

CHAPTER 3:

WHY DO DOMESTIC MAMMALS CHANGE IN SIZE AND SHAPE?

'It is striking how an environmental factor such as the level of nutrition changes the size and form of the cannon bone and consequently even more the shape of other later maturing parts of the skeleton, thus altering the conformation of the animal as a whole' (Pálsson & Vergés 1952a: 68)

3.1 INTRODUCTION

Bones are made up of a variety of living tissues and are as such organs, the function of which is to provide strength and stability to the body. Bones continue to grow with the rest of the body until an animal reaches maturity. Therefore the size and shape of individual bones is dictated by the genetic makeup of an animal. In order to achieve their genetic potential however bones need the correct environmental conditions i.e. enough energy and the correct raw materials for the tissues to be able to grow; the growth of bones is therefore also influenced by a series of environmental factors.

The factors affecting the size and shape of bones can be divided into two main groups; genetic factors and environmental factors. The two key genetic factors are the sex of the animal (i.e. male or female) and the breed or type of animal. Wild animals are affected by two key environmental factors: climate and available nutrition. Domestication and the consequent human interference provide two additional environmental variables, in particular the nature of husbandry (i.e. the provision of stalling and fodder) and the possibility of castration. This chapter will

examine these six key factors and look at evidence found by other researchers for how they affect body and consequently bone size and shape.

3.2 SEXUAL DIMORPHISM

Sexual dimorphism in both wild and domestic species is widely studied in archaeozoology (e.g. Greenfield 2006; Weinstock 2006; Howard 1963; Davis 2000). The identification of sex is key to the understanding of hunting or animal husbandry strategies. This section begins by looking at the evolutionary significance of sexual dimorphism and the purpose it may serve, before examining some of the broader trends of sexual dimorphism in mammals and reviewing the literature examining sexual dimorphism in specific elements; this not only looks at cattle and sheep but other, closely related taxa, in particular a variety of caprines and cervids, both of which demonstrate a high degree of sexual dimorphism. The final part of this section will look at some of the problems with trying to detect sexual dimorphism in archaeological samples/populations.

3.2.1 Evolutionary Significance

In order to fully understand sexual dimorphism and why some bones are more dimorphic than others it is first important to understand why males and females have different sizes. In the majority of known sexually reproducing animal species the female is bigger than the male (e.g. Arachnida, Cephalopoda, Crustacea, Annelida and Lophiiformes (angler fish), Fairbairn 2007: 3). The reason for this is that in these taxonomic groups the females must carry large quantities of young or eggs and the males do not (Lindenfors *et al.* 2007: 16). In most mammals (and birds) the opposite

is true; almost without exception male mammals are bigger than their female counterparts. Female mammals carry much fewer young and expend a much greater amount of time and energy on caring for them after birth than do other taxa. For male mammals, in particular those of polygamous species, it is of great advantage to be bigger; the likelihood of breeding depends on their ability to secure quality territory, i.e. for most ungulates this means good grazing land where females will come to feed. The larger a male is the more likely he is to win a fight for territory and hence access to females, and therefore have a higher chance of successful mating (Capellini 2007; Lindenfors *et al.* 2007). Therefore natural selection favours large body size in males of polygamous mammal species.

3.2.2 Broad Trends in Sexual Dimorphism of Polygamous Mammals

As we have seen from the preceding section, in general male mammals are larger than females of the same species. However this difference is much more marked in total body weight than it is in bone size; female Ibex (*Capra ibex*) are half the body weight of the males while their bone weights are approximately 80-85% of that of the males (Fernández & Monchot 2007). Mitchell and Grant (1981) noted a similar pattern in Red deer (*Cervus elaphus*). Additionally in male-biased sexually size dimorphic species the greater the average body mass of a species the greater the difference in size between males and females; this is known as Rensch's rule (Fairbairn 1997; Lindenfors *et al.* 2007). It is therefore likely that cattle would show a greater degree of sexual dimorphism than sheep.

In addition to males being larger over all, their bones tend to be more robust in order to support a greater muscle mass; bone measurements therefore tend to show a greater degree of sexual dimorphism in breadth dimensions than in length dimensions (e.g. Howard 1963), this will be seen more specifically in the following section where differences in individual elements will be examined. One final trend worthy of mention is that noted by Bartosiewicz (1984b), that later fusing bones have a greater chance of being affected by the influence of gonadal hormones and are therefore more likely to show signs of sexual dimorphism.

3.2.3 Patterns of Sexual Dimorphism in Individual Elements

The following section gives brief descriptions of individual elements that display metric variation between males and females. Elements are listed in anatomical order starting with the horncores and finishing with the phalanges.

Horncores

In sheep and cattle horns are not always present and in many modern breeds are often absent in both males and females. However hornedness can vary between types of sheep and cattle from both males and females displaying horns to neither having them. Soay rams have large horns while ewes have either considerably smaller horns than the rams or none at all (Clutton-Brock *et al.* 1990). For cattle Grigson (1982) noted that bulls had longer and stouter horns than cows but that males and females could only be identified when examining one type of cattle and not when examining mixed populations. Sykes and Symmons (2007) managed to somewhat overcome this problem: they found that the basal circumference and the

minimum basal diameter of cattle horncores were the most sexually dimorphic measurements. When plotted against each other they could provide total separation of males and females for mixed breeds of medium and long horn types, i.e. providing that short horn varieties (those with an outer curve measurement <195mm) were excluded there was no overlap between males and females on a scatter plot of these two measurements.

Skull

Clutton-Brock *et al.* (1990) noted that on average male Soays had longer skulls than females. For cattle, Howard (1963) noted that males had relatively broader skulls than females and examination of the data she presents shows the frontal breadth of the skull to be absolutely larger in bulls; only female *Bos primigenius* measurements overlapped with those for modern bulls. Grigson (1982) noted that the length of the base of the skull was very similar in cows and bulls but that other lengths and breadths were larger in bulls than in cows.

Mandibles and Teeth

Grigson (1982) noted that there was no sex difference in the cattle maxillary tooth row or in individual teeth. In addition Clutton-Brock *et al.* (1990: 22) noted that 'when separate from the skull it is not possible to establish the sex of the mandible of the Soay'. However studies of caribou (*Rangifer tarandus*) have shown these animals to be sexually dimorphic (males larger) in a variety of mandible length measurements (Bergerud 1964; Miller 1974; Morrison & Whitridge 1997); of most interest was that the tooth row was found not to be a good discriminator for sex (Morrison &

Whitridge 1997) but total length (found to be closely correlated with diastema length (Miller 1974)) and the length from the third molar to the mental foramen were good sexual indicators. This suggests that the majority of the sexual dimorphism in mandible length comes from the diastema. Examination of Clutton-Brock *et al.*'s (1990: 48) data for Soay sheep shows the means and ranges for total mandible length and the length of horizontal ramus, both of which include the diastema, to be very similar for males and females indicating that the pattern noted in caribou is not likely to be present in sheep.

Atlas and Axis

For cattle Grigson (1982) listed both of these elements to be larger in bulls than in cows and Boessneck (1969) reports that the vertebrae are thicker and 'more massive' in male sheep and goats than in females. Likewise Clutton-Brock *et al.* (1990) report that these bones are much more robust in Soay rams than in ewes due to the necessity of supporting much heavier sets of horns in rams. This would tend to indicate that this difference would be less pronounced in a hornless type of sheep or cattle.

Scapula

Riedel (1977 from Grigson 1982) suggests that a difference of over 20% could be observed between males and females in cattle distal scapula measurements, but Grigson (*ibid.*) treats this with caution as it was difficult to establish how divisions between the sexes were made and castrates were not identified. Davis (2000) found a 7-9% difference between Shetland ram and ewe mean scapula measurements.

Humerus

In the Ibex (*Capra ibex*) Fernández and Monchot (2007) found the humerus SD (smallest breadth of the diaphysis) measurement to be one of the most sexually dimorphic from a range of limb bone measurements; the mean measurement for females was less than 80% of the mean measurement for males. The same measurement in sheep was found to be only 7% different between Shetland rams and ewes (i.e. female measurements were 93% of male measurements) (Davis 2000). However Davis (*ibid.*) also found that the GLC (greatest length from the caput) was 11% larger in Shetland rams than ewes and that this measurement was one of the more sexually dimorphic dimensions from the selection that he took.

