vacuno no experimenta infertilidad periódica, aunque su estrategia reproductiva está relacionada con la disponibilidad estacional de alimento. El pastor puede modular este sistema sólo hasta cierto punto. La restricción del período de nacimiento es llevada a cabo controlando físicamente las parejas. La extensión de la estación de nacimiento en la oveja no puede llevarse a cabo fuera de la programación definida por el fotoperíodo sin intervención de luz artificial y tratamientos con hormonas. En el ganado vacuno se requiere suplementar a las parejas con alimento *ad libitum* durante todo el año. Esto sugiere que restricciones fisiológicas y ambientales pudieron haber sido fuertes en el manejo reproductivo y en la cría temprana de ovejas y bovinos. Es más probable que la reproducción de las ovejas y el ganado vacuno fuera estacional. Dentro de este contexto queda por definir cuán restringida ha sido la estación de nacimiento. La determinación de la estacionalidad del nacimiento a partir de mediciones de isótopos estables ($\delta^{18}O$) en dientes fueron realizados en conjuntos del Neolítico nor-occidental de Knap de Howar (ca. 3600 BC), Holm de Papa Westray

PALABRAS CLAVE
Estacionalidad de nacimiento,
oveja,
ganado vacuno,
Neolítico,
Europa nor-occidental,
isótopos estables del oxígeno,
esmalte dentario.

(comienzos del 3e milenio BC) y Er Yoh (segunda mitad del 4e milenio BC). Los resultados sugieren que en Knap de Howar la estación de nacimiento fue más restringida para el ganado vacuno y la oveja que la observada más tarde, tanto en Holm de Papa y Er Yoh. Sin embargo, no es aún posible desentrañar los factores climáticos de los biológicos y culturales responsables de esta diferencia. Estas observaciones deben ser puestas a prueba con una serie de datos más grande.

INTRODUCTION

Wild animals have developed a series of physiological adaptations to seasonal fluctuations in environmental conditions. One of them is a predictive reproductive strategy restricting sexual activity to a certain time of the year to ensure that births occur at a time supporting lactation and promoting maximal growth of the offspring. Domestication, by providing protection against the adversity of environmental conditions, may have minimised the natural selective pressure, leading to the attenuation or suppression of some of the physiological expressions of seasonality. However, domesticated small ruminants have retained most of them. Moreover, in domestic species breeding throughout the year such as cattle, primitive breeds seem to have kept a seasonal reproductive strategy when raised outdoors in extensive herding systems (Ortavant *et al.* 1985). After a brief review of recent literature on the environmental constraints and physiological mechanisms of sheep and cattle reproductive strategy, we evaluate to what extent the herder can manipulate this system. The reproductive pattern of sheep and cattle in Neolithic assemblages from North-western Europe is then investigated using stable oxygen isotope analysis in teeth.

SEASONAL REPRODUCTIVE STRATEGY IN SHEEP AND CATTLE

SHEEP

Under tropical conditions, where the manifestation of seasonality is low, local breeds of sheep are non-seasonal breeders, or exhibit a weak seasonality of reproductive activity: females ovulate almost the whole year round (Mason 1980).

Under temperate latitudes, sheep are seasonal breeders. The female experiences seasonally a period of infertility (anoestrus), with no behavioural or ovarian activity (Hafez 1952; Thiéry *et al.* 2002). The seasonality of sexual activity is also expressed in the male, whose daily sperm production, although never suppressed, is dramatically reduced for part of the year (Dacheux *et al.* 1981; Avdi *et al.* 2004). Birth seasonality is mainly under photoperiodic control (Karsch *et al.* 1984). Indeed the most reliable environmental clue to set lambing at the optimal time of the year is the seasonal cycle of day length, which does not vary from a year to another and therefore allows good predictability. The photoperiodic information is perceived by the retina and transmitted to the pineal gland where this signal modulates the rhythm of melatonin secretion (Legan & Karsch 1983; Karsch *et al.* 1984). Melatonin is a time keeping hormone: significant secretion of melatonin occurs only at night. Consequently the duration of melatonin secretion changes under different photoperiods. This rhythm of melatonin secretion sets the frequency of release of hormones triggering ovulation (Karsch *et al.* 1984).

The existence has been demonstrated of a circannual endogenous cycle of reproductive activity under the natural conditions of temperate climates: photoperiod does not drive the annual breeding cycle but synchronises it and imposes a period equal to a year (Karsh *et al.* 1989; Malpaux *et al.* 1997). A consequence of the photoperiodic control of reproductive activity in temperate conditions, is that the length of the breeding season differs with latitude, getting gradually shorter at higher latitudes (Hafez 1952).

Moreover, under a given latitude, all breeds do not exhibit the same pattern of annual sexual activity. Their breeding period is more or less extended, and its length depends mainly on how early its onset is (Hafez 1952). Lincoln *et al.* (1990), comparing different sheep breeds living outdoors under similar environmental conditions, have highlighted variability in the date when maximal sexual activity is attained in the male. Crossbred rams showed reproductive cycles intermediate in timing between the characteristic of the parents, suggesting a genetic basis for this character.

Interestingly, the onset of the breeding season was shown to occur earlier in modern domestic breeds than in the European mouflon (*Ovis ammon musimon*). Sheep is a short day breeder. The onset of sexual activity occurs early in the summer in some domestic breeds, whereas it does not start until fall in European mouflon, in males (Lincoln *et al.* 1990; Lincoln 1998; Santiago-Moreno *et al.* 2005) as well as in females (Santiago-Moreno *et al.* 2000; Garel *et al.* 2005). This shift, together with the diversity observed in domestic breeds, was interpreted as a consequence of domestication, which both removed natural selective pressure and allowed genetic selection for a longer mating season and greater prolificity (Lincoln *et al.* 1990; Thiéry *et al.* 2002). The European mouflon included in these studies cannot be considered as the wild ancestor of domestic breeds, first because the original populations were initially introduced to Corsica and Sardinia by human communities in the late Neolithic: this mouflon descends from Neolithic domestic sheep returned to the wild (Poplin 1979; Vigne 1988), and second because when native populations from Corsica and Sardinia were introduced to continental Europe, some crossing occurred with domestic and feral sheep (Garel *et al.* 2005). However, the European mouflon could be considered as the closest living representative of early domestic breeds. A late onset of the breeding season in European mouflon compared to improved breeds therefore suggests either that this character is reversible or that the selection for an earlier mating season occurred later in the course of domestication (a reason for this selection could be that birth in winter may have enabled animals to reach faster an adult body weight because of large food availability in spring, and to reach puberty during the next breeding season whereas births in spring would not allow animals to breed in their first year). In this point of view it would be interesting to determine whether Neolithic sheep had a restricted breeding season with a late onset, or if it was already capable of mating earlier in the summer.

Cattle

Domestic cattle do not experience seasonal anoestrus and can breed throughout the year. However, their reproductive performances (frequency of oestrus cycles, length of post-partum anoestrus) vary seasonally, the main restricting factor being nutritional level (Mukasa-Mugerwa 1989; Ezanno *et al.* 2005). When kept outdoors in extensive conditions with no control of breeding, primitive breeds tend to give birth seasonally, at the time of the year of greatest food availability. This behaviour was observed both under temperate climates, where calving occurs within two to three months (Lecomte & Le Neveu 1986; Reinhardt *et al.* 1986) and tropical climates, where peaks for calving are also clearly observed (Bailey 1982; Bekure *et al.* 1991) although births are less strictly restricted in time and occur the whole year round.

WHAT LATITUDE FOR THE HERDER?

In modern husbandry, the considerable efforts brought into shifting cattle mating season outside of the period defined in natural conditions by the annual cycle of pasture (Garcia & Holmes 1999) suggest it might not have been an easy thing to do in early herding systems. For this purpose small stock might have been easier to manipulate, although only in certain conditions, and partly because their reproductive cycle is shorter. For this reason the following considerations concern mainly sheep.

EXTENDING THE BREEDING SEASON

In sheep, under temperate climates, modern manipulation of the reproductive cycle to stretch the period of sexual activity includes the use of light treatments simulating decreasing photoperiod, hormonal treatments with monitored melatonin injections (Abi Salloum & Claus 2005) and manipulation of the social structure of the herd through introduction of sexually active males to cause reactivation of sexual activity in anoestrus females ("male effect"; Thimonier *et al.* 2000; Gelez & Fabre-Nys 2004). The latter requires the rams to be artificially sexually activated. Such treatments were not available to the early herder.

