The Late Pleistocene Reindeer (*Rangifer tarandus*, Linnaeus, 1758) of Britain and Western Europe: Past Migrations, Seasonality and Palaeodiet

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Declaration of Authorship

I, Emily Charlotte Wiesendanger, hereby declare that this thesis and the work presented in it is entirely my own. Where I have consulted the work of others, this is always clearly stated.

Enierendeneg Signed:

Date: 23/11/2020

Abstract

During the last glaciation, reindeer (*Rangifer tarandus,* Linnaeus, 1758), a highly specialised cold adapted ungulate, was extremely common throughout Britain and western Europe, in marked contrast to the Arctic and Subarctic distribution of herds today. This study investigates the palaeobiogeography of this species over a Late Pleistocene temporal transect (c. 82,000-11,700 years BP) and a geographical range across Britain and north-west Europe, to enable the impacts of climatic, environmental and anthropogenic changes on reindeer ecology to be more precisely understood. This is particularly important given the recent global declines in both the body masses and population sizes of modern reindeer and their now vulnerable conservation status.

As bi-annual migrators, reconstructions of reindeer palaeobiogeography were achieved by examining the seasonality of site occupations through the recognition of seasonal aggregations. The selection and development of non-destructive techniques for the ageing and sexing of dental, postcranial and antler remains in this thesis, has demonstrated spatial and temporal variability in the seasonality of site occupations by reindeer, although both migratory and sedentary niches were represented during the Late Pleistocene. In addition to the varying climatic and environmental conditions, this emphasises the importance of the influence of herd-specific factors such as density, snow conditions and human activity on reindeer palaeobiogeography. The impact of these factors was particularly evident from the reconstruction of body masses in modern mountain and forest reindeer, which were then used as the model for reconstructions of Late Pleistocene body mass.

Where multiple seasons of occupation were reconstructed for British sites from the Early (Windy Knoll) and Middle (Kents Cavern and Pin Hole Cave) Devensian, dental microwear analysis was conducted to provide insight into the palaeodiet of reindeer. Forage is an important influence on reindeer migrations and the monthly precision of dentition aged in this study has enabled seasonal variability in the dietary signals of microwear to be identified in both modern and fossil reindeer. For the two Middle Devensian sites, strontium isotope analysis was also conducted on dentition in a pilot study, demonstrating the differing scales of mobility at the two sites.

Acknowledgements

I would like to start by thanking my supervisor Danielle Schreve, having now supervised three projects I really wouldn't be here without her amazing guidance over the years and I am forever grateful. I also would like to thank my second supervisor Ian Candy, for his continued support during both this project and throughout my time at Royal Holloway. I am so lucky to have been part of the wonderful Department of Geography at Royal Holloway and wish to thank everyone for making it the incredibly friendly and supportive place that it is.

Of course, it would not have been possible to complete this thesis without the help of the museums and institutions that allowed me to study their reindeer material. I wish to thank the following people not only for granting me access to their collections, but for making me feel so welcome during my visits and sharing their knowledge of the collections with me: Spyridoula Pappa and Pip Brewer (Natural History Museum, London), David Gelsthorpe and Kate Sherburn (Manchester Museum), Dennis Parsons (South West Heritage Trust), Andrew Kitchener and Zena Timmons (National Museums Scotland, Edinburgh), Linda Wilson, Allan Summerfield and Wendy Russ (University of Bristol Spelaeological Society), Glen Roadley and Alison Nicholls (The Potteries Museum and Art Gallery, Stoke-on-Trent), Neil Owen (Leeds Discovery Centre), Barry Chandler (Torquay Museum), Jan Freedman (Plymouth Museum), Annelise Folie and Cécilia Cousin (Royal Belgian Institute of Natural Sciences), Kristian Murphy Gregersen (Natural History Museum Denmark), Peter Vang Petersen (National Museum of Denmark), Thomas Schossleitner (Museum of Natural History, Berlin), Sabine Gaudzinski-Windheuser, Babette Ludowici and Michaela Scheffler (Braunschweig Landesmuseum, Wolfenbüttel), Bram Langeveld (Natural History Museum Rotterdam), Hanneke Meijer (University Museum of Bergen), Daniella Kalthoff (Swedish Museum of Natural History, Stockholm), Göran Sjöberg (Ájtte Swedish Mountain and Sami Museum, Jokkmokk), Neil Duncan and Sara Ketelsen (American Museum of Natural History).

I would like to thank Spyridoula Pappa for teaching me everything that I now know about dental microwear analysis and for taking the time during her maternity leave to help me. I always enjoyed our chats whilst either in the museum or staring down a microscope. I would also like to thank Adrian Palmer for his help in making all of the microwear casts. I am also very grateful to Jane Evans at the British Geological Survey, for both her advice regarding the strontium isotope analysis and for kindly fitting me in to a busy schedule just in time to complete this work.

Finally, I would like to thank all of my friends and family, especially my parents and my sister, who have together kept this 'Reindeer Lady' relatively sane.

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Chapter 1. Introduction

1.1. Context and Justification

The intermediate-sized cervid Rangifer tarandus (Linnaeus, 1758), referred to as reindeer in Eurasia or caribou in North America, is a cold-tolerant species that today occupies areas of Arctic tundra, Subarctic taiga and mountainous regions between 50-81°N (Gunn, 2016). This is primarily due to a combination of morphological, physiological and behavioural adaptations that allow R. tarandus to tolerate snow cover and permafrost at temperatures between -45°C and +15°C (Sommer et al., 2011). As such, R. tarandus fossils have been used as cold-climate indicators in both palaeoenvironmental and palaeoclimatic reconstructions (Polly and Eronen, 2011; Sommer et al., 2014). The large numbers of R. tarandus that are evident within northern European Late Pleistocene fossil records indicate that large herds of *R. tarandus* were an important component of the open steppe tundra environments of Late Pleistocene cold stages (Stewart and Lister, 2001). Such high densities of herbivores and any changes in abundance would have had significant impacts on ecosystem processes. Herbivores play an important role in maintaining grassland environments such as the steppe tundra, as the higher rate of decomposition in the stomachs of animals improve nutrient cycling and the uptake of carbon and nitrogen into soils, thereby supporting the growth of the highly-productive grasses and herbs required to sustain this ecosystem (Zimov et al., 2012).

R. tarandus are also significant as the last northern hemisphere ungulate to undertake large-scale bi-annual migrations. Several factors may influence the movement of herds from their open tundra summer ranges towards tundra-taiga winter pastures (Skogland, 1980; Tablado *et al.*, 2014). However, migrations primarily occur in response to the reduced forage quality and access during winter, as the strong seasonality of high latitudes significantly affects resource availability (Tablado *et al.*, 2014). In turn, the seasonality of *R. tarandus* occupying different sites throughout the year affects the availability of this prey to predators, which included early hominins. The timing of herd movements between annual sites has been an important part of human subsistence strategies for millennia (Schaefer *et al.*, 2000; Price *et al.*, 2017). By intercepting herds which show high levels of fidelity towards specific sites and migration routes, hunters can reliably exploit large numbers of *R. tarandus* (Burch, 1972). Today, it is estimated that for individuals consuming the meat, fat, bone marrow and stomach contents, a total of

50 animals per persons would be required each year to meet nutritional requirements (Kelsall, 1968). However, carcasses also provide raw materials such as skins, used to make clothing and covers for tents and boats, antlers and bones, used to make needles and other utensils, and back sinews, which can be made into thread (Burch, 1972). R. tarandus exploitation is still an important part of the sociocultural identity of indigenous people throughout Arctic and Subarctic regions (Jernslettern and Klokov, 2002; Vors and Boyce, 2009). While communities in Alaska, Canada and Greenland rely on the subsistence hunting of wild *R. tarandus* (Vors and Boyce, 2009), of which the global population currently sits at 2,890,400 individuals (Gunn, 2016), a further 2,000,000 R. tarandus are domestic (Klokov, 2007). As such, for the Sámi in Scandinavia, as well as numerous cultures across Siberia, the herding and management of R. tarandus is essential to their economy (Jernslettern and Klokov, 2002; Vors and Boyce, 2009). Numerous rich Late Pleistocene R. tarandus assemblages in Northern Europe have therefore been investigated in order to establish patterns of tracking, selection, processing and transport of materials by hominins throughout the Palaeolithic (Gordon, 1988; Gaudzinski and Roebroeks, 2000; Weinstock, 2000a; Weinstock, 2000b; Costamagno et al., 2006; Britton, 2010; Britton et al., 2011; Niven et al., 2012; Fontana, 2017; Niven and Martin, 2018).

Despite the importance of *R. tarandus* herds, it is the evidence reconstructed from individual animals that is fundamental for our understanding of the palaeoenvironment and palaeoecology (Britton et al., 2009), through patterns of diet, seasonal habitats and migrations. The high levels of sexual and demographic segregation expressed within the herd during seasonal aggregations serve as an analogue for reconstructing past seasonality and migration patterns. This can be identified using two forms of evidence; age at death measures the age structure present in an assemblage, whereas season of death, identified through sexual dimorphism, recognises the changing ratio of sexes and ages within seasonal aggregations. Modern reference material, used for both ageing and sexing techniques, can be applied in the interpretation of the fossil record due to the high synchronicity of *R. tarandus* calving in May (Gordon, 1990; Paoli et al., 2018). The present study develops these techniques and applies them to Late Pleistocene assemblages, in order to determine the seasonal presence, and inferred migration pathways, of the fossil *R. tarandus* remains. The results have significant implications for R. tarandus seasonality and pathways of movement under varying climatic and environmental conditions, especially given the fluctuating terrestrial connection between Britain and continental Europe during the Late Pleistocene.

More precise reconstructions of *R. tarandus* palaeobiogeography can provide important information on the varying climatic and environmental impacts on *R. tarandus* ecology.

This also has a bearing on understanding *R. tarandus* resilience, which is particularly significant in view of current global-scale threats to the species. The IUCN Red List of Threatened Species has described *R. tarandus* as 'Vulnerable', after a 40% population decline over the last 30 years (Gunn, 2016) affected 34 out of 43 of the World's major herds (Vors and Boyce, 2009). Rising Arctic temperatures and precipitation are clearly important factors in *R. tarandus* population decline (Albon et al., 2016) and have been linked to the reductions in body mass, starvation and range shifts observed in modern populations (Hansen et al., 2010; Albon et al., 2016). Clearly, Arctic and Subarctic regions are among the most susceptible to predicted changes in global climates (Courault et al., 2017); nevertheless, distinguishing the causal effects of climatic changes from those of increasing anthropogenic disturbances can be difficult. The expansion of infrastructure, both for industry and recreational activities, has similarly been linked to R. tarandus forage depletion, range shifts and an increased abundance of predators (Newton et al., 2015; Sandström et al., 2016; St. John et al., 2016; Lafontaine et al., 2017). Although the anthropogenic impacts on Late Pleistocene R. tarandus would have been considerably different to today, understanding the response of this species to both of these threats will be essential to the future conservation of *R. tarandus*.

1.2. Research Aims, Objectives and Hypotheses

1.2.1. Aims

- To reconstruct the palaeobiogeography, including seasonal movements, of Late Pleistocene *Rangifer tarandus* in Britain and western Europe.
- To establish patterns of palaeodiet in the Late Pleistocene Rangifer tarandus.
- To assess morphological variations of modern and historical specimens of *Rangifer tarandus* in western Europe in response to environmental and climatic change.

1.2.2. Objectives

- Dental and skeletal material from recent and historical specimens will be used to compose modern training sets, for comparison of the age and sex of Late Pleistocene specimens.
- Morphometric assessments will be applied to determine the developmental stage and sex of individuals, inferring season of deposition through the comparison of modern published evidence regarding seasonal aggregations.
- A self-contained study of strontium isotope analyses of dentition will be conducted, in order to determine migration pathways for individuals from Middle Devensian sites, by comparison to modern published strontium bioavailability.
- Dental microwear analysis will be carried out to determine the diet of individuals based on the modern training set, in particular establishing whether grazing, browsing or mixed feeding niches were occupied.
- Morphometric analysis of the body mass of modern and historical specimens will be conducted to quantify recent variations in response to environmental and anthropogenic stressors.

1.2.3. Hypotheses

Hypothesis 1: There will be a difference in the seasonality of site occupations by *Rangifer tarandus* both spatially across north west Europe and temporally throughout the Late Pleistocene.

Null Hypothesis 1: There will be no difference in the seasonality of site occupations by *Rangifer tarandus* both spatially across north west Europe and temporally throughout the Late Pleistocene.

Hypothesis 2: The fluctuating presence of a landbridge connecting Britain to the European mainland during the last glaciation will dictate migration routes undertaken by Late Pleistocene *Rangifer tarandus*.

Null Hypothesis 2: The fluctuating presence of a landbridge connecting Britain to the European mainland during the last glaciation will not dictate migration routes undertaken by Late Pleistocene *Rangifer tarandus*.

Hypothesis 3: Changing climatic and environmental conditions during the Late Pleistocene in north west Europe will lead to the formation of distinct ecotypes in *Rangifer tarandus*.

Null Hypothesis 3: Changing climatic and environmental conditions during the Late Pleistocene in north west Europe will not lead to the formation of distinct ecotypes in *Rangifer tarandus*.

Hypothesis 4: There will be a difference in the body sizes of historical through to modern populations of *Rangifer tarandus* from north west Europe as a result of changing Holocene climatic and anthropogenic influences.

Null Hypothesis 4: There will be no difference in the body sizes of historical through to modern populations of *Rangifer tarandus* from north west Europe as a result of changing Holocene climatic and anthropogenic influences.

1.3. Selection of Late Pleistocene Rangifer tarandus

Temporally, the Late Pleistocene scope of this study encompasses R. tarandus records from the Last Glacial or cold stage, referred to as the Devensian in Britain or the Weichselian in continental northern Europe. This is a period characterised by rapid fluctuations between stadials and interstadials, as millennial to sub-millenial scale Dansgaard-Oeschger (D-O) events caused the oceanic and atmospheric conditions to oscillate between cold and temperate conditions (Dansgaard et al., 1982; Rasmussen et al., 2014). This is clearly reflected in the δ^{18} O or δ D values of the long ice core records from Greenland (NGRIP, GISP and GISP2) and Antarctica (EPICA), as well as deepocean sediments (Johnsen et al., 2001; Lisiecki and Raymo, 2005; Parrenin et al., 2007), which measure the changes in global ice volume and can therefore be used as a proxy for the predominance of either cold or temperate climates on land (Lisiecki and Raymo, 2005). In turn, these records have been used to define the glacial/interglacial Marine Oxygen Isotope Stages (MIS) and phases therein from the long marine records (Lisiecki and Raymo, 2005), as well as the more highly resolved Greenland Stadials (GS) and Greenland Interstadials (GI) (Rasmussen et al., 2014). The fossil sites selected for this study could therefore be divided into those from the Early Devensian and specifically MIS 5a (82-71 kyr), the Middle Devensian/Weichselian or MIS 3 (57-29 kyr) and the Late Devensian/Weichselian, specifically the Lateglacial GI-1 and GS-1 (14.6-11.7 kyr) (Figure 1.1). Material from each of these stages was selected from units/layers from which specimens had either been directly dated, or which were strongly associated with a particular Mammal Assemblage-Zone (MAZ). Nevertheless, it is important to consider the timespan of individual deposits (where known). Where assemblages represent long periods of accumulation, patterns of *R. tarandus* palaeobiogeography may potentially be obscured by the palimpsest nature of the assemblage.

The selection of Late Pleistocene sites containing fossil *R. tarandus* remains was concentrated on western Europe (**Figure 1.2**). While sites in Belgium, France and the Netherlands represented the most likely source populations for the colonisation of Britain by *R. tarandus* (Gaffney *et al.*, 2009), the inclusion of material from Germany and Denmark provided a wider scope for the analysis of seasonal movements across Britain and western Europe. In addition to well-known assemblages, lesser studied sites were also included in this research in order to broaden the study range. Each site was selected for its abundant and often dominant *R. tarandus* remains. **Table 1.1** outlines the collections from which material was accessed; however, for a number of otherwise suitable assemblages, collections were either unavailable for study or visits could not be accommodated within the timescale of this project. While for some sites, including Westeregeln in Germany and both Abri de la Madeleine and Abri de Laugerie Haute in

the French Dordogne, this resulted in the study of only a small sub-sample of what are large collections of *R. tarandus*, other notable and well-studied sites were inevitably omitted. As such, also considered for this research but not accessed were the Belgian sites of Remouchamps, Spy, Trou de l'Abîme, Trou da Somme and Bois Laiterie, the French sites of Pincevent, Verberie, Etiolles, Beauvais, Tureau des Gardes, Grotte du Renne, Grotte aux Ours, La Roche-Cotard, Fontenioux, Les Pradelles, Roc de Combe, Combe-Grenal, Abri de Facteur and Vergisson, the German sites of Stellmoor and Meiendorf, Wildscheuer, Andernach, Gonnersdorf, Geißenklösterle, Vogelherd, Hohlenstein, Schussenguelle and Petersfels, and the Dutch sites of Maasvlakte, Woerden and Den Bosch. Although these exclusions had some influence on the overall sampling distribution, particularly in France and Germany, the spatial distribution of fossil-bearing study sites also varies between each stage, as the proximity of sites to expanding and retreating ice fronts fluctuates together with the variations in the suitability of depositional environments and taphonomic processes for fossil preservation. It is therefore important to understand the taphonomy of an assemblage in the reconstruction of *R. tarandus* palaeobiogeography. Nevertheless, the distribution of sites in this study was sufficient for the reconstruction of *R. tarandus* palaeobiogeography and associated dietary changes, representing broadly north-south and east-west transects from each climatic stage.



Figure 1.1. Chronostratigraphy of the Late Pleistocene Sites Studied. Marine Oxygen Isotope Stages are determined from the LR04 stack of marine record of δ¹⁸O of benthic foraminifera, while Greenland Stadials and Interstadials are shown against the Greenland Ice Core Chronology (GICC05) of δ¹⁸O (Source: Lisiecki and Raymo, 2005; Andersen *et al.*, 2006; Rasmussen *et al.*, 2006).



Figure 1.2. Location of the Late Pleistocene Sites Studied.

| Site | Museum/Institution |
|--|--|
| Britain | |
| Banwell Bone Cave | South West Heritage Trust |
| | Natural History Museum, London |
| Brixham Cave | Natural History Museum, London |
| | Torquay Museum |
| Chelm's Combe | Natural History Museum, London |
| Church Hole Cave | Manchester Museum |
| | Natural History Museum, London |
| Gully Cave | Royal Holloway University of London |
| Feltham | Natural History Museum, London |
| Inchnadamph (Bone Cave and Reindeer Cave) | National Museums Scotland, Edinburgh |
| Isleworth | Natural History Museum, London |
| Kents Cavern | Natural History Museum, London |
| | Torquay Museum |
| | South West Heritage Trust |
| | Plymouth Museum |
| | Leeds Discovery Centre |
| Mammoth Cave | Manchester Museum |
| Ossom's Cave | The Potteries Museum and Art Gallery, Stoke-on-Trent |
| Picken's Hole | University of Bristol Spelaeological Society |
| Pin Hole Cave | Manchester Museum |
| | Natural History Museum, London |
| Robin Hood Cave | Manchester Museum |
| Sandford Hill | South West Heritage Trust |
| Soldier's Hole | Manchester Museum |
| Stump Cross Cavern | Natural History Museum, London |
| Tornewton Cave (Reindeer Stratum) | Natural History Museum, London |

 Table 1.1. Location of Late Pleistocene Rangifer tarandus Material Studied from Museum/Institution Collections.

| Windy Knoll | Leeds Discovery Centre |
|---------------------------|---|
| | Manchester Museum |
| | Natural History Museum, London |
| Wookey Hole (Hyaena Den) | South West Heritage Trust |
| | Manchester Museum |
| Belgium | |
| Goyet (Troisième Caverne) | Royal Belgian Institute of Natural Sciences |
| Caverne Marie-Jeanne | Royal Belgian Institute of Natural Sciences |
| Trou Al'Wesse | Royal Belgian Institute of Natural Sciences |
| Trou de Chaleux | Royal Belgian Institute of Natural Sciences |
| Trou Magrite | Royal Belgian Institute of Natural Sciences |
| Trou du Moulin | Royal Belgian Institute of Natural Sciences |
| Trou des Nutons | Royal Belgian Institute of Natural Sciences |
| Trou du Sureau | Royal Belgian Institute of Natural Sciences |
| Denmark | |
| Køge Bugt | Natural History Museum Denmark |
| Nørre Lyngby | Natural History Museum Denmark |
| | National Museum of Denmark |
| Slotseng | Natural History Museum Denmark |
| | National Museum of Denmark |
| France | |
| Abri de Laugerie Haute | Natural History Museum, London |
| Abri de la Madeleine | Natural History Museum, London |
| | Museum of Natural History, Berlin |
| | National Museum of Denmark |
| Germany | |
| Salzgitter-Lebenstedt | Braunschweig Landesmuseum, Wolfenbüttel |
| Westeregeln | Museum of Natural History, Berlin |
| The Netherlands | |
| Ellewoutsdijk | Natural History Museum Rotterdam |
| Raalte | Natural History Museum Rotterdam |

1.3.1. The Early Devensian

Only *R. tarandus* from Britain were studied from the Early Devensian MIS 5a (Table 1.2). Although MIS 5a represents a warmer interstadial in the Early Devensian, it nevertheless encompasses significant climatic variability between palaeoenvironmental proxies in Britain. The vertebrates from this stage were typical of a cold boreal fauna. The bone deposit of Banwell Bone Cave in Somerset represents a low diversity assemblage containing abundant remains of bison (Bison priscus, Bojanus, 1827) and R. tarandus (most numerous), in addition to a large form of brown bear (Ursus arctos, Linnaeus, 1758) (Currant and Jacobi, 2011). The composition of the fauna led Currant and Jacobi (1997, 2001, 2011) to designate the assemblage as the type for their Banwell Bone Cave MAZ, which they assigned to the Early Devensian. Uranium-series dating by Gilmour et al. (2007) on other sites yielding Banwell Bone Cave MAZ assemblages has corroborated an age within MIS 5a, c. 87-71 ka. The open, grassland environment implied by this assemblage was further recognised in the pollen records at both Isleworth and Feltham in the Middle Thames Valley, where grasses and sedges dominated the treeless landscape (Kerney et al., 1982; Coope et al., 1997). Temperature reconstructions from Coleoptera at Isleworth of 17-18°C for the warmest month and -2-1°C coldest month (Coope and Angus, 1975) were similar to the mean July temperatures of 17-18°C and mean December temperatures of -4 to +4°C, also reconstructed from coleopteran remains indicative of woodland conditions at the co-eval site of Cassington, Oxfordshire (Maddy et al., 1998). It has accordingly been suggested that the Banwell Bone Cave MAZ represents a relict island fauna (Gilmour et al., 2007; Currant and Jacobi, 2011). As global sea level increased by >40 m into the MIS 5a interstadial (Chappell et al., 1996; Cutler et al., 2003), Britain was isolated from continental Europe, leaving the cold stage fauna of the preceding MIS 5b stadial trapped. This also explains why there is no evidence in Britain for the megafauna otherwise observed from the Early Weichselian in Europe (Currant and Jacobi, 2011). Nevertheless, the prevailing palaeoenvironmental evidence still support the presence of open grassland and likely snow cover during the winter months, in order to sustain the cold stage fauna of Britain.

| Site | Unit/Layer | Age | Species List | Reference |
|---|---------------------------------|--|--|--|
| Britain | | | | |
| Banwell Bone Cave, Somerset (ST 3822 5881) | Bone deposit | Banwell Bone Cave MAZ | Lepus timidus Microtus oeconomus Canis lupus Vulpes vulpes Vulpes lagopus Ursus arctos (large form) Gulo gulo Rangifer tarandus Bison priscus | Currant and Jacobi, 1997; 2001; 2011; |
| Feltham, Middlesex (TQ 078 729) | Organic silts | Banwell Bone Cave MAZ | Rangifer tarandus Bison priscus | Coope <i>et al</i> ., 1997 |
| Isleworth, Middlesex (TQ 158 746) | Dark grey laminated silts | Banwell Bone Cave MAZ | <i>Rangifer tarandus Bison priscus</i> (small form) | Coope and Angus, 1975; Currant and Jacobi, 2011 |
| Picken's Hole, Somerset (ST 3964 5500) | Unit 5 | Banwell Bone Cave MAZ | Canis lupus Vulpes vulpes Ursus arctos Rangifer tarandus Bison priscus | Tratman, 1964; Mullan, 2018; Scott, 2018 |
| Stump Cross Cavern, North Yorkshire (SE 089 634) | Reindeer Chamber | Banwell Bone Cave MAZ, 73.86+1.20/- 1.19 ka | Canis lupus Vulpes vulpes Gulo gulo Rangifer tarandus Bison priscus | Collins, 1959; Sutcliffe <i>et al.</i> , 1985; Gilmour <i>et al.</i> , 2007 |
| Tornewton Cave, Devon (SX 817 674) | Reindeer Stratum | Banwell Bone Cave MAZ, 76-77 ka | Canis lupus Ursus arctos Rangifer tarandus Bison priscus | Widger, 1892; Sutcliffe and Zeuner, 1962; Gilmour <i>et al.</i> , 2007; Currant and Jacobi, 2011 |
| Windy Knoll, Derbyshire (SK 1263 8303) | Yellow clay deposit | Banwell Bone Cave MAZ, >51,700 ¹⁴ C years BP | Lepus sp. Leporidae sp. Arvicola cantiana Canis lupus Vulpes vulpes Ursus arctus Rangifer tarandus Bison priscus Bos primigenius | Dawkins, 1875; Pennington and Dawkins, 1877; Higham <i>et al</i> , 2006 |

 Table 1.2. Details of the Early Devensian Sites Studied.

1.3.2. The Middle Devensian/Weichselian

R. tarandus from Britain, Belgium, The Netherlands and Germany were studied from the Middle Devensian/Weichselian (Table 1.3). Despite representing an overall warmer phase of the Last Glacial, the climate of the Middle Devensian/Weichselian is highly variably, characterised by multiple short-term fluctuations (Rasmussen et al., 2014). From Whitemoor Haye Quarry in Staffordshire, mean July temperatures of 8-11°C and mean December temperatures of -22 to -16°C have been reconstructed from coleopteran remains, while pollen analysis suggests that the landscape was relatively treeless, dominated instead by grasses and sedges (Schreve et al., 2013). Referred to as the Mammoth Steppe, this open grassland and shrub tundra environment of dwarf birch (Betula nana), cold adapted willows (Salix polaris, Salix herbacea) and mountain avens (Dryas octopetala), extended across the northern European range of this study (Schutrumpf, 1991; Van Geel et al., 2019) providing abundant grazing to support a number of large herbivores. This is apparent from the Pin Hole Cave MAZ in Derbyshire, which Currant and Jacobi (1997, 2001, 2011) designated the type assemblage for the Middle Devensian and correlated with MIS 3, based on radiocarbon dating of the sites Lower Cave Earth to 55-44 Ka ¹⁴C years BP (Currant and Jacobi, 2011). Characterised by woolly mammoth (Mammuthus primigenius, Blumenbach, 1799), woolly rhinoceros (Coelodonta antiquitatis, Blumenbach, 1799), lion (Panthera spelaea, Goldfuss, 1810) and particularly spotted hyaena (Crocuta crocuta, Erxleben, 1777), the relativity diverse range of species from the Mammoth Steppe fauna of Britain, also referred to as the 'Age du Mammouth' or Mammoth Age in Belgium (Dupont, 1873), is observed in both the Middle Devensian and Weichselian records, due in part to the reconnection of Britain to continental Europe as sea level was lowered by >70 m (Cutler et al., 2003; Currant and Jacobi, 2011).

| Site | Unit/Layer | Age | Species List | Reference |
|---------------|------------|----------|-------------------------|--------------------|
| Britain | | | | |
| Brixham Cave, | Layer 3 | Pin Hole | Lepus sp. | Pengelly et al., |
| Devon | | Cave MAZ | Panthera spelaea | 1873; |
| (SX 92457 | | | Crocuta crocuta | McFarlane et |
| 55983) | | | Ursus arctos | <i>al</i> ., 2010; |
| | | | Meles meles | Currant and |
| | | | Mammuthus primigenius | Jacobi, 2011 |
| | | | Equus ferus | |
| | | | Coelodonta antiquitatis | |
| | | | Cervus elaphus | |
| | | | Capreolus capreolus | |
| | | | Rangifer tarandus | |
| | | | Bos primigenius | |

 Table 1.3. Details of the Middle Devensian/Weichselian Sites Studied.

