Journal of Archaeological Science: Reports xxx (2015) xxx–xxx

Contents lists available at ScienceDirect

Journal of Archaeological Science: Reports

journal homepage: http://ees.elsevier.com/jasrep

The Sheep Project (2): The effects of plane of nutrition, castration and the timing of first breeding in ewes on dental eruption and wear in unimproved Shetland sheep

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ARTICLE INFO

Article history:
Received 26 March 2015
Received in revised form 6 October 2015
Accepted 22 October 2015
Available online xxxx

Keywords:
Sheep
Zooarchaeology
Tooth wear
Tooth eruption

ABSTRACT

The skeletons of 356 unimproved Shetland sheep from flocks kept at two nutritional levels are used to investigate the effects of nutritional level on the timing of mandibular dental eruption, and of wear in the mandibular fourth premolar and molars; comparisons are also made between entire and early-castrated males and between unbred, early-bred and late-bred ewes. Sheep weights and counts of permanent anterior teeth recorded during life are also investigated. The skeletal dental data are compared to timing of bone fusion recorded for the same individuals (Popkin et al., 2012).

Results show small differences in the timing of eruption and tooth wear between males and females, and that these processes are only marginally affected by castration and the timing of first breeding in ewes. Small differences between sheep at the two nutritional levels are also present; however the difference between the two feeding regimes was moderate, and more marked nutritional differences might have larger effects.

The implication of our data is that marked intra-assemblage differences cannot be explained exclusively by changes in the management variables explored in this study. Further, as sex and castration have little effect on the timing of dental eruption and wear, but substantially delay epiphyseal fusion (Popkin et al., 2012), we support previous hypotheses that comparison of the two datasets may provide a method for investigating flock structure in past animal husbandry. Our results are of most relevance to domestic sheep assemblages from similar environments to the UK, and to the Shetland breed, but can assist zooarchaeologists worldwide in interpreting dental data.

1. Introduction

The sheep project was set up to investigate the effect of nutrition, sex, castration and pregnancy on skeletal development, in order to inform and improve zooarchaeological interpretations of sheep husbandry. These themes are explored in our previous publication (Popkin et al., 2012), which focused on their significance to bone maturation and post-cranial biometry, and demonstrated clear influences of sex, castration and nutrition in the timing of bone fusion. Osteological implications of breeding age in ewes were also considered by Baker et al. (2014).

This paper presents data for the timing of tooth eruption and rate of tooth wear, and their relationship with nutrition, sex, castration and pregnancy, within a flock of 356 domestic sheep (*Ovis aries*) of known life history with age at death resolved to the day. Impact of sex and management is discussed in relation to individual teeth; age estimation, including derived mandible wear stages, is not considered. The flock comprises unimproved Shetland sheep, raised outdoors in Scotland. The data are of direct relevance to similar environmental conditions and breeds, but can also contribute to understanding domestic sheep assemblages elsewhere.

1.1. Tooth eruption and wear: factors influencing sequence and timing

Sheep teeth erupt, wear down and are replaced in a known sequence. The progression of this sequence, particularly in anterior teeth, is traditionally used to age and assess the quality of farm stock, and has therefore been commonly recorded in live animals (for example, Botkin et al., 1988, 8–9; Brown, 1913, 45–51; McGregor, 2011; Simonds, 1854). The sequence of eruption is consistent between domestic sheep breeds, and varies only slightly between domestic sheep and goats (*Capra hircus*) (Jones, 2006). Inconsistencies between wild sheep species, for example *Ovis dalli* and *Ovis canadensis* (Hemming, 1969), are not relevant to British assemblages, which comprise only domestic sheep and goats.

The timing of sheep tooth eruption differs between breeds (e.g., for anterior teeth see Aitken and Meyer, 1982; Arrowsmith et al., 1974; Wiener and Purser, 1957) and sexes (Section 2.1.1), reflecting their different rates of maturation, and is associated with weight gain

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http://dx.doi.org/10.1016/j.jasrep.2015.10.029
2352-409X/

(McGregor, 2011). The timing of eruption is also suggested to vary in sheep subject to differing environmental factors, for example nutrition (Section 2.2.1) and stocking levels. Tooth wear is the progressive attrition of enamel. Its rate reflects the time that the tooth has been in occlusion (and therefore any influences on timing of eruption) together with the morphology and robusticity of the tooth enamel in question (both of which may reflect genetic and environmental variation), the abrasiveness of ingested food and contaminants (including seasonal variations), and time spent eating, ruminating or tooth grinding (Every et al., 1998). Eating behaviours may themselves be influenced by the sexes differing nutritional requirements for growth and reproduction, food availability (Galvani et al., 2010), forage preference (sheep are selective grazers; Guðmundsson and Dýmundsson, 1989) including influence of territorial and social behaviour (Dumont and Boissy, 2000), stocking levels (Guðmundsson, 1993), and even weather conditions (for example temperature, Kennedy, 1983).

Since the 1960s, zooarchaeology has increasingly investigated the sequence of dental eruption and wear in archaeological sheep mandibles. Several methods for categorising the progressive eruption of teeth and exposure of dentine have been published (for example, Ewbank et al., 1964; Grant, 1975; Grant, 1982; Payne, 1973; Payne, 1987). More recently, research has begun to investigate the relationship between dental succession, age, sex, breed, castration and nutrition, using modern collections of sheep (Clutton-Brock et al., 1990; Greenfield and Arnold, 2008; Hatting, 1983; Jones, 2006; McGregor, 2011; Moran and O'Connor, 1994; Zeder, 2006).