Among other factors known to influence reproductive performance, a good nutritional level can help in improving productivity within the period of fertility but does not allow to stretch it outside the limits defined by the photoperiod (Rosa & Bryant 2003). Food is a more important parameter under tropical conditions where ewes show no seasonal anoestrus and where nutritional management can therefore help in ensuring regular reproductive cycles throughout the year (Mahieu *et al.* 1997; Rosa & Bryant 2003).

In the case of extended breeding season some breeds have the ability to go through a complete reproductive cycle and become receptive again before the end of the mating season. If the herder wishes to favour a second gestation, and therefore produce three lambing in two years, this is all the more easily achieved if the period of infertility succeeding to lambing, including post-partum and lactational anoestrus, is shortened. The length of post-partum anoestrus was shown to be season dependent, and a good nutritional level can help reducing it (Mahieu *et al.* 1997). As for lactational anoestrus, it can be shorten by artificially reducing the suckling period. This can be achieved simply by preventing access of the young to the udder by covering it. This procedure was observed by MB in a traditional sheep husbandry among the Jordanian Bedouins in 2005.

RESTRICTING THE BREEDING SEASON

Under tropical conditions where sheep breeds have been shown to be sexually active the whole year round or to exhibit weak seasonality, a strong effect of the mating season on the productivity of the herd has been shown. The restricting factor is mainly food availability both at the time preceding mating season, during which the females build a body reserve, and at lactation time (Peacock 1982; Bekure *et al.* 1991; Mukasa-Mugerwa *et al.* 2000). When foddering is not possible in order to maintain the herd to a good nutritional level the whole year round, a solution to improve productivity is often to restrict the breeding season.

Other reasons to restrict the breeding season include reduction of breeding rate (Mace 1993), preventing two gestations within a year which could exhaust the females (Dahl & Djort 1976; Bernus 1988; Mace 1993), residential mobility — in nomadic societies, births might be scheduled to ensure that young animals and lactating females are strong enough when the time has come for long distance mobility (Barth 1961; Digard 1981; Bernus 1988), and the wish to concentrate in time the effort required for assistance in mating and, later, lambing and nursing, in order to reduce time conflicts with other tasks at other times of the year (Digard 1981).

In all cases, controlling the breeding season can be achieved by separating males and females part of the year, or by preventing mating by attaching an apron to the male (Peacock 1982; Balasse *et al.* 2003) or to the female (Jean-Brunhes-Delamarre 1970) or by tying the male's penis to the scrotum (Bernus 1988). The antiquity of such practices is not known.

CONCLUSION FOR EARLY HERDING SYSTEMS

In conclusion it appears that in temperate conditions, the physiological and environmental constraints were probably very strong on early husbandry both for sheep and cattle raising. Within this strict framework however, in certain circumstances the reproductive pattern can be manipulated by the herder, although in all cases restricting the breeding season seems easier than extending it. Within this strict framework again, diversity was observed in the reproductive pattern between different modern breeds. Consequently it is difficult to predict with certainty the reproductive pattern in early domestic breeds: it is most likely that births occurred seasonally both in cattle and in sheep, but how narrow the birth period was still needs to be determined. In this point of view, a direct assessment from faunal remains might reveal very useful.

ASSESSING SEASONALITY OF BIRTH IN TOOTH ENAMEL

PRINCIPLE

Seasonality of birth can be investigated using stable oxygen isotope analysis in tooth enamel (Bryant *et al.* 1996a, 1996b; Balasse *et al.* 2003). Tooth enamel mineral (hydroxyapatite, hereafter referred to as bioapatite) is a calcium phosphate which contains phosphate and carbonate ions. The oxygen isotope composition ($\delta^{18}O$) of enamel phosphate and carbonate is linked to that of ingested water: mainly drinking and plant water, *i.e.* meteoric water for domestic animals (Land *et al.* 1980; Longinelli 1984; Luz *et al.* 1984). The $\delta^{18}O$ of precipitation varies according to numerous parameters, some of which are seasonal: temperature at high and middle latitudes (Gat 1980), and amount of precipitation at low latitudes (Dansgaard 1964; Rozanski *et al.* 1996). These seasonal variations are recorded in tooth enamel during tooth development and they are not remodelled once enamel mineralization is completed. Moreover tooth enamel bioapatite has been shown to be fairly resistant to diagenetic alteration (Lee-Thorp *et al.* 1989; Lee-Thorp & Van der Merwe 1991; Zazzo *et al.* 2004).

By performing a sequential sampling following the tooth growth axis, it is possible to access the seasonal variation in enamel bioapatite $\delta^{18}O$ and to reconstruct the seasonal cycle. Repeating this protocol on the same tooth from several individuals in the faunal assemblage and comparing the pattern of $\delta^{18}O$ variations along the tooth allows the estimation of seasonality of birth: because the timing of tooth development is fixed within a species, individuals born at the same season record the same sequence of the seasonal cycle in the same portion of the tooth. In individuals born at different seasons, the sequences are shifted (Balasse *et al.* 2003).

EXPERIMENTAL TEST ON MODERN INDIVIDUALS

The protocol was applied to two distinct populations with radically different reproductive pattern: North Ronaldsay sheep and Small East African goats. For the purpose of this demonstration, comparing patterns in sheep on the one hand and goats on the other hand is acceptable given that their molars are very similar both in morphology and in the pattern of enamel mineralization (Suga 1982) and that we are only interested in the way lags between seasonal sequences were recorded in teeth with no consideration for the reproductive patterns as such.

The North Ronaldsay sheep are kept on North Ronaldsay island in the Orkney archipelago (Fig. 1). Under this high latitude (59°N), with constraining climatic conditions, births are restricted to a short period of the year, occurring essentially in the end of April and beginning of May (Morris 1999). This period corresponds to the time when temperature starts to increase, and when wind and precipitation are the lightest (Davidson & Jones 1990). Four lower left third molars were sampled within the assemblage collected by K. Dobney on the shoreline of North Ronaldsay in 1988.

The Small East African goat teeth were collected at the Maasai village of Enkorika in the Narok District (Kenya), at a low latitude (01°S), where they breed throughout the year (F. Kuriain 2001, personal communication). Four second molars were sampled. They belong to four different individuals which were slaughtered on different occasions during field work.

Teeth were boiled in distilled water and dried at room temperature. The enamel surface was cleaned by abrasion with a tungsten drill bit. Sequential sampling of enamel powder was performed using a diamond drill bit. Each sample is a one-millimetre wide groove perpendicular to the tooth growth axis, taken through the whole thickness of the enamel layer. Enamel powder was treated for bioapatite extraction as described