| Church Hole Cave, Derbyshire (SK 534 741) | Cave Earth | Pin Hole Cave MAZ, Middle and Upper Palaeolithic artefacts | Lepus timidus Panthera spelaea Canis lupus Vulpes vulpes Ursus arctos Mustela putorius Crocuta crocuta Mammuthus primigenius Equus ferus Coelodonta antiquitatis Megaloceros giganteus Rangifer tarandus Bison priscus | Dawkins, 1977; Currant and Jacobi, 2001 |
|--|--|---|--|--|
| Gully Cave, Somerset (ST 505 508) | Lower Breccia | Pin Hole Cave MAZ | Crocuta crocuta Equus ferus Coelodonta antiquitatis | Danielle Schreve pers. comm |
| | | | Rangifer tarandus | |
| Inchnadamph, Bone Cave, Sutherland (NC 2679 1704) | Gravel Layer | 44-28 ka ¹⁴ C years BP | Ursus sp. Rangifer tarandus Cervus elaphus | Peach and Horne, 1917; Lawson, 1981; Murray <i>et al.</i> , 1993 |
| Inchnadamph, Reindeer Cave, Sutherland (NC 2679 1704) | Outer Chamber Gravel Layer | 44-28 ka ¹⁴ C years BP | Vulpes lagopus Ursus arctos Rangifer tarandus Cervus elaphus | Lawson, 1981; Murray <i>et al.</i> , 1993 |
| Kents Cavern, Devon (SX 934 642) | Cave Earth | Pin Hole Cave MAZ, 49,600± 220 – 30,220± 460 ¹⁴ C years BP | Homo sp. Canis lupus Vulpes vulpes Crocuta crocuta Ursus arctos Mammuthus primigenuis Equus ferus Coelodonta antiquitatis Megaloceros giganteus Cervus elaphus (large form) Rangifer tarandus | Proctor, 1996; Keen, 1998; Higham et al., 2006; Currant and Jacobi, 2011 |
| Mammoth Cave, County Cork (IG R603009) | Sand below stalagmite in Gallery of the Aged Carnivores and Elephant Hall | Pin Hole Cave MAZ, 35-33 ka ¹⁴ C years BP | Lemmus lemmus Canis lupus Vulpes lagopus Crocuta crocuta Ursus arctos Mammuthus primigenuis Megaloceros giganteus Rangifer tarandus | Scharff <i>et al.</i> , 1917-1919; Hedges <i>et al.</i> , 1997; Woodman <i>et</i> <i>al.</i> , 1997 |
| Picken's Hole, Somerset (ST 3964 5500) | Unit 3 | Pin Hole Cave MAZ, 40,200± 700 ¹⁴ C years BP | Panthera spelaea Canis lupus Vulpes lagopus Crocuta crocuta Ursus arctos Mammuthus primigenius Equus ferus Coelodonta antiquitatis | ApSimon, 1986; Jacobi <i>et al.</i> , 2009; Scott, 2018 |

| | | | Megaloceros giganteus Cervus elaphus Rangifer tarandus Psion prisous | |
|--|---------------------|---|---|--|
| Pin Hole Cave, Derbyshire (SK 533 742) | Lower Cave Earth | Pin Hole Cave MAZ, 54,000± 2900 – 40,650± 500 ¹⁴ C years BP, Mousterian Middle Palaeolithic and Upper Palaeolithic artefacts | Homo sp. Lepus timidus Spermophilus major Panthera spelaea Canis lupus Vulpes vulpes Ursus arctos Mustela erminea Mustela putorius Crocuta crocuta Mammuthus primigenius Equus ferus Coelodonta antiquitatis Megaloceros giganteus Rangifer tarandus Bison priscus | Currant and Jacobi, 1997; 2001; 2011; Higham <i>et al.</i> , 2006; Jacobi <i>et al.</i> , 2006; Jacobi <i>et al.</i> , 1998 |
| Robin Hood Cave, Derbyshire (SK 244 836) | Cave Earth | Pin Hole Cave MAZ, Middle and Upper Palaeolithic artefacts | Lepus timidus Panthera spelaea Canis lupus Vulpes vulpes Ursus arctos Crocuta crocuta Mammuthus primigenius Equus ferus Coelodonta antiquitatis Megaloceros giganteus Rangifer tarandus Bison priscus | Dawkins, 1877; Currant and Jacobi, 2001 |
| Sandford Hill, Somerset (ST 4268 5905) | Reindeer Horizon | Pin Hole Cave MAZ | Lepus timidus Panthera spelaea Vulpes vulpes Canis lupus Crocuta crocuta Ursus arctos Equus ferus Coelodonta antiquitatis Rangifer tarandus Cervus elaphus Bsion priscus | Currant, 2004 |
| Wookey Hole (Hyaena Den), Somerset (ST 5323 4794) | Cave Earth | Pin Hole Cave MAZ, 31,550± 340 ¹⁴ C years BP, Aurignacian Upper Palaeolithic artefacts | Panthera spelaea Crocuta crocuta Ursus arctos Crocuta crocuta Mammuthus primigenius Equus ferus Coelodonta antiquitatis Cervus elaphus Rangifer tarandus Bison priscus | Dawkins, 1862; Currant, 2004; Higham <i>et al.</i> , 2006; Currant and Jacobi, 2011 |
| Belgium | | | | |

| Trou Al'Wesse, Namur Carverne Marie- Jeanne, Namur | Levels 1-6 Levels 1-3 | Mammoth Age, Mousterian Middle Palaeolithic and Aurignacian Upper Palaeolithic artefacts Mammoth Age, c. 50-40 ka, Magdalenian | Lepus timidus Crocuta crocuta Ursus sp. Dicrostonyx torquantus Lemmus lemmus Arvicola terrestris Equus sp. Cervus elaphus Rangifer tarandus Bos primigenius Crocuta crocuta Equus sp. Coelodonta antiquitatis Cervus elaphus | Miller <i>et al.</i> , 2016 López-García <i>et al.</i> , 2017 |
|---|--------------------------|---|---|--|
| | | Upper Palaeolithic artefacts | Rangifer tarandus Bison priscus Bos primigenius | |
| Goyet (Troisième Caverne), Namur | Levels 1-4 | Mammoth Age, 35-27 ka ¹⁴ C years BP, Mousterian Middle Palaeolithic and Magdalenian Upper Palaeolithic artefacts | Homo sp. Lepus timidus Canis lupus Vulpes vulpes Vulpes lagopus Panthera spelaea Crocuta crocuta Ursus arctos Ursus spelaeus Mustela putorius Mammuthus primigenius Coelodonta antiquitatis Cervus elaphus Rangifer tarandus Bison priscus Rupicapra rupicapra Capra ibex | Dupont, 1873; Germonpré, 1997; Toussaint, 2006 |
| Trou Magrite, Namur | Stratum 2-5 | Mammoth Age, 41-30 ka ¹⁴ C years BP, Aurignacian Upper Palaeolithic artefacts | Lepus timidus Canis lupus Vulpes vulpes Vulpes lagopus Panthera spelaea Ursus spelaeus Meles meles Mammuthus primigenius Equus sp. Coelodonta antiquitatis Rangifer tarandus Bison priscus Rupicapra rupicapra Capra ibex | Gautier <i>et al.</i> , 1997 |
| Trou du Moulin, Namur | Levels 1 and 3 | Mammoth Age, Mousterian Middle Palaeolithic artefacts | Crocuta crocuta Ursus spelaeus Coelodonta antiquitatis Rangifer tarandus | Toussaint, 2006 |

| Trou du Sureau, Namur | Level 3-4 | Mammoth Age, Mousterian Middle Palaeolithic and Aurignacian Upper Palaeolithic artefacts | Vulpes lagopus Ursus spelaeus Mammuthus primigenius Coelodonta antiquitatis Cervus elaphus Rangifer tarandus Bison priscus | Goubel <i>et al.</i> , 2012 |
|--|--|---|--|--|
| Germany | | | | |
| Salzgitter- Lebenstedt, Lower Saxony | Unit 1 and 2 | c.58-54 ka, Middle Palaeolithic artefacts | Homo sp. Canis lupus Mammuthus primigenius Equus sp. Coelodonta antiquitatis Rangifer tarandus Bison priscus | Gaudzinski and Roebroeks, 2000 |
| Westeregeln, Saxony-Anhalt | Reddish sandy loess and Periglacial soil | Middle Palaeolithic artefacts | Canis lupus Vulpes vulpes Vulpes lagopus Panthera spelaea Ursus spelaeus Meles meles Crocuta crocuta Mammuthus primigenius Equus caballus Coelodonta antiquitatis Rangifer tarandus Bison priscus Bos primigenius | Diedrich, 2012 |
| The Netherlands | Group II | Mammath | Donthoro onologo | Karkhaff 1000 |
| Zeeland | | Steppe fauna | Virsus spelaeus Meles meles Crocuta crocuta Mammuthus primigenius Coelodonta antiquitatis Megaloceros giganteus Rangifer tarandus Bison priscus | Neiniuli, 1900 |
| Kaalte, Overijissel | Grey-blue fluviatile clay | Mammoth Steppe fauna, 39,000± 1000 ¹⁴ C years BP | Canis lupus Panthera spelaea Ursus spelaeus Crocuta crocuta Mammuthus primigenius Equus sp. Coelodonta antiquitatis Megaloceros giganteus Cervus elaphus Rangifer tarandus Bison priscus Bos primigenius Ovibos mochatus | Bosscha Erdrink <i>et al.</i> , 2001; Mol <i>et</i> <i>al.</i> , 2007 |

1.3.3. The Late Devensian/Weichselian

Late Devensian/Weichselian R. tarandus were studied from Britain, Belgium, Denmark and France (Table 1.4). Although R. tarandus were part of the restricted cold-climate faunal assemblages of the Last Glacial Maximum (LGM), the Late Devensian/Weichselian specimens are primarily preserved from the warmer Lateglacial Interstadial (GI-1) and the period of climatic deterioration of the Younger Dryas or Loch Lomond Stadial (GS-1). Sea level throughout the Late Devensian/Weichselian remained low enabling the continued connectivity across the northern European range of this study (Cutler et al., 2003; Aaris-Sørensen, 2009). This is evident from the Lateglacial Interstadial faunas in Britain, which are characterised by an absence of *C. antiquitatis*, C. crocuta and P. spelaea, but display a prevalence of horses (Equus sp.) and Late Upper Palaeolithic artefacts from both the Gough's Cave MAZ and the Belgian 'Age du Renne' or Reindeer Age assemblages (Dupont, 1873; Currant and Jacobi, 2011). Another important component of the Gough's Cave MAZ is the record of red deer (Cervus elaphus, Linnaeus, 1758), as the environment become more temperate, and first juniper and then birch woodland continued to develop. This corresponds to coleopteran and chironomid reconstructed mean July temperatures from Britain of between 9-14°C (Brooks and Langdon, 2014; Elias and Matthews, 2014). Similar patterns of vegetation succession have been observed throughout Northern Europe (Aaris-Sørensen, 2009; Costamagno et al., 2016; Bos et al., 2017), although chironomidbased July temperature reconstructions were slightly higher in mainland Europe, at 16.2-17.3°C in Belgium (Bos et al., 2017) and 17.5°C in Southwest France (Miller et al., 2012). Although the expansion of woodland progressively led to the fragmentation of R. tarandus populations in the south of western Europe (Costamagno et al., 2016), as temperatures in Britain decreased into the Younger Dryas to between 7-11°C from chironomid-inferred summer air temperatures (Lang et al., 2010; Brooks and Langdon, 2014), R. tarandus began to dominate the cold, tundra conditions. Although no formal MAZ has been defined for this stage, isolated finds indicate that the more temperate fauna of the Gough's Cave MAZ disappeared, while cold-adapted species resurged (Currant and Jacobi, 2011). Despite this limitation, the application of radiocarbon dating on samples from the Late Devensian/Weichselian has been fundamental in assigning remains more precisely. As such, only the sites of Chelm's Combe and Ossom's Cave represented Younger Dryas assemblages in this study.
| Site | Unit/Layer | Age | Species List | Reference |
|--|---|--|--|---|
| Britain | | | | |
| Chelm's Combe, Somerset (ST 4632 5445) | Layer IX | Gough's Cave MAZ, 10,150±40 - 10,995±40 ¹⁴ C years BP, Upper Palaeolithic artefacts | Lepus sp. Microtus sp. Vulpes vulpes Equus caballus Cervus elaphus Rangifer tarandus | Jackson, 1931; Harrison, 1976; Currant and Jacobi, 2011 |
| Somerset (ST 505 508) | Upper Breccia and Calcareous Breccia | 12,037- 12,409 cal years BP | Rangiter tarandus | Danielle Schreve pers. comm. |
| Ossom's Cave, Staffordshire (SK 09587 55753) | Layer C | Gough's Cave MAZ, 12-10 ka ¹⁴ C years BP, Upper Palaeolithic artefacts | Homo sapiens Lepus timidus Sorex araneus Sorex minutus Dicrostonyx torquatus Lemmus lemmus Arvicola cantiana Myodes glareolus Microtus arvalis Microtus agrestis Equus ferus Rangifer tarandus Bos/Bison sp. | Bramwell <i>et</i> <i>al.</i> , 1987 |
| Soldier's Hole, Somerset (ST 4686 5400) | Layers 9-21 | Gough's Cave MAZ, 12,465±55 ¹⁴ C years BP, Upper Palaeolithic artefacts | Lepus sp. Microtus sp. Panthera spelaea Canis lupus Vulpes vulpes Ursus arctos Mammuthus primigenius Equus caballus Cervus elaphus Rangifer tarandus Bison priscus | Jackson, 1931; Currant and Jacobi, 2011 |
| Trou de Chaleux, Namur | Level 1 | Reindeer Age, $12,375\pm$ 50- $12,630\pm$ 55 ¹⁴ C years BP, Upper Palaeolithic Magdalenian artefacts | Castor fiber Lepus timidus Canis lupus Alopex/Vulpes Ursus arctos Mustela sp. Gulo gulo Meles meles Crocuta crocuta Felis sp. Equus sp. Equus hydruntinus Sus scrofa | Charles, 1994; Patou-Mathis, 1994; Germonpré, 1997; Stevens <i>et al.</i> , 2009 |

| | | | Cervus elaphus Capreolus capreolus Rangifer tarandus Bos sp. Saiga tatarica Rupicapra rupicapra Capra ibex Capra bircus | |
|-------------------------------------|---|--|--|---|
| Trou de Nutons, Namur | Level 1 | Reindeer Age, Upper Palaeolithic Magdalenian artefacts | Lepus timidus Canis lupus Alopex/Vulpes Ursus arctos Mustela foina Mustela sp. Gulo gulo Meles meles Felis sp. Equus sp. Sus scrofa Cervus elaphus Capreolus capreolus Rangifer tarandus Bos sp. Capra hircus | Charles, 1994 |
| Denmark | | | | |
| Køge Bugt | Dredged sediments | 12-11 ka ¹⁴ C years BP | Lepus timidus Megaloceros giganteus Rangifer tarandus | Aaris- Sørensen <i>et</i> <i>al.</i> , 2007; Aaris- Sørensen, 2009 |
| Nørre Lyngby, Northern Jylland | Sand and gravel, sand and clay units | 12-11 ka ¹⁴ C years BP | Lepus timidus Castor fiber Sorex araneus Sorex minutus Arvicola terrestris Microtus gregalis Desmana moschata Ursus arctos Rangifer tarandus | Aaris- Sørensen, 1995 |
| Slotseng, Southeast Jylland | Kettle hole fill | c. 12.5 ka ¹⁴ C years BP, Upper Palaeolithic Hamburgian artefacts | Rangifer tarandus | Aaris- Sørensen <i>et</i> <i>al.</i> , 2007; |
| France | | | | |
| Abri de Laugerie Haute, Dordogne | Bone deposit | c.15-14 ka ¹⁴ C years BP, Upper Palaeolithic Perigordian, Solutrean and | Lepus sp. Canis lupus Alopex/Vulpes Ursus sp. Mammuthus primigenius Equus caballus. Cervus elaphus. | Gowlett <i>et al.</i> , 1986; Delpech, 2012 |

| | | Magdalenian artefacts | Rangifer tarandus Bos sp. Saiga tatarica Rupicapra rupicapra Capra ibex. | |
|------------|---------|--------------------------|--|-------------------|
| Abri de la | Bone | c.13-12 ka | Lepus timidus | Delibrias et al., |
| Madeleine, | deposit | ¹⁴ C years | Equus caballus | 1976; |
| Dordogne | | BP, Upper | Cervus elaphus | Fontana, 2017 |
| | | Palaeolithic | Rangifer tarandus | |
| | | Magdalenian | Bos sp. | |
| | | artefacts | Rupicapra rupicapra | |
| | | | Capra ibex. | |

1.4. Selection of Modern and Historical *Rangifer tarandus*

Modern specimens were selected only when the sex, collection location and date was known. In some instances, the age at death of the specimen was also available.

1.4.1. Scandinavian Specimens

Populations of wild mountain *R. tarandus* once extended throughout western Europe, but are today only found in Norway. Monitoring programs report that in total around 30,000-35,000 individuals persist throughout the 24 defined management areas of the country (Solberg *et al.*, 2010), of which approximately 10,000 animals belong to the largest population in Hardangervidda (Villrein, 2020). Four mainland provinces were included in the study of modern Norwegian *R. tarandus*, each representing specimens from the *Rangifer tarandus tarandus* (mountain reindeer) subspecies (**Figure 1.3**). From southern Norway, the three provinces of Hordaland, Buskerud and Oppland are examples of mountain habitats, where wild *R. tarandus* move between adjacent mountain ranges from summer pastures in the west to winter pastures in the east (Dahle *et al.*, 2008; Panzacchi *et al.*, 2013). However, the province of Finnmark in northern Norway represents part of the forest range of the semi-domesticated *R. tarandus* herded by the Sámi people (Johnsen *et al.*, 2015).

Sámi populations extend from the north of Norway into Sweden, Finland and Russia. Despite the fact that the *R. tarandus* are defined as semi-domesticated, most herds are migratory (Sandström, 2015), moving freely within their natural ranges with only occasional herding (Åhman *et al.*, 2014). The primary economy of the Sámi is meat production and as such, the limited contact with herds comes during either slaughter or supplementary feeding, each required to maintain body condition (Åhman *et al.*, 2014). The semi-domesticated *R. tarandus* are organised into geographical and administrative

areas which govern each herders' access to grazing lands and animal numbers, following the Reindeer Husbandry Act (The Sami Parliament, 2019). These are referred to as a Reinbeitedistrikt (reindeer pasture district) in Norway, a Sameby (or Sámi village) in Sweden, and a Paliskunta in Finland. In Norway, *R. tarandus* are divided between 77 Reinbeitedistrikts however, 73% of the 250,000 semi-domesticated animals are found in Finnmark (Johnsen et al., 2015). Movements generally occur between the summer coastal pastures and inland winter pastures further south (Johnsen et al., 2015). In Sweden, the semi-domesticated R. tarandus population varies between 225,000-280,000 (The Sami Parliament, 2019). Of the 51 Samebys, 33 occupy mountain areas, 10 are found in forests and 8 are concession (permit holding) herding areas (The Sami Parliament, 2019). This study includes *R. tarandus* from four provinces in the north of Sweden, all belonging to the *R. t. tarandus* subspecies (Figure 1.3). Both Jämtland and Härjedalen fall within Jämtland County and represent R. tarandus occupying mountain ranges (The Sami Parliament, 2019). For the mountain herds, R. tarandus are fully migratory, moving from summer ranges in the mountains of the north west, towards the inland and coastal coniferous forests in the south east for winter (Sandström et al., 2016; Bårdsen et al., 2017). Forest populations, on the other hand, are more sedentary, moving only within the coniferous forests throughout the year (Bårdsen et al., 2017). Norrbotten and Lappland are part of Norrbotten County and occupy entirely forest ranges in Norrbotten and both mountain and forest habitats in Lappland (The Sami Parliament, 2019).

Also included in the Scandinavian samples were specimens from the high Arctic islands of Svalbard (**Figure 1.3**). The Norwegian archipelago consists of four islands, whereby an estimated 22,435 individuals represent the subspecies *Rangifer tarandus platyrhynchus* (Svalbard reindeer) (Le Moullec *et al.*, 2019), which is endemic to Svalbard. However, only *R. tarandus* collected from the largest island, Spitsbergen, were studied. Occupying both the open tundra of inland, glacial valleys, as well as coastal pastures (Le Moullec *et al.*, 2019), the wild Svalbard *R. tarandus* are not migratory, instead undertaking small-scale movements within localised home ranges (Tyler and Oritsland, 1989).

Norwegian specimens, including those from the Svalbard archipelago, were accessed at the University Museum of Bergen and represent animals killed between 1868 and 2006. The majority of modern *R. tarandus* specimens from Sweden were accessed at the Ájtte Swedish Mountain and Sami Museum, Jokkmokk, with additional material held at the Swedish Museum of Natural History, Stockholm. The Swedish *R. tarandus* sample represents animals collected between 1909 and 1956.



Figure 1.3. Location of Modern *Rangifer tarandus* Samples from Scandinavian Provinces.

1.4.2. North American Specimens

Four provinces from North America were also included in this study, all of which were located in Canada (**Figure 1.4**). These included examples of three of the four wild *R. tarandus* subspecies found throughout the Canadian provinces and territories. Specimens of *Rangifer tarandus caribou* (boreal woodland caribou) are endemic to Canada and were studied from both Alberta and Newfoundland. Occupying boreal coniferous forest environments, an estimated 34,000 individuals are found across 51 ranges and cover nine of the Canadian provinces and territories, although the precise monitoring of populations is somewhat limited by this wide distribution (Environment

Canada, 2011). Despite separating into groups that winter either in forest or alpine areas (Kuzyk *et al.*, 1999), *R. t. caribou* are considered sedentary when compared to other *R. tarandus* subspecies (Banfield, 1961).

Conversely, the migratory *Rangifer tarandus groenlandicus* (barren-ground caribou) move between summer ranges in the tundra of the Arctic coast towards winter pastures either in the southern Arctic tundra or boreal forests (COSEWIC, 2016). An estimated 800,000 animals, in 14-15 subpopulations, are found continuously across the continental provinces and territories of Canada, even extending into the Canadian Arctic Archipelago in Nunavut Territory (COSEWIC, 2016). Specimens of *R. t. groenlandicus* in this study included those from both the Northwest Territories and Nunavut Territory.

While *R. t. groenlandicus* are an important aspect of the subsistence diets of Indigenous people (COSEWIC, 2016), the subspecies *Rangifer tarandus pearyi* (Peary caribou) is often the only *R. tarandus* subspecies available to the Inuit and Inuvialuit cultures (COSEWIC, 2015). Endemic to Canada, most populations of *R. t. pearyi* live in the tundra of the high Arctic islands of the Canadian Arctic Archipelago (Petersen *et al.*, 2010) however, only specimens from Nunavut Territory were studied. There are an estimated 13,200 individuals across four subpopulations that migrate seasonally either within the range of a single island, or by moving across the sea ice between multiple islands (COSEWIC, 2015).

The Canadian specimens were accessed at the American Museum of Natural History, New York City and represent individuals collected between 1898 and 1936.



Figure 1.4. Location of Modern *Rangifer tarandus* Samples from North American Provinces.

Chapter 2. *Rangifer tarandus* Taxonomy, Behaviour and Ecology

The chapter provides an overview of the taxonomy, behaviour and ecology of modern *Rangifer tarandus*, focussing particularly on the adaptations which enable this species to survive in Arctic and Subarctic environments. One of the most unique behavioural adaptations of *R. tarandus* is the large-scale bi-annual migrations between summer and winter grazing pastures, which are today unique amongst northern ungulates. However, the future status of *R. tarandus* herds are likely to be impacted by ongoing anthropogenic related changes and current and future global warming.

2.1. Rangifer tarandus Subspecies

Holocene *R. tarandus* represent nine subspecies, two extinct and seven extant, which have traditionally been classified into three ecological groups: tundra, woodland and high Arctic island, on the basis of their morphology, habitat use and behaviour (Banfield, 1961) (Table 2.1). Tundra R. tarandus, which include the Eurasian subspecies Rangifer tarandus tarandus and the North American subspecies Rangifer tarandus grantii and Rangifer tarandus groenlandicus, typically have wide-angled antlers with long and slender beams and undertake extensive migrations between the open tundra and boreal or taiga forests (Banfield, 1961; Flagstad and Røed, 2003). Woodland R. tarandus, on the other hand, are found predominantly in boreal coniferous forests and move within a much more localised range (Banfield, 1961). This group includes the Eurasian subspecies Rangifer tarandus fennicus and the North American subspecies Rangifer tarandus caribou, which are further characterised by larger body sizes and leg lengths than tundra *R. tarandus*, as well as shorter and more compact antlers (Banfield, 1961; Flagstad and Røed, 2003). The final ecological group describes subspecies found exclusively on high Arctic islands. This includes the Eurasian subspecies Rangifer tarandus platyrhynchus and the North American subspecies Rangifer tarandus pearyi, which in addition to their unique geographical distribution, demonstrate smaller body sizes than both tundra and woodland R. tarandus (Banfield, 1961; Flagstad and Røed, 2003).

| Ecological Group | Subspecies | Distribution |
|---------------------|---------------------------------|---------------------------------|
| Tundra | R. t. grantii | Alaska, Canada |
| | R. t. groenlandicus | Canada |
| | R. t. tarandus | Norway, Sweden, Finland, Russia |
| Woodland | R. t. caribou | Canada, USA |
| | <i>R. t. dawsoni</i> (extinct) | Graham Island (Canada) |
| | R. t. fennicus | Finland, Russia |
| High Arctic | R. t. eogroenlandicus (extinct) | Greenland |
| Island | R. t. pearyi | Canada |
| | R. t. platyrhynchus | Svalbard |

| Table 2.1. | Rangifer | tarandus | Subsp | ecies b | y Ecolo | gical Gr | oups. |
|------------|----------|----------|-------|---------|---------|----------|-------|
| | | | | | | | |

The tundra, woodland and high Arctic island *R. tarandus* are therefore distributed in both North America and Eurasia in the present day. However, genetic studies focussing on mitochondrial DNA (mtDNA) indicate that the traditional ecological groups used to define *R. tarandus* subspecies are not representative of the phylogeography and taxonomy of the species (Gravlund *et al.*, 1998; Flagstad and Røed, 2003; Cronin *et al.*, 2006; McDevitt *et al.*, 2009; Yannic *et al.*, 2014; Kvie *et al.*, 2016). Instead, the present-day geographical distribution of mtDNA haplotypes is a product of the refugial origins, colonisation and fragmentation of *R. tarandus* following the Last Glacial Maximum (LGM) (Flagstad and Røed, 2003; Yannic *et al.*, 2014).

Depending on the precise mtDNA markers used, there is some discrepancy between studies as to how many haplotypes modern *R. tarandus* originated from. Using the mitochondrial control region (CR), three main haplotypes have been identified (Flagstad and Røed, 2003) and subsequently divided into subclusters (Røed et al., 2008; Bjørnstad et al., 2012; Klütsch et al., 2012; Kvie et al., 2016). While the largest of these clusters originated from a glacial population with a continuous range from Eurasia to Beringia and has therefore influenced all extant subspecies, the two smaller clusters represent glacial refugia in North America to the south of the Wisconsin Ice Sheet, and Eurasia, possibly isolated in western Europe during Weichselian ice advance (Flagstad and Røed, 2003). However, when the protein-coding cytochrome (cytb) region was used, only the large Euro-Beringian and smaller North American refugia cluster were identified (Yannic et al., 2014). Similarly, although there is general consensus between markers that the island subspecies were derived from Euro-Beringian populations (Flagstad and Røed, 2003; Yannic et al., 2013; Kvie et al., 2016), there is still considerable uncertainty over the colonisation of high Arctic islands and whether this followed a Eurasian (Gravlund et al., 1998; Kvie et al., 2016) or North American (Banfield 1961; Flagstad and Røed, 2003) route. As such, it appears that many of the morphological and behavioural differences

observed in the modern *R. tarandus* subspecies are adaptive traits that evolved with changing postglacial environments (Flagstad and Røed, 2003). This also explains why the tundra subspecies *R. t. tarandus* can be separated into both a mountain and forest form, despite both originating from the same Euro-Beringian refugial population (Flagstad and Røed, 2003). Nevertheless, interbreeding also means that there is a continual mixing of genetics not only between the subspecies (Nieminen and Helle, 1980, Flagstad and Røed, 2003; Puputti and Niskanen, 2008), but also between the wild and semi-domesticated herds which often co-exist within their respective ranges in Fennoscandia, Russia, Alaska and Canada (Anderson *et al.*, 2017).

2.2. Adaptations to Arctic and Subarctic Environments

Today, modern *R. tarandus* occupy Arctic tundra, Subarctic taiga and mountainous regions between 50-81°N (Gunn, 2016). Therefore, in addition to the characteristics of each ecological group, *R. tarandus* have evolved a series of morphological, physiological and behavioural adaptations to be able to tolerate temperatures between -45°C and +15°C (Nilssen *et al.*, 1984; Sommer *et al.*, 2011) and snow cover for more than 40% of year (Nieminen, 1990).

The primary form of insulation for *R. tarandus* comes from a thick pelage consisting of short, hollow guard hairs which trap air close to the body (Banfield, 1961; Klein, 1992). Contrary to appearances, this is a particularly flexible form of insulation as piloerective control enables R. tarandus to exercise thermoregulation through the raising and lowering of guard hairs (Klein, 1992). In the winter, a fine and woolly insulating underfur also grows, while the brown summer coat is replaced by white tipped guard hairs consistent with the increasingly snow-covered environment, until they eventually break off during the spring (Banfield, 1961). Although the short ears and tail are constantly covered in fur to reduce heat loss, tufts of fur only cover the foot pads during the winter (Banfield, 1961). With their pads well insulated, *R. tarandus* instead use the sharp edges of their crescent-shaped hooves to provide grip on snow and ice (Nieminen, 1990). Broad hooves and prominent dew claws also help to increase foot surface area (Telfer and Kelsall, 1984; Nieminen, 1990; Klein, 1992). As well as dissipating weight so that R. tarandus can walk on the top of snow and not sink in (Nieminen, 1990), the larger size of forelimb hooves (Nieminen, 1990) enables *R. tarandus* to dig craters through the snow in search of food (Klein et al., 1987).

A large and squarish nose is also well furred and provides an important role in heat conservation through valvular nostrils. When the ambient air temperature is low, the process of nasal heat exchange reduces the temperature of exhaled air below that of the body temperature (Blix and Johnsen, 1984; Langman, 1985). By maintaining a temperature gradient along the nasal mucosa (Johnsen *et al.*, 1985), 75% of the heat and 80% of the water added during inspiration to increase the temperature of air entering the lungs, can be recovered on exhalation (Langman, 1985). Although the resting metabolic rate of *R. tarandus* is low (Blix *et al.*, 2016) and does not increase greatly until temperatures exceed 15°C (Nilssen *et al.*, 1984), nasal heat exchange greatly reduces the metabolic costs of heat conservation (Langman, 1985). As such, shivering, which is a mechanism for increasing the metabolic rate of individuals at a low critical temperature (Blix *et al.*, 2016), is a secondary response in *R. tarandus* only used in the severe cold (Soppela *et al.*, 1986). Similarly, oxygen binding in *R. tarandus* haemoglobin is not adversely affected by cold temperatures (Giardina *et al.*, 1989).

Equally important for the cold-adapted *R. tarandus* is the ability to prevent overheating during periods of high physical activity or when ambient air temperature increases towards 15°C. For this purpose, nasal heat exchange can also be used to dissipate heat by reducing the temperature gradient along the nasal mucosa (Johnsen *et al.*, 1985). As air is inhaled through the nose, even during open mouth panting, the cooled blood from the nasal mucosa continues to pass through the cavernous sinus and selectively cool both the body and brain (Johnsen *et al.*, 1987). However, panting and sweating can still be energetically costly responses to overheating (Williamsen *et al.*, 2019). Therefore, where possible, behavioural strategies for thermoregulation may be the first response (Williamsen *et al.*, 2019). This has been observed on the treeless, and therefore shadeless, tundra environment, where *R. tarandus* actively select bed sites on cooler substrates such as snow or the wet, mossy mires which overlay permafrost, when summer temperatures are >9°C (Williamsen *et al.*, 2019).

Perhaps the most unique characteristic of Arctic environments that *R. tarandus* must also contend with is strong seasonality. The extreme shift between the continuous darkness of the polar night in winter and the continuous daylight of the midnight sun in summer, has weakened the circadian rhythms of *R. tarandus* so that the frequency of daily cycles fluctuates with changes in forage availability and appetite throughout the year (van Oort *et al.*, 2005; van Oort *et al.*, 2007; Lu *et al.*, 2010; Stokkan *et al.*, 2007). While this could represent a lower photic response in *R. tarandus* (van Oort *et al.*, 2007), the visual range of this species has also adapted to cope with extended periods of darkness. Seasonal changes in the tapetum lucidum, the reflective surface behind the central retina, increase the sensitivity of *R. tarandus* to the reduced winter light levels (Stokkan *et al.*, 2013). While reflectance in the summer is golden and not unlike that of other ungulates, in the winter, the tapetum lucidum shifts towards a blue reflection wavelength which is more consistent with the ultraviolet-rich winter light associated with

Rayleigh scatter (Stokkan *et al.*, 2013). This switch greatly improves the ability of *R. tarandus* to see in dim light, but at the cost of visual acuity, a trade-off which is evidently necessary for *R. tarandus* to be able to maximise foraging and avoid predators during the Arctic winter (Stokkan *et al.*, 2013). The strong seasonality of the Arctic has also resulted in a shorter growing season, which *R. tarandus* have adapted to by selective foraging. By prioritising plants which can be rapidly digested in their relatively small rumen (Klein, 1992), *R. tarandus* may devote between 40-60% of the day to foraging to ensure that nutritional needs are met (Roby, 1978; Reimers, 1980).

2.3. Diet

The diets of modern *R. tarandus* display variability between populations (Figure 2.1), both in terms of the availability of forage and the capability to digest specific plant species (Heggberget et al., 2002). Appetites are often lowered in the winter, when the short days and snow and ice layers reduce the accessibility and productivity of forage (Heggberget et al., 2002). As such, the winter diet of R. tarandus is typically dominated by lichen, which due to its high carbohydrate and low protein content provides a large source of energy that is otherwise not exploited by other northern ungulates (Leader-Williams, 1988; Heggberget et al., 2002). In light of this, calves that have not yet been weaned will begin foraging only days after birth, with individuals selecting plants based on trial and error, thereby developing an important digestive capacity for lichens (Bergerud, 1972; Holand et al., 2012). It has been reported that lichen could account for 80% of the winter diet in *R. tarandus* (Gaare, 1997; Heggberget et al., 2002), although observed levels of lichen consumption are usually closer to 50-60% in both the tundra R. t. tarandus and the woodland R. t. caribou (Figure 2.1) (Bergerud, 1972; Gaare and Skogland, 1975; Skogland, 1984; Schaefer et al., 2016). In winter, there may be an increase in the selection of arboreal rather than terrestrial lichen which is exposed above the snow (Bergerud, 1972). However, in high Arctic islands, lichen is much less abundant than in either continental tundra or woodland environments. In Svalbard, overgrazing and trampling of terrestrial lichens has resulted in R. t. platyrhynchus having to substitute their preferred winter lichens for mosses and graminoids (dead grasses) (Reimers, 1982; Staaland et al., 1983; Skogland, 1986; Heggberget et al., 2002), thereby changing their reliance on this one food type (Figure 2.1). As summer approaches and the snowline recedes, appetite increases to take advantage of the digestible new growth forage which is high in protein and therefore important for regaining body condition in preparation for the following winter (Bergerud, 1972; Mathiesen et al., 2000). This ushers in a much more diverse diet of deciduous shrubs (willow), graminoids (grasses and sedges), forbs and lichen (Leader-Williams, 1988; Heggberget et al., 2002) in both the tundra and

woodland subspecies, although *R. t. caribou* does appear to better maintain this level of diversity throughout the year (**Figure 2.1**). Nevertheless, in order to sustain selective foraging in both the summer and winter, *R. tarandus* must move greater distances on both a daily and seasonal basis, mobility which takes the form of migrations (Klein, 1992).





(c) High Arctic Island R. t. platyrhynchus



Figure 2.1. Diet Composition of *Rangifer tarandus* Subspecies. Diet composition was determined from the rumen content of (a) tundra *R. t. tarandus* from Norway (Gaare and Skogland, 1975), (b) woodland *R. t. caribou* from Canada (Bergerud, 1972) and (c) high arctic island *R. t. platyrhynchus* from Svalbard (Staaland *et al.*, 1983).