Radius (and ulna)

As for the scapula Riedel (1977 from Grigson 1982) suggests that dimensions of the proximal radius in cattle differ by over 20% between males and females; the particular dimensions used are not mentioned by Grigson (*ibid.*) and again she holds reservations as to the reliability of this data. In the Ibex the radius was found overall to be a fairly sexually dimorphic element with the female means for both the SD and Bd (distal breadth) to be less than 80% of the male means. In addition the GL (greatest length) and Bp (proximal breadth) are only slightly over 80%. Davis (2000) also found some sexually dimorphic radius measurements (GL and SD) with a difference of 11% between GL means for rams and ewes and 17% between SD means. No mention of sexual dimorphism in the ulna could be found in any of the literature consulted.

Pelvis

It is well known that the pelvis is one of the most sexually dimorphic elements in the skeleton due to its function in the birth of offspring. The pelvis possesses a whole suite of non-metric traits that may be used to determine the sex of an individual and these have been well documented in sheep (Boessneck 1969, Hatting 1995) and as such are not discussed here. Metric variation of the pelvis has also been studied by a number of researchers and a summary is given below.

For the Soay sheep Clutton-Brock *et al.* (1990) report that the male pelvis is overall larger than the female but that the female pelvis is relatively broader. They also noted that the ilium was similar in length in males and females; this contradicted Boesneck's (1969) account which said that the ilium was longer in females. Lemppenau (1964, from Grigson 1982) and Prummel and Frisch (1986) noted that in cattle and sheep the medial wall of the acetabulum was high in males and low in females. Greenfield (2006) examined this in more detail, looking at a variety of ungulate species and found that for some species there was no overlap in the measurement for males and females and other taxa gave a strong bimodal distribution with a small amount of overlap. The data Greenfield presented for cattle showed no overlap, but the sample was small. A larger sample was studied for sheep and some overlap was shown. Problems of overlap were worsened when the samples contained mixed populations that may have been subjected to different environmental conditions (Greenfield 2006).

West (1990) achieved excellent separation of males and females for a variety of species through the plotting of pubis measurements (breadth and length), females having longer and more slender pubes than males. The best separation was achieved by plotting the pubic index $((PB \times 100)/PL)$ against pubic breadth. Excellent separation in pubis shape was achieved for cattle (small sample size) and sheep; unfortunately castrates, as would be expected, fell in between and slightly overlapped with males and females.

Femur

For GLC and SD measurements of Shetland sheep rams were found to have mean values 11% and 12% larger than ewes respectively (Davis 2000); these were the only femur measurements taken. In the Ibex (Fernández and Monchot 2007) the most dimorphic femur measurement was the Bp (breadth of the proximal end) with the mean female measurement being only 80% of that of the males. The least dimorphic was the Bd, the female mean being 82.8% of the male mean.

Tibia

Little sexual dimorphism work has been carried out on tibiae but Bartosiewicz (1985) documents that tibia length in cows is absolutely smaller than tibia length in bulls. Davis's (2000) measurements of Shetland sheep showed that tibia length is on average 12% larger in rams than ewes and SD is up to 15% larger once both the distal and proximal epiphyses were fused. Interestingly the Bd measurement was only 5-6% larger on average in rams than ewes making it one of the better measurements for looking at variation caused by factors other than sexual dimorphism. In the Ibex the

SD is again the most sexually dimorphic measurement for the tibia with the female mean being only 79.3% of the males mean; the Bd and Bp measurements show less marked sexual dimorphism (Fernández & Monchot 2007).

Astragalus and Calcaneum

Davis's (2000) study of Shetland sheep showed the astragalus and calcaneum to have a very low level of sexual dimorphism in sheep. The GL and DI (depth of the lateral half) were found to have means differing by only 2% between rams and ewes. The calcaneum GL and astragalus Bd were found to be only slightly more dimorphic differing by 5% and 7% respectively. For cattle Grigson (1982) pointed out that although some researchers have tried to identify sex from astragalus and calcaneum measurements the lack of work on specimens of known sex has hindered this greatly. Higham (1969) found that as for sheep the astragalus and calcaneum provided some of the least sexually dimorphic dimensions for cattle. A similar story is seen for the ibex: Fernández and Monchot (2007) found that the astragalus GLI (greatest length of the lateral side) was the least dimorphic measurement of all those taken for their study with the female mean being 90% of the male mean.

Metacarpals and Metatarsals

Cattle and sheep metapodial measurements show similar patterns in sexual dimorphism. Males tend to have longer metacarpals and metatarsals than do females and in addition male metapodials are broader in proportion to their length than their female counterparts (Howard 1963; O'Connor 1982; Bertaux & Guintard 1995). It

should also be noted that metatarsals are in general less sexually dimorphic than metacarpals (Higham 1969).

According to Davis's (2000) sheep measurements the most sexually dimorphic dimension of both the metacarpal and metatarsal is the SD; mean measurements for rams being 18% and 15% larger than ewes respectively. GL mean measurements are only 8% and 6% larger for rams than ewes. O'Connor (1982) found that a breadth/depth index for the distal metacarpal gave 85% accuracy in determination of sex in a sample of mixed breed. He also points out that although length/breadth ratios are good for identifying sexual dimorphism where all of the members of a sample have been subject to the same environmental conditions, this cannot be ascertained with any accuracy when examining archaeological samples (*ibid.*).

In cattle Bertaux and Guintard (1995) found Bd in both metacarpals and metatarsals to be the most dimorphic dimension. Higham (1969) also reported a high degree of sexual dimorphism in the distal width of the metacarpal and that measurements of breadth were in general more dimorphic than measurements of length. Howard (1963) found that metapodials of bulls were always broader in proportion to length than those of cows, and Grigson (1982) noted that plotting a histogram of metacarpal distal breadth measurements should show a bi-modal distribution. It is important to note however that in all these cases there is considerable overlap in the male and female measurement distributions.

In examining the metapodials of elk (*Alces alces*) Iregren (1985) found that breadth and depth measurements, particularly of the metacarpals were the best indicators of sex. In the highly sexually dimorphic Ibex the metapodials were found to be some of the less dimorphic bones; the most dimorphic measurement being the metatarsal SD with the female mean being 82% of the male mean measurement. This is compared to a number of dimensions of other bones where the female means are on average less than 80% of those of the males.

Phalanges

Identifying sexual dimorphism in the phalanges is difficult but can be done if one can separate out those from the fore and hind limb, and those from the inner and outer of the foot (Grigson 1982). Higham (1969) did separate out first phalanges from the fore and hind limbs of Aberdeen Angus cattle and found the resulting groups to be highly sexually dimorphic for the breadth measurements; length measurements were not particularly dimorphic. It should also be noted that the fore phalanges were slightly more dimorphic than the hind phalanges. Iregren (1985) also noted sexual dimorphism in the phalanges of the elk; this included first and second phalanges of the fore and hind limb examined separately. Greater sexual dimorphism was observed in the breadth measurements than length; Iregren was cautious about the use of this data as although male (bulls) mean values were always higher than female mean values it was sometimes observed that some of the female values were larger than the male mean, showing a considerable overlap in the ranges of male and female measurements (*ibid.*).

3.2.4 Summary and problems in identifying sexual dimorphism

As can be seen from the descriptions above most of the bones in the skeletons of domestic ungulates display some degree of sexual dimorphism ranging from (for a very few elements) total separation of males and females to males being, on average, slightly larger than females; often the most reliable separation is achieved when looking at indices of two different dimensions taken across different planes (e.g. Howard 1963; West 1990). The most sexually dimorphic measurements are the basal measurements of the horncores; measurements of the pubis and acetabulum in the pelvis; SD measurements of the long bones in particular for the metacarpal and finally length measurements of the tibia, femur, radius and humerus (Davis 2000). However, although separation can be achieved or at least an impression of the sexual makeup of a sample be gained, there are a number of problems, inherent of examining archaeological populations of domestic mammals, which make the identification of sexual dimorphism harder than it may first seem.

Firstly the animals that we are dealing with, principally sheep and to some extent cattle and goats, are not as sexually dimorphic as some other ungulates for example the ibex (Fernández and Monchot 2007). This means that although for the majority of measurements rams or bulls will have larger mean values than ewes or cows the ranges of the measurement values may overlap considerably and hence individual measurements will be extremely difficult to assign to one sex or the other with any certainty. This situation is severely compounded by two further considerations: castration and the possibility of having mixed populations.