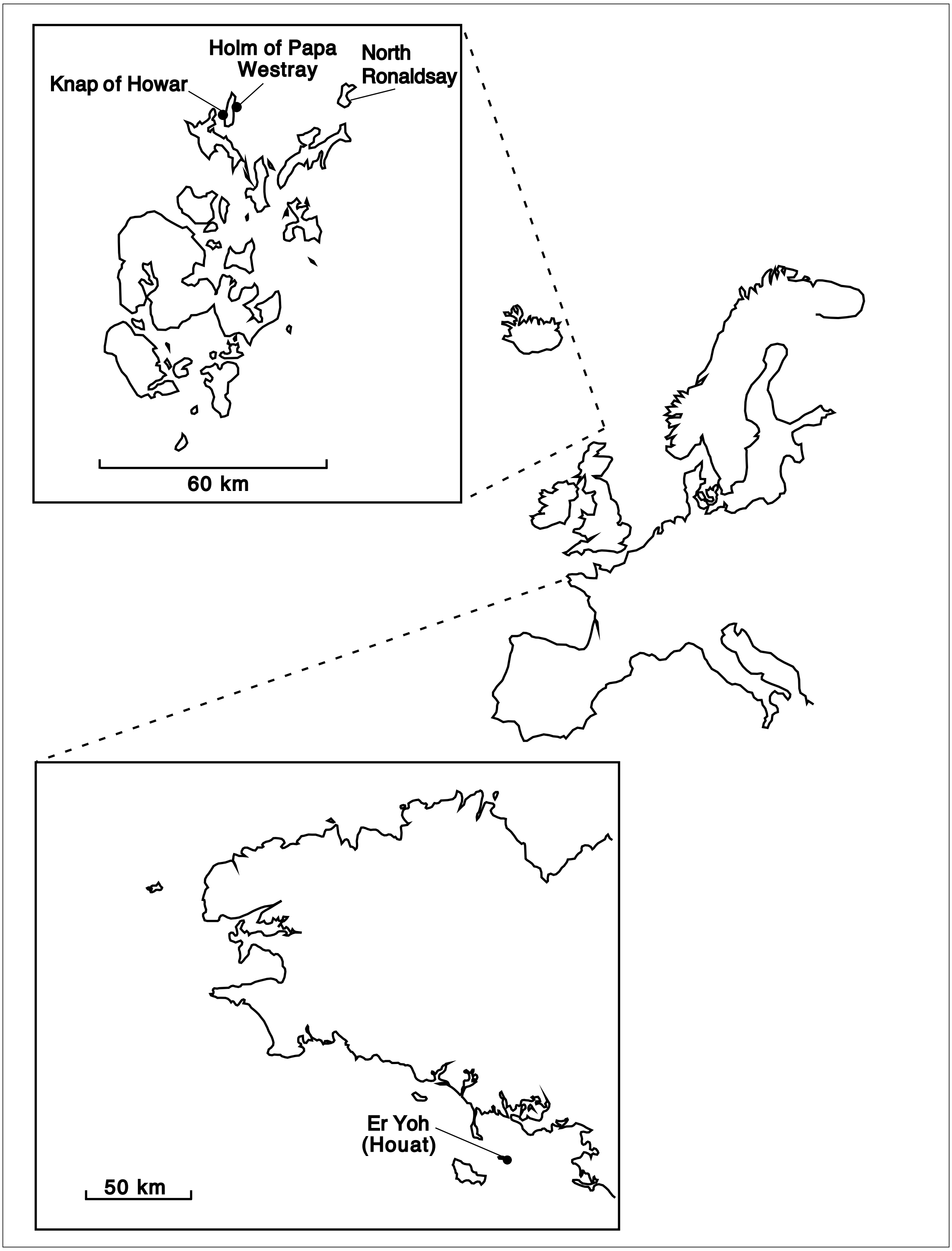

FIG. 1. – Map of North Western Europe with location of the sites included in the study. Designer: M. Balasse.

in Balasse *et al.* (2002). Briefly, enamel was treated with sodium hypochlorite 2-3% (24 h) to remove organic matter, and then with 0.1 M acetic acid (4 h, 0.1 ml/mg) to remove exogenous carbonate. Bioapatite samples weighing around 600 to 700µg were reacted with 100% phosphoric acid at 70°C in individual vessels in an automated cryogenic distillation system (Kiel III device), interfaced with a Finnigan MAT 252 isotope ratio mass spectrometer. The $\delta^{18}O$ values are expressed versus VSMOW. The analytical precision is 0.13 ‰, defined by analysis of 42 aliquots of the international standard NBS 19 over the period of analysis of these bioapatite samples.

Results from analysis are shown in Table 1 (in appendix) and Fig. 2. The pattern of variation of carbonate $\delta^{18}O$ along the tooth, *i.e.* with age, is very similar in the four individuals from North Ronaldsay. The inter-individual variability observed in the $\delta^{18}O$ values, on the y-axis, might be related to inter-annual variability in temperature, as these individuals might have been born in different years. Seasonality related information is read on the x-axis. In all four sheep, the highest $\delta^{18}O$ values, corresponding to the warmest yearly temperatures at this latitude (Gat 1980), were recorded in the same part of the enamel crown at around 5 to 8.5 mm from the neck (Fig. 2). This is in agreement with a narrow lambing period for this breed, although it is difficult to estimate precisely what this amplitude of variation (3.5 mm) represents in time.

Inversely, in the four Small East African goats from Enkorika the sequence of the seasonal cycle recorded in the second molar is shifted from one individual to another (Fig. 2), reflecting the variability in the period of birth.

Variability in patterns of reproductive strategies in archaeological assemblages might reveal more subtle differences than between these two extreme examples. Disentangling intra-individual variability in tooth development from a difference in the date of birth requires more work on modern reference individuals with known date of birth. This work is currently in progress in sheep and is also needed for cattle. It is likely that inter-individual variability in tooth growth will be enhanced when measurements are performed in

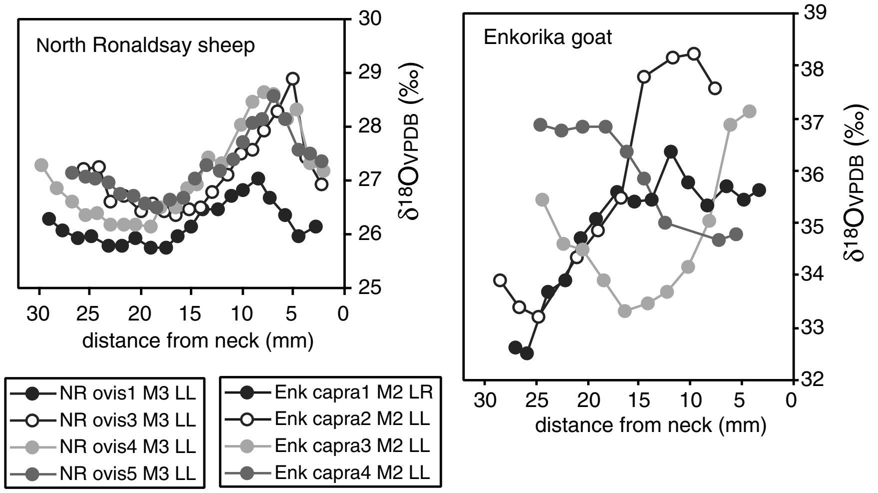

FIG. 2. – Variations in carbonate oxygen isotope ratios ($\delta^{18}O$ VSMOW) along the tooth crown of the third molar (M3) of modern sheep from North Ronaldsay and modern goats from Enkorika.

cattle teeth because they are larger than sheep teeth. Moreover, in all cases, part of the observed variability is also due to measurement precision for localisation of the enamel samples along the crown height and variability in tooth morphology which is affecting the location of the neck.

APPLICATION TO ARCHAEOLOGICAL ASSEMBLAGES

This protocol was applied earlier to the Late Stone Age assemblage of Kasteelberg (latitude 33°S, Cape Province, South Africa) where the analysis highlighted two birth seasons for sheep. This result was in accordance with observations by Europeans colonists of two lambing seasons for indigenous sheep in the Cape (Balasse *et al.* 2003). We are now applying the procedure to Neolithic assemblages from sites distributed at different latitudes in the North hemisphere and dated to the 4th millennium BC. This research is part of a project (ECLIPSE II) whose primary goal is to evaluate the climatic constraints on the development of Neolithic husbandry in Western Europe at the Atlantic/Sub-Boreal boundary. In the long term the objective is to map sheep and cattle birth seasonality and to evaluate the consequences on herding systems, with the potential to be able to disentangle herding options from environmental constraints. At this point we are presenting the results from three sites, two of which should be enlarged very soon. We would like to stress the fact that the conclusions were raised from small data sets and must be considered as preliminary.

MATERIAL AND METHODS

The Knap of Howar (KH) is a small Neolithic farmstead located on Papa Westray Island (latitude 59°N; Fig. 1) dated to ca. 3600 BC (Ritchie 1983). It corresponds to the very first colonisation of the Orkney archipelago by farming communities. The site includes two dry stone houses and a large midden. These yielded several thousand bone fragments, including a high proportion of cattle and sheep. Sheep husbandry seems to have been mostly oriented toward meat production, as documented by the kill off pattern obtained on the basis of tooth wear analysis (Tresset, unpublished), which reveals a slaughtering peak between six and twelve months, most of the animals being killed before reaching three years. As for cattle, teeth include a large proportion of unworn dp4, suggesting that a significant proportion of the animals were stillborn or died shortly after birth.