2.4. Bi-annual Migrations

R. tarandus represent the last northern hemisphere ungulate to undertake large-scale migrations (Vors and Boyce, 2009). Although several factors influence the movement of R. tarandus, migrations mainly occur in response to the reduced forage quality and access during winter, necessitating the movement between pastures (Tablado et al., 2014). However, just as indigenous people will herd R. tarandus on ranges which are either small and localised or large and nomadic (Klokov, 2007), wild R. tarandus occupy both migratory and sedentary niches. Contrary to what the name suggests, sedentary herds still demonstrate some degree of nomadism or seasonal movement within their home ranges, in order to avoid resource depletion (Tyler and Øritsland, 1989). While the high Arctic R. t. platyrhynchus on the island of Svalbard are limited in this way to home ranges of only a few km² (Tyler and Øritsland, 1989), forest R. t. tarandus in Finland utilise both the woodland and surrounding tundra environments (Vors and Boyce, 2009) in annual home ranges 90-200 km² (Helle, 1981). Nevertheless, compared to migratory tundra R. tarandus, this still represents a relatively small amount of movement. In Norway, mountain R. t. tarandus occupy ranges of 8,000 km² on the Hardangervidda plateau (Skogland, 1989; Skogland, 1990), while in Canada, the Qamanirjuag barrenground R. t. groenlandicus move within a range of 310,000 km² (Mallory et al., 2020).

Migrations in tundra *R. tarandus* are bi-annual, as herds move in the autumn towards tundra-taiga winter pastures, before returning to spring and summer grounds on the open tundra (Skogland, 1980; Tablado et al., 2014). As such, the autumn rut, winter grazing, spring calving and summer grazing periods, are reflected by the occupation of different sites throughout the year. However, large aggregations of R. tarandus form only temporarily during the rut in October and calving from late May to early June (Gordon, 1990), when *R. tarandus* demonstrate strong reproductive synchrony within populations (Paoli et al., 2018). It is therefore during the autumn and spring migrations, when large numbers of animals are present together in one area, that *R. tarandus* are most at risk from anthropogenic hunting (Burch, 1972). Otherwise, herds regularly disperse into the living herd structure (Kelsall, 1968; Skoog, 1968). In a stable population, mortality will naturally fluctuate throughout the year through predation and seasonal pressures (Discamps and Costamagno, 2015), but the living structure of a herd can still be described through observations following annual calving (Steele, 2005). Ungulates tend to separate into mothers and calves, adult males and females, and solitary males (Main et al., 1996). Calves generally represent a 1:1 ratio of males to females and remain by their mother's side for their first year (Leader-Williams, 1988; Holand et al., 2012). Individuals are considered to be subadults until reaching reproductive age between 3-11 years (Thomas and Barry, 1990; Jorgensen et al., 2015). At this point, there is a shift in

the ratio of adults >2.5 years to 1:2 or 1:3 males to females; this continues into adulthood following the pressures of breeding and violence exhibited between males (Miller, 1974b; Bergerud, 1980; Skogland, 1985; Leader-Williams, 1988). Once past reproductive age, tooth wear in reindeer becomes so great that it impacts upon feeding efficiency and body condition declines significantly (Skogland, 1986). In the wild, only 2-3% of reindeer survive beyond the ages of 10-12 years (Thomas and Barry, 1990). Nevertheless. when seasonal aggregations do form, clear levels of sexual and demographic segregation are expressed within the herd (Figure 2.2).



Figure 2.2. Seasonal Aggregations of Rangifer tarandus.

The breeding season, known as the rut, occurs over a 3-4 week period in the autumn generally in the same annual location (Body et al., 2014). As a polygynous ungulate, the aggregations formed during the rut are characterised by fewer males and multiple female and calf pairs (L'Italien et al., 2012), as dominant males form harems (Holand, 2006). This is reflected in a ratio of 1:2 or 1:3 males to females for a living population on entering the rut (Weinstock, 2000a). Females move between groups to choose breeding partners (Hirotani, 1989), usually settling with males of a similar social status (Hirotani, 1989). When not part of a harem, solitary females will form small groups in order to reduce male harassment (Body et al., 2015), a significant control on female body mass during the rut especially when both a dominant male and younger males are present within a harem (Holand, 2006). The rut is also a period of high energy exertion for the males, which lose

0.3% of their pre-rut body mass for each female included in the harem (Tennenhouse *et al.*, 2011). In addition to prioritising chasing and fighting challenging males in violent displays, whilst continuing to herd females into harems, adult males have been shown to neglect feeding during this time (Holand, 2006). To mitigate the large losses in body mass, males will stop herding when a harem exceeds 22 females (Weladji *et al.*, 2017). Nevertheless, the significant depletion of male body reserves during the rut (**Figure 2.3**), as much as 34% in 77 days (Barboza *et al.*, 2004), may inevitably culminate in starvation during the early winter (Weinstock, 2000b). The younger subadult males with their lower social status will sustain negligible losses, as more time is invested in feeding than herding or challenging and therefore survival is greater (Holand *et al.*, 2012). In some large herds, the rut is considerably less organised, as males will court females during the autumn migration rather than forming distinct harems (Lent, 1965; Bergerud, 1973). However, by early winter, the large rut aggregations have disbanded into smaller groups.



Figure 2.3. Annual Variation in *Rangifer tarandus* Body Reserves. The carry-over effects from each season determine an individual's ability to survive depending on the balance of energy intake, output and storage, and recovery facilitated by the foraging opportunities and risks associated with the current season (Fauchald *et al.*, 2004; Albon *et al.*, 2016). Fat content by weight is presented for adult males (black), subadult males (grey) and females (dashed). (Source: Weinstock, 2000b; after Spiess, 1979).

As resource quality decreases throughout winter, individuals must balance the importance of energy intake with risk when selecting seasonal ranges (Bergerud and Luttich, 2003; Nieminen *et al.*, 2013; Tablado *et al.*, 2014). Although the forage at lower latitude winter grazing pastures is less restricted by snow and ice cover, the risk of predation from wolverine (*Gulo gulo*, Linnaeus, 1758), lynx (*Lynx lynx*, Linnaeus., 1758), brown bear (*Ursus arctos*, Linnaeus, 1758), wolf (*Canis lupus*, Linnaeus, 1758), red fox (*Vulpes vulpes*, Linnaeus, 1758) and golden eagle (*Aquila chrysaetos*, Linnaeus, 1758) is frequently increased (Nieminen *et al*, 2013; Tablado *et al.*, 2014). The location of winter pastures will thus vary slightly each year so that ranges are less predictable to predators like *C. lupus*, which activity hunt reindeer returning to the same locations (Schaefer *et*

al., 2000; Francis, 2016; Lafontaine *et al.*, 2017). However, forage availability remains the primary driver in range selection (Avgar *et al.*, 2015), with the tolerance for the winter tundra environments decreasing as resources are depleted (Tablado *et al.*, 2014). Throughout winter, mother and calf losses are highly dependent on maternal social status within the herd, as both will still share feeding craters throughout this first year (Kojola, 1989). Craters are dug in order to reach vegetation locked under snow and ice however, this is energetically expensive and females can lose around 32% of both fat and muscle during the winter gestation months (Adamczewski *et al.*, 1987). Females are therefore most at risk of pregnancy termination and starvation during the winter (**Figure 2.3**) (Fauchald *et al.*, 2004; Albon *et al.*, 2016).

When the winter snow cover begins to reduce and conditions ameliorate, average daily movements increase from 4.17 km to 11.98 km (Nagy, 2011) as pregnant females lead the spring migration towards calving grounds by following the new growth of vegetation along the snowline (Fauchald et al., 2004). Males, non-pregnant females and yearlings typically lag behind this movement, the yearlings having begun to develop antagonistic relations with their mothers (Hirotoni, 1990). Calving forms a particularly sexually segregated aggregation which occurs over a 4-5 week period from May to June (Lent, 1966; Dauphiné and McClure, 1974; Bergerud, 1975; Leader-Williams, 1988; Aaris-Sørensen et al., 2007). However, within an individual herd, 80-90% of calves will be born in just 10 days (Lent, 1966; Dauphiné and McClure, 1974; Bergerud, 1975paoli). The temporary formation of a large aggregation during this important and highly synchronised life cycle event therefore reduces the predation risk for each animal (Klein, 1992), by confusing predators with the mass of individuals and providing R. tarandus with the benefit of a collective awareness (Kie, 1999). It is the first and last breeding seasons that are of highest risk to females, whereby mortality increases at 2-4 years and 11-13 years (Jorgensen et al., 2015; Weinstock, 2000a). Soon after the spring calving, males and subadults re-join the herd in late June and early July to form the largest aggregation of the year, before individuals once again disperse at a rate of 14.65 km/day for the summer grazing (Burch, 1972; Nagy, 2011). When females are calving or lactating, R. tarandus demonstrate high levels of site fidelity to ensure familiarity with resources and minimise risk (Schaefer et al., 2000; Body et al., 2014; Lafontaine et al., 2017), a result of their good long-term spatial memory (Avgar et al., 2015). Calving sites in particular are used over many generations (Schaefer et al., 2000). R. tarandus therefore return to the high, open topography of their tundra ranges where the risk of predation is lower (Bergerud and Luttich, 2003). On these windy ridges, the presence of insects including mosquitoes (Aedes sp.), skin warble flies (Hyoderma tarandi) and nasal bot flies (Cephenemyia trompe) is also reduced, allowing *R. tarandus* to feed with significantly less harassment from these parasites (Mörschel and Klein, 1997; Weladji et al., 2003; Tablado et al.,

2014). This is important as the higher nutrient content of summer grazing forage supports the recovery of females from the pressures of reproduction (Heggberget *et al*, 2002) and facilitates the growth of calves (Adamczewski *et al*, 1987), so that both may avoid winter starvation (Fauchald *et al.*, 2004). Both of these are vital for ensuring body reserves rise above those required to survive an average winter (Fauchald *et al.*, 2004).

During migrations *R. tarandus* move in a variety of gaits (**Table 2.2**), but will tend to pace in single file over long distances (Kelsall, 1968; Skoog, 1968; Burch, 1972), at an average of 25-30 km/day (Kelsall, 1968; Skoog, 1968). This is not the fastest gait (**Table 2.2**), but trotting is reserved for the negotiation of more uneven terrain such as mires, tussocky meadows and steep mountain slopes, while galloping is only employed in short bursts in the evasion of predators (Burch 1972; Klein, 1992). Therefore, by selecting areas of lower topographic resistance (Burch, 1972), the only major obstacles for *R. tarandus* are deep snow and rivers with unstable or floating ice (Lent, 1966; Skoog, 1968). Otherwise, not only are *R. tarandus* well adapted for traversing snow, but their large feet and buoyant guard hairs make them competent swimmers (**Table 2.2**) (Klein, 1992).

| Movement | Speed (km/hr) | Reference |
|-------------|---------------|---|
| Walk | 7 | Pruitt (1960) |
| Pace | 10 | Skoog (1968) |
| Trot | 40 | Skoog (1968) |
| Gallop | 70-80 | Banfield (1951), Makridin (1962), Skoog (1968) |
| Swim | | Kelsall (1968) |
| undisturbed | 6.5 | |
| chased | 11 | |

 Table 2.2. Rangifer tarandus Speeds of Movement.

2.5. Current and Future Status

The IUCN Red List of Threatened Species has changed the status of reindeer from 'Least Concern' to 'Vulnerable', after a 40% population decline over the last 30 years (Gunn, 2016) affected 34 out of 43 of the World's major herds (Vors and Boyce, 2009). Climatic changes in the form of rising Arctic temperatures and precipitation are clearly important factors in *R. tarandus* population declines (Albon *et al.*, 2016), since the increase in the formation of ice-crusts has been linked to reductions in body mass, starvation and range shifts towards ice-free areas (Hansen *et al.*, 2010; Albon *et al.*, 2016).

Body mass can provide an important insight into the condition of *R. tarandus*, which appears to have been decreasing in modern animals over recent years. In a study of

females from Svalbard conducted between 1994-2015, Albon et al. (2016) observed a 12% reduction in body masses from 55 kg to 48 kg. Below the threshold of 50kg, females are more likely to produce smaller calves or even terminate pregnancies during the winter, placing pressure on the population (Albon et al., 2016). As a density-dependent species, *R. tarandus* are highly susceptible to the pressures of larger population sizes. The increased competition during either the winter or summer grazing periods reduces food availability and subsequently negatively influences the size of individuals, particularly calves (Tallian et al., 2012; Albon et al., 2016). Typically, this is a process that occurs when the population exceeds half the ecological carrying capacity (Skogland, 1985). However, in recent years, the density-dependence effect appears to be becoming less pronounced in the autumn body masses of Svalbard R. tarandus, but are visible in the spring body masses (Albon et al., 2016). This change has coincided with climatic warming of up to 5°C in the Arctic over the last century (Anisimov et al., 2007). Under climatic warming, the carrying capacity for *R. tarandus* should increase as summer plant productivity is higher and healthier, well grazed individuals enter autumn with greater fecundity and survival potential (Parker et al., 2009; Albon et al., 2016). However, the combined effect of warmer winter temperatures and increased precipitation has resulted in icing events (Albon et al., 2016). This describes the development of an impenetrable ice layer, which restricts access to winter forage through the refreezing of rain within the snow-pack due to above freezing air temperatures (Vors and Boyce, 2009). Starvation as a result of ice-locked pastures affects multiple generations in a single winter independent of density (Vors and Boyce, 2009), although whether this destabilises the population entirely depends on the frequency of such events (Hansen et al., 2019a). Given the importance of rainfall, the effect of climatic change on continental populations may not be so extreme, particularly considering their increased potential to migrate compared to their insular counterparts (Vors and Boyce, 2009). Nevertheless, the lower genetic diversity in the isolated high Arctic islands such as Svalbard, suggest that these populations are highly susceptible to future climatic changes (Yannic et al., 2014).

Warmer Arctic temperatures and the observed increase in the productivity of vegetation, as well as the length of the growing season in spring, have also affected the timings of *R. tarandus* movements (Rickbeil *et al.*, 2018; Paoli *et al.*, 2018). As snow begins to melt earlier, the spring migration in Canadian *R. tarandus* has advanced by 13.65 days, although herds are only arriving at calving sites on average 6.02 days earlier (Mallory *et al.*, 2020). This loss of days is primarily due to the poorer ice conditions *R. tarandus* experience when snow melt, and therefore movements, begin earlier (Mallory *et al.*, 2020). However, this advance in the calving date is similar to changes recorded in Finland between 1970-2016, where calving is now 7 days earlier (Paoli *et al.*, 2018). Despite the level of resilience demonstrated by *R. tarandus*, as ranges become

increasingly fragmented, it is predicted that within the next 70 years North American R. tarandus will lose 89% of their current ranges, while Eurasian R. tarandus will have lost 60% (Yannic et al., 2014). Nevertheless, distinguishing the causal effects of climatic changes from those of increasing anthropogenic disturbances can be difficult. It is anticipated that by 2050, anthropogenic activity will influence 50-80% of the Arctic, compared to the 15-20% that is affected today (Attonen et al., 2011). The expansion of roads and railways for forestry and mining enterprises, as well as recreational activities, has been linked to forage depletion and range shifts in R. tarandus (Nellemann et al., 2000; Dahle et al., 2008; Newton et al., 2015; Sandström et al., 2016; St. John et al., 2016; Lafontaine et al., 2017). Each form of infrastructure creates a different zone of influence, with R. tarandus avoiding areas within 5 km of wind turbines (Skarin et al., 2015; Skarin et al., 2018), 11-14 km of open-pit mines (Boulanger et al., 2012) and 5-10 km of tourist resorts and cabins (Nellemann et al., 2000; Dahle et al., 2008). As such, this means that the connectivity between grazing pastures is reduced (Skarin et al., 2015; Skarin et al., 2018) and may ultimately result in a shift in migrational behaviour. Although *R. tarandus* will track roads in order to find relatively undisturbed areas in which to cross, the continued development of highways and railways is already severely limiting the scale of migrations (Jordhøy, 2008; Indrelid and Hufthammer, 2011; Panzacchi et al., 2013). For example, pre-industrial development, Norwegian R. tarandus were divided into two or three populations that undertook large-scale migrations; however, these are now fragmented into 24 separate herds (Panzacchi et al., 2013). In the future, perhaps the best approach to managing both the expansion of infrastructure and *R. tarandus* will be a combination of technology-based monitoring with the exchange of knowledge between researchers, indigenous people and governments (Herrmann et al., 2014).

2.6. Summary

- Seven subspecies of *R. tarandus* exist across the Arctic and Subarctic, for which a number of morphological, physiological and behavioural adaptations enable their survival in these harsh conditions.
- One of the most unique behavioural adaptations of *R. tarandus* is the large-scale migrations still undertaken by a number of herds and driven by the strong seasonality of forage quantity and quality in the Arctic, as well as the avoidance of harassment from predators and insects.
- As part of this bi-annual cycle, regular dispersals and concentrations of individuals within herds mean that the aggregations that form throughout the year during the rut, calving and summer and winter grazing express differing and recognisable levels of sexual segregation and social organisation.

• Recent declines in population sizes and body masses of modern *R. tarandus* highlight the susceptibility of herds to both the expansion of anthropogenic presence in the Arctic, in the form of industrial infrastructure and recreational activity, and warmer and wetter winter climates.

Chapter 3. Methods

The following chapter primarily outlines the methodology for determining the seasonality of site occupations from the dental, antler and postcranial remains of *Rangifer tarandus* fossil assemblages. These can be divided into techniques that reconstruct age at death and season of death. Also included is the method for estimating average body mass from *R. tarandus* postcrania, which allows the body masses of modern and historical specimens to be compared with those from the Late Pleistocene. Methods concerning reconstructions of palaeodiet, using dental microwear analysis, and mobility, from strontium isotope analysis, are addressed in Chapters 7 and 8 respectively.

3.1. Reconstructing Age at Death

Age at death records the age structure present in an assemblage, which can then be compared to the different demographies represented during seasonal aggregations. Although both the antlers and postcrania can give an indication of age in individual animals, it is only the analysis of dentition that generates ages precise enough to provide accurate reconstructions of seasonality from a fossil site.

3.1.1. Dentition

In *R. tarandus*, age at death can be determined from the (often well preserved) mandibles and isolated teeth of fossil assemblages using two well established methods, either by counting the incremental lines in tooth cementum (Spiess, 1979; Niven *et al.*, 2012; Takken Beijersbergen, 2017a) or using the known timing of permanent tooth eruption and attritional wear (Spiess, 1979; Murray, 1994; Enloe, 1997; Niven *et al.*, 2012; Daujeard *et al.*, 2019; Fontana, 2017; Takken Beijersbergen, 2017a).

For many years, using tooth cementum was thought to be the more precise technique for determining the age of an animal based on its dentition. Initially used as an ageing tool in the Pinnipedia (Scheffer, 1950), the technique was developed for *R. tarandus* in the 1960s by McEwan (1963) in Canada, followed by Reimers and Nordby (1968) in Norway. Both Stutz (2002) and Foster (2012) provide an overview of the different approaches used by studies to prepare and analyse annulations. Acellular cementum is a mineralised deposit which is laid down below the gum line on the exterior of the tooth

root (Spiess, 1979). This process occurs throughout the life of an individual with seasonal regularity. Thick and translucent growth zones form during the summer and are separable from the narrow and dark winter rest lines, which are known as annuli (McEwan, 1963; Reimers and Nordby, 1968). Although the precise methods of cementum deposition are not well understood (Takken Beijersbergen, 2017a), age can be reliably established by directly counting the annulations of a tooth (Miller, 1974a), although this is necessarily a destructive method. Furthermore, using the degree of formation of the outermost increment of cementum, it is also possible to determine the season of death by comparing the thickness of growth and rest layers from previous years, to the progress of the microstructure at the time of death (Spiess, 1976). Although there appears to be good synchronisation between North American and European *R. tarandus* populations (Takken Beijersbergen, 2017a), a modern control population should first be assessed in order to establish when the rest line develops in specimens from comparable environments (Pike-Tay, 1995; Takken Beijersbergen, 2017a). This chronology can then be applied to the fossil assemblage.

For *R. tarandus*, analysis of dental cementum has mainly concentrated on the first incisor. The longer cervical section of the root of this tooth means that it is significantly easier to locate the first annulus from which to begin counting (Miller, 1974a; Takken Beijersbergen, 2017a). However, this approach is problematic when considering fossil assemblages in which incisors are rarely preserved (Pike-Tay, 1995; Pasda, 2009a). Unfortunately, work on the more abundant molariform fossil remains has shown that incremental lines are harder to identify in these teeth (Reimers and Nordby, 1968; Leader-Williams, 1979; Pike-Tay, 1995; Pasda, 2009a; Takken Beijersbergen, 2017a). Rest lines may be irregular or too close together to discern age, while the variability between layer thickness in individual animals has made the transition between the start of the translucent growth zone and the end of the rest line, and therefore the season of death, less distinct (Pasda, 2009a). A more accurate approach to ageing dentition is therefore required in order to reconstruct season of death consistently.

By combining the known eruption of permanent dentition with patterns of attritional wear, age at death can be determined without the use of destructive thin sectioning. Particularly when individuals are within the first two years of life, this non-invasive approach can achieve monthly precision when applied to reindeer mandibular molars and premolars, which are well studied and abundantly preserved in the fossil record (Spiess, 1979). As such, in addition to determining age structure, the high resolution of juvenile tooth ages can be used to directly infer season of death. Criticism for this technique focuses on the assumption that tooth eruption and wear must be homogeneous both within, and between, populations (Hillson, 2005; Fontana, 2017; Takken Beijersbergen, 2017a;

Gifford-Gonzalez, 2018). However, ground-truthing completed during the development of methods for this research, using modern specimens for which age at death was known, has demonstrated that this did not have any bearing on interpretations of the season of death.

Few studies have directly applied both techniques for ageing dentition to a single fossil assemblage. Where this has been attempted (Niven *et al.*, 2012; Takken Beijersbergen, 2017a, 2017b), the inferred seasonality derived from the timing of tooth eruption and wear is comparable to the precision of destructively counting incremental tooth cementum and is therefore a much more desirable technique to apply to already fragmented fossil collections.

3.1.1.1. Timing of Permanent Tooth Eruption

The permanent dentition of *R. tarandus* follow the form:

$$I\frac{0}{3}C\frac{1}{1}P\frac{3}{3}M\frac{3}{3}$$

R. tarandus possess low crowned teeth with prominent roots and a relatively narrow and long premolar tooth row (Hillson, 2005). At birth, R. tarandus deciduous teeth are either already present in the mouth (incisors and canines) or are in the process of erupting (premolars) (Miller, 1972). With the exception of the deciduous lower fourth premolar (dp₄) which displays an additional pair of cusps, these are essentially smaller, more delicate versions of the permanent dentition (Miller, 1972). Molars are the only teeth that do not have a deciduous form. Because maxillary cheek teeth have not been studied in as much detail as those of the mandibles, it is unknown whether they lead or lag established patterns of eruption and wear observed in the lower dentition (Spiess, 1979). Therefore, in addition to the exclusion of the poorly preserved incisors and canines, only mandibular molars and premolars were considered in this research. In general, there is good agreement in the timing of permanent tooth eruption across modern R. tarandus populations from Canada (Bergerud, 1970; Miller, 1972), Alaska (Skoog, 1968), Lapland and the USSR (Bromée-Skuncke, 1952). This coherence in the modern signal therefore gives support to the cross-comparison of Late Pleistocene R. tarandus remains across the Palaearctic.

Established ages were primarily taken from Miller's (1972) study of the Canadian Kaminuriak population whereby the initiation, 50% and 100% stages of tooth eruption were described (**Table 3.1**), recording the continuous nature of this process (Hillson, 2005) with monthly precision. These ages were comparable to Bromée-Skuncke's (1952) work in Lapland and the USSR, which are geographically closer to the selected

fossil sites in this study and would thus be assumed to represent similar populations. The most notable difference between the North American and European populations was the variability in the timing of the eruption of the third molar and all three of the premolars (**Table 3.1**). This has been the principal criticism for the application of eruption ages to fossil dentition, with some studies opting to use only the more precise first and second molars in order to determine age at death (Fontana, 2017). At the earliest, Skoog (1968) observed that both the premolars and the M_3 could be fully erupted in Alaskan individuals as young as 22 months. Similarly, in Banfield's (1954) study of tooth eruption in Canada, the permanent dentition of *R. tarandus* were fully erupted by 18 months, almost a year earlier than at other localities (Miller, 1972). For the premolars in particular, it is not unusual for the loss of the deciduous teeth to be somewhat delayed. In seven out of eight of the Canadian individuals studied by McEwan (1963), the deciduous premolars were still present at 23-24 months, despite the fact that eruption typically commences at 21 months. However, most studies of modern R. tarandus consistently support the later eruption of the premolars and third molar between 28-30 months (Bromée-Skuncke, 1952; Skoog, 1968; Bergerud, 1970; Miller, 1972). As such, an eruption age of 29 months was applied in this research, which assuming that the four teeth erupt simultaneously (Bromée-Skuncke, 1952), was closer to the timings from European R. tarandus (Table 3.1).

| | Canada | | | Lapland | USSR | |
|-----------------------|---------------|-----|------|----------------|------|--|
| | Miller (1972) | | | Bromée-Skuncke | | |
| Dentition | | | | | 52) | |
| | Begins | 50% | 100% | 100% | 100% | |
| P ₂ | 21 | 25 | 28 | 30 | 29 | |
| P ₃ | 21 | 25 | 28 | 30 | 29 | |
| P ₄ | 21 | 25 | 28 | 28 | 29 | |
| M ₁ | 3 | 4 | 5 | 4 | 3-5 | |
| M ₂ | 10 | 13 | 15 | 15 | 15 | |
| M ₃ | 15 | 26 | 28 | 28 | 29 | |
| Complete | | | 29 | 30 | 29 | |

Table 3.1. Ages for the Eruption of *Rangifer tarandus* Permanent Dentition. Bold values highlight the eruption ages (months) applied to *R. tarandus* specimens due to the good consistency between geographical areas. (Source: after Miller, 1972, p.611).

For each age class present at a fossil site, the minimum number of individuals (MNI) was identified. An erupting tooth was defined as one that has one or more cusps protruding above the alveolar bone, while a tooth was considered fully erupted once correctly orientated (Miller, 1972). However, measuring tooth eruption alone is limited to the point at which permanent teeth are fully erupted in mandibles (Morrison, 1997). The definable

age range of individuals in a fossil assemblage can therefore be extended by quantifying the stage of attritional tooth wear in erupting teeth.

3.1.1.2. Attritional Tooth Wear Progression

Worn dentine and enamel form distinct patterns, as continuous wear occurs from the anterior to the posterior of the tooth and cusp (Spiess, 1979). Such a progression, from an initial enamel covering to a point where only enamel borders surround the dominant darker dentine, can be used to age teeth (Grant, 1982).

In previous work on domestic animals, tooth wear profiles have been developed so that a numerical value represents the total wear across the entire mandible, combining wear stages in the M₁, M₂ and M₃ (Payne, 1973; Grant, 1982). Bouchard (1966) was the first to use patterns of tooth wear in *R. tarandus* in this way for French Palaeolithic sites, developing eleven categories of wear which covered a period from 3 weeks to 48 months in an animal's life. However, the categories were based largely on Banfield's (1954) timings for tooth eruption, which are not only inconsistent with most other modern populations (Miller, 1972), but do not account for the variability in wear which occurs independent of eruption throughout the year (Spiess, 1979). Instead, studies of fossil R. tarandus have relied on descriptions of tooth wear made by Miller (1974b) from the Canadian Kaminuriak population (Murray, 1994; Enloe, 1997; Niven et al., 2012; Daujeard et al., 2019; Fontana, 2017). Given the taphonomic context of many fossil R. tarandus assemblages, these descriptions have primarily been used to establish hominin hunting strategies, assigning teeth with broad age classes in order to determine the demography of an assemblage (Spiess, 1979; Murray, 1994; Enloe, 1997; Niven et al., 2012; Daujeard et al., 2019; Fontana, 2017; Takken Beijersbergen, 2017b). Following this approach, the stage of wear on an erupted tooth or mandible is categorised as either unworn (no dentine exposed), slightly worn (dentine exposed), or showing heavy wear (no enamel left) and can be correlated to an age class which include calves, subadults, adults and old age individuals.

The Kaminuriak population is a unique collection from which patterns of dental development can be defined, with the potential for defining age at death with greater precision than broad age classes. Having been collected by the Canadian Wildlife Service between March 1966 and July 1968, the age and season of death is known for a total of 356 individuals (Miller, 1974b). A new mandibular wear profile for *R. tarandus* has accordingly been developed by this research, which replaces indicative age stages with actual chronological ages (**Figure 3.1**). This entailed a tooth wear profile, initially based on the descriptions made by Miller (1972; 1974b), being ground-truthed using

| | Мз | M2 | Mı | dp4/P4 | dp3/P3 | dp2/P2 |
|------------------|---------------------------------------|--------------------|----------------|-----------------------|---------------------------|---------------------------|
| | | | | | – Deciduous – | |
| 0-3 months | | | | | En | |
| 3 months | | | œ | | aria | |
| 4 months | | | | | | |
| 5-10 months | | | ĊŞ | 600 | R D | |
| 10-12 months | | | E P | | | |
| 15 months | | | | *15- | 18 200 ^{*15-1} | ⁸ *15-18 |
| 16-18 months | (PD) | | | | – Permanent – | |
| 21-24 months | | | Ca | 20 | 10 | GN |
| 27 months | | | Ca. | NA | | GR |
| 29 months | C C C C C C C C C C C C C C C C C C C | | CQ | C.A.S. | CAN . | GR |
| 3-5 years | | | 62 | 1a | * | M |
| 6-9 ∣ years ∧ | | | | Va | 20 | |
| >10 I years I | 68 | | | Ĩ | æ | R |
| Ι Λ Cusps | flat bucco-lingual | y and sharp antero | -posteriorly I | Cusps flat bucco-ling | gually and antero- | posteriorly |

Figure 3.1. Ages for Patterns of *Rangifer tarandus* Attritional Tooth Wear. The diagram shows dentition from the left mandible, for erupting (outlined in grey) and fully erupted (outlined in black) molars and premolars. The mesowear of cusps is sharp unless otherwise indicated.

known age individuals from Norway, Sweden and Greenland. In total, 291 teeth from 56 modern specimens were studied (**Appendix 1**). Observations from 165 teeth of 56 fossil specimens from Britain (Wiesendanger, 2015), Belgium, France and Switzerland further contributed to the development of the wear profile (**Appendix 1**), ensuring that the morphology of wear patterns was consistent between modern and Late Pleistocene *R. tarandus*.

The resulting wear profile has provided an efficient technique by which to determine age at death and season of death for both mandibles and isolated lower cheek teeth. Although age estimates from mandibles are considered the more reliable, as they incorporate the timing of tooth eruption and wear, the ageing of isolated teeth, which might otherwise be excluded from studies, can significantly increase the MNI of fragmentary fossil assemblages. In future applications of this technique, MNI should further be increased by including the deciduous premolars. Ground-truthing has enabled the wear on these teeth, the resolution of which was previously considered too low to define age at death due to the rapid wear in the first few months of life, to be constrained with monthly precision. Therefore, where these teeth are present in the fossil record, they could provide an important indicator for the summer occupation only recognisable from calf dentition.

The ability to assign season of death independent of eruption ages is a particularly important component of the wear profile. This has been limited somewhat by the availability of known age specimens, especially as the monitoring and culling of modern specimens often occurs during the autumn, however, each of the four seasons is represented in the profile created. For some stages of wear, it was necessary to implement an age range (**Figure 3.1**). Although these could cover a period of between two and five months, this did not restrict estimates of seasonality as each age range still represents either winter (5-10 months), spring (10-12 months and 21-24 months) or autumn (16-18 months).

As reindeer mature, the precision of the technique decreases from monthly to yearly, so that seasonality can only be inferred up until the age of 29 months. Nevertheless, the ability to distinguish broad age classes throughout the natural lifespan of reindeer remains important for studies of past subsistence strategies, where the recognition of subadult, adult and old individuals can provide information on the targeting of specific age classes by Palaeolithic hominins (Gaudzinski and Roebroeks, 2000; White *et al.*, 2016). In addition to patterns of dentine and enamel wear, adults aged 3-5 years, 6-9 years and >10 years are identified by the relief, or mesowear, of the tooth crown (Miller, 1974b), as the sharp, peaked cusps of newly erupted teeth become gradually shorter and flatter throughout the life of an individual (**Figure 3.1**). This progression is also

recognisable in the deciduous premolars and can therefore be applied to individuals 10-12 months and 15-18 months old (**Figure 3.1**).