The likelihood of castrates being present in domestic livestock populations is very high as they can still be used for meat, wool and traction and can be kept in larger quantities without the problems of aggression etcetera, inherent in keeping intact, sexually active males. Measurements of castrate bones have a tendency to overlap with both male and female ranges (e.g. Howard 1963; Davis 2000); the extent of this overlap often depending on the age of castration. A more detailed discussion of the effects of castration on the size and shape of bones and how they may be distinguished from intact males and females is given below (section 3.6).

The problem of mixed populations, i.e. where a sample is made up of animals brought up under differing environmental regimes, or of animals of different type or breed, is a difficult one; this is possibly more of an issue on urban or trading sites where animals may be brought in from a variety of surrounding rural settlements (O'Connor 2003: 80) as opposed to a strictly rural or subsistence site where animals are more likely to be raised all in the same place, from the same breeding stock and under the same husbandry regime. However one must be very careful in making assumptions about the variety (or lack of it) in the populations being sampled; one can never say with certainty that the animals present at a particular site were of the same type or subjected to the same environmental conditions. In a number of the cases described above males and females were often fairly easily distinguished when a single population was being examined, however when mixed populations were examined the boundaries between male and female measurements were blurred or rather their ranges became increasingly overlapped.

A further and possibly more concerning problem is that even when complete separation (i.e. no overlap of values) of males and females can be achieved the point at which the values divide is not always obvious. Sykes and Symmons (2007) found that although their plot of basal measurements of horn-cores had no overlap between male (including castrates) and female values, experienced archaeozoologists struggled to place a dividing line in the correct location.

3.3 BREEDING

This section examines the genetic variation, other than sex, that may affect the size and shape of domestic mammals. Today in Britain it could be argued that the breed of an animal may in fact be the greatest determining factor in its final size and shape, given that the past three centuries of livestock husbandry have focused on the intensive selection and breeding of animals for the production of specific commodities. Trow-Smith (1959: 45) recognised that in the eighteenth century there were great 'opportunities for livestock husbandry' (*ibid.*) that called for swift and significant improvements in livestock in order to satisfy the 'mouths of the soaring populations' (*ibid.*). Although up until this point there had been periods of stock improvement these were gradual and did not necessarily result in a fixed type such as those seen in the stock books of today (e.g. Texel Sheep Society 2008). In that case, why is it important that we look at modern breeds and how they are configured? What can this add to our understanding of past livestock that are unlikely to have been intensively selected for a specific purpose? Firstly the region under study here consists of a reasonably diverse range of geographical and climatic situations which may have some influence on the types of animals kept there.

Secondly if animals were being kept for specific purposes then it is likely that some artificial selection is likely to have taken place, even if this is at an unconscious level. Consequently an examination of different breeds, their uses and the size and shape of their bones may prove helpful in determining the uses of archaeological livestock populations and to what extent particular traits may have been selected for. Therefore although we will not be looking at *breeds* of livestock in the past, it may be possible to identify different *types* of animals present on different sites/regions or in different time periods.

This section first introduces what we mean when talking about livestock breeds and how they come about, including a very brief history of the domestication and spread of livestock across Europe and into Britain. Secondly this section will look at how breed actually influences the size and shape of the bones of domestic livestock and what this may mean for the archaeological populations being examined in this research.

3.3.1 What is a breed and how do you make one?

The Concise Oxford Dictionary (9th edition) definition of a breed is: *'a stock of animals or plants within a species having a similar appearance and usually developed by deliberate selection'* (Thompson 1995: 160). This definition implies that although artificial selection (i.e. the selection of particular desirable genotypes by man) is the main cause of breed creation other factors may be in play. Darwin (1868) was sure that both artificial and natural selection had a role in the development of domestic breeds of all species and this is a view shared by many modern day naturalists. Hall

(1993) lists both natural selection and artificial selection as contributors towards the creation of breeds. The extent to which each of these will contribute to the final breed will depend upon where the animals are raised and what their final purpose is. For example breeds that are commercially important be it for meat, milk or wool are more likely to be influenced by artificial selection as breeders will select for desirable characteristics depending on the product required e.g. the Texel has been heavily selected for meat production (Texel Sheep Society 2008; National Sheep Association 1998: 152). Natural selection however is more likely to have a greater effect where animals are less commercially valued but may be required to withstand particular environmental constraints. An excellent example of this is the North Ronaldsay sheep of the Orkney Islands, which is kept on the foreshore and subsists almost entirely on a diet of seaweed (Tribe & Tribe 1950; Fenton 1997: 466) which is extremely low in essential copper. Experiments with cross breeding have shown that although the resulting sheep performed well on islands near to North Ronaldsay where pasture was available to them, none of these sheep could 'withstand the rigours and exposure of the North Ronaldshay (*sic*) coast' (Tribe & Tribe 1950: 106). This implies that the North Ronaldsay sheep have been naturally selected to withstand harsh environmental conditions and a low copper intake.

Hall (2004) brings together a variety of other researchers' definitions of the term 'breed'. Kohler-Rollefson (1997), Clutton-Brock (1992) and Simm (1998) are all listed as offering slightly varying interpretations of what is meant when talking about livestock breeds (Hall 2004). There are several points on which the definitions share common ground; firstly that the animals of a breed should demonstrate a high

degree of homogeneity in their phenotypic heritability. Secondly they should be almost completely genetically isolated either by geographic or reproductive separation. Thirdly their appearance may be largely determined by man and does not always represent the best strategy for survival (as for natural selection) but may represent some feature seen as desirable by their human breeders, be it aesthetic, economic or sacred (Clutton-Brock 1992, from Hall 2004).

What is also clear about domestic species is their vastly increased phenotypic variability, i.e. between breeds, when compared to their wild counterparts. Hall (1993) brings together a variety of possible causes for such increased variability and new forms of genetic expression. For example the activation of previously dormant genetic sequences through inbreeding, the placing of animals under environmental stresses not previously encountered, or the mutation of genes through contact with anthropogenic mutagens (*ibid.*). Therefore it can be seen that new phenotypes may appear quite by chance and if advantageous may be either naturally or artificially selected for. What appears to be absolutely key in the formation of a breed, as mentioned above, is genetic isolation; in the area under study here this is most likely to occur through geographic isolation. However human cultural divides such as ethnicity, language or economic group could be cause for reproductive isolation of livestock (Hall 2004: 37) within the same geographic region. In modern-day intentional selection of animals for a specific purpose a breed can be fixed within a few generations (Hall 1993). However, what we need to know now is how did we get to this point?

3.3.2 A brief history of livestock breeds in Britain and the North Atlantic

One cannot really begin to talk about livestock breeds in any region without first going back to the beginning and looking at their initial domestication. This is a subject area which has understandably long been of interest and debate among archaeozoologists (Zeuner 1963). Sheep and goats were the first livestock species to be domesticated (Clutton-Brock 1999; Ryder 1984) and until fairly recently this was thought to have occurred at around 10,000-9,500 B.P (Zeder 2008). Initial studies on domestication focused on morphological changes to distinguish between bones of wild and domestic animals (Uerpmann 1978; Rowley-Conwy 1995). One of the most noted of these morphological changes was a rapid reduction in body size upon domestication (Uerpmann 1978; Clutton-Brock 1999:78). However more recent work has questioned this automatic reduction in body size as a direct response to domestication. Zeder (2008) pointed out that one of the key differences between the bones found in deposits created by hunters and those created by herders would be *sex* rather than *size*, i.e. there was no change in body size, just a change in culling strategy; prey strategies of hunters tend to focus on larger males and conversely the harvest strategies of herders are more likely to focus on females with many of the males being killed off at a younger age. Detailed examination of age and sex profiles at a variety of sites in the Fertile Crescent (Israel, Lebanon, Syria, Iraq) has identified such harvest strategies where no morphological changes in the bones were observed (*ibid.*); these data have pushed back the date for domestication of sheep and goats by c.1000 years. Morphological changes associated with domestication such as size reduction and changes in horn morphology were found to have occurred up to 1000 years later and are likely to have been responses to new selective pressures when

animals were moved out of their natural habitat and into hotter and more arid lowlands (see section 3.4.3 below) where in addition to new habitat conditions they would have been isolated from their wild progenitors (Zeder 2006 & 2008).