The Holm of Papa Westray (HPWN) is a megalithic tomb located on a small islet, off the main island of Papa Westray in the Orkney archipelago (Fig. 1), at a latitude of 59°N (Davidson & Henshall 1989). Part of its filling, composed mostly of thousands of bones of very young lambs and sheep foetuses, is likely to be a natural accumulation (Tresset 2003). Several radiocarbon dates clearly demonstrate that this accumulation is Neolithic, dated to the beginning of the 3rd millennium BC, probably between 2900 and 2600 cal BC. This implies that the tomb has been open for a long time during that period, providing the animals with a shelter against strong winds and precipitation. This also suggests the existence of an extensive herding strategy, where flocks wander freely.

Er Yoh is a Neolithic settlement located on an islet which was very likely part of the island of Houat at this period (latitude 47°N, Morbihan, France: Fig. 1), as it is attached to it at low tide nowadays. Excavated in 1924-1925 by Zacharie Le Rouzic, it is dated to the second half of the 4th millennium. The assemblage includes a significant proportion of sheep and cattle (Tresset 2003; Schulting *et al.* 2004). Complete neonatal sheep were recovered, that likely died of natural cause (Schulting *et al.* 2004). The kill off pattern established on the basis of tooth wear, characterised by a slaughtering peak between six and twelve months and a significant proportion of older animals, suggests a combination of meat production and the exploitation of the so-called “secondary products” (milk and maybe hair).

Three sheep third molars (M3) from the Knap of Howar, three sheep M3 and five cattle M3 from the

Holm of Papa Westray and five sheep M2 and three cattle M3 from Er Yoh were selected for sampling. We were careful in choosing teeth which did not match and most likely belonged to different individuals. At the Knap of Howar and the Holm of Papa Westray, this first data set will be soon extended with additional sheep and cattle teeth. The teeth were sampled and the enamel treated and analysed as described above for the modern sheep and goat teeth. Results from the analyses are shown in Tables 2 and 3 (in appendix) and Figs. 2 and 3.

SEASONALITY OF BIRTH IN ARCHAEOLOGICAL SHEEP

The patterns observed at the Knap of Howar suggest seasonal breeding with a restricted period of birth for sheep (Fig. 3). The lambing period seems less restricted at the Holm of Papa Westray as reflected by the shift in the sequence of the seasonal cycle recorded in HPWN ovis 3 and HPWN ovis 4 compared to HPWN ovis 2 (Fig. 3). For the reasons highlighted above, it is difficult to estimate more precisely what this shift represents in time.

Fig. 4 compares the pattern of variation of δ^{18}O along the tooth in archaeological (KH and HPWN) and modern sheep (NR) from the Orkney archipelago. If the pattern observed on a limited number of individuals at KH is confirmed, these sheep recorded the highest δ^{18}O values further away (~12 mm) from the tooth neck than the NR sheep (~ 5 to 8.5 mm). This suggests that when the KH sheep reached summer, their third molar was at an earlier development stage than in the NR sheep. If this is not explained by interbreed difference in the timing of tooth development, it could alternatively mean that KH sheep were born later in the year than the NR sheep. No such clear difference is observed when the NR sheep are compared to the sheep from HPWN.

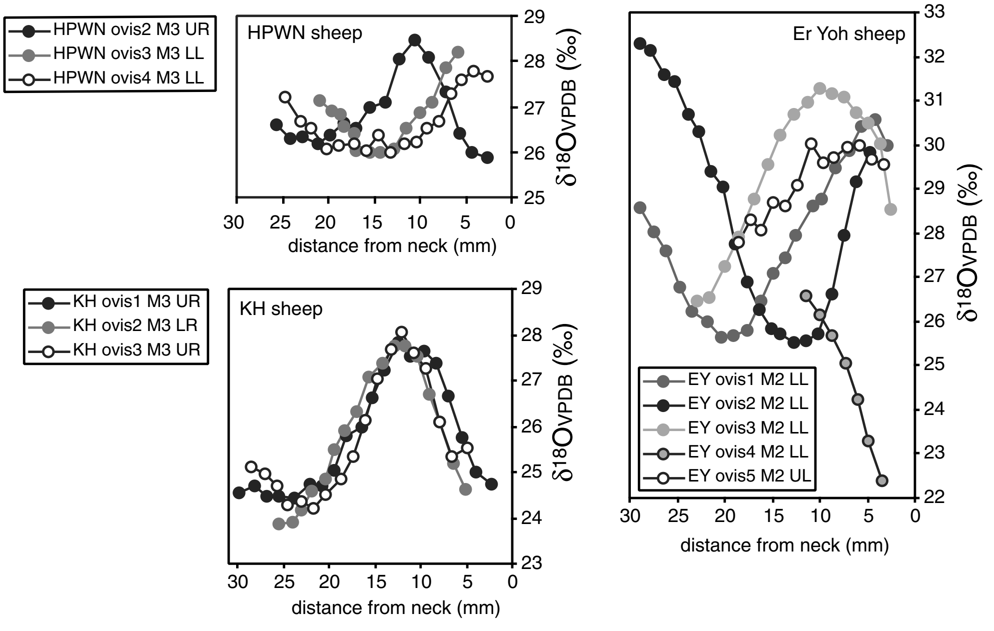

FIG. 3. – Variations in carbonate oxygen isotope ratios (δ^{18}O VSMOW) along the tooth crown of the sheep molars from the Holm of Papa Westray (HPWN), the Knap of Howar (KH) and Er Yoh.

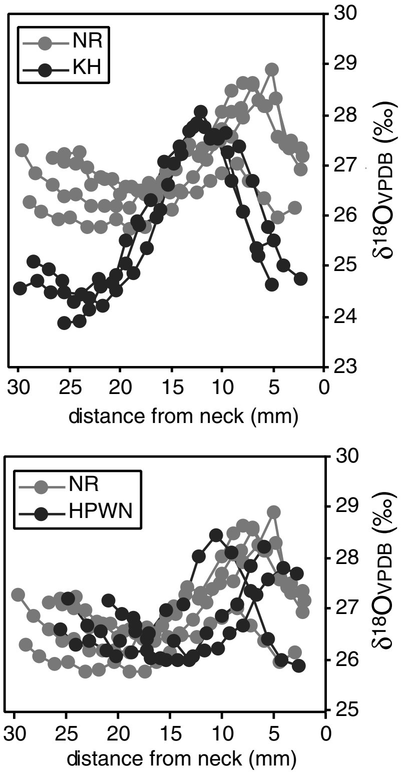

FIG. 4. – Comparison of the variations in carbonate oxygen isotope ratios ($\delta^{18}O$ VSMOW) along the tooth crown of modern sheep from North Ronaldsay (NR) and Neolithic sheep from the Knap of Howar (KH) and the Holm of Papa Westray (HPWN).

If a later onset of the breeding season is confirmed at Knap of Howar, compared to what is observed at Holm of Papa Westray, this might reflect progressive adaptation of the herding system to the environmental conditions of the archipelago. The occupation at Holm of Papa Westray post-dates the occupation at Knap of Howar by several centuries. Genetic selection could have occurred over this time. Moreover, it is likely that the scarcity of pasture at winter time put a serious constraint on the first herding communities at Knap of Howar, especially under moist climatic conditions making fodder storage difficult. At Holm of Papa Westray, it is interesting to note that sheep included marine resources in their winter diet (probably seaweed) as evidenced by stable carbon isotope analysis in their teeth, whereas marine resources did not contribute in a significant manner to the diet of sheep or cattle at the Knap of Howar (Balasse *et al.* 2006). Spontaneous or controlled supplementation of the winter sheep diet with marine resources might have helped in advancing the onset of the lambing season. However, at the same time, consumption of very high amounts of seaweed has been shown to have negative effects on ewes in the latter half of the gestation, occasioning a nervous disorder frequently fatal to the young (Hallson 1964). This might partly explain the high incidence of perinatal lambs in the assemblage of the Holm of Papa Westray (Harman, ms; Tresset, unpublished), although these sheep were shown to rely on a mixture of terrestrial and marine resources during winter rather than exclusive consumption of marine plants (Balasse *et al.* 2006). It is also likely that north-western Europe and more generally the North Atlantic area experienced particularly severe climatic conditions at that time, as suggested by the very low $\delta^{18}O$ ratios recorded several times between 2900 and 2600 cal BC in the GISP2 ice core from Greenland (Meese *et al.* 1997; Steig *et al.* 1994; Stuiver *et al.* 1995, 1997). This may have had an important impact on animal survival.