Some studies have also used crown height to assign age at death by measuring the distance between the neck and the biting surface of the crown on the mesial cusp of a tooth (Murray, 1994; Enloe, 1997). Although the rapid wear of the dp₄ can be aged to the first or second year of life (Murray, 1994; Enloe, 1997), Pike-Tay (1993) has developed a more precise approach using known age *R. tarandus* to modify a guadratic regression first applied by Klein et al. (1983) to red deer (Cervus elaphus). Expanding the usable dentition to include the dp₃, dp₄ and all three permanent molars, the equation allows the average age of a mandible to be calculated in months (Pike-Tay, 1993). However, the mesowear of a tooth is more strongly correlated with diet (Rivals et al., 2007) and in particular the quality of winter forage available (Skogland, 1988), than it is to age. This was apparent from the ground-truthing of modern specimens completed during this research. In some adult individuals from both modern and fossil collections, the wear of the dentine and enamel corresponded to that of a 6-9 year old, while the sharp relief of the tooth itself was more consistent with a 3-5 year old. The actual age of the modern mandibles was within the 6-9 year age band, potentially reflecting the influence of diet on the mesowear of teeth, compared to the patterns of enamel and dentine wear which are much more representative of age. Therefore, although it is sufficient to use the relief of a tooth in conjunction with the tooth wear profile to age adults, exact measurements of crown height are an unreliable ageing technique.

3.2. Reconstructing Season of Death

In addition to the monthly precision afforded by ageing the eruption and wear of juvenile teeth, season of death is identified using the sexual dimorphism which exists between male and female *R. tarandus* postcrania, antlers and associated crania. The ratio of sexes and ages present within an assemblage is then compared to those of the different seasonal aggregations or, in some instances, can be used to directly infer season of death.

3.2.1. Antlers and Crania

Unlike other cervids, both male and female *R. tarandus* bear antlers throughout their lives. For males, antlers are a defensive weapon, improving reproductive success and dominance during the intrasexual competition of the rut (Pruitt, 1966; Bubenik, 1972). The unique presence of antlers in female *R. tarandus* also improves the social rank of

individuals within the herd, but as a more offensive weapon (Espmark, 1964; Bubenik, 1968; Henshaw, 1969; Kjos-Hanssen, 1973; Reimers, 1993; Holand *et al.*, 2004). In winter, when conditions are harsh and pregnant females still have last spring's calves at heel, carrying antlers means that females are significantly more effective at deterring antlerless *R. tarandus* away from valuable feeding craters (Espmark, 1964; Bubenik, 1968; Henshaw, 1969; Kjos-Hanssen, 1973; Reimers, 1993; Hirotani, 1990: Holand *et al.*, 2004). Competition for these craters could be either intrasexual or intersexual. Therefore, considering that both body mass and age have a far greater influence on female social rank than antler size (Holand *et al.*, 2004), the feeding advantage afforded by females growing and carrying antlers during the winter must far outweigh the costs associated with their annual growth (Baksi and Newbrey, 1989; Holand *et al.*, 2004; Loe *et al.*, 2019).

Within the first few days of life, permanent pedicles have formed on the frontal bone of *R. tarandus* calves and the first antlers begin to grow (Blake *et al.*, 1998). Growing antlers are composed of a soft and flexible cartilage (Kjos-Hanssen, 1973), covered with a skin of dark, furry velvet and a complex network of blood vessels and nerves (Lichti *et al.*, 2016). For healthy individuals, antler growth typically averages about 1 cm/day (Nikolaevskii, 1968), although recent 3D imaging completed by Lichti *et al.* (2016) suggest that over a seven-week period, the velocity was closer to 7-9 mm/day. As growth progresses from the distal tip, the proximal cartilage begins to ossify and stiffen (Kjos-Hanssen, 1973). Once ossified along the length of the antler, the now loose velvet is scraped off on the surrounding environment (Kjos-Hanssen, 1973). Between one and three weeks before casting, when an antler is shed ready for regrowth the next year, a shedding line appears at the antler base just above the burr (Fontana, 2017).

Although there is some uncertainty over the cause of pedicle initiation, this is potentially a function of mass, as it appears to occur independent of the overall antler cycle which is controlled by steroid hormones (Lincoln and Tyler, 1992; 1994; Bubenik *et al.*, 1997; Blake *et al.*, 1998). Testosterone in males, and estradiol in females, act to regulate the annual growing and shedding of antlers, reaching their peak during periods of ossification, before minimum steroid levels trigger the annual casting (Lincoln and Tyler, 1992; 1994; Bubenik *et al.*, 1997; Blake *et al.*, 1998). The two hormones also act to synchronise the seasonality of the antler cycle with that of the reproductive cycle (Lincoln and Tyler, 1994), so that not only is the timing of antler growth and shedding between the two sexes different, but it allows season of death to be directly inferred from antler and cranial remains.

3.2.1.1. Seasonal Antler Cycles

Despite the prevalence of antlers in many fossil assemblages, there is little consistency in the application of antler cycles from modern populations (Kjos-Hanssen, 1973; Spiess, 1979; Aaris-Sørensen *et al.*, 2007; Fontana, 2017; Takken Beijsbergen, 2017b). Therefore, for the purpose of this research, the antler cycles of calves, males and females of subadult (yearling to 2.5 years) and adult (>2.5 years) age (**Figure 3.2**), have been derived from Scandinavian *R. tarandus* from Norway and Finland (Kjos-Hanssen, 1973; Høymork and Reimers, 2002; Aaris-Sørensen *et al.*, 2007; Reimers *et al.*, 2013), being geographically proximal to the fossil sites selected.

| | Antler circumference | Antlers unshed | Antlers shedding | Antlerless crania |
|------------------|-------------------------|-------------------|------------------|----------------------|
| Calves | <6 cm | Oct-May | May-Jun | Jun-Sept |
| Subadult females | 6-7 cm | Oct-Mar | Mar-Jun | Jun-Sept |
| Adult females | 8-9 cm | Oct-May | May-Jun | Jun-Sept |
| Subadult males | ² 10-11 cm | Sept-Nov | Nov-Apr | Apr-Aug |
| Adult males | >12 cm | Sept-Nov | Nov-Dec | Dec-Aug |

Figure 3.2. The Seasonal Antler Cycles of *Rangifer tarandus*. Antler circumference (cm) based on measurements by Høymork and Reimers (2002) is used to age and sex *R. tarandus* antler remains and correlate the timing of antler growth and shedding periods.

As previously stated, calves born in May begin growing antlers almost immediately. Growth is complete by September, with shedding taking place the following May-June (Kjos-Hanssen, 1973; Aaris-Sørensen *et al.*, 2007). The antlers of both subadult and adult females also grow from June to September (Aaris-Sørensen *et al.*, 2007), after which, there is a slight deviation between the seasonality of antler shedding for pregnant and non-pregnant cows. Pregnant females generally cast their antlers within a week of giving birth in May-June (Lent, 1965; Espmark, 1971; Kjos-Hanssen, 1973; Høymork and Reimers, 2002; Aaris-Sørensen *et al.*, 2007), while shedding in barren females can occur as early as March, but often overlaps the calving in May-June (Høymork and Reimers, 2002; Aaris-Sørensen *et al.*, 2007). Although in some Canadian populations, 13.5% of pregnant females have been observed to shed their antlers up to two weeks before calving (Gagnum and Barrette, 1992), this would not alter the spring seasonality of shed

female antlers if this timing also occurred in Late Pleistocene populations. Of course, whether or not a female is pregnant is generally unrecognisable from the fossil record and certainly not from the antlers alone. As such, in fossil assemblages, adult antlers were assumed to follow the antler cycle of pregnant females, while subadult antlers were assumed to be consistent with the timing of antler shedding in barren females. The antlers of males begin growing in April and are fully grown by August-September (Kjos-Hanssen, 1973; Aaris-Sørensen *et al.*, 2007). Shedding occurs from November onwards (**Figure 3.2**); the older, adult males are the first to lose their antlers in November-December, while younger subadult males cast their antlers later in the winter (Kjos-Hanssen, 1973; Aaris-Sørensen *et al.*, 2007). In Alaskan and Canadian *R. tarandus*, this may take place as late as April (Skoog, 1968; Fuller and Keith, 1980), timings which were adopted by this research due to the lack of precision for subadult shedding in modern Scandinavian populations.

Following the identification of antlers, the MNI for the shed and unshed antlers, as well as antlerless crania, of each age-sex class were established and correlated to the season of death for that phase of the antler cycle, as well as the age-sex ratio of the different seasonal aggregation. However, because the seasonality of reindeer antler cycles varies considerably with sex, age and shedding state, accurate identifications of antler and cranial remains are of vital importance.

3.2.1.2. Identifying the Shedding State of Antlers

Shed antlers are recognisable by their almost flat burr surface, which could display either a convex or concave depression in the centre (Spiess, 1979). Where numerous, the antlers would be suggestive of occupation during the months when shedding occurs (Kjos-Hanssen, 1973; Spiess, 1979). However, the susceptibility of shed antlers to postdepositional transport (for example as a food or other resource) significantly reduces their reliability in reconstructions and care must therefore be taken to address the taphonomic context of any such remains (Spiess, 1979). Fortunately, cranial fragments which are either still attached to antlers and therefore unshed, or display pedicles indicative of recent shedding, are more informative in this respect since they reflect actual site occupation by individual animals and can contribute to MNI reconstruction (Spiess, 1979; Aaris-Sørensen *et al*, 2007).

3.2.1.3. Identifying the Age and Sex of Antlers

Visually, unambiguous identifications can be made between the straight, tine-less antlers of calves less than one year old and the more complex adult forms. Although some females do carry tine-less antlers, these are somewhat more robust than the spikes of calves (Figure 3.3). Apart from male spikes being slightly taller and thicker than females (Høymork and Reimers, 2002), it is not possible to sex the calves themselves and this would have no bearing on the season of death anyway (Figure 3.2). In yearlings, however, the increasing sexual dimorphism of antlers enables the identification of males and females (Kjos-Hanssen, 1973). The antlers of male R. tarandus are larger, reaching their maximum size between the ages of 5-9 years, at which point, antler size begins to decrease (Skoog, 1968; Kjos-Hanssen, 1973; Nieminen, 1985; Melnycky et al., 2013). Male antlers are also a lot more complex in terms of the number and split-offs of tines (Høymork and Reimers, 2002), consistently displaying a brow tine on one or both antlers (Kjos-Hanssen, 1973). If this appendage is present in females, it will only be as thick as a finger (Kjos-Hanssen, 1973), as female antlers are not only simpler in form, but much smaller, plateauing in size around 2-5 years (Skoog, 1968; Nieminen, 1985; Melnycky et al., 2013).



Figure 3.3. Tine-less *Rangifer tarandus* Antlers. Examples of the spikes (left) of a calf 0.5 years old and the straight, simplified antlers sometimes observed in adult females (right), here an individual >2.5 years old. Both *R. tarandus* are from Hardangervidda, Norway.

Complete antlers extending beyond the brow tine are rarely preserved in the fossil record. The ratio of males to females at a site is therefore determined using the presence

of the more robust shed and unshed antler bases. Bouchud (1966) suggested that the shape of the base of shed antlers can be used to sex *R. tarandus*. Following this method, if the shedding surface of an antler is convex it belongs to a male, while the curvature of female antlers is concave (Bouchud, 1966). This technique has been tested against individuals of known sex from Scotland (Murray, 1994), North America and Greenland (Spiess, 1979), but has been shown to be unreliable, with each sex displaying distinct variability in the basal curvature. A more quantitative technique for separating subadult and adult individuals was developed by Banfield (1960) and involves counting the annulations of pedicle cross-sections in order to age individual antlers. Unlike the annulations of dental cementum, the precision afforded by this approach is yearly, not monthly (Banfield, 1960), and the annuli of antlers have been observed to fade with age (Banfield, 1960). It is therefore unsurprising that this destructive method has not been widely applied to the fossil record.

Fortunately, Høymork and Reimers (2002) have categorised the size range of a series of morphometric parameters for each sex from Norwegian R. tarandus, which can be applied to both shed and unshed antler bases. Although these parameters include antler height, circumference, the total number of tines, the number of tine split-offs and the maximum width between left and right antlers (Figure 3.4), antler circumference, taken at the first measurable point above the burr with a soft tape measure (cm) to one decimal place (Høymork and Reimers, 2002), is the only parameter that is consistently well preserved and allows differentiation between antler age as well as sex. However, exact measures of antler circumference can be strongly population-dependent (Høymork and Reimers, 2002; Wiesendanger, 2015). While *R. tarandus* demonstrate good memory for the same shape and structure of antlers throughout adulthood (Kjos-Hanssen, 1973; Lichti et al., 2016), annual size is significantly affected by the quantity and quality of nutrition, as well as the amount of winter snowfall (Kjos-Hanssen, 1973; Bergerud, 1976; Høymork and Reimers, 2002). This variability should not be a problem in large assemblages, where the limits of antler circumference can be adjusted to reflect the broad size patterns of the fossil population. The measurements of antler circumference (Figure 3.2) should therefore only be used as a guideline, to be compared closely to the visual characteristics and morphologies (number of tines, robustness) of antlers of different ages and sexes. Nevertheless, in smaller assemblages, where such comparisons cannot be made, it may be necessary to exclude antler remains from analyses of season of death.

This approach has been particularly useful for distinguishing between the more ambiguous antlers of subadult males and adult females. Visually, the size and complexity of these antlers are very similar (**Figure 3.5**), an overlap which prompted Spiess (1979)

to advise that only the instantly recognisable large adult males and calves should be used in studies of seasonality. Therefore, the difference in antler circumference has enabled the distinct seasonality represented by these two antler cycles to be included in this research (**Figure 3.2**).



Figure 3.4. Position of Morphometric Measurements for *Rangifer tarandus* Antlers. Høymork and Reimers (2002) developed a series of measurements for ageing and sexing antlers including antler height (dashed line), antler circumference (arrows) and the number of tine and tine split-offs. Only antler circumference (cm) was applied to this research. (Source: after Høymork and Reimers, (2002), p.76.).



Figure 3.5. Antlers of Subadult Male and Adult Female *Rangifer tarandus*. Examples of the similarities between the size and complexity of the antlers of a 2 year old subadult male (top) and a 3 year old adult female (bottom). Both *R. tarandus* are from Sweden.

The seasonality of adult females may also be problematic to identify when individuals are antlerless (Figure 3.6). Although it is rare for *R. tarandus* to be consistently antlerless throughout their life (around 2% of individuals) (Loe et al., 2019), usually between 0-7.5% of females within a population may be antlerless in any given year (**Table 3.2**). There are a number of explanations as to why an individual might not bear antlers either sporadically or throughout its lifetime. While the trait is rarely observed amongst the descendants of domesticated or captive R. tarandus (Cronin et al., 2003), populations with a higher proportion of antlerless females have been associated with poorer nutrition (Reimers, 1993; Cronin et al., 2003). Furthermore, in Norway, increased herd density has also seen the number of antlerless females rise to 17%, as physical condition is reduced due to the competition for resources (Reimers, 1993). However, in woodland R. tarandus herds, where the number of individuals and therefore competition is lower, antlerless females are also more prevalent (Cronin et al., 2003). This potentially highlights the significance of genetic selection for certain environments (Reimers, 1993). The fact that the herds with the highest percentage of antlerless females were observed from island populations (Table 3.2), where bottle necks and genetic drift have been evident, could facilitate the selection of antlerless individuals throughout time independent of density and resource pressure (Jacobsen et al., 1998). Nevertheless, while the presence of female crania with pedicles but no antlers would ordinarily represent site occupation from June to September, this seasonality would be expanded if the female were antierless. However, the small percentage of antierless females within modern populations suggests that antlerless females would not significantly alter interpretations of the season of death in large assemblages, although, where possible, antlers should not be used in isolation when analysing season of death.

1861 stat. vilt.

Figure 3.6. Antlerless Adult Female *Rangifer tarandus*. Example of an antlerless female (1.5 years old) from Hardangervidda, Norway.
| Country/Herd | Subspecies | Year | Antlerless Females | Reference |
|---------------------------|---------------------|-----------|-----------------------|--|
| Alaska | | | | |
| Central Arctic | R. t. granti | 1994-2002 | 4.0-6.4% | Cronin <i>et al.</i> (2003) |
| Porcupine | R. t. granti | 1983-1990 | 5.0% | Whitten (1995) |
| Western Arctic Herd | R. t. granti | 1961-1964 | 0.9-3.0% | Lent (1965) Skoog (1968) |
| Forty Mile | R. t. granti | 1952-1955 | 0.6% | Skoog (1968) |
| Nelchina | R. t. granti | 1957-1962 | 1.4-2.3% | Skoog (1968) |
| Canada | | | | |
| West of Hudson Bay | R. t. groenlandicus | 1900s | 0.3% | Steffanson (1913) |
| Queen Charlotte Island | R. t. dawsoni | 1956 | 100% | Banfield (1961) Cowan and Guiguet (1956) |
| Finland | R. t. fennicus | 1970 | 7.5% | Espmark (1971) |
| Greenland | R. t. groenlandicus | 1977-1984 | 21-78% | Reimers (1993) Thing <i>et al.</i> (1986) |
| Norway | R. t. tarandus | 1948-1983 | 0-17% | Reimers (1993) |
| Svalbard | R. t. platyrhynchus | 1972-1994 | 0-50% | Thing <i>et al.</i> (1986) Reimers (1993) Jacobsen <i>et al.</i> (1998) |

Table 3.2. Percentage of Antlerless Females in Modern Rangifer tarandus Populations.(Source: after Cronin et al., (2003), p.68.).

3.2.2. Postcrania

By the age of one, the sexual dimorphism seen in the antlers is also recognisable in *R. tarandus* postcrania, reflecting the increasingly different body masses of the two sexes. Although there is a distinct overlap in the weights of modern *R. tarandus*, with males generally weighing between 70-150 kg and females weighing between 40-100 kg (Herre, 1986), patterns of sexual dimorphism in individual populations are strong. In Norway, male *R. tarandus* have been recorded as weighing 2.1-2.4 times that of females (Reimers 1972; Solberg *et al.*, 2008), while their Canadian counterparts weigh 1.2-1.6 times that of the females (McEwan 1968; Dauphine, 1976; Jarman, 1983; Geist and Bayer, 1988). This clear level of sexual dimorphism in *R. tarandus* has been demonstrated to extend into both the archaeological and Pleistocene record (Weinstock 1997; 2000a; 2000b; 2002; Wiesendanger, 2015; Takken Beijersbergen, 2017b; Castaños and Castaños, 2018).

The close correlation of skeletal dimensions with body mass in mammalian families is not unexpected (Scott, 1990). As body mass increases, the corresponding rise in compressive and bending forces on weight-bearing elements requires postcranial bones to be of a sufficient thickness to withstand them (Scott, 1990; Collinge, 2001). Postcrania therefore appear to follow interspecific allometry, with elements maintaining their functionality at different sizes by changing dimensions (Scott, 1985). Fortunately, ungulates follow these scaling relationships (Scott, 1985; 1987). As such, reconstructions of body mass from *R. tarandus* postcrania can be used to determine the season of death by comparing the ratio of males to females, established from the clustering that is apparent when measurable postcranial dimensions are compared on an element by element basis, to known levels of sexual segregation expressed within seasonal aggregations.

Using single elements to compare the body size of populations is significantly limited by the variable, and often low, abundance of elements recovered from fossil sites (Weinstock, 2000a). Previous studies comparing osteological measures of *R. tarandus* body size have applied Uerpmann's (1979; 1982) "Variability Size Index" (VSI) method (Weinstock, 1997; 2000a; 2002; Pasda, 2009b; Kuntz and Costamagno, 2011; van Kolfschoten et al., 2011; Castaños and Castaños, 2018; Takken Beijersbergen, 2017b). This allows dimensions from all postcranial elements to be compared simultaneously by relating fragmentary fossil records to a standard population, thereby increasing sample size. Measurements of skeletal dimensions produce an index indicative of body mass, which is either larger (positive) or smaller (negative) than the standard population placed at zero (Weinstock, 2000a). Compared to similar techniques, such as the logarithmic size index (LSI), the definition of the standard as a population rather than a single individual, enables the variation in different dimensions and elements to be considered (Uerpmann, 1982). However, it is unclear whether any nominal modern "standard" can adequately capture variation in a heterogeneous population. Even when a standard uses individuals from the same biological population, over- or under-representation of certain individuals can still alter the reliability of this approach. In the Norwegian modern standard used by Takken Beijersbergen (2017b), the presence of only one male individual had to be considered when interpreting the scale of positive or negative skew of the VSI of the studied sites. The population therefore had to be treated as an archaeological, rather than biological, population (Takken Beijersbergen, 2017b).

Many studies that investigate body size in *R. tarandus* using VSI have relied upon one archaeological population in particular (Pasda, 2009b; Kuntz and Costamagno, 2011; van Kolfschoten *et al.*, 2011; Castaños and Castaños, 2018), the Ahrensburgian layer of the German site of Stellmoor, as developed by Weinstock (1997; 2000a; 2002). An

abundant and well-preserved assemblage that accumulated under rapid deposition, this site has been the frequent focus of study as the material represents a homogeneous, if not biological, population (Weinstock, 2000a). Adopting the same standard population means that it is possible to compare multiple studies and sites. However, because the VSI operates as an isometric scaling relationship, which is relatively rare in nature, reconstructions of body size will be highly dependent on the sex ratio of the fossil assemblage which can be hard to distinguish based on the VSI alone (Kuntz and Costamagno, 2011). Although a bimodal distribution of body sizes roughly corresponds to the presence of males and females at a site (Weinstock, 1997), the presence of multiple peaks may obscure this distribution pattern (Takken Beijersbergen, 2017b). Only Pasda (2009b) has attempted to calculate VSI separately for males and females by first sexing elements, emphasising the importance of understanding the demography of a site before analysing size (Meadow, 1999). Nevertheless, the reconstruction of body sizes generated by VSI and other size indices remain a coarse estimation of body mass (Meadow, 1999). As an alternative and more precise approach, this research utilises the development of individual predictive equations for body mass, in order to reconstruct the average body masses of male and female *R. tarandus*.

3.2.2.1. Average Mass Equation

Reconstructions of body mass follow an average mass equation based on work by Scott (1990) and developed by Collinge (2001) (Equation 1), which functions as an allometric scaling relationship between skeletal measures and body mass (Scott, 1985). Biologically, this provides a more accurate estimate of size than methods based on isometric relationships, such as VSI (Kuntz and Costamagno, 2011). The technique was originally developed for bovids (Scott, 1983), but has since been expanded to a range of families including Suidae, Equidae, Rhinocerotidae, Canidae, Ursidae, Felidae, and, most importantly for this research, Cervidae (Scott, 1987; Scott, 1990; Collinge, 2001). For each family, an individual predictive equation has been developed (Scott, 1990; Collinge, 2001), reflecting the way in which different skeletal morphologies respond to changes in body size (Scott, 1983). These were constructed using an average of body weights from wild-collected adult individuals of both sexes (Scott, 1990). By using an average, predictive equations were able to account for the seasonal variations in body mass otherwise obscured by one-time capture weights (Scott, 1983), as well as adjust for any trophy or zoo individuals included in the collections (Scott, 1990). The scaling relationship was determined by least squares regression, using Log₁₀ transformed data to determine the linear relationship between skeletal measures and body mass (Scott, 1990; Collinge, 2001). Care was taken to ensure that the dimensions of skeletal

measures selected were roughly comparable between the different taxa (Scott, 1990). Therefore, by using the predictive equation for Cervidae, values of skeletal measures can be substituted to calculate average estimates of body mass (kg) (Collinge, 2001).

Log Body Mass = m(log measure) + c

measure = parameter measured (cm)

m = slope of line

c = y-intercept

Equation 1.

Collinge (2001) did not attempt to differentiate between the sexes when making reconstructions of Pleistocene body masses, instead presenting an average for each site. However, using the sexual dimorphism exhibited by *R. tarandus*, Wiesendanger (2015) demonstrated that it is possible to distinguish between sexes when reconstructing body mass from the fossil record. As such, not only do reconstructions of body mass facilitate the determination of sex ratios and therefore season of death from an assemblage, but they also provide insight into the geographical and temporal variations in the body masses of fossil *R. tarandus*. As an equation operating as a scaling relationship, this technique is also applicable to the skeletal measurements of modern *R. tarandus*, allowing the direct comparison of variations in fossil *R. tarandus* to the recent decreases in body mass observed in modern populations (Albon *et al.*, 2016). This is an especially useful tool when considering critical thresholds for *R. tarandus* and how the body sizes of the species might be expected to respond in the future, given Late Pleistocene reconstructions.

3.2.2.2. Statistical Analysis of Body Mass

Following the reconstruction of body mass using the average mass equation, statistical analysis was completed using SPSS (v.26 2019), in order to ascertain whether:

- There was a significant difference between the average body masses of male and female *R. tarandus*, thereby recognising the extent of sexual dimorphism.
- There was a significant difference between the average body masses of modern *R. tarandus* subspecies, thereby recognising genetic variation.
- There was a significant difference between the average body masses of modern *R. tarandus* from different localities and dates, thereby recognising geographical and temporal variation.

- There was a significant difference between the average body masses of fossil *R. tarandus* from sites of the same age, thereby recognising geographical variation.
- There was a significant difference between the average body masses of fossil *R*. *tarandus* from different Late Pleistocene stages, thereby recognising temporal variation.

For all tests, males and females were tested separately with the null hypothesis (H₀):

• There is no significant difference between the average body masses of independent *R. tarandus* samples. Critical significance level p=0.05

Prior to the statistical analysis of body mass estimates, outliers were removed following the visual inspection of histograms and Q-Q plots. Males and females from each fossil site or modern locality were then assessed for normality using the Shapiro-Wilks test. Where the results of these analyses showed a statistically non-significant non-normal distribution at p>0.05, this ensured that parametric tests for difference which assume a normal distribution within a dataset could be reliably applied. To compare variances of independent samples and assess whether these can be singularly explained by sample errors (Sokal and Rohlf, 1995), two tests were used, the independent sample t-test (ttest) and the one-way analysis of variance (ANOVA). Where comparisons were made between two sample means, the t-test was calculated for separate variance estimates and reported based on whether Levene's test for equal variance was non-significant (p>0.05) and therefore equal, or significant (p<0.05) and therefore unequal. However, to test more than two independent samples, it is not appropriate to repeatably use t-tests as this increases the chance of incorrectly rejecting the null hypothesis, referred to as Type 1 errors (Campbell, 1981). Therefore, a one-way ANOVA was applied instead, which in addition to data that is independent and normally distributed, requires homogeneous variances (Sokal and Rohlf, 1995). Where p<0.05 and there was a statistically significant difference between samples reported by the ANOVA, Levene's test for equal variance was subsequently applied to determine which post hoc test should be used to compare the differences between individual samples. When Levene's test was non-significant (p>0.05) and indicative of equal variances, the Tukey Honest Significant Difference (HSD) test was applied, but when Levene's test was significant (P<0.05) and indicative of unequal variances, Dunnett's T3 test was used.

3.2.2.3. Selection of Skeletal Elements and Measurements

Measurements of postcranial dimensions were taken from the fully-fused epiphyses following standard measurements outlined by Von den Driesch (1976), Weinstock

(2000a) and Collinge (2001) (**Appendix 2**), using digital callipers in order to improve the accuracy of measurements (mm) to two decimal places. **Figure 3.7** shows the postcranial elements utilised in the reconstruction of *R. tarandus* body size from both modern and fossil specimens. Unfortunately, the average mass equation only applies to postcranial long bones and metapodials and so reconstructions from dimensions of the ulna (LO, SDO, DPA, BPC) and calcaneum (GL, GB), as well as the depth of distal radii (Dd), are not possible. However, the raw measurements of these elements still provide a useful indication of the ratio of males and females present at the site and were therefore used to determine the season of death for fossil assemblages.



Figure 3.7. *Rangifer tarandus* Postcranial Element Selection. Forelimb and hindlimb elements used for reconstructing *R. tarandus* body size from modern and fossil specimens (highlighted in grey). The average body mass could be calculated from all dimensions with the exception of the ulna and calcaneum.

Where mass estimating equations are applicable (**Appendix 3**), Collinge (2001) excluded a number of measurements from both modern and fossil specimens on account of these generating either inconsistent results (T3, Mc1, Mt1), or consistently overestimating (Mc4, Mt4) or underestimating (Mc5, Mt5) reconstructions of body mass. In addition to those highlighted by Collinge (2001), distinct variations were also observed in this study from estimates of modern *R. tarandus*. Further dimensions identified for omission could, again, be separated into measures that overestimated (F3, Mc3, Mt3), or underestimated (H3, H6, T1) body mass, in addition to those which displayed larger

values of standard deviation (H6, F3, F4) (**Figure 3.8**). Any anomalous outliers observed in the skeletal measures of individual specimens were excluded from average estimates.



Figure 3.8. Measures Excluded from Average Body Mass Estimates. A number of measurements were excluded from average body mass estimates from the (a)
Humerus (H3, H6), (b) Metapodials (Mc3, Mt3), (c) Femur (F3, F4) and (d) Tibia (T1). These outliers are shown for Norwegian *Rangifer tarandus* populations for males (squares) and females (diamonds), with the standard deviation.

Although a greater number of measurements will increase the accuracy of the average body mass (Scott, 1990), averages derived from only one or two measures should not vary greatly from those generated from a complete element (Scott, 1983). In the fossil record, complete elements are rarely preserved, while isolated proximal or distal ends dominate assemblages. As such, estimates of body mass from fossil assemblages depended completely on measurements of breath and depth, as measures of length (H1, H2, R1, F1, T1) could not be collected. Fortunately, non-length measures are thought to correspond more closely to body mass than length measures, as compressive and bending forces have a greater impact on bone thickness (breadth and depth) than length (Scott, 1990). Additional elements excluded from reconstructions included the femur and the proximal humerus, which are both consistently poorly preserved. In addition to the over- or underestimations of certain measurements, differences have also been observed by this study between the body masses calculated from the individual epiphyses of different postcranial elements. This was particularly noticeable when comparing the smaller body masses reconstructed from the proximal radius, to larger estimates derived from elements such as the distal tibia. As the proximal radius represents an earlier-fusing epiphysis, the calculation of consistently lower body masses could be attributed to the inclusion of a larger number of younger and therefore smaller animals. However, this pattern was recognisable regardless of age from both subadult and adult specimens in the fragmentary fossil record, as well as modern R. tarandus of known-age. As such, the differences between epiphyses could instead be linked to the performance of the mass estimating equation when applied to separate postcranial elements (Scott, 1983). In cervids, it is not uncommon for estimates of body mass to be lower in the forelimb than the hindlimb, something that has typically been associated with species-level specialisations for locomotion (Scott, 1983). Morphological variations of this kind have already been identified in R. tarandus from the distal metapodials (Collinge, 2001), but could also have a more significant influence on the forelimbs than previously thought. Nevertheless, as the measurements from all elements, and therefore epiphyses, contribute to the average estimates of body mass, the variability observed in *R. tarandus* should not negatively impact the final calculation.

In order to determine the sex ratio present within a fossil assemblage, the best elements for providing body mass estimates are those of the forelimb (Collinge, 2001). This corresponds to the strong sexual dimorphism that exists in *R. tarandus* between the larger antiered males and the smaller antiered females, with R. tarandus forelimbs supporting a greater proportion of the body's weight than is expressed through the hindlimbs (Weinstock, 2000b). Reconstructions of body mass from the forelimbs therefore represent an estimate which is closer to an individual's actual weight (Scott, 1983), enabling a much clearer distinction between the sexes. Furthermore, Weinstock (2000b) recorded that sexual dimorphism is most distinct in the late-fusing epiphyses, namely the distal radius and proximal humerus. However, work by Wiesendanger (2015) has demonstrated that these elements show weak patterns of dimorphism. Instead, the clearest representations of sexual dimorphism were taken from the distal humerus and proximal radius, as well as the ulna, calcaneum and the distal tibia (Wiesendanger, 2015). This is supported by recent work by Takken Beijersbergen (2017b), which studied modern Norwegian specimens of known sex and found that elements such as the calcaneum and proximal radius, traditionally excluded from analyses of sexual dimorphism, were 90% effective at assigning sex to fossil specimens.