The other key discussion on the subject of domestication is that of which wild species were domesticated. For example do sheep have a single wild ancestor or were there several occurrences of domestication of two or more wild sheep species? Examination of chromosome numbers showed that the mouflon (*Ovis orientalis*), having 54 chromosomes, was the most likely wild ancestor of the domestic sheep (*Ovis aries*), which also has 54 chromosomes; other Asian wild species had higher chromosome numbers (Ryder 1984; Clutton-Brock 1999). However it is possible for different species to hybridize; a hybrid ewe offspring from the argali (*Ovis ammon*) having 56 chromosomes and a mouflon having 54 chromosomes was found to have just 55 chromosomes and even more interestingly these ewes produced ova with just 27 chromosomes suggesting a selection towards a lower chromosome number. This would indicate that wild sheep with greater than 54 chromosomes could not be ruled out as possible contributors to the ancestry of the domestic sheep (Ryder 1984). However, more recent studies on domestic sheep genetics have been able to throw much more light on the subject. Bruford and Townsend (2006) examined mitochondrial DNA sequences from a variety of domestic and wild sheep. The results of this study indicated that all domestic sheep were likely to have descended from the Asiatic mouflon (*Ovis orientalis*), and that other potential wild ancestors could most likely be ruled out.

How then did domestic mammals get from the Near East across Europe, into Britain and beyond? The Mesolithic-Neolithic transition in Europe has been widely studied and is still under much scrutiny with scientific advances in genetic studies, stable isotope analysis and dating techniques all helping to shed light on this fundamental subject. Models for the transition from hunting and gathering to sedentary agriculture have varied widely from 'demic diffusion', the migrations of farmers originating from south-east Europe (Ammerman & Cavalli-Sforza 1984), to hunter-gatherers themselves downing their spears and taking up the tools of agriculture (e.g. Whittle 1996).

Recent evidence leans more towards the 'demic diffusion' model, but not without some input from hunter-gatherer societies. Bentley *et al.* (2003) interpreted differences in strontium isotope values between males (local, alluvial lowlands) and females (non-local, uplands) from Neolithic cemeteries in Germany as evidence for intermarriage between hunter-gatherer females and male farmers. This was supported by the genetic evidence which seemed to suggest that in the early part of the transition colonisation was the principal activity, while later in north-west Europe there was much more input from the indigenous populations (*ibid.*).

However the uptake of farming does not appear to have taken place in a steady linear march across Europe; Bocquet-Appel *et al.* (2009) plotted early Neolithic radiocarbon dates on a vector map in order to examine the nature of the spread of the Neolithic package across Europe and identified several areas of renewed

expansion and contact zones with a number of significant barriers being crossed, finally expanding into 'marginal zones' (including Britain) around 5000-4000 BC.

Adoption of the Neolithic package in Britain, presumably including domestic livestock, has been examined by Brown (2007) through the examination of radiocarbon dates from early charred cereal grains. These were interpreted as showing that between 3950-3800 cal. BC there was a limited uptake of cereal cultivation followed by a much greater uptake between 3800-3000 cal. BC (*ibid.*). Further definition of what may have occurred between 3950-3800 cal. BC was not possible from radiocarbon dates alone due to a plateau in the calibration curve at this point (*ibid.*). The dates for cultivated cereals also agreed well with dates for Megalithic tombs; therefore it appears that once the Neolithic package arrived in Britain it was swiftly adopted (*ibid.*), a view shared by some other researchers (e.g. Schulting & Richards 2002).

In the Northern and Western Isles of Scotland sheep (and pigs and cattle) have been present since the Neolithic (Watson 1931) and are still prolific today. The principal sheep breeds from these islands (Hebridean, Shetland and North Ronaldsay) are all hardy, prolific and fine boned, and are thought to have changed little since their introduction to the islands; sheep bones found at Jarlshof were likened to the Soay (Platt 1934). Some researchers have suggested that when the Vikings arrived in these islands they brought new sheep along with them (e.g. Fenton 1997), although there is little positive evidence of this.

3.3.3 What do different breeds look like and why?

As can be seen above, the improvement of livestock for various purposes has long been a priority for agriculturalists in Britain and Europe. In addition it seems obvious that some of these improvements will have had an effect on the size and shape of the animals in question. The most recent studies in livestock improvement (e.g. Rius-Vilarrasa *et al.* 2009) pay great attention to genetic parameters and pay less attention to physical features such as body size. In addition, those that are interested in carcass measurements tend to use measurements less useful to the archaeozoologist (e.g. buttocks circumference, Lambe *et al.* 2009). However, in the early to mid nineteenth century when such genetic methods were unavailable, measurements of muscle, fat and of particular use here, bone were key tools to those studying animal husbandry and livestock improvement (e.g. Hammond 1932) and it is these studies which are mostly drawn upon here.

The majority of sheep breeds can be grouped into one of the following types; meat, wool, milk and mixed/primitive/unimproved (Guintard & Lallemand 2003). Primitive breeds are likely to be less affected by human selection and more so by their geographical location and local climatic conditions and hence natural selection (e.g. see the North Ronaldsay discussed above). Wool breeds will tend to be selected for increased wool yield, fineness and quality of their fibres (it is interesting to note here that Fraser (1951: 214) noted that animals raised on poor pasture had finer wool than those of the same breed raised on good quality pasture) and milk or dairy breeds will be selected for increased milk yields. Finally livestock used in meat production will be selected for increased meat yield, and quality and flavour of meat;

this selection has the most influence on the size and shape of bones as it is the bones that have to support an increase in meat (muscle and fat) mass.

It is highly likely that all of the bones recovered for the archaeological sites examined in this research, with perhaps the exception of those being examined from the Post Medieval layers at Old Scatness, are likely to fall into the 'primitive' group (Guintard & Lallemand 2003). However, as mentioned above it is important to examine the stature of the other groups as well so that tendencies towards specialisation may be detected.

In order to see how sheep had been improved for meat production Hammond (1932) undertook a comprehensive study of the mutton carcass through examination of the weight, distribution, quality etcetera, of muscle, fat and bone in a variety of sheep breeds of differing age, sex, size, level of improvement and utilization. One of the key developments in improving livestock for meat production is the breeding of early maturing animals (Hammond 1952: 164). The important effect of early maturity is not necessarily that an animal reaches full size and hence slaughter weight sooner than a slow maturing breed, but that its body conformation is changed in order that the meaty parts become meatier. This in turn has a considerable affect on the size and shape of the bones supporting the extra muscle. An initial impression of the effect of early maturity is given by comparing the body proportions of an early maturing breed such as the Suffolk to a primitive sheep such as the Mouflon (figure 3.1). The Suffolk lamb has similar body proportions in term of depth of body compared to leg length to that of an adult Mouflon ewe (*ibid.*). So how does this

happen? First we must understand that all parts of the body do not grow at the same rate at the same time; the body develops in a particular order. The skeletal system is relatively early to develop and mature, followed by the musculature and last comes the laying down of fat deposits. The skeletal system also develops in a particular order starting with the head and feet; these are the most developed parts at birth, baby animals being largely composed of head and legs. Skeletal growth then proceeds from the extremities towards the thorax in a 'growth wave' (Warmington & Kirton, 1990); the vertebrae being the last bones to ossify. Therefore in early maturing animals the bones fuse sooner, muscle and fat development starts sooner and progresses further. This results in shorter bones and greater overall quantity of muscle and fat in an animal, imparting blockier joints of meat with a greater fat content. This will provide more meat that is also less likely to dry out before and during cooking, and will probably be tastier and higher in calorific value. It is worth noting here that although keeping a meat joint moist is desirable in most modern communities this was possibly not always favourable in prehistoric times as drying is a useful form of meat preservation; in Shetland salt or smoke cured *reested* mutton is still popular today (Fenton 1997: 450) as is *skerpikjøt*, well aged, dried mutton in the Faroe Islands (Proctor 2004).

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Figure 3.1 Body proportion of the Mouflon (left) and the Suffolk sheep (right) after Hammond (1932: figures 2 & 8). Body proportions are scaled to height at the withers. Note the difference in depth of the body and relative leg length. (Illustration by D. Bashford).