The pattern of $\delta^{18}O$ variation measured at Er Yoh (Fig. 2) is more difficult to interpret partly because of the loss of a significant part of the information on heavily worn teeth (EY ovis 4 and EY ovis 5). It seems however, that the variability in the timing of birth (the amplitude of variation in the location of the highest $\delta^{18}O$ values in the crown) is comparable to that observed at HPWN, assuming a similar rate of enamel formation for the second and third molar. Today, the local Ouessant sheep breed gives birth between February and September, with a peak in February and March. This breeding pattern is indeed more extended than that observed in North Ronaldsay. The variability in the range of intra-tooth variation of $\delta^{18}O$ from one individual to another is high at Er Yoh: EY ovis 4, in particular, shows very low values compared to the other sheep (Fig. 2). This could be explained by inter-annual variability in temperature, or a different drinking source for this individual. However, the possibility of intrusive material cannot be ruled out especially in the "upper layer" (LeRouzic 1930) from which EY ovis 3, EY ovis 4 and EY ovis 5 derive.

SEASONALITY OF BIRTH IN ARCHAEOLOGICAL CATTLE

At the Knap of Howar, the pattern of variation of $\delta^{18}O$ measured in cattle teeth is very similar in all five individuals, suggesting a strong seasonality of birth (Fig. 5). As observed for sheep, seasonality of birth in cattle seems less restricted at Er Yoh than at the Knap of Howar (Fig. 5). It is interesting to note that at the Knap of Howar, cattle remains include a significant number of unworn deciduous fourth premolars (dP4). The high occurrence of these dental buds reflects a significant perinatal mortality. The strict restrictions imposed by the harsh climatic conditions of Scottish Islands and Highlands on cattle herd management, especially in birth timing, has been extensively discussed by F. McCormick (1998): late calving would lead to a situation where the young is still too weak to confront the winter to come, and early calving would put too much pressure on the mother, still very weakened by the long Scottish winter. For this reason, in the 18th and 19th centuries, calves born unseasonably were slaughtered, to save the scarce fodder available for fitter animals, enhancing their chances to survive the winter. It is possible that births occurred over a more extended period than suggested by the results, but within this period the most favourable window allowing a good chance of survival could have been short, which would account for the fact that the individuals who eventually survived the first year were all born about the same time of the year, the others being slaughtered or dead from natural causes. This hypothesis will be soon tested by measuring the variation in $\delta^{18}O$ recorded in the unworn dP4 on the one hand, and in the heavily worn dP4 on the other hand, and comparing how the seasonal cycle was recorded in both groups.

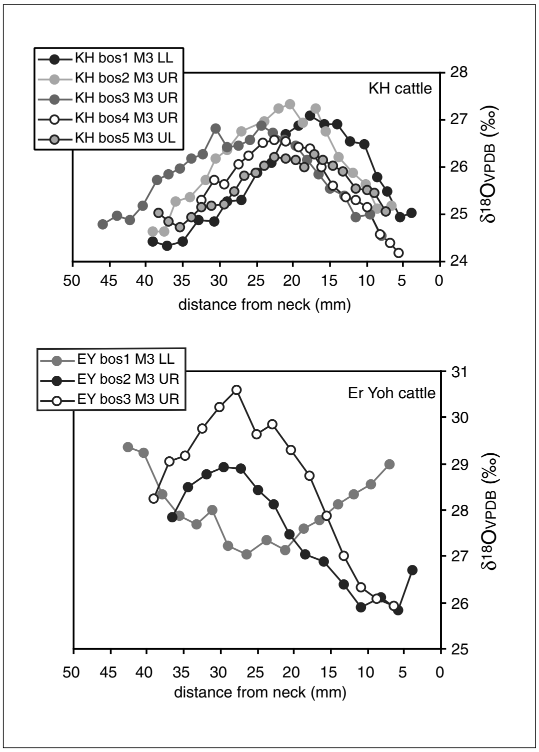

FIG. 5. – Variations in carbonate oxygen isotope ratios ($\delta^{18}O$ VSMOW) along the tooth crown of the cattle third molars (M3) from the Knap of Howar (KH) and Er Yoh.

CONCLUSIONS AND PERSPECTIVES

Physiological and environmental parameters are important components of the herding strategies and must be taken into account when evaluating herding systems. Animal husbandry is a cultural manipulation of a biological system. This biological system, including animal physiology and climatic and environmental settings, is constraining. Defining more precisely to what extent it can be culturally altered should lead us to more realistic reconstruction of past husbandry strategies.

It is most likely that in temperate conditions, the biological constraints on sheep and cattle reproductive timing were very strong in early husbandry. Direct assessment of birth seasonality from isotope measurements in teeth should however allow us to get a closer picture of the actual timing and duration of birth season in Neolithic assemblages from each site, rather than a general statement. The first results obtained on Neolithic assemblages from North Western Europe suggest that this picture might have been different for the first farming communities at the Knap of Howar, with a more restricted birth season — both for cattle and sheep — than subsequently at the Holm of Papa Westray and at Er Yoh. However it is not possible yet to disentangle the roles of climatic, biological and cultural factors responsible for this difference: fluctuations in weather conditions, technical adaptation to new environmental conditions, demographic management, intentional or unintentional genetic selection. These first observations must be challenged after enlargement of the data set with forthcoming measurements on additional specimens from the same assemblages. More work will then be conducted for comparison with other Neolithic assemblages from lower latitudes in western Europe.

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REFERENCES

ABI SALLOUM B. & CLAUS R. 2005. — Interaction between lactation, photoperiodism and male effect in German Merino ewes. *Theriogenology* 63: 2181-2193.

AVDI M., BANOS G., STEFOS K. & CHEMINEAU P. 2004. — Seasonal variation in testicular volume and sexual behavior of Chios and Serres rams. *Theriogenology* 62: 275-282.

BAILEY C.R. 1982. — *Cattle husbandry in the communal areas of Eastern Botswana*. PhD Cornell University. Ann Arbor, University Microfilms International.

BALASSE M., AMBROSE S.H., SMITH A.B. & PRICE T.D. 2002. — The seasonal mobility model for prehistoric herders in the south-western Cape of South Africa assessed by isotopic analysis of sheep tooth enamel. *Journal of Archaeological Science* 29: 917-932.

BALASSE M., SMITH A.B., AMBROSE S.H. & LEIGH S.R. 2003. — Determining sheep birth seasonality by analysis of tooth enamel oxygen isotope ratios: the Late Stone Age site of Kasteelberg (South Africa). *Journal of Archaeological Science* 30: 205-215.

BALASSE M., TRESSET A. & AMBROSE S.H. 2006. — First evidence for seaweed winter foddering in the Neolithic of Scotland. *Journal of Zoology* 270: 170-176.

BALASSE M., TRESSET A., DOBNEY K. & AMBROSE S.H. 2005. — The use of isotope ratios to test for seaweed eating in sheep. *Journal of Zoology* 266: 283-291.

BARTH F. 1961. — *The Nomads of South Persia*. Humanities Press, New York.

BEKURE S., DE LEEUW P.N., GRANDIN B.E. & NEATE P.J.H. 1991. — *Maasai herding. An analysis of the livestock production system of Maasai pastoralists in eastern Kajiado District, Kenya*. International Livestock Centre for Africa Systems study 4. ILCFA, Addis Ababa.

BERNUS E. 1988. — Seasonality, climatic fluctuations, and food supplies (Sahelian nomadic pastoral societies), in DE GARINE I. & HARRISON, G. A. (eds), *Coping with Uncertainty in Food Supply*. Clarendon Press, Oxford: 318-336.

BRYANT J.D., FROELICH P.N., SHOWERS W.J. & GENNA B.J. 1996a. — A tale of two quarries: biologic and taphonomic signatures in the oxygen isotope composition of tooth enamel phosphate from modern and Miocene equids. *Palaios* 11: 397-408.