3.2.2.4. Ages of Epiphyseal Fusion

Because both the distal humerus and proximal radius represent early-fusing epiphyses, it is particularly important to consider the age that each element represents in the interpretation of a site's demography (Weinstock, 2000b). However, when sex ratios are determined from the measurements of early-fusing epiphyses, it can be hard to separate patterns of smaller body sizes from those of juvenile individuals. This is because the number of elements with this epiphysis fully fused is increased and, as such, a wider spectrum of ages could be included in bivariate plots. This effect is often exaggerated in large assemblages, with patterns of sexual dimorphism becoming so blurred that the size transition from females to males appears to be continuous. Although such high levels of postcranial preservation are rare for most fossil sites, by recording whether or not an element represents an isolated fragment, as well as ageing all epiphyses present, the fully fused postcrania of adults can be easily identified in order to clarify sex ratios.

Postcranial bones are aged using the stage of epiphyseal fusion. Timings for each element have been determined from direct measurements of 70 Norwegian *R. tarandus* from the 1940s, 1970s and 2000s made by Hufthammer (1995) and Takken Beijersbergen and Hufthammer (2012) (**Table 3.3**). For each skeleton, the date of death was known and the calving date, when 50% of population is thought to have given birth, was placed at the 15th May. Postcrania were allocated to one of three stages that correlate with an age. Epiphyses were classified as (1) unfused, or younger than the lowest age, (2) fused, or older than the upper age limit, and (3) fusing, which placed the element between initiation and completion of epiphyseal fusion. In addition, the presence of a faint epiphyseal line on completely fused elements indicates a state within one year of the upper age limit of epiphyseal fusion (Spiess, 1979). Nevertheless, the technique is subjective and is limited to a maximum age limit of 66 months (5½ years) or younger in the case of most elements.

| Element | End | Approx. Age of Fusion (months) |
|-----------------------|----------|-----------------------------------|
| Humerus | Proximal | 42 - 54 |
| | Distal | 6 - 15 |
| Radius | Proximal | 4 - 10 |
| | Distal | 36 - 48 |
| Ulna | Proximal | 42- 48 |
| Radius-Ulna Diaphysis | | 18 - 30 |
| Metacarpal | Distal | 18 - 30 |
| Femur | Proximal | 36 - 48 |
| | Distal | 36 - 48 |
| Tibia | Proximal | 36 - 48 |
| | Distal | 18 - 30 |
| Metatarsal | Distal | 18 - 30 |
| Calcaneum | Proximal | 18 - 42 |

Table 3.3. Approximate Ages of Epiphyseal Fusion for *Rangifer tarandus*. Definitions of the timing of fusion stages in *R. tarandus* were taken from Takken Beijersbergen and Hufthammer (2012).

3.2.2.5. Foetal Postcrania

While the age classes of epiphyseal fusion are too broad to constrain patterns of seasonality in individuals, a more precise season of death can be determined directly from postcranial remains when delicate foetal bones can be identified. This method uses the rapid growth rate of foetuses to correlate the length of the hind-foot (from the calcaneum to the last phalange) to developmental age (in days), following a straight-line regression (**Equation 2**) (Spiess, 1979). In an incomplete fossil record, hind-foot length is determined using the more measurable length of long bone diaphyses (**Figure 3.9**), the growth of which is thought to be proportional throughout gestation (Spiess, 1979).

Age (days) = $\frac{1}{2}$ x hind-foot length (mm) + 70

Equation 2.

Assuming that the rut occurs on the 15th October (Spiess, 1979), the foetal age therefore represents the season of death for the adult female, providing a more precise indication of winter occupation than tooth ages during this season (Fontana, 2017). However, further work is required to test this method. The original straight-line regression was developed by Spiess (1979) using the postcrania of only four foetal specimens measured by Kelsall (1957). Measurements taken by Spiess (1979) on an additional six specimens confirmed this regression however, it is advisable that specimens covering a greater variety of ages and populations should be included in the future development of this method. Furthermore, the poor preservation of foetal diaphyses means that the technique is rarely applicable to fossil assemblages. Foetal bones younger than 60 days have yet to develop a hard cortex and so are significantly less likely to be preserved

(Spiess, 1979). Even in particularly abundant assemblages such as that from the Magdalenian site of La Madeleine in France, where the number of identifiable specimens of *R. tarandus* exceeds 7000, only twelve measurable foetal bones were preserved (Fontana, 2017). Throughout the course of this research, no remains were found for which this method could be applied.



Figure 3.9. Rangifer tarandus Foetal Diaphyses. The delicate remains of foetal postcrania are rarely preserved in the fossil record. Examples presented here are from Schweizer Bild, Switzerland.

3.3. Summary

- The seasonality of site occupations is established using techniques that reconstruct either the age at death or season of death, from the dentition, antlers, crania and postcrania of Late Pleistocene *R. tarandus*.
- The eruption and wear ages of teeth provide the most precise assessment of *R*. *tarandus* age at death, which, in juveniles, can further be used to determine the month and therefore season of death.
- Season of death is mainly identified using the sexual dimorphism observed between male and female *R. tarandus*, which varies between seasonal aggregations. The ratio of sexes present in an assemblage can be determined from the antlers, crania and postcrania. The season of death can also be assigned directly using the annual shedding cycle of antlers from both sexes.
- In addition to identifying the sex ratio, postcranial reconstructions of average body mass using a mass estimating equation also enable the direct comparison of size variations between modern and fossil *R. tarandus*.

Chapter 4. Body Mass in Modern and Late Pleistocene Rangifer tarandus

This chapter presents the body mass estimates of *Rangifer tarandus* specimens from both modern and historical populations, as well as those from Late Pleistocene assemblages. It will discuss the mechanisms for variations in body size and how these relate to the recent changes observed in different *R. tarandus* populations. Where estimates from Late Pleistocene assemblages enable the identification of sexual dimorphism, and therefore the prediction of body masses of male and female *R. tarandus* in the fossil record, the temporal and spatial variations in size will be discussed. This will be complemented by discussion of the way in which such morphological variations affect palaeoenvironmental and palaeoclimatic reconstructions from the Late Pleistocene.

4.1. Body Mass in Modern and Historical Rangifer tarandus

A total of 130 males and 97 females were studied in order to estimate the average body mass of modern and historical *R. tarandus*. Following the criteria outlined in Chapter 3 for the exclusion of specific skeletal dimensions, any additional anomalous outliers are listed in **Appendix 4.1**. The final number of individuals included from each locality is outlined in **Table 4.1**. For several of the specimens from Norrbotten 1950s and Lappland 1950s (mountain) in Sweden (**Appendix 4.2**), the sex was incorrectly labelled and has been altered accordingly (Göran Sjöberg, pers. comm.). The full list of specimens studied, as well as the individual estimates of body mass, is included as Supplementary Data **(SD 9-10)**.

Prior to the statistical analysis of body mass estimates, outliers were removed following the visual inspection of histograms and Q-Q plots. Males and females from each locality were subsequently assessed for normality using the Shapiro-Wilks test. The results of these analyses all showed a statistically non-significant non-normal distribution at p>0.05 (**Appendix 4.3**), enabling the reliable application of parametric tests for difference which assume a normal distribution within a dataset.

| Country | Subspecies | Locality and Date of | Number of | | |
|----------|---------------------|-------------------------|-----------|---------|--|
| | | Collection | Indiv | viduals | |
| | | | Males | Females | |
| Canada | R. t. caribou | Alberta 1930s | 1 | 1 | |
| | R. t. groenlandicus | Northwest Territories | 1 | | |
| | | 1911 | | | |
| Norway | R. t. tarandus | Finnmark 1869 | 1 | | |
| | | Oppland 1947 | 1 | | |
| | | Buskerud 1948 | 6 | 3 | |
| | | Buskerud 1970 | 3 | 7 | |
| | | Hordaland 1970s | 7 | 10 | |
| | | Oppland 2006 | 1 | 5 | |
| Sweden | R. t. tarandus | Norrbotten 1909 | 6 | | |
| | | Jämtland 1950s | 23 | 23 | |
| | | Härjedalen 1950s | 13 | 15 | |
| | | Lappland 1950s (forest) | 5 | | |
| | | Lappland 1950s | 37 | 10 | |
| | | (mountain) | | | |
| | | Norrbotten 1950s | 4 | 5 | |
| Svalbard | R. t. platyrhynchus | Spitsbergen 1861 | 1 | | |
| | | Spitsbergen 1960 | 1 | | |
| | | Spitsbergen 1975 | 2 | 1 | |

 Table 4.1. Modern and Historical Rangifer tarandus Specimens. The number of individuals that body mass was reconstructed for are presented by subspecies, location and collection date.

4.1.1. Rangifer tarandus Subspecies

Figure 4.1 compares the average estimated body masses of modern *R. tarandus* subspecies. The small sample sizes of the two North American subspecies, *Rangifer tarandus caribou* and *Rangifer tarandus groenlandicus* (**Table 4.1**), could only be used to provide a broad comparison with the better represented European *Rangifer tarandus tarandus* in the context of this study. Nevertheless, the largest estimates of body mass from modern *R. tarandus* subspecies were recorded from male and female *R. t. caribou* from Canada. Male *R. t. caribou* weighed 216.23 \pm 9.53 kg, while an average body mass of 167.21 \pm 3.83 kg was recorded from the females. From the second North American subspecies, *R. t. groenlandicus*, the average body mass from a Canadian male was 141.41 kg.

Examples of the European subspecies *R. t. tarandus* were measured from Norway and Sweden. Although the average estimated body masses from both sexes were heavier from Sweden, where males weighed 124.81 ± 12.22 kg and females weighed 99.43 ± 9.53

kg, whereas from Norway, males weighed 110.20 ± 19.61 kg and females weighed 81.98 ± 8.84 kg, there was an overlap in the male and female 95% confidence levels from the two countries. To ascertain whether there was a significant difference between the total average body mass of the Norwegian and Swedish *R. t. tarandus*, a t-test was used. For males, there was no significant difference (t_{10} =1.626 p=0.135) in the body mass of individuals from Norway, where n=6, mean=110.20 kg and SD=18.69 kg, and Sweden, where n=6, mean=124.81 kg and SD=11.64 kg. For females, however, there was a significant difference (t_6 =4.271 p=0.005) in the body mass of individuals from Norway, where n=4, mean=81.98 kg, SD=5.56 kg, and Sweden, where n=4, mean=99.43 kg and SD=6.00 kg. Equal variances were assumed from Levene's test which was non-significant for both males (F_{10} =2.412 p=0.151) and females (F_6 =0.053 p=0.826).



Figure 4.1. Average Estimated Body Mass of *Rangifer tarandus* Subspecies. Body mass was reconstructed from the postcrania of modern specimens of *R. t. caribou* (*R.t.c.*), *R. t. groenlandicus* (*R.t.g.*), *R. t. tarandus* (*R.t.t.*) and *R. t. platyrhynchus* (*R.t.p.*). Males are represented by a square and females are shown as a diamond. The 95% confidence interval is also presented. The legend gives an indication of the colour representing each country.

The total average body mass for the combined *R. t. tarandus* subspecies was 117.50 ± 10.61 kg for males and 90.71 ± 8.99 kg for females. Although smaller than either of the North American subspecies, the lightest estimates of body mass for both males and females were instead measured from *Rangifer tarandus platyrhynchus*, a subspecies only found on the Norwegian archipelago of Svalbard. Males were recorded as weighing 75.83 kg, while females weighed 56.23 kg. Again, the small sample size of female *R. t. platyrhynchus* prohibited statistical tests for difference between the subspecies however, it was possible to use the t-test on male body size. There was a

significant difference (t_{13} =3.979, p=0.002) between the average body mass of *R. t. tarandus*, where n=12, mean=117.50 kg, SD=16.69, and *R. t. platyrhynchus*, where n=3, mean=75.83 kg, SD=13.34. Equal variances were assumed from Levene's test which was non-significant (F_{13} =0.737, p=0.406).

4.1.2. Norwegian and Swedish Rangifer tarandus tarandus

The *R. tarandus* specimens studied in this research primarily represented individuals from the *R. t. tarandus* subspecies found across Norway and Sweden, covering a period between 1869-2006 (**Table 4.1**). As sex was known for these specimens, it was possible to test whether there was a statistically significant difference in the size of males and females, when the average mass equation was used to estimate body mass. **Table 4.2** shows the result of t-tests completed on each of the Scandinavian localities where both sexes were represented. Equal variances were assumed from Levene's test which was non-significant for all localities, with the exception of Buskerud 1948 and Jämtland 1950s where Levene's test was significant and equal variances were not assumed. Nevertheless, there was a significant difference between the body masses of males and females at each of the localities studied, and, therefore, the sexual dimorphism of *R. t. tarandus*.

Table 4.2. Results of Levene's Test and Independent Samples T-Test for Scandinavian
Rangifer tarandus tarandus. R. t. tarandus were tested to determine whether a
significant difference was evident between the body masses of males and females at
each locality. Results were significant at p<0.05.</th>

| Locality and | Sex | n | mean | SD | Levene's test | t-test |
|--------------|-----|-----|--------|-------|-----------------------------|------------------------------|
| Date of | | | | | | |
| Collection | | | | | | |
| Buskerud | М | 85 | 103.26 | 9.57 | F _{130.727} =9.555 | t _{130.727} =17.727 |
| 1948 | F | 50 | 78.70 | 6.50 | p=0.002 | p=0.0001 |
| Buskerud | М | 37 | 92.64 | 9.28 | F ₂₀₄ =0.008 | t ₂₀₄ =8.972 |
| 1970 | F | 169 | 77.39 | 9.39 | p=0.930 | p=0.0001 |
| Hordaland | М | 128 | 93.35 | 10.78 | F ₃₃₉ =0.006 | t ₃₃₉ =9.458 |
| 1970s | F | 213 | 82.08 | 10.57 | p=0.939 | p=0.0001 |
| Oppland | М | 14 | 105.12 | 7.18 | F ₁₁₅ =3.335 | t ₁₁₅ =4.907 |
| 2006 | F | 103 | 89.77 | 11.36 | p=0.070 | p=0.0001 |
| Jämtland | М | 45 | 110.92 | 16.66 | F _{75.273} =4.648 | t _{75.273} =5.656 |
| 1950s | F | 41 | 94.05 | 10.56 | p=0.034 | p=0.0001 |
| Härjedalen | М | 49 | 117.31 | 14.34 | F ₇₅ =3.456 | t ₇₅ =4.219 |
| 1950s | F | 28 | 100.23 | 21.11 | p=0.067 | p=0.0001 |
| Lappland | М | 75 | 117.85 | 13.02 | F ₉₃ =0.699 | t ₉₃ =6.907 |
| 1950s | F | 30 | 95.91 | 10.95 | p=0.405 | p=0.0001 |
| (Mountain) | | | | | | |
| Norrbotten | Μ | 29 | 135.62 | 17.16 | F ₃₉ =0.400 | t ₃₉ =4.944 |
| 1950s | F | 12 | 107.54 | 14.88 | p=0.531 | p=0.0001 |

Figure 4.2. shows the average estimates of body mass from Norwegian provinces and included specimens from Buskerud, Hordaland and Oppland in southern Norway, as well as from the northern province of Finnmark. Male average body mass was largest in Norway from Finnmark during 1969 and Oppland in 1947, with estimates of 134.63 ± 4.80 kg and 132.18 ± 11.37 kg respectively. Individuals from Oppland were also measured from 2006. During this later collection period, the male average body mass of 105.11 ± 4.14 kg was smaller than during the 1940s, while females weighed 88.63 ± 2.22 kg. A decrease in body size from observations during the 1940s was also observed from Buskerud. In 1948, male *R. t. tarandus* weighed 104.76 ± 2.06 kg and females weighed 81.18 ± 1.85 kg, but by 1970, average body mass was 94.43 ± 3.09 kg for males and 77.39 ± 1.43 kg for females. Body sizes of individuals from 1970s Buskerud overlapped with males and females from 1970s Hordaland, weighing 93.72 ± 1.89 kg and 81.80 ± 1.42 kg respectively.



Figure 4.2. Average Estimated Body Mass of Norwegian *Rangifer tarandus tarandus*. Body mass was reconstructed from the postcrania of modern specimens of *R. t. tarandus* from provinces in Norway (Buskerud, Finnmark Hordaland, Oppland). Males are represented by a square and females are shown as a diamond. The 95% confidence interval is also presented. The legend gives an indication of the colour representing each country.

Estimates of average body mass from Swedish *R. t. tarandus* are presented in **Figure 4.3**. Most of the specimens measured were collected during the 1950s, although *R. t. tarandus* from Norrbotten were also available from 1909. The largest estimates of male average body mass were measured from the Norrbotten *R. tarandus*, which weighed 141.78 \pm 4.87 kg in 1909 and 137.01 \pm 6.53 kg during the 1950s. While the male forest *R. t. tarandus* from 1950s Lappland weighed less than those from Norrbotten, at

 126.20 ± 16.04 kg, they exceeded the size of males from mountain areas of Lappland that weighed 117.85 ± 3.00 kg and were more consistent with the average male body mass of 117.31 ± 4.12 kg from Härjedalen 1950s. The smallest estimate of male body mass from Swedish *R. t. tarandus* of 110.92 ± 5.01 kg was recorded from Jämtland 1950s. The females from Norrbotten 1950s were also the heaviest reconstructed, at 107.54 ± 9.45 kg, with smaller estimates of body mass reconstructed from Jämtland, at 94.05 ± 3.33 kg, Härjedalen, at 100.23 ± 8.18 kg, and Lappland, at 95.91 ± 5.13 kg.



Figure 4.3. Average Estimated Body Mass of Swedish *Rangifer tarandus tarandus*. Body mass was reconstructed from the postcrania of modern specimens of *R. t. tarandus* from provinces and states in Sweden (Jämtland, Härjedalen, Lappland, Norrbotten). The individuals from Lappland represent *R. tarandus* occupying forest (F) and mountain (M) Reindeer Husbandry Areas of Sweden. Males are represented by a square and females are shown as a diamond. The 95% confidence interval is also presented. The legend gives an indication of the colour representing each collection date.

Because the same subspecies, *R. t. tarandus*, was represented throughout the two Scandinavian countries, it was also possible to make comparisons between the different localities throughout time. A one-way ANOVA was used to separately test the differences between male and female body masses. Between the male populations from each locality, the one-way ANOVA was significant ($F_{(11,541)}=79.352$, p=0.0001) and therefore there was a statistically significant difference in body mass. Levene's test for equal variance was also significant ($F_{(11,541)}=4.119$, p=0.0001) and indicative of unequal variances. Therefore, body masses could be further analysed using the *post hoc* test Dunnett's T3 to compare the differences between each locality (**Table 4.3**). The results of this test are summarised below.

- There was no significant difference between the body masses of male populations from the Norwegian provinces of Finnmark 1969 and Oppland 1947 and the Swedish provinces of Norrbotten 1909 and Norrbotten 1950s.
- There was a significant difference between the larger body masses of male populations from Finnmark 1869, Norrbotten 1909 and Norrbotten 1950s and the smaller body masses of males from Buskerud 1948, Buskerud 1970, Hordaland 1970, Oppland 2006, Jämtland 1950s, Härjedalen 1950s and Lappland 1950s (mountain).
- There was no significant difference between the body masses of male populations from the Norwegian provinces of Buskerud 1948 and Oppland 2006, and the Swedish province of Jämtland 1950s.
- There was no significant difference between the body masses of male populations from the Norwegian provinces of Buskerud 1970 and Hordaland 1970s, but there was a significant difference between the males from these two provinces and all other localities.
- There was a significant difference between the larger body masses of male populations from Buskerud 1948, Oppland 2006 and Jämtland 1950s and the smaller body masses of males from Buskerud 1970 and Hordaland 1970s.
- There was no significant difference between the body masses of male populations from the Swedish provinces of Jamtland 1950s, Harjedalen 1950s, Lappland 1950s (mountain) and the Norwegian province of Oppland 1947.
- There was a significant difference between the larger body masses of male populations from Härjedalen 1950s, Lappland 1950s (mountain) and Oppland 1947 and the smaller body masses of males from Buskerud 1948, Buskerud 1970, Hordaland 1970s and Oppland 2006.
- There was no significant difference between the body masses of the male population from the Swedish province of Lappland 1950s (forest) and all other localities.

Table 4.3. Results of Dunnett's T3 Test for Male *Rangifer tarandus tarandus* from Scandinavia. *R. t. tarandus* were tested to determine whether a significant difference was evident between the body masses of males from Scandinavian localities. The mean difference is significant (*) at p<0.05.

| Locality and | Locality and | Mean | Std. | Sig. | 95% Co | nfidence |
|----------------|------------------------------|------------------------|---------|-------|----------------|----------------|
| Date of | Date of | Difference | Error | | Inte | rval |
| Collection (I) | Collection (J) | (I-J) | | | Lower Bound | Upper Bound |
| Finnmark | Oppland 1947 | 2.45313 | 4.99597 | 1.000 | -20.9909 | 25.8972 |
| 1869 | Buskerud 1948 | 31.37092* | 2.54465 | 0.000 | 22.0698 | 40.6721 |
| | Buskerud 1970 | 41.99210 [*] | 2.77947 | 0.000 | 32.0146 | 51.9696 |
| | Hordaland 1970s | 41.28980 [*] | 2.51118 | 0.000 | 32.0748 | 50.5048 |
| | Oppland 2006 | 29.52909* | 3.01270 | 0.000 | 18.5761 | 40.4820 |
| | Norrbotten 1909 | -6.33520 | 3.35917 | 0.968 | -18.1187 | 5.4483 |
| | Jämtland 1950s | 23.71658 [*] | 3.40104 | 0.000 | 11.7598 | 35.6733 |
| | Härjedalen 1950s | 17.32358 [*] | 3.09796 | 0.000 | 6.3814 | 28.2657 |
| | Lappland 1950s (mountain) | 16.78333 [*] | 2.76732 | 0.000 | 6.8771 | 26.6896 |
| | Lappland 1950s (forest) | 8.43480 | 6.95356 | 0.999 | -24.7893 | 41.6589 |
| | Norrbotten 1950s | -0.98417 | 3.94399 | 1.000 | -15.0372 | 13.0689 |
| Oppland | Finnmark 1869 | -2.45313 | 4.99597 | 1.000 | -25.8972 | 20.9909 |
| 1947 | Buskerud 1948 | 28.91778 [*] | 4.54296 | 0.023 | 4.5216 | 53.3140 |
| | Buskerud 1970 | 39.53896* | 4.67853 | 0.004 | 15.5897 | 63.4882 |
| | Hordaland 1970s | 38.83667* | 4.52430 | 0.006 | 14.3651 | 63.3082 |
| | Oppland 2006 | 27.07595 [*] | 4.82074 | 0.025 | 3.3735 | 50.7784 |
| | Norrbotten 1909 | -8.78833 | 5.04453 | 0.944 | -32.1326 | 14.5560 |
| | Jämtland 1950s | 21.26344 | 5.07250 | 0.083 | -2.0751 | 44.6020 |
| | Härjedalen 1950s | 14.87044 | 4.87448 | 0.356 | -8.6610 | 38.4019 |
| | Lappland 1950s (mountain) | 14.33020 | 4.67133 | 0.370 | -9.6301 | 38.2905 |
| | Lappland 1950s (forest) | 5.98167 | 7.90666 | 1.000 | -28.7251 | 40.6885 |
| | Norrbotten 1950s | -3.43730 | 5.45145 | 1.000 | -26.9165 | 20.0419 |
| Buskerud | Finnmark 1869 | -31.37092 [*] | 2.54465 | 0.000 | -40.6721 | -22.0698 |
| 1948 | Oppland 1947 | -28.91778 [*] | 4.54296 | 0.023 | -53.3140 | -4.5216 |
| | Buskerud 1970 | 10.62118 [*] | 1.84506 | 0.000 | 4.1600 | 17.0823 |
| | Hordaland 1970s | 9.91888 [*] | 1.40884 | 0.000 | 5.1123 | 14.7255 |
| | Oppland 2006 | -1.84183 | 2.18063 | 1.000 | -10.2026 | 6.5189 |
| | Norrbotten 1909 | -37.70612* | 2.63871 | 0.000 | -46.9426 | -28.4696 |
| | Jämtland 1950s | -7.65434 | 2.69181 | 0.301 | -17.1502 | 1.8415 |
| | Härjedalen 1950s | -14.04734* | 2.29698 | 0.000 | -22.0800 | -6.0147 |
| | Lappland 1950s (mountain) | -14.58758* | 1.82670 | 0.000 | -20.8613 | -8.3138 |

| | Lappland 1950s | -22.93612 | 6.63557 | 0.252 | -56.7850 | 10.9128 |
|-----------|------------------------------|------------------------|----------|-------|----------|----------|
| | Norrbotten | -32.35508 [*] | 3.35169 | 0.000 | -44.6067 | -20.1035 |
| | 1950s | 44.0004.0* | 0 770 47 | 0.000 | F4 0000 | 22.04.40 |
| Buskerud | Finnmark 1869 | -41.99210 | 2.77947 | 0.000 | -51.9696 | -32.0140 |
| 1970 | Oppland 1947 | -39.53696 | 4.07000 | 0.004 | -03.4002 | -15.5697 |
| | Buskerud 1948 | -10.02110 | 1.04000 | 0.000 | -17.0023 | -4.1000 |
| | Hordaland 1970s | -0.70230 | 1.79002 | 1.000 | -7.0157 | 5.0111 |
| | Oppland 2006 | -12.46301 [*] | 2.45058 | 0.001 | -21.5142 | -3.4118 |
| | Norrbotten | -48.32730 [*] | 2.86583 | 0.000 | -58.3036 | -38.3510 |
| | Jämtland 1950s | -18.27552 [*] | 2.91480 | 0.000 | -28.4796 | -8.0714 |
| | Härjedalen | -24.66852* | 2.55467 | 0.000 | -33.5629 | -15.7741 |
| | 1950s | 05.00070* | | | 00.0004 | 17 700 1 |
| | Lappland 1950s (mountain) | -25.20876 | 2.14174 | 0.000 | -32.6284 | -17.7891 |
| | Lappland 1950s (forest) | -33.55730 | 6.72912 | 0.050 | -67.1695 | 0.0549 |
| | Norrbotten 1950s | -42.97626 [*] | 3.53328 | 0.000 | -55.7223 | -30.2303 |
| Hordaland | Finnmark 1869 | -41.28980 [*] | 2.51118 | 0.000 | -50.5048 | -32.0748 |
| 1970s | Oppland 1947 | -38.83667* | 4.52430 | 0.006 | -63.3082 | -14.3651 |
| | Buskerud 1948 | -9.91888 [*] | 1.40884 | 0.000 | -14.7255 | -5.1123 |
| | Buskerud 1970 | 0.70230 | 1.79862 | 1.000 | -5.6111 | 7.0157 |
| | Oppland 2006 | -11.76071 [*] | 2.14148 | 0.001 | -20.0419 | -3.4796 |
| | Norrbotten 1909 | -47.62500 [*] | 2.60645 | 0.000 | -56.7630 | -38.4870 |
| | Jämtland 1950s | -17.57322 [*] | 2.66020 | 0.000 | -26.9754 | -8.1711 |
| | Härjedalen 1950s | -23.96622* | 2.25985 | 0.000 | -31.8836 | -16.0489 |
| | Lappland 1950s | -24.50647* | 1.77979 | 0.000 | -30.6206 | -18.3923 |
| | (mountain) | | | | | |
| | Lappland 1950s (forest) | -32.85500 | 6.62281 | 0.058 | -66.7400 | 1.0300 |
| | Norrbotten 1950s | -42.27397* | 3.32636 | 0.000 | -54.4616 | -30.0863 |
| Oppland | Finnmark 1869 | -29.52909 [*] | 3.01270 | 0.000 | -40.4820 | -18.5761 |
| 2006 | Oppland 1947 | -27.07595 [*] | 4.82074 | 0.025 | -50.7784 | -3.3735 |
| | Buskerud 1948 | 1.84183 | 2.18063 | 1.000 | -6.5189 | 10.2026 |
| | Buskerud 1970 | 12.46301 [*] | 2.45058 | 0.001 | 3.4118 | 21.5142 |
| | Hordaland | 11.76071* | 2.14148 | 0.001 | 3.4796 | 20.0419 |
| | Norrbotten | -35.86429 [*] | 3.09255 | 0.000 | -46.8339 | -24.8946 |
| | Jämtland 1950s | -5.81251 | 3.13798 | 0.971 | -16.9748 | 5.3498 |
| | Häriedalen | -12.20551* | 2.80664 | 0.005 | -22.2756 | -2.1354 |
| | 1950s | | | / | | |
| | Lappland 1950s (mountain) | -12.74575 | 2.43679 | 0.001 | -21.7071 | -3.7844 |
| | Lappland 1950s (forest) | -21.09429 | 6.82876 | 0.347 | -54.5261 | 12.3375 |
| | Norrbotten 1950s | -30.51325* | 3.71954 | 0.000 | -43.9342 | -17.0923 |
| | Finnmark 1869 | 6.33520 | 3.35917 | 0.968 | -5.4483 | 18.1187 |

| Norrbotten | Oppland 1947 | 8.78833 | 5.04453 | 0.944 | -14.5560 | 32.1326 |
|------------|----------------|------------------------|---------|-------|----------|----------|
| 1909 | Buskerud 1948 | 37.70612* | 2.63871 | 0.000 | 28.4696 | 46.9426 |
| | Buskerud 1970 | 48.32730 [*] | 2.86583 | 0.000 | 38.3510 | 58.3036 |
| | Hordaland | 47.62500* | 2.60645 | 0.000 | 38.4870 | 56.7630 |
| | 1970s | | | | | |
| | Oppland 2006 | 35.86429* | 3.09255 | 0.000 | 24.8946 | 46.8339 |
| | Jämtland 1950s | 30.05178 [*] | 3.47197 | 0.000 | 18.0200 | 42.0835 |
| | Häriedalen | 23.65878* | 3.17567 | 0.000 | 12.6657 | 34.6518 |
| | 1950s | | | | | |
| | Lappland 1950s | 23.11853 [*] | 2.85405 | 0.000 | 13.2126 | 33.0245 |
| | (mountain) | | | | | |
| | Lappland 1950s | 14.77000 | 6.98853 | 0.800 | -18.3856 | 47.9256 |
| | (forest) | | | | | |
| | Norrbotten | 5.35103 | 4.00532 | 1.000 | -8.7853 | 19.4873 |
| | 1950s | | | | | |
| Jämtland | Finnmark 1869 | -23.71658 [*] | 3.40104 | 0.000 | -35.6733 | -11.7598 |
| 1950s | Oppland 1947 | -21.26344 | 5.07250 | 0.083 | -44.6020 | 2.0751 |
| | Buskerud 1948 | 7.65434 | 2.69181 | 0.301 | -1.8415 | 17.1502 |
| | Buskerud 1970 | 18.27552 [*] | 2.91480 | 0.000 | 8.0714 | 28.4796 |
| | Hordaland | 17.57322 [*] | 2.66020 | 0.000 | 8.1711 | 26.9754 |
| | 1970s | | | | | |
| | Oppland 2006 | 5.81251 | 3.13798 | 0.971 | -5.3498 | 16.9748 |
| | Norrbotten | -30.05178 [*] | 3.47197 | 0.000 | -42.0835 | -18.0200 |
| | 1909 | | | | | |
| | Härjedalen | -6.39300 | 3.21993 | 0.942 | -17.5812 | 4.7952 |
| | 1950s | | | | | |
| | Lappland 1950s | -6.93324 | 2.90321 | 0.672 | -17.0699 | 3.2035 |
| | (mountain) | | | | | |
| | Lappland 1950s | -15.28178 | 7.00875 | 0.768 | -48.4176 | 17.8540 |
| | (forest) | | | | | |
| | Norrbotten | -24.70074 [*] | 4.04050 | 0.000 | -38.9679 | -10.4336 |
| | 1950s | | | | | |
| Härjedalen | Finnmark 1869 | -17.32358 [*] | 3.09796 | 0.000 | -28.2657 | -6.3814 |
| 1950s | Oppland 1947 | -14.87044 | 4.87448 | 0.356 | -38.4019 | 8.6610 |
| | Buskerud 1948 | 14.04734* | 2.29698 | 0.000 | 6.0147 | 22.0800 |
| | Buskerud 1970 | 24.66852 [*] | 2.55467 | 0.000 | 15.7741 | 33.5629 |
| | Hordaland | 23.96622* | 2.25985 | 0.000 | 16.0489 | 31.8836 |
| | 1970s | | | | | |
| | Oppland 2006 | 12.20551* | 2.80664 | 0.005 | 2.1354 | 22.2756 |
| | Norrbotten | -23.65878* | 3.17567 | 0.000 | -34.6518 | -12.6657 |
| | 1909 | | | | | |
| | Jämtland 1950s | 6.39300 | 3.21993 | 0.942 | -4.7952 | 17.5812 |
| | Lappland 1950s | -0.54024 | 2.54144 | 1.000 | -9.3454 | 8.2649 |
| | (mountain) | | | | | |
| | Lappland 1950s | -8.88878 | 6.86680 | 0.997 | -42.2240 | 24.4465 |
| | (forest) | | | | | |
| | Norrbotten | -18.30774 | 3.78892 | 0.001 | -31.7858 | -4.8297 |
| L | 1950s | 10 700* | 0 70755 | 0.000 | 00.0000 | 0.077 |
| Lappland | Finnmark 1869 | -16.78333 | 2.76732 | 0.000 | -26.6896 | -6.8771 |
| 1950s | Oppland 1947 | -14.33020 | 4.67133 | 0.370 | -38.2905 | 9.6301 |
| (mountain) | Buskerud 1948 | 14.58758 | 1.82670 | 0.000 | 8.3138 | 20.8613 |
| | Buskerud 1970 | 25.20876 | 2.14174 | 0.000 | 17.7891 | 32.6284 |
| | Hordaland | 24.50647 | 1.77979 | 0.000 | 18.3923 | 30.6206 |
| | 1970s | 40 74575* | 0.40070 | 0.001 | 0.70.1.1 | 04 707 1 |
| | Oppland 2006 | 12.74575 | 2.43679 | 0.001 | 3.7844 | 21.7071 |

| | Norrbotten | -23.11853 [*] | 2.85405 | 0.000 | -33.0245 | -13.2126 |
|------------|------------------------------|------------------------|---------|-------|----------|----------|
| | Jämtland 1950s | 6.93324 | 2.90321 | 0.672 | -3.2035 | 17.0699 |
| | Härjedalen 1950s | 0.54024 | 2.54144 | 1.000 | -8.2649 | 9.3454 |
| | Lappland 1950s (forest) | -8.34853 | 6.72411 | 0.998 | -41.9694 | 25.2723 |
| | Norrbotten 1950s | -17.76750 [*] | 3.52373 | 0.001 | -30.4697 | -5.0653 |
| Lappland | Finnmark 1869 | -8.43480 | 6.95356 | 0.999 | -41.6589 | 24.7893 |
| 1950s | Oppland 1947 | -5.98167 | 7.90666 | 1.000 | -40.6885 | 28.7251 |
| (forest) | Buskerud 1948 | 22.93612 | 6.63557 | 0.252 | -10.9128 | 56.7850 |
| | Buskerud 1970 | 33.55730 | 6.72912 | 0.050 | -0.0549 | 67.1695 |
| | Hordaland 1970s | 32.85500 | 6.62281 | 0.058 | -1.0300 | 66.7400 |
| | Oppland 2006 | 21.09429 | 6.82876 | 0.347 | -12.3375 | 54.5261 |
| | Norrbotten 1909 | -14.77000 | 6.98853 | 0.800 | -47.9256 | 18.3856 |
| | Jämtland 1950s | 15.28178 | 7.00875 | 0.768 | -17.8540 | 48.4176 |
| | Härjedalen 1950s | 8.88878 | 6.86680 | 0.997 | -24.4465 | 42.2240 |
| | Lappland 1950s (mountain) | 8.34853 | 6.72411 | 0.998 | -25.2723 | 41.9694 |
| | Norrbotten 1950s | -9.41897 | 7.28770 | 0.998 | -42.4000 | 23.5620 |
| Norrbotten | Finnmark 1869 | 0.98417 | 3.94399 | 1.000 | -13.0689 | 15.0372 |
| 1950s | Oppland 1947 | 3.43730 | 5.45145 | 1.000 | -20.0419 | 26.9165 |
| | Buskerud 1948 | 32.35508 [*] | 3.35169 | 0.000 | 20.1035 | 44.6067 |
| | Buskerud 1970 | 42.97626 [*] | 3.53328 | 0.000 | 30.2303 | 55.7223 |
| | Hordaland 1970s | 42.27397* | 3.32636 | 0.000 | 30.0863 | 54.4616 |
| | Oppland 2006 | 30.51325* | 3.71954 | 0.000 | 17.0923 | 43.9342 |
| | Norrbotten 1909 | -5.35103 | 4.00532 | 1.000 | -19.4873 | 8.7853 |
| | Jämtland 1950s | 24.70074 [*] | 4.04050 | 0.000 | 10.4336 | 38.9679 |
| | Härjedalen 1950s | 18.30774 [*] | 3.78892 | 0.001 | 4.8297 | 31.7858 |
| | Lappland 1950s (mountain) | 17.76750* | 3.52373 | 0.001 | 5.0653 | 30.4697 |
| | Lappland 1950s (forest) | 9.41897 | 7.28770 | 0.998 | -23.5620 | 42.4000 |