So what affect does selection for early maturing, meat producing animals have on the size and shape of their bones? The aim of producing early maturing animals is to reduce the size of the non-meaty parts and increase the size of the meaty parts of an animal. Therefore one is looking for greater development of the pelvis, lumbar vertebrae, ribs and upper limbs; all of which develop later in life. The metapodials, skull and neck all become shortened; this is due to earlier ossification of the

epiphyses, which can be brought about by heavy feeding (Hammond 1932). Due to this decrease in size of the metapodials and corresponding increase in the size of later maturing bones in improved animals, these later maturing bones will be relatively larger in improved animals than in unimproved animals (*ibid.*: 184). In particular there is an increase in bone thickness which leads to an overall increase in skeletal weight (*ibid.*: 386). Guintard & Lallemand (2003) found that metapodial measurements of meat breeds fell almost exclusively into the morphological type 'small' (short) and 'heavy' or 'fat'. It is possible that this thickening of the bone is a reaction to increased muscle and fat weight i.e. an animal will need more robust bones to support a greater meat weight. However, Hammond (1932) thought 'probably thickness of bone and ultimate body size [*i.e. muscle and fat weight*] are both influenced by the same factor – body nutrition' (*ibid.*: 387). He also thought there to be two types of nutrition that influenced growth in different ways. Hammond (*ibid.*: 388) thought that 'energy nutrition', e.g. fats, protein and carbohydrates, influenced bone thickness and that 'generative ferment', e.g. vitamins and minerals, controlled length growth; however no further evidence has been found to support this. Nutrition is discussed more fully in Section 3.5 below, but the comments of Shetland sheep breeder Agnes Leask are worthy of note here 'The older type sheep is smaller..... they're slower maturing. They're leaner. They don't put on the same depth of meat that the flock book ones do. If you put them on very good grazing, oh yes they put on condition, but then you've got a greater layer of fat to meat' (Leask 2003: 153). One other possibility for reducing the size of the head and feet other than by changing the nutritional regime is constant selection for smaller heads and feet (Hammond 1932: 388). It is interesting to note here that in a sheep

breeding experiment carried out by the Animal Breeding Research Organisation (ABRO), ewes selected for increased cannon bone length were considerably more prolific (greater number of twins and improved lamb survival) than either the control group or those selected for short cannon length (Purser 1980).

Less research into the size and shape of the bones of wool and dairy breeds appears to have been carried out; presumably due to animal size or weight being of less importance in these breeds than in meat producing ones. However Hammond (1932) did show that in general wool breeds tended to be more similar to wild or primitive breeds than to meat types (Hammond 1932). This was also demonstrated by Guintard and Lallemand's (2003) plots of metapodial dimensions where wool types and 'rustic' types were all small and light. Pitchford (1993) noted wool breeds to have a lower meat to bone ratio. A similar pattern has been noted between meat and dairy cattle, the latter being more slender (Hammond 1932).

Therefore in summary, animals bred for meat production and early maturity have shorter and thicker bones than later maturing animals. In addition the size of later maturing bones, such as the femur, are increased in size in particular in comparison to earlier maturing bones like the metapodials. It is extremely worthy of note here that such changes can not only be brought about by human selection but also by increased feeding (Hammond 1932). Bones of wool and dairy breeds are more similar in appearance to primitive or unimproved types than to meat breeds.

3.4 BIOGEOGRAPHICAL FACTORS

Biogeography studies the relationship between an organism and its geographical situation. An animal's geographical situation in terms of altitude, latitude, ambient temperature and available water and nutrition has an influence over its growth; in order to explain this, ecologists have developed a number of biogeographical rules. These and their effects on the growth of an animal are discussed in turn below.

3.4.1 Allan's Rule

Allan's rule, sometimes known as the proportion rule, states that animals living in cold climates have shorter extremities than those in warmer climates. This results in a reduction in body surface area and a consequent reduction in heat loss (Hugget 2004; Weaver & Ingram 1969). To investigate this rule Weaver and Ingram (1969) raised pigs from the same litter at different temperatures. Pigs raised at 5°C and 35°C were found to vary considerably in body shape. The animals raised at 5°C were of a much stockier build having shorter limbs and snout than those raised at 35°C, giving them a smaller surface area to weight ratio. A third set of pigs raised at 20°C were found to have body dimensions intermediate to the two extremes. This experiment appears to validate Allan's rule, however the temperature changes examined were extreme; a difference of 30°C is probably much larger than any temperature difference to be examined in the current study area. However differences were also noted in the intermediate group to a lesser extreme. Assuming that Allan's rule can be applied to the current study area then one would expect to see animals with longer more slender limbs in the warmer, more southerly regions and shorter, more robust animals in the colder regions.

3.4.2 Bergman's Rule

Bergmann's rule, or the size rule, is probably one of the best known of the biogeographical rules and has been widely quoted to explain size differences within mammalian species (Davis 1981; Weaver & Ingram 1969). The basic premise of the rule is that members of a particular genus or species will be larger in areas of cold habitat than members of the same genus/species living in a warmer climate (Hugget 2004). This reason for this being, once again, a matter of reducing the available surface area (or more strictly the surface area to volume ratio) over which heat can be lost. A number of researchers have found that with increasing latitude and resulting decrease in temperature animals of the same or related species increase in size (e.g. Schrieder 1950). Conversely, Davis (1981) found that with an increase in temperature in Israel in the late Pleistocene a whole array of mammal species decreased in size. Referring to this work Lister (1997) points out that this size change in mammals may not be directly related to temperature but rather to increased aridity, which in turn would be related to the increase in temperature, but probably more importantly would affect the quantity of available food.

3.4.3 Guthrie's or Geist's Rule

Lister (1997) is by no means alone in casting doubt upon Bergmann's rule and its validity. Geist's (1987) paper '*Bergmann's rule is invalid*' makes a very clear stand. In this work Geist points out that although many researchers found an increase in body size with increasing latitude, some also found the opposite to be true (McNab 1971). Geist (1987) looked at data from a number of deer species and wolves, both of which have habitats spreading a wide range of latitudes including those around 60° N. The

results showed that the animals increased in size with latitude up to around 60-65°N, at which point the trend towards greater size was reversed and animals started to get smaller with increasing latitude (*ibid.*).

Geist's (1987) explanation for this distribution of mammal sizes was that instead of body size being dependent on temperature it was actually dependant on available nutrition, or more precisely the length of the 'annual productivity pulse' i.e. the quantity and quality of vegetative nutrition available during the peak growth season. At more southerly latitudes a dry climate reduces the quality and quantity of vegetation compared with that found in more northerly, temperate regions. However if one travels further north where the length of summer is considerably shorter and the angle of the sun much lower the growing season ('annual productivity pulse') is again shortened. Therefore, in the temperate region below 60°N the 'annual productivity pulse' is greatest and mammals at their largest; move either north or south from here and there is a reduction in the 'annual productivity pulse' and the mammals gradually decrease in size.

Guthrie's (1984) work, looking at changes in mammal size between the late Pleistocene and the Holocene, argued that during this time changes in the plant communities meant that in any one place resources were less varied and had shorter growing seasons. This in turn shortened the somatic (skeletal) growth season of herbivores which Guthrie believed was fundamental to dwarfing in the late glacial. Guthrie purports the growth season was critical to body size and 'better accounts for Bergmann's law than any other factor' (Guthrie 1984: 269).

Therefore both Guthrie (1984) and Geist (1987), believe that although mammalian body size does vary with latitude, the key factor in determining this is not temperature but available nutrition. Moreover this is not just the year long average of available nutrients but the duration of the peak in quality growth resources i.e. quality forage high in usable protein needed for somatic growth (Guthrie 1984).

3.4.4 Island Dwarfism

One final biogeographical factor that is of particular relevance here is the phenomenon of island dwarfism; large mammals that colonise islands become smaller over time. This phenomenon has been noted in a variety of species in a variety of places. As mentioned above dwarfing has also taken place in continental regions during the late Pleistocene.

The reasons for both of these forms of dwarfing are essentially the same and come down to a shortage of resources (Marshall & Corruccini 1978; Guthrie 1984; Schule 1993: 403). Large mammals have higher total rates of metabolism than do smaller mammals (McNab 1990: 15) and consequently need greater amounts of energy to sustain them; therefore in times and places of shortage small body size is an advantage. In the late Pleistocene climate changes and competition with humans led to a greater scarcity of resources and hence a reduction in body size (Marshall & Corruccini 1978; Guthrie 1984). On an island there is a finite quantity of terrestrial resources, which can be better exploited by more small individuals than fewer large

individuals. Island populations are frequently genetically isolated and therefore it is crucial that as much genetic variability as possible is maintained through high population numbers (Kurtén 1968: 252, from Marshall & Corruccini 1978: 114f). Once a population is isolated on an island a decrease in size, in response to lack of resources, can take place very rapidly (Marshall & Corruccini 1978).