BRYANT J.D., FROELICH P.N., SHOWERS W.J. & GENNA B.J. 1996b. — Biologic and climatic signals in the oxygen isotopic composition of Eocene-Oligocene equid enamel phosphate. *Palaeogeography, Palaeoclimatology, Palaeoecology* 126: 75-90.

DACHEUX J.L., PISSELET C., BLANC M.R., HOCHEREAU-DE-REVIER M.T. & COUROT M. 1981. — Seasonal variations in rete testis fluid secretion and sperm production in different breeds of ram. *Journal of Reproduction and Fertility* 61: 363-371.

DAHL G. & HJORT A. 1976. — *Having Herds. Pastoral Herd Growth and Household Economy*. Stockholm University, Stockholm.

DANSGAARD W. 1964. — Stable isotopes in precipitation. *Tellus* 16: 436-468.

DAVIDSON D.A. & JONES R.L. 1990. — The environment of Orkney, in RENFREW C. (eds.), *The Prehistory of Orkney (4000 BC-1000 AD)*. Edinburgh University Press, Edinburgh: 10-35.

DIGARD J.-P. 1981. — *Techniques des Nomades Baxtyâri d'Iran*. Éditions de la Maison des Sciences de l'Homme, Paris.

EZANNO P., ICKOWICZ A. & LANCELOT R. 2005. — Relationships between N'Dama cow body condition score and production performance under an extensive range management system in Southern Senegal: calf weight gain, milk production, probability of pregnancy, and juvenile mortality. *Livestock Production Science* 92: 291-306.

GARCIA S.C. & HOLES C.W. 1999. — Effects of time of calving on the productivity of pasture-based dairy systems: a review. *New Zealand Journal of Agricultural Research* 42: 347-362.

GAREL M., CUGNASSE J.-M., GAILLARD J.-M., LOISON A., GIBERT P., DOUVRE P. & DUBRAY D. 2005. — Reproductive output of female mouflon (*Ovis gmelini musimon* x *Ovis* sp.): a comparative analysis. *Journal of Zoology* 266: 65-71.

GAT J.R. 1980. — The isotopes of hydrogen and oxygen in precipitation, in FRITZ P. & FONTES J.-C. (eds), *Handbook of Environmental Isotope Geochemistry*. Vol. 1. *The Terrestrial Environment*. Elsevier, Amsterdam: 21-42.

GELEZ H. & FABRE-NYS C. 2004. — The "male effect" in sheep and goats: a review of the respective roles of the two olfactory systems. *Hormones and Behavior* 46: 257-271.

HAFEZ E.S.E. 1952. — Studies on the breeding season and reproduction of the ewe. *Journal of Agricultural Science* 42: 189-231.

HALLSON S. V. 1964. — *The uses of seaweeds in Iceland. Proceedings of the Fourth International Seaweeds Symposium, Biarritz 1961*. Pergamon Press, Oxford: 398-405.

JEAN-BRUHNES-DELAMARRE M. 1970. — *Le berger dans la France des villages*. Études et Documents de l'Institut d'Ethnologie de l'Université de Paris I. CNRS Éditions, Paris.

KARSCH F.J., BITTMAN E.L., FOSTER D.L., GOODMAN R.L., LEGAN S.J. & ROBINSON J.E. 1984. — Neuroendocrinal basis of seasonal reproduction. *Recent Progress in Hormone Research* 40: 185-232.

KARSCH F.J., ROBINSON J.E., WOODFILL C.J.I. & BROWN M.B. 1989. — Circannual cycles of luteinizing hormone and prolactin secretion in ewes during prolonged exposure to a fixed photoperiod: evidence for an endogenous reproductive rhythm. *Biology of Reproduction* 41: 1034-1046.

LAND L.S., LUNDELIUS E.L. & VALASTRO S. 1980. — Isotopic ecology of deer bones. *Palaeogeography, Palaeoclimatology, Palaeoecology* 32: 143-151.

LECOMTE T. & LE NEVEU C. 1986. — *Le Marais Vernier. Contribution à l'étude et à la gestion d'une zone humide*. Thèse de dotorat. Université de Rouen Haute-Normandie, Rouen.

LEGAN S.J. & KARSCH F.J. 1983. — Importance of retinal photoreceptors to the photoperiodic control of seasonal breeding in the ewe. *Biology of Reproduction* 29: 316-325.

LEE-THORP J.A., SEALY J.C. & VAN DER MERWE N.J. 1989. — Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. *Journal of Archaeological Science* 16: 585-599.

LEE-THORP J.A. & VAN DER MERWE N.J. 1991. — Aspects of the chemistry of modern and fossil biological apatites. *Journal of Archaeological Science* 18: 343-354.

LE ROUZIC Z. 1930. — *Carnac : Fouilles faites dans la région. Îlot d'Er Yoh (Le Mulon), commune de Houat, 1924-1925*. Imprimerie Lafolye et Lamarzelle, Vannes.

LINCOLN G.A., LINCOLN C.E. & MCNEILLY A.S. 1990. — Seasonal cycles in the blood plasma concentration of FSH, inhibin and testosterone, and testicular size in rams of wild, feral and domesticated breeds of sheep. *Journal of Reproduction and Fertility* 88: 623-633.

LINCOLN G.A. 1998. — Reproductive seasonality and maturation throughout the complete life-cycle in the mouflon ram (*Ovis musimon*). *Animal Reproduction Science* 53: 87-105.

LONGINELLI A. 1984. — Oxygen isotopes in mammal bone phosphate: a new tool for paleohydrological and paleoclimatological research. *Geochimica et Cosmochimica Acta* 48: 385-390.

LUZ B., KOLODNY Y. & HOROWITZ M. 1984. — Fractionation of oxygen isotopes between mammalian bone-phosphate and environmental drinking water. *Geochimica et Cosmochimica Acta* 48: 1689-1693.

MACE R. 1993. — Nomadic pastoralists adopt subsistence strategies that maximize long-term household survival. *Behavioral Ecology and Sociobiology* 33: 329-334.

MAHIEU M., AUMONT G. & ALEXANDRE G. 2003. — Élevage intensif des ovins tropicaux à la Martinique. *INRA Productions Animales* 10: 21-32.

MALPAUX B., VIGUIÉ C., SKINNER D.C., THIÉRY J.C. & CHEMINEAU P. 1997. — Control of the circannual rhythm of reproduction by melatonin in the ewe. *Brain Research Bulletin* 44: 431-438.

MASON J.L. 1980. — *Les ovins tropicaux prolifiques.* Étude FAO : Production et Santé animales 17. United Nations, Rome.

MEESE D.A., GOW A.J., ALLEY R.B., ZIELINSKI G.A., GROOTES P.M., RAM M., TAYLOR K.C., MAYEWSKI P.A. & BOLZAN J.F. 1997. — The Greenland Ice Sheet Project 2 depth-age scale: Methods and results. *Journal of Geophysical Research* 102(C12): 26, 411-426.

MORRIS J. 1999. — North Ronaldsay Sheep (seaweed-eating sheep of Orkney), in KELLY A. (eds), *Proceedings of the 5th World Congress on Coloured sheep and their Products.* Deakin University, Geelong: 41-46.

MUKASA-MUGERWA E. 1989. — *A review of a productive performance of female Bos indicus (zebu) cattle.* International Livestock Centre for Africa Monograph 6. ILCA, Addis Ababa.

MUKASA-MUGERWA E., ANINDO D., SOVANI S., LAHLOU-KASSI A., TEMBELY S., REGE J.E.O. & BAKER R.L. 2002. — Reproductive performance and productivity of Menz and Horro sheep lambing in the wet and dry seasons in the highlands of Ethiopia. *Small Ruminant Research* 45: 261-271.

ORTAVANT R., PELLETIER J., RAVAULT J.P., THIMONIER J. & VOLLAND-NAIL P. 1985. — Photoperiod: main proximal and distal factor of the circannual cycle of reproduction in farm animals. *Oxford Reviews of Reproductive Biology* 7: 306-345.

PEACOCK C.P. 1982. — Seasonal breeding effects on productivity, in GATENBY R.M. & TRAIL J.C.M. (eds), *Small ruminant breed productivity in Africa. Proceedings of a seminar held at ILCA, Addis Ababa, Ethiopia in October 1982.* International Livestock Center for Africa, Adis Ababa: 77-80.