Between the female populations from each locality, the one-way ANOVA was significant ($F_{(7,628)}$ =40.660, p=0.0001) and therefore there was a statistically significant difference in body mass between localities. Levene's test for equal variance was also significant ($F_{(7,628)}$ =9.513, p=0.0001) and indicative of unequal variances. Therefore, body masses could be further analysed using the *post hoc* test Dunnett's T3 to compare the differences between each locality (**Table 4.4**). The results of this test are summarised below.

• There was no significant difference between the body masses of female populations from the Norwegian province of Buskerud 1948 and both Buskerud

1970 and Hordaland 1970s, but there was a significant difference between the smaller body masses of female populations at Buskerud 1970 and the larger body masses of females at Hordaland 1970s.

- Similarly, there was no significant difference between the body masses of female populations from the Swedish provinces of Jämtland 1950s, Härjedalen 1950s, Lappland 1950s (mountain) and Norrbotten 1950s.
- There was a significant difference between the smaller body masses of female populations from the Norwegian provinces of Buskerud 1948, Buskerud 1970 and Hordaland 1970s, and the larger body masses of females from the Swedish provinces of Jamtland 1950s, Harjedalen 1950s and Lappland 1950s (mountain).
- There was also a significant difference between the larger body mass of female populations from Norrbotten 1950s and the smaller body masses of females at Buskerud 1948, Buskerud 1970, Hordaland 1970s and Oppland 2006.
- There was a significant difference between the larger body masses of female populations at Oppland 2006 and the smaller body masses of females at Buskerud 1948, Buskerud 1970 and Hordaland 1970s.

| Table 4.4. Results of Dunnett's T3 Test for Female Rangifer tarandus tarandus from | | | | | | | | | |
|--|------------|---------|--------------|----------|--|--|--|--|--|
| Scandinavia. <i>R. t. tarandus</i> were tested to determine whether a significant difference | | | | | | | | | |
| was evident between the body masses of fema | les from S | candina | vian localit | ies. The | | | | | |
| mean difference is significant (*) at p<0.05. | | | | | | | | | |
| | | | | | | | | | |

| Locality and Date of | Locality and Date of | Mean Difference | Std. Error | Sig. | 95% Cor Inte | nfidence rval |
|-------------------------|---------------------------------|------------------------|---------------|-------|-----------------|------------------|
| Collection (I) | Collection (J) | (I-J) | | | Lower Bound | Upper Bound |
| Buskerud | Buskerud 1970 | 1.30924 | 1.16853 | 1.000 | -2.4137 | 5.0322 |
| 1948 | Hordaland 1970s | -3.38360 | 1.16991 | 0.118 | -7.1089 | 0.3417 |
| | Oppland 2006 | -11.07690* | 1.44829 | 0.000 | -15.6694 | -6.4845 |
| | Jämtland 1950s | -15.35848* | 1.88832 | 0.000 | -21.4832 | -9.2338 |
| | Härjedalen 1950s | -21.53467* | 4.09338 | 0.000 | -35.4185 | -7.6508 |
| | Lappland 1950s (mountain) | -17.21110 [*] | 2.61617 | 0.000 | -26.2480 | -8.1742 |
| | Norrbotten 1950s | -28.83943* | 4.39150 | 0.001 | -45.6724 | -12.0064 |
| Buskerud | Buskerud 1948 | -1.30924 | 1.16853 | 1.000 | -5.0322 | 2.4137 |
| 1970 | Hordaland 1970s | -4.69284 [*] | 1.02275 | 0.000 | -7.9019 | -1.4838 |
| | Oppland 2006 | -12.38614 [*] | 1.33224 | 0.000 | -16.5956 | -8.1767 |
| | Jämtland 1950s | -16.66772* | 1.80085 | 0.000 | -22.5392 | -10.7963 |
| | Härjedalen 1950s | -22.84391* | 4.05378 | 0.000 | -36.6375 | -9.0503 |

| | Lappland | -18.52034 [*] | 2.55376 | 0.000 | -27.4261 | -9.6146 |
|--------------|---------------------|------------------------|----------|-------|----------|----------|
| | 1950s | | | | | |
| | (mountain) | | | | | |
| | Norrbotten | -30.14867* | 4.35461 | 0.000 | -46.9545 | -13.3429 |
| | 1950s | | | | | |
| Hordaland | Buskerud 1948 | 3.38360 | 1.16991 | 0.118 | -0.3417 | 7.1089 |
| 1970s | Buskerud 1970 | 4.69284* | 1.02275 | 0.000 | 1.4838 | 7.9019 |
| | Oppland 2006 | -7.69330 [*] | 1.33345 | 0.000 | -11.9052 | -3.4814 |
| | Jämtland | -11.97488 [*] | 1.80175 | 0.000 | -17.8483 | -6.1015 |
| | 1950s | | | | | |
| | Härjedalen 1950s | -18.15107 | 4.05418 | 0.003 | -31.9455 | -4.3566 |
| | Lappland | -13.82750 [*] | 2.55439 | 0.000 | -22.7343 | -4.9207 |
| | 1950s | | | | | |
| | (mountain) | | | | | |
| | Norrbotten | -25.45583 [*] | 4.35498 | 0.002 | -42.2618 | -8.6498 |
| | 1950s | | | | | |
| Oppland 2006 | Buskerud 1948 | 11.07690 [*] | 1.44829 | 0.000 | 6.4845 | 15.6694 |
| | Buskerud 1970 | 12.38614 [*] | 1.33224 | 0.000 | 8.1767 | 16.5956 |
| | Hordaland | 7.69330* | 1.33345 | 0.000 | 3.4814 | 11.9052 |
| | 1970s | | | | | |
| | Jämtland | -4.28158 | 1.99377 | 0.599 | -10.6991 | 2.1359 |
| | 1950s | 40 45777 | 4.4.4000 | 0.005 | 04.45.40 | 0 500 4 |
| | Harjedalen 1950s | -10.45777 | 4.14309 | 0.335 | -24.4549 | 3.5394 |
| | Lappland | -6.13420 | 2.69328 | 0.508 | -15.3347 | 3.0663 |
| | 1950s | | | | | |
| | (mountain) | | | | | |
| | Norrbotten | -17.76253 [*] | 4.43787 | 0.035 | -34.6329 | -0.8922 |
| | 1950s | | | | | |
| Jämtland | Buskerud 1948 | 15.35848 [*] | 1.88832 | 0.000 | 9.2338 | 21.4832 |
| 1950s | Buskerud 1970 | 16.66772* | 1.80085 | 0.000 | 10.7963 | 22.5392 |
| | Hordaland | 11.97488 [*] | 1.80175 | 0.000 | 6.1015 | 17.8483 |
| | 1970s | | | | | |
| | Oppland 2006 | 4.28158 | 1.99377 | 0.599 | -2.1359 | 10.6991 |
| | Härjedalen 1950s | -6.17619 | 4.31664 | 0.981 | -20.6017 | 8.2493 |
| | Lappland | -1.85262 | 2.95330 | 1.000 | -11.7171 | 8.0119 |
| | 1950s | | | | | |
| | (mountain) | | | | | |
| | Norrbotten | -13.48096 | 4.60031 | 0.201 | -30.5359 | 3.5740 |
| Häriedalen | Buskerud 1948 | 21.53467 [*] | 4.09338 | 0.000 | 7.6508 | 35.4185 |
| 1950s | Buskerud 1970 | 22.84391 [*] | 4.05378 | 0.000 | 9.0503 | 36.6375 |
| | Hordaland | 18.15107 [*] | 4.05418 | 0.003 | 4.3566 | 31.9455 |
| | 1970s | | | | | |
| | Oppland 2006 | 10.45777 | 4.14309 | 0.335 | -3.5394 | 24.4549 |
| | Jämtland | 6.17619 | 4.31664 | 0.981 | -8.2493 | 20.6017 |
| | 1950s | | | | | |
| | Lappland | 4.32357 | 4.68103 | 1.000 | -11.1603 | 19.8075 |
| | 1950s | | | | | |
| | (mountain) | | | | | |
| | Norrbotten | -7.30476 | 5.86114 | 0.996 | -27.2189 | 12.6094 |
| | 1950s | · | | | | |
| | Buskerud 1948 | 17.21110 [*] | 2.61617 | 0.000 | 8.1742 | 26.2480 |

| Lappland | Buskerud 1970 | 18.52034 [*] | 2.55376 | 0.000 | 9.6146 | 27.4261 |
|------------|---------------|-----------------------|---------|-------|----------|---------|
| 1950s | Hordaland | 13.82750* | 2.55439 | 0.000 | 4.9207 | 22.7343 |
| (mountain) | 1970s | | | | | |
| | Oppland 2006 | 6.13420 | 2.69328 | 0.508 | -3.0663 | 15.3347 |
| | Jämtland | 1.85262 | 2.95330 | 1.000 | -8.0119 | 11.7171 |
| | 1950s | | | | | |
| | Härjedalen | -4.32357 | 4.68103 | 1.000 | -19.8075 | 11.1603 |
| | 1950s | | | | | |
| | Norrbotten | -11.62833 | 4.94383 | 0.470 | -29.3156 | 6.0589 |
| | 1950s | | | | | |
| Norrbotten | Buskerud 1948 | 28.83943 [*] | 4.39150 | 0.001 | 12.0064 | 45.6724 |
| 1950s | Buskerud 1970 | 30.14867* | 4.35461 | 0.000 | 13.3429 | 46.9545 |
| | Hordaland | 25.45583 [*] | 4.35498 | 0.002 | 8.6498 | 42.2618 |
| | 1970s | | | | | |
| | Oppland 2006 | 17.76253 [*] | 4.43787 | 0.035 | 0.8922 | 34.6329 |
| | Jämtland | 13.48096 | 4.60031 | 0.201 | -3.5740 | 30.5359 |
| | 1950s | | | | | |
| | Härjedalen | 7.30476 | 5.86114 | 0.996 | -12.6094 | 27.2189 |
| | 1950s | | | | | |
| | Lappland | 11.62833 | 4.94383 | 0.470 | -6.0589 | 29.3156 |
| | 1950s | | | | | |
| | (mountain) | | | | | |

4.1.3. Svalbard Rangifer tarandus platyrhynchus

As demonstrated in **Figure 4.1**, the lowest average body mass estimates for both males and females were observed from the Svalbard subspecies R. t. playtrhynchus. Specimens from Svalbard were measured from the island of Spitsbergen from 1861, 1960 and 1975 (Table 4.1). Although females were only present from the 1975 collection date, as with the Scandinavian R. t. tarandus, a t-test showed that there was a statistically significant difference (t₄₄=4.119 p=0.0001) between the body masses reconstructed for R. t. platyrhynchus males, where n=21, mean=62.18 kg and SD=4.35 kg, and females, where n=25, mean=56.23 kg and SD=5.28 kg, from 1975. Equal variances were assumed from Levene's test which was non-significant (F_{44} =1.332 p=0.255). In 1861, the average body mass reconstructed from a single male from Svalbard was 76.50±3.61 kg (Figure 4.4). Although a larger average body mass of 88.83±4.56 kg was estimated from one male almost one hundred years later in 1960, the smallest estimates of male body mass were observed from Svalbard in 1975 at 62.17±1.98 kg (Figure 4.4). As male populations were present from all three collection dates, a one-way ANOVA was also employed to determine whether there was a significant difference in the body masses of male R. t. playtrhynchus over time. The results of this test were significant (F_(2,84)=39.97, p=0.0001) and therefore there was a statistically significant difference in body mass over the collection dates. Levene's test for equal variance was also significant ($F_{(2,84)}$ =8.096, p=0.001) and indicative of unequal variances. Therefore, body masses could be further analysed using the *post hoc* test Dunnett's T3 which identified differences between each of the three weights (**Table 4.5**). Although no temporal comparison could be made for females, the average estimated body mass from 1975 was 56.23 ± 2.18 kg (**Figure 4.4**).



Figure 4.4. Average Estimated Body Mass of Svalbard *Rangifer tarandus platyrhynchus*. Body mass was reconstructed from the postcrania of *R. t. platyrhynchus* from the island of Spitsbergen in the Svalbard archipelago. Males are represented by a square and females are shown as a diamond. The 95% confidence interval is also presented.

Table 4.5. Results of Dunnett's T3 Test for Male *Rangifer tarandus platyrhynchus* from Svalbard. *R. t. platyrhynchus* were tested to determine whether a significant difference was evident between the body masses of males from different collection dates. The mean difference is significant (*) at p<0.05.

| Locality and Date of | Locality and Date of | Mean Difference | Std. Error | Sig. | 95% Confidence Interval | |
|-------------------------|-------------------------|------------------------|---------------|-------|----------------------------|----------------|
| Collection (I) | Collection (J) | (I-J) | | | Lower Bound | Upper Bound |
| Spitsbergen 1861 | Spitsbergen 1960 | -12.33443* | 2.96968 | 0.000 | -19.6274 | -5.0415 |
| | Spitsbergen 1975 | 14.31969 [*] | 2.01057 | 0.000 | 9.3529 | 19.2865 |
| Spitsbergen 1960 | Spitsbergen 1861 | 12.33443 [*] | 2.96968 | 0.000 | 5.0415 | 19.6274 |
| | Spitsbergen 1975 | 26.65412 [*] | 2.56456 | 0.000 | 20.2748 | 33.0334 |
| Spitsbergen 1975 | Spitsbergen 1861 | -14.31969* | 2.01057 | 0.000 | -19.2865 | -9.3529 |
| | Spitsbergen 1960 | -26.65412 [*] | 2.56456 | 0.000 | -33.0334 | -20.2748 |

4.2. Mechanisms for Variations in Rangifer tarandus Body Size

Specimens from two subspecies of *R. tarandus*, *R. t. tarandus* and *R. t. platyrhynchus*, were studied with a view to identifying the mechanisms responsible for variations in the body sizes of modern populations.

4.2.1. Latitude and Bergmann's Rule

The samples from provinces in Norway and Sweden provide a north-south transect of *R. t. tarandus* from Arctic and Subarctic populations (**Figure 1.3**). As such, the significant differences in body mass observed within Scandinavia (**Table 4.3 and 4.4**) could represent a response to Bergmann's Rule. This stipulates that in the colder climates at higher latitudes, a larger body size and therefore surface area to volume ratio should be favourable within an endothermic species (Mayr, 1956; 1963). This could account for the significant difference in body size between the larger individuals in Finnmark, Norrbotten, and to a smaller extent Jämtland, Härjedalen and Lappland, all more northerly provinces, and the smaller specimens from Buskerud and Hordaland in southern Norway, identifiable both visually (**Figure 4.5**) and statistically (**Table 4.3 and 4.4**) in males and females. The mean difference in body mass between higher and lower latitude provinces ranged from 17.57-42.00 kg for males and 12.00-30.15 kg for females.



Figure 4.5. Average Estimated Body Mass of *Rangifer tarandus tarandus* by Latitude. Reconstructions of Body mass are plotted for Scandinavian mainland provinces, with males represented by a square and females shown as a diamond. The 95% confidence interval is also presented.

An exception to this pattern was observed in the individuals from Oppland (**Figure 4.5**), a province located in southern Norway. The average body mass of 132.18 ± 11.37 kg for males collected during 1947 was more consistent with the size of individuals from Finnmark and Norrbotten in the north, than the more southernly Buskerud or Hordaland (**Table 4.3**). By 2006, the average male body mass from Oppland was 105.11 ± 4.14 kg, significantly lighter than specimens from both Finnmark and Norrbotten, this weight was instead more similar to those from Buskerud 1948 (**Table 4.3**). Because the 1947 average was generated from only one animal, the risk of bias associated with using museum specimens that were potentially derived from trophy hunting must be considered (Collinge, 2001). However, this does suggest that *R. tarandus* do not necessarily obey Bergmann's Rule. As such, a better approach to geographical variations in body size is to focus on determining the mechanisms which account for these differences, rather than using rules of conformity (McNab, 2010; Teplitsky and Millien, 2014).

4.2.2. Mountain and Forest Habitats

The most notable variations in estimates of average body mass were the differences observed between R. tarandus subspecies (Figure 4.1). The morphologies of R. tarandus can be divided into the larger woodland or forest Rangifer tarandus caribou (North America) and Rangifer tarandus fennicus (Europe), and the much smaller barrenground Rangifer tarandus groenlandicus (North America) and mountain Rangifer tarandus tarandus (Europe) (Nieminen and Helle, 1980) (Figure 4.6). The Norwegian and Swedish specimens included in this study all belonged to R. t. tarandus. However, despite representing a mountain rather than woodland subspecies, populations throughout Scandinavia can be further separated into herds that occupy either mountainous or forest regions, between which significant differences persisted. Reconstructions of body mass in both males and females found that there was a significant difference between the larger average estimates of body mass from the forest R. t. tarandus of Finnmark 1969 and Norrbotten (1909 and 1950s), and the smaller average estimates of body mass from Buskerud 1948, Buskerud 1970, Hordaland 1970s and Oppland 2006, which all represent Norwegian mountain herds (Table 4.3 and 4.4). In males, there was also a difference between the Jämtland 1950s, Härjedalen 1950s and Lappland 1950s (mountain) Swedish mountain R. t. tarandus, and the forest specimens (Table 4.3).



Figure 4.6. Body Size Variations in *Rangifer tarandus* Subspecies. Examples of left humeri demonstrate the difference in body size between the woodland *R. t. caribou* subspecies and the mountain *R. t. tarandus* subspecies.

The larger size of the Finnmark and Norrbotten *R. t. tarandus* could be reflective of the taiga forest environments they inhabit, as variations in the consistency of winter snow and ice cover can have an adaptational bearing on *R. tarandus* leg length (Nieminen and Helle, 1980). In hard-packed tundra snow regions, such as the Norwegian mountains, shorter leg lengths are preferred, while deep, soft, taiga snow benefit the longer legs observed in the Fennoscandian wild forest *R. t. fennicus* (Nieminen and Helle, 1980). Therefore, the tolerance for traveling through deep snow, up to 65 cm, is greater in those individuals adapted to taiga areas, compared to the mountains where depths in excess of 50-60 cm cannot be readily traversed (Nieminen and Helle, 1980). The average snow depth recorded from the Abisko station in northern Sweden between 1913-2004 was 51.50 cm (Kohler *et al.*, 2006). This is within the range of *R. tarandus* more suited to taiga snow conditions, which could therefore be an important factor contributing to the larger size of forest *R. t. tarandus* in Scandinavia.

Such variability within a single subspecies is also recognisable in the woodland *R. t. caribou* of North America. *R. t. caribou* can be separated into groups that winter either in forest or alpine areas (Kuzyk *et al.*, 1999). This behaviour is similar to the segregation observable between the migratory mountain and non-migratory forest herds of Norway and Sweden (Jordhøy, 2008; Indrelid and Hufthammer, 2011; Bårdsen *et al.*, 2017). However, although the shoulder height of *R. t. caribou* wintering in forests was around 14 cm larger, snow cover in these areas was not necessarily deeper than in the winter 101

alpine ranges (Kuzyk *et al.*, 1999). As both the mountain and forest wintering individuals registered similar overall body conditions, the variations in body size could not be attributed to either genetic or nutritional controls (Kuzyk *et al.*, 1999). As such, additional factors are clearly significant in determining body size.

External factors may also be responsible for the notable differences observed separately between either mountainous or forest herds. From the forest R. t. tarandus, although there was no significant difference in the size of males from Lappland 1950s (forest), Finnmark and Norrbotten, the size of Lappland 1950s (forest) individuals was not significantly different from any of the mountain herds studied (Table 4.3). Reconstructions of male average body mass from Lappland 1950s (forest) of 126.20+16.04 kg were comparable to known weights of domestic *R. tarandus*, around 128 kg (Puputti and Niskanen, 2008). However, the larger male body masses of 140.97 ± 4.87 kg (1909) and 135.62 ± 6.53 kg (1950s) from Norrbotten, and 134.63 ± 4.80 kg from Finnmark 1969, compared much more favourably with the wild forest *R. tarandus* weights of 143 kg (Puputti and Niskanen, 2008). One explanation for this size difference could be the interbreeding which has been common across northern Fennoscandia between predominantly female R. t. tarandus and male R. t. fennicus, resulting in increasingly similar body sizes and postcranial morphologies (Nieminen and Helle, 1980, Puputti and Niskanen, 2008). However, interbreeding has not been apparent from the genetic studies of populations from this region. In Sweden, although the Norrbotten R. tarandus do appear to be genetically distinct from other mountain R. t. tarandus in Sweden, they can still be attributed to this subspecies (Göran Sjöberg, pers. comm.). Similarly, from both male and female mountain R. t. tarandus, there was a significant difference between the heavier Swedish herds from Härjedalen 1950s and Lappland 1950s (mountain), as well as Jämtland 1950s in females, and the lighter Norwegian herds from Buskerud 1948, Buskerud 1970 and Hordaland 1970s (Table 4.3 and 4.4). Mean differences between the Swedish and Norwegian herds ranged from 14.05-25.14 kg for males and 11.97-22.84 kg for females, suggesting that size in both mountain and forest provinces must also be attributed to more localised herd dynamics.

4.2.3. Herd Size and Population Density

After 40 years of collecting data from multiple *R. tarandus* populations in Svalbard, the Climate-Ecological Observatory for Arctic Tundra (COAT) monitoring programme has demonstrated that the processes which are most influential in determining herd and body size are density and weather (FRAM, 2019). As a density-dependent species, *R. tarandus* are highly susceptible to the pressures exerted by population sizes. Typically,

density dependency occurs when the population exceeds half the ecological carrying capacity (Skogland, 1985). The increased competition during either the winter or summer grazing periods reduces food quantity as well as quality, which has adverse effects on body size, particularly in calves (Courturier *et al.*, 2010; Tallian *et al.*, 2012; Albon *et al.*, 2016). In turn, density also directly affects the response of the herd to climatic conditions, increasing their sensitivity at higher densities (Bårdsen *et al.*, 2017). The Svalbard *R. t. platyrhynchus* are a good example of the density dependence effect; the large herd sizes with a density of 1.75 individuals/km² (Skogland, 1986), unrestricted by predators, have resulted in individuals of much smaller body sizes (Reimers, 1982).

Because both the forest and mountain Swedish *R. t. tarandus* represent semi-domestic herds where meat production is the primary economic goal, body condition should be somewhat regulated (Åhman *et al.*, 2014). This is controlled using a combination of annual slaughter and supplementary feeding, with the aim of stabilising the herd's density below the ecological carrying capacity (Åhman *et al.*, 2014). The fact that the body mass of mountain *R. tarandus* of Sweden from Jämtland, Härjedalen and Lappland (mountain) consistently exceeds their Norwegian counterparts from Buskerud and Hordaland (the last wild mountain herds in Europe) could therefore be indicative of the differences between wild and semi-domestic herds. Although the semi-domesticated herds in Sweden rely more heavily on natural forage than supplementary feeding (Sandström *et al.*, 2016), the provision of additional resources during particularly harsh winters could account for the maintenance of their higher body conditions. However, it is not uncommon for fluctuations in body size to occur, irrespective of this management (Åhman *et al.*, 2014).

The annual monitoring of Swedish *R. t. tarandus* by the individual Sameby's means that data on herd dynamics is available from the Sami Parliament (**Figure 4.7**). For Norrbotten County, which includes both Norrbotten and Lappland, the total number of *R. tarandus* between 1995-2018 averaged 134,920 individuals. This is three times the number of *R. tarandus* recorded for the same period from Jämtland County, which includes Jämtland and Härjedalen, where an average of 44,172 individuals persisted. In contrast, the number of individuals per group in Jämtland was 419, more than double the 184 individuals present in Norrbotten herds. Although the number of *R. tarandus* per group is in itself an average, as the herd sizes of each group manager will vary, this nevertheless provides an overview of the different densities represented by each county. In Norrbotten County, the smaller number of individuals per group and 1950s and Lappland 1950s (forest) to achieve larger body masses, despite the greater total number of *R. tarandus*.



Figure 4.7. Herd Statistics for Swedish *Rangifer tarandus tarandus*. The number of individuals represent the *R. tarandus* present in winter herds, counted after the annual autumn slaughter but before the spring calving. Groups are defined as the number of *R. tarandus* under the responsibility of the group manager. (Source: The Sami Parliament, 2019).

The opposite is therefore true for the Jämtland County *R. tarandus*, whose significantly smaller male and female sizes (**Figure 4.3, Table 4.3**) are potentially the product of the higher densities generated by larger herds, irrespective of the smaller total number of *R. tarandus* present in the region. However, this only reflects the herd statistics for the last 20 years, whereas the *R. tarandus* in this study were mostly collected during the 1950s. Although it is generally understood that *R. t. tarandus* herding in Sweden has become increasingly less regulated during the last century, with more and more free-ranging herds, average densities have remained similar, thereby supporting these differences in

body mass between the forest herds of Norrbotten and the mountain herds of Jämtland County (Moen and Danell, 2003; Bårdsen *et al.*, 2017).

In Norway, Sami populations also herd semi-domestic *R. t. tarandus* across large areas of the north. The largest average estimate of body mass from the Norwegian specimens was from the northern province of Finnmark 1869 and weighed 134.63 ± 4.80 kg. As this was generated from only one animal, there was initial concern that this body mass might not be representative of the size of individuals in this area, instead demonstrating museum collection bias (Collinge, 2001). Furthermore, the reconstruction of a large body mass would appear to contradict the overabundance, and therefore higher density, of *R. tarandus* documented in Finnmark today (Holand *et al.*, 2010). However, the similarity between the Finnmark specimen and the average estimates of body mass from Norrbotten 1909 and 1950s and Lappland 1950s (forest) (**Table 4.3**), where sample sizes were larger (**Table 4.1**), suggest that this was probably not the case. Instead, the Finnmark *R. tarandus* probably follows the same pattern demonstrated in Norrbotten County, where a higher population but smaller individual group size has resulted in individuals with a larger body mass.

The male average body mass from Oppland 1947 was also not significantly different at 132.18±11.37 kg from either the Finnmark 1869, Norrbotten 1909 and 1950s or Lappland 1950s (forest) individuals (Table 4.3). Semi-domestic Norwegian herds extend as far south as Oppland (Villrein, 2020) and could, therefore, account for the size of these individuals. However, Oppland, together with Buskerud and Hordaland, also falls within the range of the wild mountain *R. tarandus* that occupy southern Norway (Villrein, 2020). Although it is unknown from which specific herds the modern Norwegian R. tarandus originated, of the 23 wild *R. tarandus* management areas in southern Norway, herds are divided into those from the central Langfjella mountains, which extend into western Buskerud, or those from the Dovre regions of Oppland (Villrein, 2020). Both Buskerud and Hordaland provide part of the range of the largest wild *R. tarandus* herd in Norway, that of the Hardangervidda plateau. With animal numbers between 6,000 and 19,000 individuals over 8,000 km², the density of the Hardangervidda herd is 0.74 to 2.34 individuals/km² and much higher than any of the Swedish herds (Skogland, 1989; Skogland, 1990). Similarity between the average body masses of R. tarandus from Buskerud and Hordaland collected during the 1970s is therefore to be expected (Figure 4.2), although this was statistically only observed in estimates of males (Table 4.3 and **4.4**), with males of the two provinces weighing 94.43 ± 3.09 kg (Buskerud) and 93.34 ± 1.89 kg (Hordaland) and females weighing 77.39 ± 1.43 kg (Buskerud) and 82.08±1.43 kg (Hordaland). In the Dovre regions of Oppland, a number of smaller herds persist. Representative of these is the Knutshø herd, which contains 500 to 800 animals

over 1,600 km², giving a density of 0.3 to 0.5 individuals/km² (Skogland, 1989). A comparison between the Dovre/Oppland and Hardangervidda/Buskerud herds could be made from samples collected during the 1940s. In addition to the Oppland 1947 sample, male average body mass was also estimated from Buskerud in 1948, but was significantly smaller at 103.26 ± 2.06 kg (**Figure 4.2**, **Table 4.3**). The lower density of *R*. *t. tarandus* in the Dovre region, regardless of whether the Oppland *R. tarandus* belonged to semi-domestic or wild mountain herds, could therefore explain the difference in male body mass between the Oppland 1947 weight and other populations of Norwegian wild mountain *R. t. tarandus*.