However island dwarfism is not always a simple ecophenotypic change i.e. growing less big in response to shortage, but eventually will become a genetic change and may result in the evolution of a new species or sub-species, for example *Candiacervus ropalophorus* a Cretan dwarf deer (Lister 1996). From Lister's (1996) examination of deer and elephant fossils he concluded that there were two key stages to the process of dwarfism.

The first stage comes about with a need for a reduction in size due to a shortage of resources, this begins with the ecophenotypic change mentioned above, but then may go beyond the ecophenotypic range (normal size range); at this point there is actual genetic change/evolution. This change can happen fairly rapidly occurring over a time span of a few thousand years. It should also be noted that ecophenotypic change alone can take place very quickly, for example British red deer which reduced in size during the Holocene due to forest clearance returned to their original size within 15-20 years of being introduced to the lush pasture of New Zealand (Lister 1997). Although genetically different to their mainland ancestors the smaller island animals may not yet be truly speciated. Good examples of this are the Jersey red deer (Lister 1995 & 1996) and the Wrangel mammoths (Lister 1996).

If dwarf animals are isolated for long enough and survive then the second stage will come into play and further, genetic, modifications will take place. These changes will help retain the structural integrity of an animal and may include the reduction of tooth size to return to the original ratio of tooth to bone size or a modification of limb morphology to account for smaller body size (Lister 1996). Examples of animals that have reached this second stage of dwarfing development are the Cretan deer and the Californian and Mediterranean elephantids (Lister 1996).

3.4.5 Summary of biogeographical effects

With the exception of Allen's rule, which does appear to be directly connected to environmental temperature, all of the other biogeographical effects seem to be linked with available nutrition. On islands the available nutrition is limited by the area available for plant (food resource) growth and on all land masses available nutrition is limited by the 'annual productivity pulse' which is affected by rainfall, angle of the sun and soil fertility etcetera, which are in turn are affected by latitude, altitude and geology. All of these factors then have an effect on the quality and quantity of available nutrition. Therefore in areas where the 'annual productivity pulse' is reduced, by whatever means, the amount of available nutrition and hence individual body size (see section 3.5) will also be reduced. It should however be noted that the research behind Gurthrie's and Geist's rule (the latitude rule) is based entirely on wild species and so caution may be required when applying this rule to domestic species.

3.5 NUTRITION

The subject of nutrition has come up several times throughout this chapter and it is clearly a very important factor when dealing with bone growth and eventual size. Plentiful, good quality nutrition is required for animals to reach their full genetic potential (Pálsson & Vergés 1952a: 68f) and this is not always (or even often) likely to occur in the marginal North Atlantic environment being studied here (see Chapter 4).

Therefore how does nutrition or more pertinently lack of it, affect the growth and hence bone size and shape of an animal or more specifically a sheep? Growth and production performance in domestic livestock is very important to modern agriculture; a wide variety of experiments have been employed in the past to assess the affect of inadequate nutrition on sheep and other livestock. A small number of these studies have examined skeletal growth, most notable of which, in relation to this research is Pálsson and Vergés' (1952a & b) work on the '*Effects of the plane of nutrition on growth and the development of carcass quality of lambs*'. From this work a number of basic principles in (skeletal) growth relating to nutrition can be established. These ideas were also touched upon by Hammond (1932) and are as follows; the lower the level of nutrition an animal receives the less it will grow and the smaller its adult size will be. Later maturing bones (and body tissues) will be more greatly affected, in terms of growth retardation, by a low plane of nutrition than will more early maturing bones (or body tissues). Growth in bone thickness will be more greatly affected than growth in bone length and finally the timing of shorter periods of poor nutrition will determine which bones are most greatly affected. Each of these factors will be discussed in more depth below.

3.5.1 Nutrition and Overall Growth

A variety of experiments have shown that animals which have higher planes of nutrition grow to a larger size. Animals receiving poorer nourishment grow more slowly, mature later and cannot attain the proportions of well fed animals (McCance *et al.* 1968; Pálsson & Vergés 1952a).

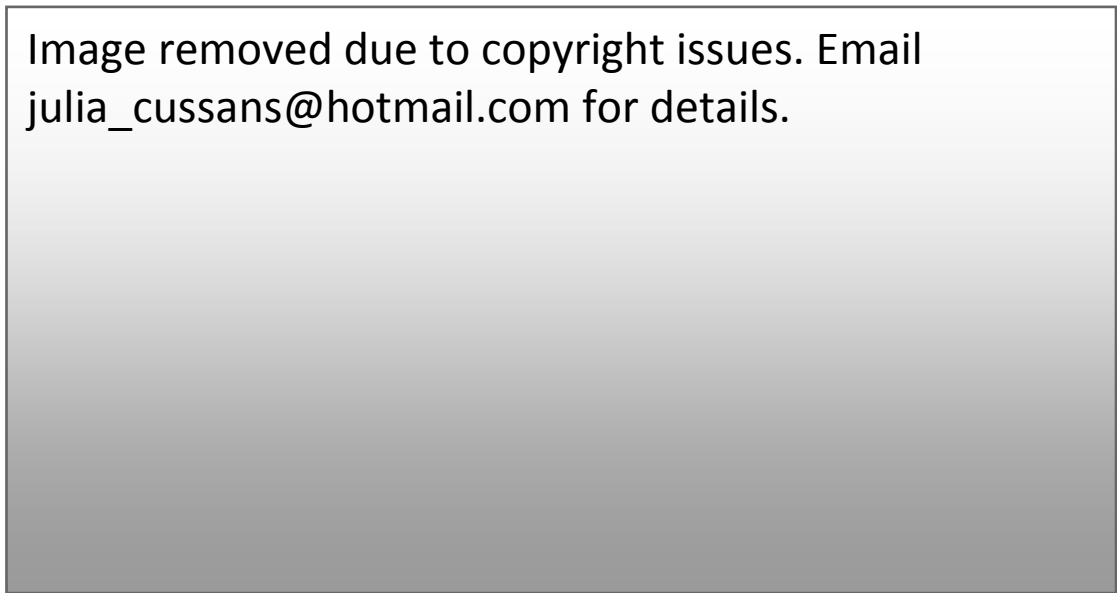


Figure 3.2 Outlines of sheep carcasses raised on different nutritional regimes and slaughtered at the same carcass weight, high-high (HH), high-low (HL), low-high (LH) and low-low (LL), after Vergés (1939), taken from Hammond (1952). Note the more robust proportions of the high-high animal compared to the low-low animal. (Illustration by D. Bashford).

Pálsson and Vergés (1952a) work showed that animals reared on high and low planes of nutrition had vastly different carcass sizes when slaughtered at the same age; those being reared on a high plane of nutrition being the larger. Dickerson and McCance's (1961) work on under-nutrition in pigs compared undernourished pigs to well fed pigs of the same weight, but a younger age and those of the same age but

heavier weight. Finally, Allen and Lamming's (1961) work on ewe lambs showed that ewes fed on a high plane of nutrition grew considerably larger and started puberty at a younger age than lambs reared on a moderate plane of nutrition.

3.5.2 Differential effects of poor nutrition on the skeleton

It is mentioned earlier in section 3.3.3 that growth occurs in a wave starting at the extremities and gradually moving inwards towards the centre of the body. Therefore the skeleton does not mature all together at the same time but in stages, starting at the head and feet and working inwards. It is also true that the skeletal tissue is one of the earlier maturing tissues in the body; muscle and fat maturing later in life. Dickerson and McCance (1961) found that pigs fed on different nutritional planes, slaughtered at the same weight but different ages, undernourished pigs had larger (heavier) humeri than pigs which had been well fed, indicating that for undernourished pigs a greater proportion of their body weight was accounted for by the skeleton, which had been preferentially fed over other tissues given the limited available nutrition. Therefore in poorly nourished animals skeletal growth takes president over muscle and fat growth.