1.2. Zooarchaeological research potential

Zooarchaeological interpretation is often comparative, investigating evidence for social, cultural, chronological or spatial similarity and difference in husbandry and animal utilisation. Sheep dental data is used to estimate age at death and suggest flock structures and product utilisation, quality of meat consumed, and seasonality of slaughter whether for everyday or festive/ceremonial activities. The validity of intra- or inter-site comparison often relies on assumed minimal influence of forage quality (associated with status, geography and topography) and management practices (including castration and breeding of ewes) on dental data. However, these factors do influence post-cranial skeletal development (growth and fusion) in the population under study (Popkin et al., 2012).

The known life history dental data presented here therefore offer two primary opportunities. Firstly, to refine and clarify understanding of the influence of forage quality and flock management on dental eruption and tooth wear, and secondly to investigate whether any differences seen in dental processes can be compared to variation in epiphyseal fusion, in order to investigate sheep management practices for comingled assemblages, or to confirm sex in articulated skeletons. The implications of our data on age at death estimation are considered elsewhere (Worley et al., in preparation).

2. Background

This section reviews previous research into the impact of sex and nutrition on tooth development and wear. It also summarises previous research into how sex and nutrition affected other maturation and growth characteristics of the study population (i.e., osteometric and bone fusion data).

2.1. Impact of breed, sex and management (castration of rams, breeding age in ewes) on sheep

2.1.1. Comparative research on tooth eruption and wear with reference to breed, sex and management

In a precursor to this research, Moran and O'Connor (1994) noted that there are few reliable data regarding differences in tooth eruption. The majority of research has focussed on incisor eruption. Comparing males and ewes, some sources suggest male first incisors erupt slightly earlier (Field et al., 1990; Simonds, 1854, 87), while others found little or no difference (Ho et al., 1989), even in large samples (Matika et al., 1992). Castration has been reported to result in earlier eruption by some authors (Clutton-Brock et al., 1990 incisor and cheek tooth data, Ho et al., 1989 incisor data for Finn x Whiteface), while others have found little effect (for example Davis, 2000 cheek tooth data, Hatting, 1983 incisor data), although some wethers exhibited advanced eruption in Hatting's small dataset. Differences in eruption between rams, wethers and ewes are also impacted by breed (as shown in Ho et al., 1989).

We are not aware of studies on tooth eruption in relation to age at first mating in ewes. It is possible that breeding ewe lambs (under 12 months) impacts on tooth eruption through reduced live weight (McGregor, 2011, 81; see Kenyon et al., 2011, 327 for live weight studies), though a direct effect of early breeding on eruption has not been reported. Studies of breeding age and tooth wear have indicated that ewes successfully bred when young (<12 months) may suffer a greater incidence of broken mouth, and incisor wear and loss when adult (6 years and older), which can impact on their condition and productivity (McGregor, 2011, 82, 83).

There are few studies of the effect of sex on tooth wear. Davis found slight accelerated wear in Shetland rams relative to wethers (Davis, 2000), but Jones (2006) found no difference between ewes and rams for some mandible wear stages in 3 to 8 month old animals. She considered her dataset for older sheep too small to draw useful conclusions, although her data show slight advanced median mandible wear stage for ewes at 13 months (Jones, 2006, Fig. 14).

2.1.2. Previous results of sex, castration and breeding impacts on other maturation and growth characteristics of the subject population

2.1.2.1. Sex, castration, breeding and growth (osteometric data). Popkin et al. (2012) demonstrated that bone growth is not uniform across the skeleton, but varies by element portion and by plane of growth depending on the sex and castration status of the individual. In general terms, sex has the strongest influence on bone growth with ewes being smaller than both rams and wethers. Wether elements are always longer than ewe elements but wether femur, humerus, astragalus and calcaneus are not always longer than the ram counterparts. Differences in bone growth between the sexes also vary by plane of nutrition, as described below. Breeding and early breeding limit the potential for skeletal growth (size, shape, variability) in ewes (Baker et al., 2014).

2.1.2.2. Sex, castration, breeding and skeletal maturity (bone fusion data). Popkin et al. (2012) demonstrated that both sex and nutrition significantly affect the timing of fusion in post-cranial skeletal elements. In later fusing elements, castration leads to a delay in epiphyseal fusion of up to 12 months relative to rams and up to 21 months relative to ewes. Ewes consistently show the earliest onset and completion of fusion relative to both wethers and rams. Early breeding impacts completion of fusion in ewes, which may be due to slowing of the fusion process or, in some cases, to a delay in the onset of fusion (Baker et al., 2014).

2.2. Impact of nutrition on sheep

2.2.1. Comparative research on tooth eruption and wear with reference to nutrition

Moran and O'Connor's (1994) research noted a general dearth in data on the impact of nutrition on dental development, citing Tschirvinsky (1909), Franklin (1950) and a series of papers published in the 1960s (Cutress and Healy, 1965; Healy et al., 1967; Healy and Ludwig, 1965) as exceptions. Research into the impact of nutritional mineral and vitamin deficits (for example, Franklin, 1950; see also

Please cite this article as: Worley, F., et al., The Sheep Project (2): The effects of plane of nutrition, castration and the timing of first breeding in ewes on dental eruption a..., Journal of Archaeological Science: Reports (2015), http://dx.doi.org/10.1016/j.jasrep.2015.10.029