Despite the variation between Buskerud and Oppland, male body masses in both regions have decreased significantly from the 1940s (Figure 4.2, Table 4.3). From Buskerud, male average body mass decreased by 9% from 1948 to 1970, whereas from Oppland, male average body mass decreased by 20% from 1947 to 2006. However, throughout the circumpolar range of *R. tarandus*, populations are in decline. The 'Vulnerable' IUCN Red List of Threatened Species status of *R. tarandus*, follows a 40% decline over just three generations - approximately 21-27 years (Gunn, 2016). Similarly, Vors and Boyce (2009) have observed population reductions of 57% in 34 out of 43 of the world's major herds, suggesting global scale threats to the future survival of *R. tarandus*. Although wild Norwegian *R. tarandus* population numbers are partially maintained by hunting quotas (Skogland, 1990), Vors and Boyce (2009) categorise Norway as having a decreasing wild population. Furthermore, between individual R. tarandus herds, the decline in population is not the same everywhere (Figure 4.8). For the Oppland herds of Rondane and Snøhetta, populations have been increasing or stabilising from the 1970s to 2006 (Figure 4.8). In Rondane, this increased recruitment rate has almost doubled the number of animals in the herd (Solberg et al., 2010), with resultant increases in density potentially explaining the lowered average body masses from Oppland 1947 to Oppland 2006. In Buskerud, Hardangervidda population levels have decreased from 1950 to 1970 (Figure 4.8) which would otherwise be expected to increase rather than decrease the size of R. tarandus. However, in recent years, it appears that factors such as weather and hunting have had a much larger influence on the Hardangervidda herds than density dependence (Bargmann et al., 2019).

4.2.4. The Effect of Climate on Recent Decreases in Body Size

In addition to the larger forest individuals already discussed, Norrbotten was also the only Swedish province from which samples were available from two separate collection



Figure 4.8. Herd Statistics for Norwegian *Rangifer tarandus tarandus*. The number of individuals represent the population abundance of herds from Buskerud and Hordaland (Hardangervidda) and Oppland (Rondane and Snøhetta) (Source: Uboni *et al.*, 2016; p.4.).

dates, 1909 and the 1950s. Although male average body mass decreased by 3% over this period, local observations suggest that the *R. tarandus* from Norrbotten are not only significantly smaller today, but almost indistinguishable from the Swedish mountain R. tarandus (Göran Sjöberg and Kjell-Åke Aronsson, pers. comm.). The R. tarandus samples from Norrbotten are from the Rödingträsk group, which belongs to the Udtja herding district. Slaughter data in the form of carcass weights from Udtja show that from 2012-2017, males measured on average 34 kg, equivalent to a live weight of 68 kg (Birgitta Åhman, pers. comm.). Although over the last 20 years (1996-2017), body masses from the region have been relatively stable, or even increasing slightly (Birgitta Åhman, pers. comm.), Norrbotten R. tarandus have nevertheless undergone a 52% reduction in their size since the 1950s. Instead, the Norrbotten 2012-2017 body mass of 68 kg was more consistent with the size of males from Svalbard 1975, which were estimated at 62.17 ± 1.98 kg. The Svalbard R. t. platyrhynchus are characterised by their small size (Flagstad and Røed, 2003), but it is the proximity of recent weights to the 50 kg threshold which is of particular concern. Below this weight, females are more likely to produce smaller calves, or even terminate pregnancies during the winter, placing pressure on the population (Albon et al., 2016). Unfortunately, the equivalent female body mass data has not been available from Norrbotten for 2012-2017. However, an average body mass of 56.23±2.18 kg has been estimated from the Svalbard 1975 females, demonstrating the critical levels these animals are approaching.

On Svalbard, critically low body masses have been attributed to the changing climatic regime. With warmer winter temperatures, the carrying capacity for *R. tarandus* should increase, as summer plant productivity is higher and well grazed individuals enter autumn with greater fecundity and survival potential (Parker *et al.*, 2009; Albon *et al.*, 2016). However, since the 1990s, warmer temperatures have been accompanied by increased levels of precipitation (Peeters *et al.*, 2019). It is this combination of above

freezing air temperatures and the refreezing of rain within the snow-pack (rain-on-snow), which causes the development of a thick, impenetrable ice layer (Vors and Boyce, 2009). This basal ice encapsulates the vegetation, which in Arctic environments is low lying to begin with, to create ice-locked pastures (Peeters *et al.*, 2019). Winter survival is therefore highly dependent on the reserves accumulated during summer grazing, with mass starvation and reductions in body mass affecting multiple generations in a single winter, independent of herd density (Vors and Boyce, 2009; Albon *et al.*, 2016). This, in turn, triggers a cascading effect on the food web, as predators such as the arctic fox exploit the increase in *R. tarandus* remains on the landscape (Hansen *et al.*, 2013).

Between 1994-2015, Albon *et al.* (2016) observed a 12% reduction in the body masses of Svalbard *R. t. platyrhynchus* from 55 kg to 48 kg, which they attributed to increased icing events. Evidently, the significant decrease in body mass from 88.83 ± 4.85 kg in 1960 to 62.17 ± 1.98 kg in 1875 (**Table 4.5**) observed by this research, together with an average female body mass of 56.23 ± 2.18 kg, confirm this trend of lowering body masses to near-critical levels.

Rain-on-snow events are still relatively uncommon throughout the Arctic. However, as a high Arctic island, Svalbard may represent an early warning for the pressures which may already be apparent in Norrbotten (Hansen et al., 2019a). In addition to decreases in body mass to near critical levels (Albon et al., 2016), research on the response of Svalbard R. t. platyrhynchus has lent support to the resilience of R. tarandus during these icier winters. Following a rain-on-snow event the population collapses. However, using demographic population modelling, work by Hansen et al. (2019a) suggests that instead of destabilising the population entirely, this leaves a herd composed of more resilient individuals, primarily those of prime age and health. Now part of a lower density herd, these individuals continue to build their reserves and reduce the sensitivity of the population to frequent rain-on-snow events. It was estimated that it would take seven years to return to the pre-collapse population structure. Therefore, if rain-on-snow events occur less often than this, the population will once again crash. Studies of multiple R. tarandus herds between 1945-2012 have not found any indication that Swedish populations have been experiencing large-scale herd collapses as would be expected from increases in rain-on-snow events (Åhman et al., 2014; Bårdsen et al., 2017). Where significant declines have been observed on the local scale, these have been associated with increasing predation from either lynx (Lynx lynx, Linnaeus, 1758) or wolverine (Gulo gulo, Linnaeus, 1758), rather than changes in body condition or density (Åhman et al., 2014; Bårdsen et al., 2017).
4.2.5. Vegetation Changes and Dietary Plasticity

A further buffer against the effects of climatic changes is the ability of *R. tarandus* to occupy both grazing and browsing niches (Hansen *et al.*, 2019b). As such, *R. tarandus* are generalists whose dietary plasticity enables them to exploit a range of vascular plants, bryophytes and lichens in order to survive (Skogland, 1984; Hansen *et al.*, 2019b). Nowhere is this more evident than in Svalbard. As the amount of sea-ice has decreased, *R. tarandus* on Svalbard have become increasingly isolated in their ranges (Hansen *et al.*, 2019b). With access to terrestrial forage further restricted by ice-locked pastures, the *R. tarandus* of Svalbard have responded by utilising marine resources, in particular kelp (Hansen *et al.*, 2019b). These appear to be comparable to terrestrial plants in terms of their nutritional value and demonstrates the underlying adaptability of *R. tarandus* to changing environments (Hansen *et al.*, 2019b).

Nevertheless, in Sweden, without substantial evidence for either population crashes or the frequency of rain-on-snow and ice-locked pastures, neither effect can directly account for the large reduction in body mass observed from Norrbotten. One change in the Swedish landscape, which has also occurred from the 1950s to the present day, is the decline in lichen-rich habitats. For both the forest and mountain *R. t. tarandus*, lichen provides an important winter resource in open coniferous forests (Sandström et al., 2016). Between 1953-2013, data from the Swedish National Forest Inventory has reported a 71% decline in the amount of productive lichen-rich forests, with only 0.41 million ha remaining (Sandström et al., 2016). Furthermore, these declines vary regionally, with Jämtland County losing 55% of lichen cover, compared to the inland and coastal areas of Norrbotten County which have lost 78% and 74% respectively (Sandström et al., 2016). As forest herds, the non-migratory R. tarandus of Norrbotten are dependent on the coniferous forests year-round. The loss of this important winter resource is clearly not counteracted by either supplementary feeding or the dietary plasticity of *R. tarandus*. The substantial decline in lichen from the 1950s onwards could therefore explain the reduction in male average body mass from 135.62 ± 6.53 kg during the 1950s, to 68 kg in the 2010s.

Overgrazing is a common cause for the decline of lichen, with *R. t. platyrhynchus* from Svalbard typifying the reductions in body mass associated with the loss of this resource (Reimers, 1982). However, the vegetational change in Sweden has been synchronous throughout the country, including areas outside of the defined herding ranges of *R. tarandus* (Sandström *et al.*, 2016). Human activity can also have a negative impact on the availability of *R. tarandus* forage. In northern Sweden, forestry and husbandry practices have co-existed for many years but, as forestry expands, lichen decreases as new forest growth increases the density of coniferous stands (St. John *et al.*, 2016). As

denser forests provide insufficient light levels for lichen growth, the increasing precipitation of Arctic environments instead supports the growth of the mosses which are now dominating 73% of the once lichen-rich forests (Sandström *et al.*, 2016). Similar changes in vegetation have also been observed in Norway in the Dovre region of Oppland. Lichen is a key component of winter diets in Dovre *R. tarandus*, but between 2001-2015, there has been a decline in lichen richness as bryophytes such as mosses outcompete them (Bignon-Lau *et al.*, 2017; Vanneste *et al.*, 2017). Such forage limitation could therefore have contributed to the significantly reduced body mass of Oppland *R. tarandus* in 2006. A primary cause of this vegetation change has been suggested to be climate, linked to a 0.87°C rise in temperature and 18% increase in precipitation recorded between 1900-2014 in Norway (Vanneste *et al.*, 2017). However, like Sweden, forestry is also an important component of the inland regions of southern Norway, which account for 75% of the domestic commercial timber supply (Vanneste *et al.*, 2017). Therefore, the interaction between forestry and climatic changes are likely to have been as significant for lichen growth in southern Norway as they have been in northern Sweden.

4.2.6. Expansion of Human Infrastructure

In addition to the expansion of forestry in Sweden, recent human induced behavioural changes have come from the investment in wind turbines. During both the construction and operation phases, the wind turbines not only require the clearing of old, open coniferous forest, but limit the connectivity between grazing pastures as R. tarandus alter their movements to avoid these sights and sounds by up to 5 km (Skarin et al., 2015; Skarin et al., 2018). For both the Hardangervidda and Dovre R. tarandus herds, the construction of highways and railways in particular, have also provided substantial barriers to migration pathways (Jordhøy, 2008; Indrelid and Hufthammer, 2011). While this has limited the scale of north-south migrations made by the Hardangervidda R. tarandus, west-east migrations are now thought to have completely ceased amongst animals in the Dovre region (Jordhøy, 2008; Indrelid and Hufthammer, 2011). Variations in migrational ranges can have a detrimental effect on *R. tarandus* body size on even a decadal scale (Couturier et al., 2010). For herds undergoing migrations frequently, and over long distances, energy expenditure is proportionally higher for individuals with shorter legs meaning migratory populations will often select for longer leg lengths (Klein et al., 1987; Couturier et al., 2010). As ranges of Norwegian herds contract, the smaller body sizes in Buskerud, Hordaland and Oppland from 1970 onwards could therefore be the result of a more sedentary existence by the respective herds.

4.2.7. Summary of Modern and Historical Body Masses

With the exception of morphological differences at the subspecies level, body mass in modern R. tarandus is dependent on a number of herd specific factors. Broadly, the R. tarandus occupying taiga forest habitats are larger than those from alpine tundra dominated mountain regions, primarily in response to differences in snow and ice cover, as well as group size. However, variations have also been recognised within herds, particularly stemming from changes in population size and therefore density, whether human or naturally induced. In recent years, body mass in a number of herds has approached the near-critical threshold of 50 kg. In Svalbard, this has been linked to warmer temperatures and higher precipitation during the winter, reducing access to forage trapped under ice layers and leading to population crashes. However, similar decreases in body mass observed in Sweden, and to a lesser extent Norway, have instead coincided with reduced lichen growth caused both by the expansion of forestry activities and higher levels of precipitation. Forestry is not the only human impact affecting *R. tarandus*. The expansion of roads and railways have provided substantial barriers to migration routes, in turn reducing the adaptive advantage for longer leg lengths. As such, while the changing climatic conditions of the Arctic will test the resilience of *R. tarandus* in the future, the impacts of human activity could be just as damaging.

4.3. Body Mass in Late Pleistocene Rangifer tarandus

Unlike the modern specimens included in this study where sex was known, for Late Pleistocene *R. tarandus*, the identification of males and females was based on the sexual dimorphism expressed within postcranial skeletal elements. This clustering of measurements enabled the average body mass to be reconstructed for individuals of both sexes. **Tables 4.6, 4.7 and 4.8** outline the minimum number of individuals (MNI) included in the average estimates of body mass from the Early Devensian, Middle Devensian/Weichselian and Late Devensian/Weichselian sites studied. These included five British sites from the Early Devensian, 19 sites from Middle Devensian/Weichselian Britain and Ireland, Belgium, Germany and the Netherlands, and 10 Late Devensian/Weichselian sites that ranged from Britain, Belgium, Denmark and France. The full list of speciments studied, as well as the individual estimates of body mass, is included as Supplementary Data **(SD 1-8, SD 10)**.

As with the modern specimens, outliers were removed following the visual inspection of histograms and Q-Q plots, prior to the statistical analysis of body mass estimates. Males and females from each site were subsequently assessed for normality using the Shapiro-

Wilks test. The results of these analyses all showed a statistically non-significant nonnormal distribution at p>0.05 (**Appendix 4.3**), enabling the reliable application of parametric tests for difference which assume a normal distribution within a dataset.

| Country | Site | MNI | | |
|---------|------------------------|-------|---------|--|
| | | Males | Females | |
| Britain | Banwell Bone Cave | 5 | 6 | |
| | Isleworth | 4 | 2 | |
| | Picken's Hole (Unit 5) | 3 | 1 | |
| | Stump Cross Cavern | 1 | 1 | |
| | Windy Knoll | 1 | 2 | |

Table 4.6. Early Devensian Rangifer tarandus Specimens by Sex. The number of individuals that body mass was reconstructed for are presented by site.

Table 4.7. Middle Devensian/Weichselian Rangifer tarandus Specimens by Sex. The number of individuals that body mass was reconstructed for are presented by site.

| Country | Site | I | MNI |
|-------------|---------------------------|--------|---------|
| | | Males | Females |
| Britain | Brixham | 4 | 1 |
| | Gully Cave | 1 | 2 |
| | Inchnadamph, Bone Cave | 1 | 1 |
| | Kents Cavern | 3 | 2 |
| | Mammoth Cave | 1 | 1 |
| | Picken's Hole (Unit 3) | 1 | |
| | Pin Hole Cave | 2 | 3 |
| | Robin Hood Cave | | 1 |
| | Sandford Hill | 3 | 8 |
| Polaium | Covet (Traisiàma Coverna) | 2 | G |
| Deigium | Governe Maria Jaanna | 3 | 0 E |
| | | 1 | ວ ວ |
| | Trou Mogrito | ו ס | 2 |
| | | 3 | 3 |
| | | 1 | 1 |
| | riou du Suleau | Z | 4 |
| Germany | Salzgitter-Lebenstedt | 29 | 18 |
| · | Westeregeln | 2 | |
| The | Ellewoutsdiik | 1 | 1 |
| Netherlands | Raalte | 2 | 4 |

| Country | Site | MNI | |
|---------|------------------------|-------|---------|
| | | Males | Females |
| Britain | Chelm's Combe | 3 | 2 |
| | Gully Cave | 2 | 1 |
| | Ossom's Cave | 2 | 1 |
| | Soldier's Hole | 5 | 5 |
| Belgium | Trou de Chaleux | 1 | 2 |
| | Trou des Nutons | | 3 |
| Denmark | Køge Bugt | 5 | 3 |
| | Nørre Lyngby | 1 | 1 |
| France | Abri de Laugerie Haute | 4 | 4 |
| | Abri de la Madeleine | 11 | 19 |

Table 4.8. Late Devensian/Weichselian Rangifer tarandus Specimens by Sex. The number of individuals that body mass was reconstructed for are presented by site.

4.3.1. Early Devensian Body Mass

Early last cold stage *R. tarandus* were only measured from sites in Britain (**Table 4.6**). As both sexes were identified from all sites, t-tests were applied to determine whether there was a statistically significant difference in the size of males and females, when the average mass equation was used to estimate body mass from Late Pleistocene specimens where sex was only inferred and not known. From each of the Early Devensian sites, the average body mass of males and females were significantly different (**Table 4.9**). However, at Stump Cross Cavern, only one male was recorded and therefore the sample size was small. Equal variances were assumed from Levene's test which was non-significant for all localities, with the exception of Banwell Bone Cave where Levene's test was significant and equal variances were not assumed.

The average estimated body mass for males from three of the five British sites was higher than 130 kg (**Figure 4.9**). At Isleworth, males weighed 135.32 ± 6.38 kg, at Banwell Bone Cave, they weighed 131.49 ± 4.86 kg, while at Windy Knoll, a large standard error of 13.39 kg was associated with the male average body mass of 134.07 kg. Similar weights were also observed from the female *R. tarandus* at these sites. At Isleworth, females were recorded as slightly heavier at 102.79 ± 6.11 kg, but from Banwell Bone Cave and Windy Knoll, the average estimated body mass for females was 96.63 ± 2.63 kg and 92.52 ± 6.78 kg respectively. This was also consistent with the female average body mass from Stump Cross Cavern of 94.62 ± 5.03 kg, as well as the Early Devensian layer (Unit 5) from Picken's Hole, whereby an average body mass of 92.93 ± 12.47 kg was reconstructed. However, from both these sites, the male average body masses of 119.06

kg from Stump Cross Cavern and 124.05 ± 10.78 kg from Picken's Hole were the smallest in Britain.

Table 4.9. Results of Levene's Test and Independent Samples T-Test for Early Devensian *Rangifer tarandus*. *R. t. tarandus* were tested to determine whether a significant difference was evident between the body masses of males and females at each site. Results were significant at p<0.05.

| Site | Sex | n | mean | SD | SE of | Levene's test | t-test |
|---------------|-----|----|--------|-------|-------|------------------------------|-----------------------------|
| | | | | | mean | | |
| Banwell | М | 42 | 131.49 | 15.61 | 2.41 | F _{65.472} = 14.651 | t _{65.473} =12.697 |
| Bone Cave | F | 65 | 96.64 | 10.62 | 1.32 | p=0.0001 | p=0.0001 |
| Isleworth | М | 18 | 135.32 | 12.82 | 3.02 | F ₃₀ =1.363 | t ₃₀ =7.669 |
| | F | 14 | 102.79 | 10.58 | 2.83 | p=0.252 | p=0.0001 |
| Picken's | М | 10 | 124.05 | 15.07 | 4.77 | F ₁₂ =0.725 | t ₁₂ =3.859 |
| Hole (Unit 5) | F | 4 | 92.93 | 7.84 | 3.92 | p=0.411 | p=0.002 |
| Stump Cross | М | 1 | 119.06 | | | | t ₁₁ =2.964 |
| Cavern | F | 12 | 94.62 | 7.92 | 2.29 | | p=0.013 |
| Windy Knoll | Μ | 4 | 134.08 | 8.41 | 4.21 | F ₈ =0.539 | t ₈ =8.874 |
| | F | 6 | 92.52 | 6.46 | 2.64 | p=0.484 | p=0.0001 |



Figure 4.9. Average Estimated Body Mass of *Rangifer tarandus* from Early Devensian Sites. Body mass is reconstructed from the postcrania of Early Devensian *R. tarandus* from sites in Britain including Banwell Bone Cave (BBC), Isleworth (I), Picken's Hole Unit 5 (PicH), Stump Cross Cavern (STC) and Windy Knoll (WK). Males are represented by a square and females are shown as a diamond. The 95% confidence interval is also presented.

Comparisons were also made between the Early Devensian sites using a one-way ANOVA, to separately test the differences between male and female body mass reconstructions. Between the male populations from each site, which did not include the individual from Stump Cross Cavern due to the small sample size (n<2), the one-way ANOVA was non-significant ($F_{(3,70)}$ =1.311, p=0.278) and therefore there was no significant difference in body mass between the Early Devensian sites. Levene's test for

equal variance was non-significant ($F_{(3,70)}$ =1.451, p=0.235) and indicative of equal variances. Between the female populations from each site, the one-way ANOVA was also non-significant ($F_{(4.96)}$ =1.797, p=0.136) indicating that there was no significant difference in body masses. Levene's test for equal variance was non-significant ($F_{(4.96)}$ =0.426, p=0.789) and assumed equal variances.

4.3.2. Middle Devensian/Weichselian Body Mass

Average estimates of body mass were reconstructed for Middle Devensian/Weichselian R. tarandus from five countries: Britain and Ireland, Belgium, Germany and the Netherlands (Table 4.7). With the exception of Picken's Hole (Unit 3), Robin Hood Cave and Westeregeln, both sexes were identified from all mid last cold stage sites. As such, t-tests were applied to determine whether there was a significant difference in the size of males and females when the average mass equation was used to estimate body mass. There was no significant difference in male and female body mass at the sites of Inchnadamph Bone Cave, Trou Al'Wesse, Trou du Moulin and Ellewoutsdijk (Table **4.10**). However, at all four sites, small sample sizes were recorded for at least one of the sexes (Table 4.7). Small sample sizes were also observed from Mammoth Cave (Table 4.7), but at this site, together with all remaining sites from the Middle Devensian/Weichselian, there was a statistically significant difference between the body masses of males and females (Table 4.10). Equal variances were assumed from Levene's test which was non-significant for all localities apart from Trou du Sureau and Salzgitter-Lebenstedt, where Levene's test was significant and equal variances were not assumed.

For Britain and Ireland (**Figure 4.10**), body mass appeared to be consistent between the males and females from the sites of Pin Hole Cave, where males weighed 112.86 ± 8.33 kg and females weighed 89.47 ± 7.00 kg, Sandford Hill, where males weighed 110.46 ± 5.76 kg and females weighed 84.61 ± 3.20 kg, Robin Hood Cave, where females weighed 90.63 kg, and the Middle Devensian layer at Picken's Hole (Unit 3), where males weighed 114.23 kg. Slightly larger individuals were evident from the sites of Gully Cave, where males weighed 123.49 ± 10.58 kg and females weighed 103.74 ± 3.74 kg, and Inchnadamph Bone Cave, where males weighed 120.06 kg and females weighed 92.64 ± 14.20 kg. However, the smallest estimates of body mass from Britain were reconstructed from the site of Brixham Cave, where males weighed 98.92 ± 3.87 kg and females weighed 76.93 ± 5.61 kg. Furthermore, at both Kent's Cavern and Mammoth Cave, the difference in size between the males and females was more pronounced than at other British sites. For males, the average body mass reconstructed from the two sites

was 123.13 ± 6.00 kg at Kent's Cavern and 119.04 kg at the Irish site of Mammoth Cave, compared to the females of 87.41 ± 4.34 kg and 80.19 ± 9.21 kg respectively.

Table 4.10. Results of Levene's Test and Independent Samples T-Test for Middle Devensian/Weichselian *Rangifer tarandus*. *R. t. tarandus* were tested to determine whether a significant difference was evident between the body masses of males and females at each site. Results were significant at p<0.05.

| Site | Sex | n | mean | Std. Dev | Levene's test | t-test |
|---------------|-----|-----|--------|-------------|-----------------------------|------------------------------|
| Brixham | Μ | 16 | 98.92 | 7.25 | F ₂₀ =0.523 | t ₂₀ =6.730 |
| Cave | F | 6 | 76.93 | 5.34 | p=0.478 | p=0.0001 |
| Gully Cave | Μ | 7 | 123.49 | 11.44 | F ₁₅ =1.883 | t ₁₅ =4.835 |
| | F | 10 | 103.74 | 5.23 | p=0.190 | p=0.0001 |
| Inchnadamph | Μ | 1 | 120.06 | | | t ₂ =4.153 |
| Bone Cave | F | 3 | 92.64 | 5.72 | | p=0.053 |
| Kents | Μ | 21 | 123.13 | 13.17 | F ₃₇ =1.941 | t ₃₇ =9.801 |
| Cavern | F | 18 | 87.41 | 8.72 | p=0.172 | p=0.0001 |
| Mammoth | Μ | 2 | 119.04 | 14.75 | F ₆ =1.043 | t ₆ =4.747 |
| Cave | F | 6 | 80.19 | 8.78 | p=0.347 | p=0.003 |
| Pin Hole | Μ | 13 | 112.86 | 13.79 | F ₂₆ =0.276 | t ₂₆ =4.681 |
| Cave | F | 15 | 89.47 | 12.65 | p=0.604 | p=0.0001 |
| Sandford Hill | Μ | 15 | 110.46 | 10.39 | F ₆₅ =0.185 | t ₆₅ =7.820 |
| | F | 52 | 84.61 | 11.51 | p=0.669 | p=0.0001 |
| Goyet | Μ | 15 | 122.66 | 14.04 | F ₄₉ =0.148 | t ₄₉ =7.470 |
| (Troisième | F | 36 | 91.77 | 13.21 | p=0.702 | p=0.0001 |
| Caverne) | | | | | | |
| Caverne | Μ | 6 | 120.60 | 8.38 | F ₂₆ =0.102 | t ₂₆ =6.159 |
| Marie- | F | 22 | 91.41 | 10.70 | p=0.752 | p=0.0001 |
| Jeanne | | | | | | |
| Trou | Μ | 1 | 122.42 | | | t ₆ =2.279 |
| Al'Wesse | F | 7 | 92.93 | 12.11 | | p=0.063 |
| Trou Magrite | Μ | 16 | 134.65 | 11.98 | F ₄₂ =3.542 | t ₄₂ =11.089 |
| | F | 28 | 86.73 | 14.70 | p=0.067 | p=0.001 |
| Trou du | Μ | 1 | 120.17 | | | t₅=2.436 |
| Moulin | F | 6 | 95.90 | 9.23 | | p=0.59 |
| Trou du | Μ | 20 | 127.42 | 19.94 | F _{29.910} =4.178 | t _{29.910} =7.023 |
| Sureau | F | 28 | 91.83 | 12.74 | p=0.047 | p=0.001 |
| Salzgitter- | Μ | 251 | 107.10 | 9.23 | F _{334.065} =9.939 | t _{334.065} =23.319 |
| Lebenstedt | F | 137 | 85.73 | 7.40 | p=0.002 | p=0.0001 |
| Ellewoutsdijk | Μ | 2 | 119.32 | 4.77 | | t ₁ =5.205 |
| | F | 1 | 88.94 | | | p=0.121 |
| Raatle | Μ | 16 | 112.08 | 8.56 | F _{22.827} =6.504 | t _{22.827} =10.657 |
| | F | 19 | 86.36 | 4.85 | p=0.016 | p=0.0001 |

The largest estimates of body mass from Middle Weichselian *R. tarandus* were reconstructed from sites located in Belgium (**Figure 4.10**). From the Troisième Caverne at Goyet, males weighed 122.66 ± 7.77 kg and females weighed 91.77 ± 4.47 kg, from Caverne Marie-Jeanne, males weighed 120.60 ± 8.79 kg and females weighed of 91.41 ± 4.74 kg, from Trou Al'Wesse, males weighed 122.42 kg and females weighed 92.93 ± 11.20 kg, and from Trou du Moulin, males weighed 120.17 kg and females

weighed 95.90 ± 9.68 kg. However, it was the sites of Trou Magrite and Trou du Sureau that yielded both the heaviest male and lightest female estimates of average body mass. Male average body mass was estimated at 134.65 ± 6.38 kg for Trou Magrite and 127.42 ± 9.33 kg for Trou du Sureau, while female average body masses were estimated at 86.73 ± 5.70 kg for Trou Magrite and 91.83 ± 4.94 kg for Trou du Sureau.

From Germany (**Figure 4.10**), the males measured from Salzgitter-Lebenstedt, which weighed 107.10 ± 1.15 kg, were lighter than those from Westeregeln, which weighed 125.42 ± 9.37 kg. Females were only recorded from Salzgitter-Lebenstedt and weighed 85.73 ± 1.25 kg. However, from the Netherlands, both male and female body mass was reconstructed from the two sites of Ellewoutsdijk and Raalte (**Figure 4.10**). Male average body mass was estimated at 119.32 kg for Ellewoutsdijk and 112.08 ± 4.56 kg for Raalte, while female average body masses were estimated at 88.94 kg for Ellewoutsdijk and 86.36 ± 2.34 kg for Raalte.



Figure 4.10. Average Estimated Body Mass of *Rangifer tarandus* from Middle Devensian/Weichselian Sites. Body mass is reconstructed from the postcrania of Middle Devensian/Weichselian *R. tarandus* from sites in Britain and Ireland including Brixham Cave (BC), Gully Cave (GC), Inchnadamph Bone Cave, (In-B), Kent's Cavern (KC), Mammoth Cave (MC), Picken's Hole Unit 3 (PicH), Pin Hole Cave (PHC), Robin Hood Cave (RHC) and Sandford Hill (SH), sites in Belgium including Goyet Troisième Caverne (G3e), Caverne Marie-Jeanne (CMJ), Trou Al'Wesse (TAW), Trou Magritte (TMa), Trou du Moulin (TMo) and Trou du Sureau (TS), sites in Germany including Salzgitter-Lebenstedt (SL) and Westeregeln (W), and sites in The Netherlands including Ellewoutsdijk (E) and Raalte (R). Males are represented by a square and females are shown as a diamond. The 95% confidence interval is also presented. The legend gives an indication of the colour representing each country.

Comparisons were also made between the Middle Devensian/Weichselian sites using a one-way ANOVA, to separately test the differences between male and female body mass

reconstructions. The sites of Inchnadamph Bone Cave, Mammoth Cave, Picken's Hole (Unit 3), Trou Al'Wesse, Trou du Moulin and Ellewoutsdijk were not included in the analysis of males due to small sample sizes (n<2). Between the male populations from each site, the one-way ANOVA was significant ($F_{(11,394)}$ =22.961, p=0.0001) and therefore there was a significant difference in body mass. Levene's test for equal variance was significant ($F_{(11,394)}$ =3.955, p=0.0001) and indicative of unequal variances. Therefore, body masses could be further analysed using the *post hoc* test Dunnett's T3 to compare the differences between each site (**Table 4.11**). The results of this test are summarised below.