As well as the early maturing skeleton being preferentially fed over later maturing tissues, the skeleton itself is differentially affected by poor nutrition, and as with the different tissues it is the later maturing parts that are most affected. Pálsson and Vergés' (1952a & b) studies showed that the bones of the head and feet were less affected in terms of growth retardation than the upper limbs, ribs and vertebrae. In low nutritional plane lambs the weight of the skull and the lower jaw was found to

make up a much greater proportion of total skeletal weight than in lambs reared on a high plane of nutrition. Later maturing bones, such as the scapula and ribs were found to make up a smaller proportion of the total skeletal weight in the low plane lambs than the high plane lambs. McCance *et al.* (1968) also found that in pigs the teeth were much less affected by under-nutrition than the body as a whole.

The likely explanation for this phenomenon is that the more essential elements of the body develop first. The skull is important in protecting the brain, the skull and the lower jaw together are needed for eating (the acquisition of nutrients), and the feet are needed for moving around (finding food) and escaping predators. These elements are therefore given nutritive preference. Pálsson and Vergés (1952a) give an excellent example of this preferential distribution of nutrition: in young lambs that were undernourished during the last eight weeks of foetal life it was found that the growth of the feet was most affected, as this is a time when the feet have a high growth intensity. However the skull also has a high growth intensity at this time but was found to be much less affected by the low nutritional plane than the feet. This was thought to be because of the greater importance of the skull in the overall success of the body and therefore the little nutrition available was focused on the growth of the skull rather than the feet at this time (*ibid.*).

3.5.3 Effects of poor nutrition on bone shape

Not only does the nutritional level of an animal affect different parts of the skeleton preferentially it also differentially affects bone growth in different dimensions. Bone length is more early maturing than bone thickness (breadth) and therefore bone

breadth is more greatly retarded by poor nutrition than bone length; hence bone shape is more greatly affected or altered than bone size (Pálsson & Vergés 1952a & b). Low plane lambs are relatively much skinnier than high plane lambs as described here: 'The cannons of the Low-Plane lambs at 41 weeks though 10% shorter as an absolute figure than those of the High-Plane ones at the same age are, relative to their thickness, much longer, having 36% less weight: length ratio.' (Pálsson & Vergés 1952a: 68). Measurements of bone length, minimum circumference and weight of bone per 10cm length were measured for bones of the hind limb (Pálsson & Vergés 1952a) and these compared between the high plane and low plane lambs. Least difference was found in the length measurements and the most difference between the weight per 10cm, indicating that bone thickness and possibly epiphysial breadth was most greatly affected by poor nutrition (*ibid.*).

More recent research, carried out by the English Heritage 'Sheep Project', has found some similar results in that bone breadth shows a relatively greater increase in size than bone length with increased nutrition (low quality pasture versus high quality pasture and supplements) (P. Popkin pers. comm.). However the difference between the two is greatly dependant on the sex of the animal in question. For instance in terms of distal breadth measurements all of those examined showed an increase between low nutrition females and high nutrition females (*ibid.*). A slightly larger difference was noted between low nutrition males and high nutrition males. Conversely, in castrates, many of the distal breadth measurements showed little or no difference between low and high planes of nutrition; increases were found in astragalus, tibia and humerus distal breadth measurements (*ibid.*).

3.5.4 Timing of poor nutrition

When discussing poor nutrition above it has so far been assumed that this is a sustained state i.e. that an animal will suffer from poor or a lower nutritive state for the majority of its life; this is not necessarily the case. Livestock may suffer poor nutrition for only a relatively short period of their life, for example in a winter following a bad harvest when fodder supplies are low, or during a season of particularly adverse weather conditions (see Section 3.7 below).

As well as studying animals raised entirely on a low or high plane of nutrition Pálsson and Vergés (1952b) also studied animals whose plane of nutrition had been changed part way through their lives, rearing some on a high and then low nutritional plane and some on a low and then high plane. We have already discussed the fact that different parts of the skeleton mature at different times and this means that different bones have varying growth intensities throughout life. Therefore if a period of low nutrition comes at a time when a particular bone should be having a period of high growth intensity then this bone will suffer more in terms of retarded growth than will other bones. For example late maturing bones such as the lumbar vertebrae were considerably more retarded in growth in the High-Low group of lambs than in the Low-High group (*ibid.*). Similarly the early maturing jaw was more retarded in growth in the Low-High group than in the High-Low group (*ibid.*). Therefore short periods of poor nutrition may only affect certain areas of the body and would probably be difficult to detect unless complete or almost complete skeletons were available for study.

3.5.5 Summary and further considerations

From the above it can be seen that level of nutrition has a substantial effect on bone size and shape. Inadequate nutrition will reduce bone size, although not to the extent that overall body size will be reduced. It will also differentially effect later and earlier maturing body parts; later maturing parts being the most affected. Bone breadth will be more greatly retarded than will bone length and the timing of short periods of poor nutrition will most affect bones that should have a high growth intensity at the time of poor nutrition.

Although studies such as Pálsson and Vergés (1952a & b) are excellent and yield a great deal of useful information there are some factors that need to be taken into consideration when using them to make inferences on archaeological data. Although some linear bone measurements are used the majority of studies of this nature tend to use bone weight as a measure of bone size. There are several reasons why weight may not always be directly related to bone length or breadth i.e. bone weight may be affected by factors other than their external linear dimensions.

Dickerson and McCance (1961) found that in pigs undernourished animals had a thin and brittle bone cortex and that the marrow cavity was enlarged via the process of medullary erosion. In addition Pratt and McCance (1964) found that animals subjected to severe, prolonged poor nutrition had very thin and very dense cortical bone. These factors would not necessarily affect the external measurements of a bone but would most certainly affect its weight. In addition Dickerson and McCance's

(1961) research also found that the bones of undernourished animals contained a much greater percentage of water than those of well fed animals and conversely a much lower proportion of substances such as fat, collagen and calcium. This may also have had an effect on the bone weight. Nutritional stress occurring in pregnant and lactating ewes triggers the resorption of minerals from the skeleton, decreasing bone weight but not external measurements (Benzie *et al.* 1955).

Finally none of the papers discussed above examine fully adult animals (i.e. all bones fused); the oldest animals studied by Pálsson and Vergés (1952a & b) were 41 weeks old. They also showed that from three slaughtering ages of birth, nine weeks and 41 weeks, size differences between high and low plane lambs were least at birth, greatest at nine weeks old and intermediate at 41 weeks; this suggests that some of the early shortfall in growth had been made up later in life. To what extent this catch up continues into adulthood is difficult to determine although it seems unlikely to be complete.

3.6 CASTRATION

Castration of male domestic mammals is an important part of modern day animal husbandry and has been practiced for centuries (see Davis 2000 for a brief review of historical sources) for a variety of reasons, partly to give human control over animal breeding and partly for reasons of product (meat, wool etc.) quality. The removal of the testes has various physiological effects on skeletal growth; formation of the horn-cores is particularly affected as is the maturation of the limb bones.

The effects on the growth of the horn-core in sheep range from the complete lack of a horn-core to having an appearance closer to that of a ewe than the ram to being just slightly reduced in size (Hatting 1975 & 1983). The extent of the 'deformation' depends partly on the type of sheep and partly on the timing of castration. Those being castrated early being most greatly affected (*ibid.*) and castrated rams born of hornless ewes being most likely to be hornless (Clutton-Brock *et al.* 1990). In addition to being changed in size and shape so that the horn-core of a castrate is more like that of a ewe than a ram there are other, non-metric, changes that take place in the bone structure of the horn-core: the bone surface becomes smoother, the wall of the core become thinner and the cavities inside the horn-core become larger (Hatting 1975 & 1983).

The horn-core is not the only part of the skeleton to be affected by castration, maturation of the skeleton, principally fusion of the epiphyses (Davis 2000; Hatting 1983), is also affected. Interestingly tooth eruption appears to be unaffected (*ibid.*) although wear on the teeth can be reduced compared to rams. This is probably due to a lower food intake in castrates than rams (Davis 2000), which need a greater energy intake particularly prior to the mating season; the difference in tooth wear between rams and wethers increases with age (*ibid.*). Clutton-Brock *et al.*'s (1990) study of the Soay sheep did not find any evidence for a long delay in bone fusion caused by castration, but did note that this may be due to a lack suitable comparative material. Hatting (1983) noted that long bone fusion may be delayed by over a year in some castrates compared to fertile animals and Davis (2000) noted that although

bone fusion was greatly variable it generally occurred much later in wethers again with some examples of fusion being delayed by over a year.