POPLIN F. 1979. — Origine du Mouflon de Corse dans une nouvelle perspective paléontologique, par marronnage. *Annales de génétique et de sélection animale* 11 : 133-143.

REINHARDT C., REINHARDT A. & REINHARDT V. 1986. — Social behaviour and reproductive performance in semi-wild Scottish Highland cattle. *Applied Animal Behaviour Science* 15: 125-136.

RITCHIE A. 1983. — Excavation of a Neolithic farmstead at Knap of Howar, Papa Westray, Orkney. *Proceedings of the Society of Antiquaries of Scotland* 113: 40-121.

RITCHIE A. 2001. — Knap of Howar, Papa Westray. *Discovery and Excavation in Scotland* 2000: 124-125.

ROSA H.J.D. & BRYANT M.J. 2003. — Seasonality of reproduction in sheep. *Small Ruminant Research* 48: 155-171.

ROZANSKI K., ARAGUAS-ARAGUAS L. & GONFIANTINI R. 1996. — Isotope patterns of precipitation in the East African Region, in JOHNSON C. (eds), *The Limnology, Climatology and Paleoclimatology of the East African Lakes.* Gordon & Breach, Amsterdam: 79-93.

SANTIAGO-MORENO J., LOPEZ-SEBASTIAN A., GONZALEZ-BULNES A., GOMEZ-BRUNET A. & CHEMINEAU P. 2000. — Seasonal changes in ovulatory activity, plasma prolactin, and melatonin concentration, in Mouflon (*Ovis gmelini musimon*) and manchega (*Ovis aries*) ewes. *Reproduction, Nutrition, Development* 40: 421-430.

SANTIAGO-MORENO J., GOMEZ-BRUNET A., GONZALEZ-BULNES A., TOLEDANO-DIAZ A., MALPAUX B. & LOPEZ-SEBASTIAN A. 2005. — Differences in reproductive pattern between wild and domestic rams are not associated with inter-specific annual variations in plasma prolactin and melatonin concentrations. *Domestic Animal Endocrinology* 28: 416-429.

SCHULTING R., TRESSET A. & DUPONT C. 2004. — From harvesting the sea to stock rearing along the Atlantic façade of North-West Europe. *Environmental Archaeology* 9: 143-154.

STEIG E.J., GROOTES P.M. & STUIVER M. 1994. — Seasonal precipitation timing and ice core records. *Science* 266: 1885-1886.

STUIVER M., GROOTES P.M. & BRAZIUNAS T.F. 1995. — The GISP2 $\delta^{18}O$ climate record of the past 16,500 years and the role of the sun, ocean, and volcanoes. *Quaternary Research* 44: 341-354.

STUIVER M., BRAZIUNAS T.F., GROOTES P.M. & ZIELINSKI G.A. 1997. — Is There Evidence for Solar Forcing of Climate in the GISP2 Oxygen Isotope Record? *Quaternary Research* 48: 259-266

SUGA S. 1982. — Progressive mineralization pattern of developing enamel during the maturation stage. *Journal of Dental Research* 61: 1532-1542.

THIÉRY J.C., CHEMINEAU P., HERNANDEZ X., MIGAUD M. & MALPAUX B. 2002. — Neuroendocrinal interactions and seasonality. *Domestic Animal Endocrinology* 23: 87-100.

THIMONIER J., COGNIÉ Y., LASSOUED N. & KHALDI G. 2000. — L'effet mâle chez les ovins : une technique actuelle de maîtrise de la reproduction. *INRA Production Animales* 13: 223-231.

TRESSET A. 2003. — French Connections II: of cows and men, in ARMIT A., MURPHY E., NELIS E.L. & SIMPSON D.D.A. (eds), *Neolithic Settlement in Ireland and western Britain.* Oxbow, Oxford: 18-30.

VIGNE J.-D. 1988. — *Les mammifères postglaciaires de Corse. Étude archéozoologique.* CNRS Éditions, Paris.

ZAZZO A., LÉCUYER C. & MARIOTTI A. 2004. — Experimentally-controlled carbon and oxygen isotope exchange between bioapatites and water under inorganic and microbially-mediated conditions. *Geochimica et Cosmochimica Acta* 68: 1-12.

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APPENDIX

TABLE 1. – Oxygen stable isotope ratios (δ^{18}O VSMOW) of carbonate from enamel sampled along the tooth crown of the third molar (M3) of five modern sheep from North Ronaldsay (NR ovis 1-5) and five modern goats from Enkorika (Enk capra 1-5).
For each sample, distance from the crown neck is reported in mm.

mm	δ^{18}O (‰)	mm	δ^{18}O (‰)	mm	δ^{18}O (‰)	mm	δ^{18}O (‰)
NR ovis1 M3		**NR ovis3 M3**		**NR ovis4 M3**		**NR ovis5 M3**	
29,0	26,3	25,6	27,2	29,7	27,3	26,7	27,1
27,7	26,1	24,1	27,2	28,3	26,8	25,5	27,1
26,1	25,9	22,9	26,6	26,7	26,6	24,4	27,0
24,9	26,0	21,6	26,7	25,5	26,4	23,2	27,0
23,2	25,8	20,0	26,4	24,3	26,4	22,0	26,8
21,9	25,8	18,9	26,6	22,9	26,2	20,8	26,7
20,5	25,9	17,6	26,4	21,6	26,2	19,5	26,6
19,0	25,8	16,5	26,4	20,5	26,2	18,4	26,5
17,5	25,8	15,2	26,4	19,0	26,1	17,2	26,6
16,4	26,0	14,1	26,5	18,0	26,5	15,8	26,7
15,0	26,1	12,9	26,8	16,5	26,5	14,7	27,0
14,0	26,5	11,5	27,1	15,5	26,9	13,5	27,3
12,5	26,5	10,2	27,5	14,5	26,9	12,2	27,2
11,1	26,7	9,0	27,6	13,3	27,4	11,0	27,4
10,0	26,8	7,9	27,9	12,0	27,3	10,0	27,7
8,5	27,0	6,5	28,3	10,1	28,1	9,0	28,1
7,3	26,7	5,1	28,9	9,0	28,5	8,1	28,2
5,9	26,4	3,7	27,4	7,9	28,6	7,0	28,6
4,5	26,0	2,2	26,9	7,0	28,6	5,9	28,2
2,9	26,2			5,7	28,2	4,5	27,6
				4,8	28,3	3,3	27,5
				3,4	27,3	2,2	27,3
				2,1	27,2		

mm	δ^{18}O (‰)	mm	δ^{18}O (‰)	mm	δ^{18}O (‰)	mm	δ^{18}O (‰)
Enk capra1 M2		**Enk capra2 M2**		**Enk capra3 M2**		**Enk capra4 M2**	
27,0	32,6	28,5	33,9	24,4	35,5	24,6	36,9
25,8	32,5	26,6	33,4	22,3	34,6	22,5	36,7
23,9	33,7	24,7	33,2	20,4	34,5	20,4	36,9
22,1	33,9	21	34,3	18,4	33,9	18,2	36,8
20,7	34,7	19	34,8	16,3	33,3	16,1	36,4
19,1	35,1	16,7	35,5	14,2	33,5	14,5	35,9
17,2	35,6	14,6	37,8	12,2	33,7	12,5	35,0
15,5	35,4	11,7	38,2	10,2	34,2	7,3	34,7
13,8	35,5	9,7	38,2	8,1	35,0	5,5	34,8
12,0	36,3	7,6	37,6	6,1	36,9		
10,2	35,8			4,2	37,1		
8,4	35,3						
6,6	35,7						
4,8	35,4						
3,3	35,6						

TABLE 2. – Oxygen stable isotope ratios ($\delta^{18}O$ VSMOW) of carbonate from enamel sampled along the tooth crown of the third molar (M3) of sheep from the Holm of Papa Westray (HPWN ovis) and the Knap of Howar (KH ovis) and cattle from Er Yoh (EY Bos). For each sample, distance from the crown neck is reported in mm.

mm	$\delta^{18}O$ (‰)	mm	$\delta^{18}O$ (‰)	mm	$\delta^{18}O$ (‰)
HPWN ovis2 M3		**HPWN ovis3 M3**		**HPWN ovis4 M3**	
25,7	26,6	21,0	27,2	24,8	27,2
24,2	26,3	19,7	26,9	23,1	26,7
22,8	26,4	18,6	26,8	21,8	26,5
21,2	26,2	18,3	26,6	20,2	26,1
19,8	26,4	17,2	26,4	18,8	26,2
18,3	26,7	16,9	26,0	17,2	26,2
17,0	26,5	15,5	26,0	15,9	26,0
15,4	27,0	14,3	26,0	14,6	26,4
13,8	27,1	12,9	26,1	13,2	26,0
12,2	28,0	11,5	26,5	11,7	26,2
10,5	28,5	10,0	26,9	10,4	26,2
9,1	28,1	8,6	27,1	9,2	26,5
7,2	27,3	7,2	27,8	8,0	26,7
5,6	26,4	5,9	28,2	6,6	27,3
4,3	26,0			5,5	27,6
2,6	25,9			4,1	27,8
				2,7	27,7
mm	**$\delta^{18}O$ (‰)**	**mm**	**$\delta^{18}O$ (‰)**	**mm**	**$\delta^{18}O$ (‰)**
KH ovis1 M3		**KH ovis2 M3**		**KH ovis3 M3**	
29,8	24,5	25,5	23,9	28,5	25,1
28,2	24,7	24,0	23,9	27,1	24,9
26,9	24,5	23,0	24,2	25,7	24,7
25,5	24,5	22,0	24,6	24,5	24,3
23,8	24,4	20,5	24,8	23,0	24,4
22,2	24,7	19,5	25,5	21,8	24,2
20,7	24,7	18,3	25,9	20,4	24,5
19,5	25,1	17,1	26,3	18,8	24,9
18,2	25,8	15,7	27,1	17,3	25,3
16,5	26,0	14,1	27,4	16,0	26,1
15,3	26,6	12,9	27,8	14,7	27,0
13,9	27,2	11,7	27,8	13,2	27,7
12,5	27,8	10,4	27,5	12,1	28,0
11,2	27,5	9,0	26,7	10,7	27,6
9,7	27,7	7,9	26,1	9,4	27,3
8,4	27,4	6,5	25,2	8,0	26,1
6,9	26,7	5,1	24,6	6,6	25,4
5,5	25,8			4,9	25,5
4,0	25,0				
2,2	24,8				
mm	**$\delta^{18}O$ (‰)**	**mm**	**$\delta^{18}O$ (‰)**	**mm**	**$\delta^{18}O$ (‰)**
EY Bos1 M3		**EY Bos2 M3**		**EY Bos3 M3**	
42,6	29,4	36,5	27,9	39,2	28,2
40,4	29,2	34,5	28,5	36,9	29,1
38,0	28,3	31,9	28,8	34,9	29,2
35,7	27,9	29,6	28,9	32,4	29,8
33,3	27,7	27,2	28,9	30,1	30,2
31,1	28,0	24,9	28,4	27,9	30,6
28,9	27,2	22,7	28,1	25,1	29,6
26,5	27,0	20,6	27,5	23,0	29,9
23,8	27,4	18,5	27,0	20,5	29,3
21,2	27,1	16,0	26,9	17,9	28,7
18,7	27,6	13,3	26,4	15,6	27,9
16,5	27,8	10,8	25,9	13,2	27,0
14,1	28,1	8,2	26,1	10,8	26,3
11,8	28,3	5,9	25,8	8,7	26,1
9,5	28,6	3,9	26,7	6,5	25,9
7,1	29,0				

TABLE 3. – Oxygen stable isotope ratios ($\delta^{18}O$ VSMOW) of carbonate from enamel sampled along the tooth crown of the third molar (M3) of cattle from the Knap of Howar (KH Bos) and the second molar (M2) of sheep from Er Yoh (EY ovis).
For each sample, distance from the crown neck is reported in mm.

mm	$\delta^{18}O$ (‰)	mm	$\delta^{18}O$ (‰)	mm	$\delta^{18}O$ (‰)	mm	$\delta^{18}O$ (‰)	mm	$\delta^{18}O$ (‰)
KH Bos 1 M3		**KH Bos 2 M3**		**KH Bos 3 M3**		**KH Bos 4 M3**		**KH Bos 5 M3**	
39,1	24,4	39,1	24,6	46,0	24,8	32,5	25,3	38,3	25,0
37,1	24,3	37,5	24,6	44,0	25,0	30,7	25,7	36,9	24,9
35,0	24,4	35,9	25,3	42,3	24,9	29,4	25,6	35,4	24,7
32,9	24,9	34,0	25,4	40,5	25,2	27,5	26,1	33,9	24,9
30,7	24,9	32,0	25,7	38,5	25,7	26,0	26,2	32,4	25,2
29,0	25,3	30,5	26,2	37,0	25,9	24,2	26,5	31,2	25,2
27,0	25,3	28,9	26,4	35,5	26,0	22,6	26,6	29,3	25,2
25,0	25,9	27,1	26,8	33,9	26,2	21,0	26,6	28,0	25,5
23,0	26,1	23,9	27,0	32,2	26,3	19,2	26,4	26,7	25,8
21,0	26,7	21,9	27,2	30,6	26,8	17,7	26,4	25,1	25,9
19,2	26,9	20,4	27,3	28,9	26,4	16,2	26,0	24,0	26,0
17,7	27,1	18,7	26,9	27,5	26,4	14,5	25,6	22,5	26,2
15,8	26,9	17,0	27,2	25,9	26,6	12,9	25,4	21,0	26,2
14,0	26,9	15,5	26,8	24,4	26,9	11,5	25,3	19,7	26,1
12,3	26,5	13,8	26,2	22,8	26,7	10,0	25,2	18,4	26,0
10,4	26,5	11,9	25,9	21,2	26,6	8,2	24,6	17,2	26,3
8,6	25,8	10,2	25,6	19,7	26,5	6,8	24,4	16,0	26,2
7,2	25,5	8,5	25,1	18,0	26,1	5,7	24,2	14,5	26,0
5,5	24,9	6,7	25,2	16,5	25,8			13,2	25,9
3,9	25,0			14,9	25,5			11,5	25,6
				13,0	25,4			10,0	25,5
				11,5	24,9			8,9	25,5
				9,5	25,0			7,4	25,1
				8,0	24,5				

mm	$\delta^{18}O$ (‰)	mm	$\delta^{18}O$ (‰)	mm	$\delta^{18}O$ (‰)	mm	$\delta^{18}O$ (‰)	mm	$\delta^{18}O$ (‰)
EY ovis1 M2		**EY ovis2 M2**		**EY ovis3 M2**		**EY ovis4 M2**		**EY ovis5 M2**	
28,9	28,6	29,0	32,3	23,0	26,5	11,4	26,6	18,5	27,8
27,5	28,0	27,8	32,1	21,7	26,5	10,0	26,2	17,3	28,3
26,1	27,6	26,4	31,6	20,0	27,3	8,7	25,7	16,1	28,1
24,8	26,8	25,2	31,4	18,5	27,9	7,2	25,1	14,9	28,7
23,4	26,2	23,9	30,7	17,0	28,8	6,0	24,2	13,6	28,6
21,8	26,0	22,7	30,3	15,5	29,6	5,0	23,3	12,3	29,1
20,4	25,6	21,5	29,4	14,1	30,2	3,4	22,4	10,9	30,0
19,1	25,7	20,2	29,0	12,7	30,7			9,6	29,6
17,6	25,8	19,0	27,8	11,2	31,0			8,5	29,7
16,2	26,5	17,6	26,9	10,0	31,3			7,1	30,0
15,0	27,1	16,3	26,3	8,8	31,2			5,9	30,0
13,7	27,4	15,1	25,8	7,4	31,1			4,5	29,7
12,5	27,9	14,1	25,7	6,1	30,7			3,2	29,6
10,8	28,6	12,8	25,5	4,9	30,5				
9,8	28,8	11,4	25,6	3,6	30,0				
8,3	29,5	10,2	25,7	2,5	28,6				
7,0	29,9	8,8	26,6						
5,6	30,4	7,5	27,9						
4,2	30,6	6,1	29,2						
3,0	30,0	4,8	29,8						