The delay in bone fusion in castrates allows for a longer period of growth and hence results in longer limb bones. This is not to say that limb growth is speeded up at all; castrated and intact cattle were found to have no difference in leg length when slaughtered at the same age (18 months) (Lazzaroni & Biagini 2008). Similar results were found for goats (Koyuncu *et al.* 2007); it should be noted that in both of these cases the measurements taken were carcass measurements and not bone measurements. Differences in the length of mature (i.e. fully fused) long bones of rams and wethers were found by both Davis (2000) and Clutton-Brock *et al.* (1990). The same pattern was found for bulls and steers by Howard (1963). For both cattle and sheep castrates have, on average, the longest limb bones compared to rams and ewes; Clutton-Brock *et al.* (1990) noted that the extremities of the skeleton, the facial region and lower limbs, seemed to be most affected. This does not appear to be supported by Davis's (2000) data as the long bones showing the greatest length differences (radius, metacarpal, femur, tibia and metatarsal) all show a 7% increase in length compared to rams with the exception of the metatarsal which shows an 8% increase; the phalanges and skull however were not measured. Hammond (1932, 381) also mentions the observations of another researcher: 'Geddes (1910-11) found that castration caused increased lengthening of the bones, more particularly in the distal segments of the limbs' and noted that the effects of castration appeared to be the opposite to those of early maturity. This makes sense of course when the cause of the lengthening of the bones is the delay in bone fusion and thus skeletal maturity.

As discussed above (Section 3.3.3 & 3.5.1) it is possible that an increased level of nutrition can help to bring about early maturity. Could there be a nutritional reason behind why the bones of castrates fuse later than those of intact males? Koyuncu *et al.* (2007) noted that the daily live weight gain of goat kids fed *ad libitum* was less in castrates than intact males. Haddad *et al.* (2006) examining Awassi lambs found that although there was no difference between intact males and castrates in terms of carcass weight or average daily gain there was a difference in the efficiency of feed utilization i.e. the rams made better use of the food they imbibed than did the castrates. This does suggest that nutrition, or at least the ability to utilize nutrients may be part of the reason that castration delays bone fusion. Further evidence would however be needed to confirm this.

Bone breadth is also affected by castration; in sheep for example greatest length of limb bones is on average longest in castrates and shortest in ewes, whereas in term of bone breadth rams are the largest and ewes the smallest with wethers being intermediate. The difference in length to breadth ratios means that the shape of the bones in the three 'sexes' is different. Ewes are short and slender, rams are tall and broad and wethers are tall and slender (Davis 2000). The same goes for cows, bulls and steers (Howard 1963). Referring back to the paragraph above the decrease in bone breadth between rams and wethers may also be an indication that nutrition (see Section 3.5) possibly plays a role in skeletal growth of castrates.

Howard (1963) used breadth and length measurements of metapodia to calculate indices (bone breadth as a percentage of bone length) to help distinguish between

cows, bulls and steers. Separation of cows and bulls was ok with only small areas of overlap between the ranges for the two sexes. Unfortunately, in the main the steers tended to overlap almost entirely with the female range and also partly with the male range; therefore using the indices alone it is not possible to identify the presence of castrates. However scatter plots of breadth to length indices against length does give reasonable, although not total, separation of the three 'sexes' (Davis 2000: Figure 8). Therefore although individuals cannot necessarily be identified as castrates one can get an idea of the sexual makeup of the sample being examined. Davis (2000) tried plotting archaeological data from Launceston Castle in this way but found it difficult to determine the sexual make up of the sample as these sheep fell into a different size range to his Shetland sheep data, the sheep at Launceston being larger. It may however be easier to make comparisons between the North Atlantic data being examined here and Davis's Shetland sheep.

In summary castration has particular effect on the appearance of the horn-cores and on the growth of the limb bones, with possibly those at the extremities being most affected. Limb bones of castrates are on average longer than those of intact males and also more slender and it may be possible to determine their presence through the use of shape indices and scatterplots. It is interesting to note that there are similarities between the effects of castration on bone growth and the effects of poor nutrition.

3.7 PROVISION OF SHELTER

All domestic mammals (in fact all mammals) are homeotherms, meaning that they maintain a constant core body temperature. For sheep the air temperature requiring the least thermoregulatory effort is c. 4-20°C (McArthur 1991). Above or below this optimum, energy that would have otherwise been used in growth must be expended to regulate temperature (McArthur 1991; Smith 1964). Heat loss is also increased by the occurrence of wind and/or rain (*ibid.*). Therefore in an outdoor environment where livestock were exposed to wind and rain on a regular basis, it is likely that bone size will be affected due to the diversion of energy from body growth to heat production.

This effect was demonstrated by the construction of a mathematical model by Higgins and Dodd (1989); the model calculated the growth of beef steers in weather conditions determined from data collected from several different locations around Scotland and was run over five winters comparing cattle kept outside with no shelter to those kept inside over the winter period. Food intake was calculated for a target daily weight gain of 0.75kg. The live-weight deficits of cattle from the outside conditions, compared to those kept inside, were calculated, the largest being for the Kirkwall (Orkney) weather data with outside cattle calculated as having a 73kg live-weight deficit and most of the heat loss being due to high wind speed. Feeding on a higher plane of nutrition (target daily gain of 0.9kg) lessened the deficit to just 16kg between no shelter and full shelter (Higgins & Dodd 1989); this shows that cold stress can be countered by the provision of extra food. However, two other types of shelter were also examined; roof only and walls only (*ibid.*). While both lowered the weight deficit to some extent 'walls only' was found to be more efficient, reducing the live-

weight deficit to 15.6kg on the lower plane of nutrition and to just 2.4kg on the higher plane of nutrition for the Kirkwall data (*ibid.*). Therefore the provision of shelter would cut heat loss and 'improve the efficiency with which the animals use feed for productive purposes' (McArthur 1991: 104) and thus reduce the need to provide extra fodder during periods of adverse weather.

Experimental data quoted by Higgins and Dodd found that cattle housed inside made greater weight gains than those housed in a walled but unroofed structure, but that the weight differences were not significant (Petchey & Mitchell 1979, from Higgins & Dodd 1989). This is not surprising as the mathematical model found walls only to be the best type of shelter after roof and walls (Higgins & Dodd 1989).

It can therefore be seen that animals kept in inclement weather conditions (low air temperature, high wind and rain fall) are likely to grow less than those with access to shelter. However the exact effect of this on the size and shape of bones is unknown. The best one can estimate in the absence of empirical data is that the effect is similar to that of low calorific intake (see Section 3.5 above). It should also be noted that although live weight may be quite severely affected the growth of the skeleton should be less so due to its early maturing status as discussed above (Section 3.5.2).

3.8 SUMMARY

Overall it can be seen that the final size and shape of the bones of domestic mammals is influenced by a variety of interacting genetic and environmental factors. It is clear that sex and breeding have considerable influence on bone growth but also

that nutrition, not surprisingly, plays a vital role. In broad terms the effect of sex on the bones is that those of males tend to be overall larger and relatively broader than those of females from the same population. The most sexually dimorphic bones are the pelvis, horncores and metapodials. Animals bred for meat production have shorter and broader limb bones than those of unimproved or milk breeds, but it should be noted that animals cannot reach their full genetic potential without the adequate provision of nutrition.

The amount of nutrition available to an animal for skeletal growth is controlled by a variety of environmental factors such as latitude, temperature and precipitation which all affect the local availability and quality of vegetation; the availability of shelter determines how much of the available nutrition has to be spent on other functions such as maintaining core body temperature. The availability of food to domestic mammals is also determined by cultural and economic factors such as the amount of land owned by a particular farm or the introduction of a new crop.

In general improvements in the availability of nutrition will cause bones to grow larger overall but also to make greater increases in breadth over length, therefore in well nourished animals, bones are larger and relatively broader than those in poorly nourished animals. The timing of a period of good or poor nutrition in an animal's life will have varying effects on different parts of the body depending on what stage of the 'growth wave' an animal is at.

Other environmental variants appear to have a more direct effect on skeletal growth. In the case of Allen's rule, temperature affects skeletal dimensions causing shortening of the limbs in cooler conditions as a means of reducing body surface area and hence saving on heat loss. Castration of animals causes a delay in bone fusion and consequent lengthening of bones.

When examining biometrical data all of these factors must be considered as possibilities for causing differences between sites or regions or changes over time at a single site or locale. Through careful consideration of the archaeological and environmental evidence available and of which bones are affected and how, some idea of the possible reasons for observed changes in bone size or shape may be gained.