- There was no significant difference between the body masses of male populations from the British sites of Brixham Cave, Pin Hole Cave and Sandford Hill, but there was a significant difference between the smaller body masses of male populations at Brixham Cave and all remaining Middle Devensian/Weichselian sites.
- There was a significant difference between the smaller body masses of male populations at Salzgitter-Lebenstedt and the larger body masses of males at Kent's Cavern, Goyet, Trou du Sureau and Trou Magrite, as well as the smaller body masses of males at Brixham Cave.
- There was a significant difference between the larger body masses of male populations at Trou Magrite and the smaller body masses of males at Brixham Cave, Pin Hole Cave, Sandford Hill, Salzgitter-Lebenstedt and Raalte.
- There was no significant difference between all remaining combinations of sites.

| | | | | - | | |
|----------|--------------------------|------------------------|---------------|-------|-----------------|------------------|
| Site (I) | Site (J) | Mean Difference | Std. Error | Sig. | 95% Cor Inte | nfidence rval |
| | | (I-J) | | | Lower Bound | Upper Bound |
| Brixham | Gully Cave | -24.56277 [*] | 4.68742 | 0.025 | -46.4055 | -2.7200 |
| Cave | Kents Cavern | -24.20039 [*] | 3.39800 | 0.000 | -36.6795 | -11.7213 |
| | Pin Hole Cave | -13.94024 | 4.23314 | 0.176 | -30.6652 | 2.7847 |
| | Sandford Hill | -11.53429 | 3.23884 | 0.081 | -23.7364 | 0.6679 |
| | Goyet | -23.73029 [*] | 4.05354 | 0.001 | -39.3449 | -8.1157 |
| | Caverne Marie- Jeanne | -21.68229 [*] | 3.87191 | 0.018 | -39.8638 | -3.5008 |
| | Trou Magrite | -35.72875 [*] | 3.50073 | 0.000 | -48.9275 | -22.5300 |
| | Trou du Sureau | -28.49663 [*] | 4.81409 | 0.000 | -46.6277 | -10.3655 |
| | Westeregeln | -26.49263* | 4.52063 | 0.003 | -45.4245 | -7.5608 |
| | Salzgitter- | -8.17240 [*] | 1.90500 | 0.023 | -15.6395 | -0.7053 |
| | Lebenstedt | | | | | |
| | Raalte | -13.15312 [*] | 2.80564 | 0.004 | -23.5504 | -2.7559 |

Table 4.11. Results of Dunnett's T3 Test for Male *Rangifer tarandus* from Middle Devensian/Weichselian Sites. *R. tarandus* were tested to determine whether a significant difference was evident between the body masses of males from different fossil sites. The mean difference is significant (*) at p<0.05.

| Gully Cave | Brixham Cave | 24.56277* | 4.68742 | 0.025 | 2.7200 | 46.4055 |
|------------|----------------|------------------------|---------|-------|----------|---------|
| , | Kents Cavern | 0.36238 | 5.19023 | 1.000 | -21.6514 | 22.3762 |
| | Pin Hole Cave | 10.62253 | 5.77162 | 0.940 | -12.8365 | 34.0816 |
| | Sandford Hill | 13.02848 | 5.08745 | 0.560 | -8.9695 | 35.0264 |
| | Govet | 0.83248 | 5.64121 | 1.000 | -22.1644 | 23.8294 |
| | Caverne Marie- | 2.88048 | 5.51215 | 1.000 | -20.9730 | 26.7339 |
| | Jeanne | | | | | |
| | Trou Magrite | -11.16598 | 5.25806 | 0.813 | -33.3673 | 11.0354 |
| | Trou du Sureau | -3.93386 | 6.21028 | 1.000 | -28.1641 | 20.2964 |
| | Westeregeln | -1.92986 | 5.98566 | 1.000 | -26.4043 | 22.5445 |
| | Salzgitter- | 16.39037 | 4.36132 | 0.188 | -5.9750 | 38.7558 |
| | Lebenstedt | | | | | |
| | Raalte | 11.40964 | 4.82324 | 0.673 | -10.4043 | 33.2236 |
| Kents | Brixham Cave | 24.20039 [*] | 3.39800 | 0.000 | 11.7213 | 36.6795 |
| Cavern | Gully Cave | -0.36238 | 5.19023 | 1.000 | -22.3762 | 21.6514 |
| | Pin Hole Cave | 10.26015 | 4.78394 | 0.830 | -7.7805 | 28.3008 |
| | Sandford Hill | 12.66610 | 3.93150 | 0.147 | -1.7235 | 27.0557 |
| | Govet | 0.47010 | 4.62577 | 1.000 | -16.6796 | 17.6198 |
| | Caverne Marie- | 2.51810 | 4.46747 | 1.000 | -16.0636 | 21.0998 |
| | Jeanne | | | | | |
| | Trou Magrite | -11.52836 | 4.14991 | 0.370 | -26.7085 | 3.6518 |
| | Trou du Sureau | -4.29624 | 5.30491 | 1.000 | -23.7569 | 15.1644 |
| | Westeregeln | -2.29224 | 5.04011 | 1.000 | -22.1053 | 17.5209 |
| | Salzgitter- | 16.02799 [*] | 2.93183 | 0.001 | 4.8022 | 27.2538 |
| | Lebenstedt | | | | | |
| | Raalte | 11.04726 | 3.58304 | 0.200 | -2.0451 | 24.1396 |
| Pin Hole | Brixham Cave | 13.94024 | 4.23314 | 0.176 | -2.7847 | 30.6652 |
| Cave | Gully Cave | -10.62253 | 5.77162 | 0.940 | -34.0816 | 12.8365 |
| | Kents Cavern | -10.26015 | 4.78394 | 0.830 | -28.3008 | 7.7805 |
| | Sandford Hill | 2.40595 | 4.67223 | 1.000 | -15.4381 | 20.2500 |
| | Goyet | -9.79005 | 5.26981 | 0.954 | -29.5845 | 10.0044 |
| | Caverne Marie- | -7.74205 | 5.13141 | 0.994 | -28.4200 | 12.9359 |
| | Jeanne | | | | | |
| | Trou Magrite | -21.78851 [*] | 4.85745 | 0.009 | -40.1617 | -3.4153 |
| | Trou du Sureau | -14.55638 | 5.87496 | 0.597 | -36.2202 | 7.1074 |
| | Westeregeln | -12.55238 | 5.63700 | 0.772 | -34.3640 | 9.2593 |
| | Salzgitter- | 5.76784 | 3.86894 | 0.993 | -10.4205 | 21.9561 |
| | Lebenstedt | | | | | |
| | Raalte | 0.78712 | 4.38307 | 1.000 | -16.2689 | 17.8431 |
| Sandford | Brixham Cave | 11.53429 | 3.23884 | 0.081 | -0.6679 | 23.7364 |
| Hill | Gully Cave | -13.02848 | 5.08745 | 0.560 | -35.0264 | 8.9695 |
| | Kents Cavern | -12.66610 | 3.93150 | 0.147 | -27.0557 | 1.7235 |
| | Pin Hole Cave | -2.40595 | 4.67223 | 1.000 | -20.2500 | 15.4381 |
| | Goyet | -12.19600 | 4.51015 | 0.434 | -29.1203 | 4.7283 |
| | Caverne Marie- | -10.14800 | 4.34764 | 0.693 | -28.6909 | 8.3949 |
| | Jeanne | | | | | |
| | Trou Magrite | -24.19446 [*] | 4.02062 | 0.000 | -39.1126 | -9.2763 |
| | Trou du Sureau | -16.96233 | 5.20440 | 0.143 | -36.2055 | 2.2808 |
| | Westeregeln | -14.95833 | 4.93420 | 0.281 | -34.6391 | 4.7224 |
| | Salzgitter- | 3.36189 | 2.74578 | 1.000 | -7.7007 | 14.4245 |
| | Lebenstedt | | | | | |
| | Raalte | -1.61883 | 3.43247 | 1.000 | -14.4283 | 11.1906 |
| Goyet | Brixham Cave | 23.73029 [*] | 4.05354 | 0.001 | 8.1157 | 39.3449 |
| | Gully Cave | -0.83248 | 5.64121 | 1.000 | -23.8294 | 22.1644 |
| | Kents Cavern | -0.47010 | 4.62577 | 1.000 | -17.6198 | 16.6796 |

| | Pin Hole Cave | 9.79005 | 5.26981 | 0.954 | -10.0044 | 29.5845 |
|-------------|----------------|-----------------------|---------|-------|----------|---------|
| | Sandford Hill | 12.19600 | 4.51015 | 0.434 | -4.7283 | 29.1203 |
| | Caverne Marie- | 2.04800 | 4.98428 | 1.000 | -17.9913 | 22.0873 |
| | Jeanne | | | | | |
| | Trou Magrite | -11.99846 | 4.70175 | 0.542 | -29.5179 | 5.5210 |
| | Trou du Sureau | -4.76633 | 5.74690 | 1.000 | -25.8370 | 16.3043 |
| | Westeregeln | -2.76233 | 5.50340 | 1.000 | -24.0019 | 18.4772 |
| | Salzgitter- | 15.55789 [*] | 3.67156 | 0.036 | 0.6586 | 30.4572 |
| | Lebenstedt | | | | | |
| | Raalte | 10.57717 | 4.20986 | 0.574 | -5.4367 | 26.5910 |
| Caverne | Brixham Cave | 21.68229* | 3.87191 | 0.018 | 3.5008 | 39.8638 |
| Marie- | Gully Cave | -2.88048 | 5.51215 | 1.000 | -26.7339 | 20.9730 |
| Jeanne | Kents Cavern | -2.51810 | 4.46747 | 1.000 | -21.0998 | 16.0636 |
| | Pin Hole Cave | 7.74205 | 5.13141 | 0.994 | -12.9359 | 28.4200 |
| | Sandford Hill | 10.14800 | 4.34764 | 0.693 | -8.3949 | 28.6909 |
| | Govet | -2.04800 | 4.98428 | 1.000 | -22.0873 | 17.9913 |
| | Trou Magrite | -14.04646 | 4.54610 | 0.278 | -32.9234 | 4.8305 |
| | Trou du Sureau | -6.81433 | 5.62027 | 1.000 | -28.4610 | 14.8323 |
| | Westeregeln | -4.81033 | 5.37103 | 1.000 | -26.8521 | 17.2315 |
| | Salzgitter- | 13.50989 | 3.47000 | 0.189 | -5.5446 | 32.5644 |
| | Lebenstedt | | | | | |
| | Raalte | 8.52917 | 4.03528 | 0.807 | -9.6521 | 26.7104 |
| Trou | Brixham Cave | 35.72875* | 3.50073 | 0.000 | 22.5300 | 48.9275 |
| Magrite | Gully Cave | 11.16598 | 5.25806 | 0.813 | -11.0354 | 33.3673 |
| | Kents Cavern | 11.52836 | 4.14991 | 0.370 | -3.6518 | 26.7085 |
| | Pin Hole Cave | 21.78851 [*] | 4.85745 | 0.009 | 3.4153 | 40.1617 |
| | Sandford Hill | 24.19446 [*] | 4.02062 | 0.000 | 9.2763 | 39.1126 |
| | Goyet | 11.99846 | 4.70175 | 0.542 | -5.5210 | 29.5179 |
| | Caverne Marie- | 14.04646 | 4.54610 | 0.278 | -4.8305 | 32.9234 |
| | Jeanne | | | | | |
| | Trou du Sureau | 7.23212 | 5.37129 | 1.000 | -12.5193 | 26.9835 |
| | Westeregeln | 9.23612 | 5.10993 | 0.957 | -10.8443 | 29.3165 |
| | Salzgitter- | 27.55635 [*] | 3.05030 | 0.000 | 15.3722 | 39.7405 |
| | Lebenstedt | | | | | |
| | Raalte | 22.57563 [*] | 3.68061 | 0.000 | 8.8377 | 36.3136 |
| Trou du | Brixham Cave | 28.49663* | 4.81409 | 0.000 | 10.3655 | 46.6277 |
| Sureau | Gully Cave | 3.93386 | 6.21028 | 1.000 | -20.2964 | 28.1641 |
| | Kents Cavern | 4.29624 | 5.30491 | 1.000 | -15.1644 | 23.7569 |
| | Pin Hole Cave | 14.55638 | 5.87496 | 0.597 | -7.1074 | 36.2202 |
| | Sandford Hill | 16.96233 | 5.20440 | 0.143 | -2.2808 | 36.2055 |
| | Goyet | 4.76633 | 5.74690 | 1.000 | -16.3043 | 25.8370 |
| | Caverne Marie- | 6.81433 | 5.62027 | 1.000 | -14.8323 | 28.4610 |
| | Jeanne | | | | | |
| | Trou Magrite | -7.23212 | 5.37129 | 1.000 | -26.9835 | 12.5193 |
| | Westeregeln | 2.00400 | 6.08537 | 1.000 | -20.8461 | 24.8541 |
| | Salzgitter- | 20.32423* | 4.49719 | 0.012 | 2.8822 | 37.7662 |
| | Lebenstedt | | | | | |
| | Raalte | 15.34350 | 4.94644 | 0.208 | -3.1334 | 33.8204 |
| Westeregeln | Brixham Cave | 26.49263* | 4.52063 | 0.003 | 7.5608 | 45.4245 |
| | Gully Cave | 1.92986 | 5.98566 | 1.000 | -22.5445 | 26.4043 |
| | Kents Cavern | 2.29224 | 5.04011 | 1.000 | -17.5209 | 22.1053 |
| | Pin Hole Cave | 12.55238 | 5.63700 | 0.772 | -9.2593 | 34.3640 |
| | Sandford Hill | 14.95833 | 4.93420 | 0.281 | -4.7224 | 34.6391 |
| | Goyet | 2.76233 | 5.50340 | 1.000 | -18.4772 | 24.0019 |

| | Caverne Marie- | 4.81033 | 5.37103 | 1.000 | -17.2315 | 26.8521 |
|-------------|----------------|------------------------|---------|-------|----------|----------|
| | Jeanne | 0.0004.0 | 5 40000 | 0.057 | 00.0405 | 10.0440 |
| | I rou Magrite | -9.23612 | 5.10993 | 0.957 | -29.3165 | 10.8443 |
| | Trou du Sureau | -2.00400 | 6.08537 | 1.000 | -24.8541 | 20.8461 |
| | Salzgitter- | 18.32023 | 4.18154 | 0.058 | -0.4384 | 37.0789 |
| | Lebenstedt | | | | | |
| | Raalte | 13.33950 | 4.66132 | 0.378 | -5.7896 | 32.4686 |
| Salzgitter- | Brixham Cave | 8.17240* | 1.90500 | 0.023 | 0.7053 | 15.6395 |
| Lebenstedt | Gully Cave | -16.39037 | 4.36132 | 0.188 | -38.7558 | 5.9750 |
| | Kents Cavern | -16.02799 [*] | 2.93183 | 0.001 | -27.2538 | -4.8022 |
| | Pin Hole Cave | -5.76784 | 3.86894 | 0.993 | -21.9561 | 10.4205 |
| | Sandford Hill | -3.36189 | 2.74578 | 1.000 | -14.4245 | 7.7007 |
| | Goyet | -15.55789 [*] | 3.67156 | 0.036 | -30.4572 | -0.6586 |
| | Caverne Marie- | -13.50989 | 3.47000 | 0.189 | -32.5644 | 5.5446 |
| | Jeanne | | | | | |
| | Trou Magrite | -27.55635 [*] | 3.05030 | 0.000 | -39.7405 | -15.3722 |
| | Trou du Sureau | -20.32423 [*] | 4.49719 | 0.012 | -37.7662 | -2.8822 |
| | Westeregeln | -18.32023 | 4.18154 | 0.058 | -37.0789 | 0.4384 |
| | Raalte | -4.98073 | 2.21829 | 0.756 | -13.7456 | 3.7842 |
| Raalte | Brixham Cave | 13.15312 [*] | 2.80564 | 0.004 | 2.7559 | 23.5504 |
| | Gully Cave | -11.40964 | 4.82324 | 0.673 | -33.2236 | 10.4043 |
| | Kents Cavern | -11.04726 | 3.58304 | 0.200 | -24.1396 | 2.0451 |
| | Pin Hole Cave | -0.78712 | 4.38307 | 1.000 | -17.8431 | 16.2689 |
| | Sandford Hill | 1.61883 | 3.43247 | 1.000 | -11.1906 | 14.4283 |
| | Goyet | -10.57717 | 4.20986 | 0.574 | -26.5910 | 5.4367 |
| | Caverne Marie- | -8.52917 | 4.03528 | 0.807 | -26.7104 | 9.6521 |
| | Jeanne | | | | | |
| | Trou Magrite | -22.57562 [*] | 3.68061 | 0.000 | -36.3136 | -8.8377 |
| | Trou du Sureau | -15.34350 | 4.94644 | 0.208 | -33.8204 | 3.1334 |
| | Westeregeln | -13.33950 | 4.66132 | 0.378 | -32.4686 | 5.7896 |
| | Salzgitter- | 4.98073 | 2.21829 | 0.756 | -3.7842 | 13.7456 |
| | Lebenstedt | | | | | |

Between the female populations from each site, which did not include the individual from Ellewoutsdijk due to the small sample size (n<2), the one-way ANOVA was also significant ($F_{(15,380)}$ =4.553, p=0.0001) indicating that there was a significant difference in body mass. Furthermore, Levene's test for equal variance was significant ($F_{(15,380)}$ =4.447, p=0.0001) and assumed unequal variances. Therefore, the *post hoc* test Dunnett's T3 was used to compare the differences between each site (**Table 4.12**). The results of this test are summarised below.

- There was a significant difference between the smaller body masses of female populations at Brixham Cave and the larger body masses of females at Gully Cave, Goyet, Caverne Marie-Jeanne and Trou du Sureau.
- There was a significant difference between the larger body masses of female populations at Gully Cave and the smaller body masses of females at Brixham Cave, Kents Cavern, Mammoth Cave, Sandford Hill, Goyet, Caverne Marie-Jeanne, Trou Magrite, Trou du Sureau, Salzgitter-Lebenstedt and Raalte.

• There was no significant difference between all remaining combinations of sites.

Table 4.12. Results of Dunnett's T3 Test for Female *Rangifer tarandus* from Middle Devensian/Weichselian Sites. *R. tarandus* were tested to determine whether a significant difference was evident between the body masses of males from different fossil sites. The mean difference is significant (*) at p<0.05.

| Site (I) | Site (J) | Mean | Std. | Sig. | 95% Co | nfidence |
|-------------|----------------|------------------------|----------|-------|----------|----------|
| | | Difference | Error | _ | Inte | rval |
| | | (I-J) | | | Lower | Upper |
| | | | | | Bound | Bound |
| Brixham | Gully Cave | -26.81033 [*] | 2.73795 | 0.000 | -39.4963 | -14.1244 |
| Cave | Inchnadamph | -15.71667 | 3.95771 | 0.277 | -43.3621 | 11.9287 |
| | Bone Cave | | | | | |
| | Kents Cavern | -10.48500 | 2.99832 | 0.201 | -23.4319 | 2.4619 |
| | Mammoth Cave | -1.49905 | 4.13087 | 1.000 | -20.9772 | 17.9791 |
| | Pin Hole Cave | -12.54600 | 3.92735 | 0.292 | -28.7727 | 3.6807 |
| | Robin Hood | -13.70723 | 4.62947 | 0.547 | -50.3504 | 22.9359 |
| | Cave | | | | | |
| | Sandford Hill | -7.68429 | 2.70367 | 0.516 | -19.9424 | 4.5738 |
| | Goyet | -14.84139 [*] | 3.10010 | 0.014 | -27.7649 | -1.9178 |
| | Caverne Marie- | -14.48242 [*] | 3.15649 | 0.023 | -27.7252 | -1.2396 |
| | Jeanne | | | | | |
| | Trou Al'Wesse | -15.99762 | 5.07058 | 0.388 | -40.8715 | 8.8763 |
| | Trou Magrite | -9.80262 | 3.53286 | 0.533 | -23.9941 | 4.3888 |
| | Trou du Moulin | -18.97167 | 4.35346 | 0.103 | -40.7268 | 2.7834 |
| | Trou du Sureau | -14.89869 [*] | 3.25011 | 0.019 | -28.2754 | -1.5220 |
| | Salzgitter- | -8.93672 | 2.26932 | 0.214 | -21.6743 | 3.8009 |
| | Lebenstedt | | | | | |
| | Raalte | -9.43754 | 2.45004 | 0.188 | -21.7908 | 2.9158 |
| Gully Cave | Brixham Cave | 26.81033 [*] | 2.73795 | 0.000 | 14.1244 | 39.4963 |
| | Inchnadamph | 11.09367 | 3.69257 | 0.537 | -18.9723 | 41.1596 |
| | Bone Cave | | | | | |
| | Kents Cavern | 16.32533* | 2.63848 | 0.000 | 5.8620 | 26.7886 |
| | Mammoth Cave | 25.31129* | 3.87759 | 0.008 | 6.3999 | 44.2227 |
| | Pin Hole Cave | 14.26433 | 3.66002 | 0.075 | -0.7169 | 29.2455 |
| | Robin Hood | 13.10310 | 4.40496 | 0.557 | -27.1021 | 53.3083 |
| | Cave | | | | | |
| | Sandford Hill | 19.12604 | 2.29815 | 0.000 | 10.1312 | 28.1209 |
| | Goyet | 11.96894 | 2.75360 | 0.011 | 1.4508 | 22.4871 |
| | Caverne Marie- | 12.32791 | 2.81693 | 0.015 | 1.3248 | 23.3310 |
| | | 10 91271 | 1 96646 | 0.833 | 12 0512 | 25 5767 |
| | Trou Al Wesse | 17.00771* | 3 23308 | 0.000 | 15062 | 20 /102 |
| | | 7 83867 | 1 11 201 | 0.001 | -13 718/ | 29.4192 |
| | | 11 0116/* | 2 021/15 | 0.007 | 0.6726 | 23.3330 |
| | Solzaittor | 17.87362* | 1 76678 | 0.021 | 9 90/0 | 25.8/32 |
| | Labonstadt | 17.07302 | 1.70070 | 0.000 | 3.30+0 | 20.0402 |
| | Raalta | 17.37279* | 1,99358 | 0.000 | 9.0247 | 25,7209 |
| Inchnadamph | Rrivham Cave | 15 71667 | 3 95771 | 0.000 | -11 9287 | 43.3621 |
| Rone Cave | | -11 09367 | 3 69257 | 0.537 | -41 1596 | 18 9723 |
| | Kents Cavero | 5 23167 | 3 88956 | 0.007 | -22 1708 | 32 6341 |
| | Mammoth Cave | 14 21762 | 4 81693 | 0.498 | -11 9044 | 40.3397 |
| | Pin Hole Cove | 3 17067 | 4 64358 | 1 000 | -21 2692 | 27 6105 |
| 1 | FILL HOLE Cave | 0.17007 | 7.07000 | 1.000 | 21.2032 | 21.0100 |

| | Robin Hood | 2.00943 | 5.25078 | 1.000 | -34.6930 | 38.7119 |
|--------------|----------------|------------------------|--------------------|-------|----------|---------|
| | Cave | | | | | |
| | Sandford Hill | 8.03237 | 3.66723 | 0.803 | -22.2024 | 38.2671 |
| | Goyet | 0.87528 | 3.96855 | 1.000 | -25.6358 | 27.3864 |
| | Caverne Marie- | 1.23424 | 4.01275 | 1.000 | -25.0488 | 27.5173 |
| | Jeanne | | | | | |
| | Trou Al'Wesse | -0.28095 | 5.64353 | 1.000 | -28.9112 | 28.3493 |
| | Trou Magrite | 5.91405 | 4.31507 | 0.997 | -18.7085 | 30.5366 |
| | Trou du Moulin | -3.25500 | 5.00912 | 1.000 | -30.4960 | 23.9860 |
| | Trou du Sureau | 0.81798 | 4.08680 | 1.000 | -24.8865 | 26.5225 |
| | Salzgitter- | 6.77995 | 3.35985 | 0.843 | -31.8791 | 45.4390 |
| | Lebenstedt | | | | | |
| | Raalte | 6.27912 | 3.48445 | 0.907 | -28.1286 | 40.6869 |
| Kents Cavern | Brixham Cave | 10.48500 | 2.99832 | 0.201 | -2.4619 | 23.4319 |
| | Gully Cave | -16.32533 [*] | 2.63848 | 0.000 | -26.7886 | -5.8620 |
| | Inchnadamph | -5.23167 | 3.88956 | 0.993 | -32.6341 | 22.1708 |
| | Bone Cave | | | | | |
| | Mammoth Cave | 8.98595 | 4.06562 | 0.855 | -9.8845 | 27.8564 |
| | Pin Hole Cave | -2.06100 | 3.85867 | 1.000 | -17.4759 | 13.3539 |
| | Robin Hood | -3.22223 | 4.57135 | 1.000 | -40.1307 | 33.6863 |
| | Cave | | | | | |
| | Sandford Hill | 2.80071 | 2.60290 | 1.000 | -7.1283 | 12.7297 |
| | Goyet | -4.35639 | 3.01262 | 1.000 | -15.6842 | 6.9714 |
| | Caverne Marie- | -3.99742 | 3.07061 | 1.000 | -15.7331 | 7.7382 |
| | | E E1060 | E 017E7 | 1 000 | 20.0070 | 10.0707 |
| | Trou Al Wesse | -5.51202 | 0.01707 0.45605 | 1.000 | -30.0979 | 19.0727 |
| | Trou Magrite | 0.00230 | 3.40000 | 0.026 | -12.3090 | 12 7000 |
| | | -4.41369 | 4.29100 | 1.000 | -29.1132 | 7 5637 |
| | Solzaittor | 1 54828 | 2 14827 | 1.000 | -7 2335 | 10 3301 |
| | Jaizyillei- | 1.04020 | 2.14021 | 1.000 | 1.2000 | 10.0001 |
| | Raalto | 1 04746 | 2 33836 | 1 000 | -8 2039 | 10 2988 |
| Mammoth | Brivham Cave | 1.49905 | 4.13087 | 1.000 | -17,9791 | 20.9772 |
| Cave | Gully Cave | -25.31129* | 3.87759 | 0.008 | -44.2227 | -6.3999 |
| Caro | Inchnadamph | -14.21762 | 4.81693 | 0.498 | -40.3397 | 11.9044 |
| | Bone Cave | | | | | |
| | Kents Cavern | -8.98595 | 4.06562 | 0.855 | -27.8564 | 9.8845 |
| | Pin Hole Cave | -11.04695 | 4.79202 | 0.832 | -31.4068 | 9.3129 |
| | Robin Hood | -12.20819 | 5.38250 | 0.795 | -44.2992 | 19.8828 |
| | Cave | | | | | |
| | Sandford Hill | -6.18525 | 3.85346 | 0.991 | -24.9656 | 12.5951 |
| | Goyet | -13.34234 | 4.14125 | 0.330 | -32.1564 | 5.4717 |
| | Caverne Marie- | -12.98338 | 4.18363 | 0.381 | -31.9144 | 5.9477 |
| | Jeanne | | | | | |
| | Trou Al'Wesse | -14.49857 | 5.76629 | 0.703 | -40.7601 | 11.7629 |
| | Trou Magrite | -8.30357 | 4.47443 | 0.977 | -27.5874 | 10.9802 |
| | Trou du Moulin | -17.47262 | 5.14703 | 0.270 | -41.1847 | 6.2395 |
| | Trou du Sureau | -13.39964 | 4.25471 | 0.353 | -32.3585 | 5.5592 |
| | Salzgitter- | -7.43767 | 3.56219 | 0.875 | -26.7282 | 11.8529 |
| | Lebenstedt | | | | | |
| | Raalte | -7.93850 | 3.67995 | 0.857 | -26.9564 | 11.0794 |
| Pin Hole | Brixham Cave | 12.54600 | 3.92735 | 0.292 | -3.6807 | 28.7727 |
| Cave | Gully Cave | -14.26433 | 3.66002 | 0.075 | -29.2455 | 0.7169 |
| | Inchnadamph | -3.17067 | 4.64358 | 1.000 | -27.6105 | 21.2692 |
| | Bone Cave | | | | | |

| | Kents Cavern | 2.06100 | 3.85867 | 1.000 | -13,3539 | 17,4759 |
|----------------|----------------|------------------------|---------|-------|-----------|----------|
| | Mammoth Cave | 11 04695 | 4 79202 | 0.832 | -9.3129 | 31 4068 |
| | Pobin Hood | -1 16123 | 5 22794 | 1 000 | -32 4287 | 30 1062 |
| | | 1.10120 | 0.22701 | 1.000 | 02.1201 | 00.1002 |
| | Sandford Hill | 4 86171 | 3 63445 | 1 000 | -9 9049 | 19 6283 |
| | Govet | -2 29539 | 3 93827 | 1.000 | -17 8096 | 13 2188 |
| | Goyerna Maria | -1.936/2 | 3 08281 | 1.000 | -17.6647 | 13 7018 |
| | | -1.33042 | 0.00201 | 1.000 | -17.00-77 | 10.7910 |
| | | -3 /5162 | 5 62220 | 1 000 | -28 5/16 | 21 6383 |
| | Trou Mogrito | 2 7/338 | 1 28725 | 1.000 | -13 8510 | 10 3378 |
| | Trou Magnie | -6 42567 | 4.20723 | 1.000 | -13.0010 | 15.5370 |
| | | -0.42307 | 4.90017 | 1.000 | -20.4909 | 10.0440 |
| | Trou du Sureau | -2.35269 | 4.00741 | 1.000 | -10.2430 | 13.3362 |
| | Salzgitter- | 3.00920 | 3.32403 | 1.000 | -10.6417 | 17.0003 |
| | Lebenstedt | 2 4 0 9 4 0 | 2 44004 | 1 000 | 44.0050 | 47 5500 |
| B 1 1 1 | Raalte | 3.10846 | 3.44994 | 1.000 | -11.3353 | 17.5522 |
| Robin Hood | Brixham Cave | 13.70723 | 4.62947 | 0.547 | -22.9359 | 50.3504 |
| Cave | Gully Cave | -13.10310 | 4.40496 | 0.557 | -53.3083 | 27.1021 |
| | Inchnadamph | -2.00943 | 5.25078 | 1.000 | -38.7119 | 34.6930 |
| | Bone Cave | | | | | |
| | Kents Cavern | 3.22223 | 4.57135 | 1.000 | -33.6863 | 40.1307 |
| | Mammoth Cave | 12.20819 | 5.38250 | 0.795 | -19.8828 | 44.2992 |
| | Pin Hole Cave | 1.16123 | 5.22794 | 1.000 | -30.1062 | 32.4287 |
| | Sandford Hill | 6.02294 | 4.38373 | 0.984 | -34.5099 | 46.5557 |
| | Goyet | -1.13416 | 4.63874 | 1.000 | -36.9016 | 34.6332 |
| | Caverne Marie- | -0.77519 | 4.67661 | 1.000 | -36.1133 | 34.5629 |
| | Jeanne | | | | | |
| | Trou Al'Wesse | -2.29039 | 6.13335 | 1.000 | -34.9466 | 30.3658 |
| | Trou Magrite | 3.90461 | 4.93846 | 1.000 | -28.6918 | 36.5010 |
| | Trou du Moulin | -5.26443 | 5.55517 | 1.000 | -37.7885 | 27.2596 |
| | Trou du Sureau | -1.19146 | 4.74030 | 1.000 | -35.6913 | 33.3084 |
| | Salzgitter- | 4.77052 | 4.13002 | 0.994 | -44.0828 | 53.6238 |
| | Lebenstedt | | | | | |
| | Raalte | 4.26969 | 4.23202 | 0.999 | -40.6638 | 49.2032 |
| Sandford Hill | Brixham Cave | 7.68429 | 2.70367 | 0.516 | -4.5738 | 19.9424 |
| | Gully Cave | -19.12604 [*] | 2.29815 | 0.000 | -28.1209 | -10.1312 |
| | Inchnadamph | -8.03237 | 3.66723 | 0.803 | -38.2671 | 22.2024 |
| | Bone Cave | | | | | |
| | Kents Cavern | -2.80071 | 2.60290 | 1.000 | -12.7297 | 7.1283 |
| | Mammoth Cave | 6.18525 | 3.85346 | 0.991 | -12.5951 | 24.9656 |
| | Pin Hole Cave | -4.86171 | 3.63445 | 1.000 | -19.6283 | 9.9049 |
| | Robin Hood | -6.02294 | 4.38373 | 0.984 | -46.5557 | 34.5099 |
| | Cave | | | | | |
| | Govet | -7.15709 | 2.71951 | 0.639 | -17.1868 | 2.8726 |
| | Caverne Marie- | -6.79813 | 2.78362 | 0.787 | -17.3495 | 3.7533 |
| | Jeanne | | | | | |
| | Trou Al'Wesse | -8.31332 | 4.84725 | 0.977 | -33.0314 | 16.4048 |
| | Trou Magrite | -2.11832 | 3.20410 | 1.000 | -14.2111 | 9.9745 |
| | Trou du Moulin | -11.28737 | 4.09118 | 0.578 | -32,7634 | 10.1886 |
| | | -7.21440 | 2.88935 | 0.751 | -18.0388 | 3.6100 |
| | Salzaitter- | -1,25242 | 1.71317 | 1.000 | -7.5765 | 5.0716 |
| | Lehenstedt | | | | | 0.0110 |
| | Raalte | -1,75325 | 1,94623 | 1 000 | -8 9359 | 5,4294 |
| Govet | Brixham Covo | 14 84139* | 3 10010 | 0.014 | 1 9178 | 27 7649 |
| Julyer | Gully Cave | -11 96894* | 2,75360 | 0.011 | -22 4871 | -1 4508 |
| 1 | July Cave | | | 0.011 | | |

| | Inchnadamph | -0.87528 | 3.96855 | 1.000 | -27.3864 | 25.6358 |
|--------------|----------------|------------------------|---------|-------|----------|---------|
| | Bone Cave | | | | | |
| | Kents Cavern | 4.35639 | 3.01262 | 1.000 | -6.9714 | 15.6842 |
| | Mammoth Cave | 13.34234 | 4.14125 | 0.330 | -5.4717 | 32.1564 |
| | Pin Hole Cave | 2.29539 | 3.93827 | 1.000 | -13.2188 | 17.8096 |
| | Robin Hood | 1.13416 | 4.63874 | 1.000 | -34.6332 | 36.9016 |
| | Cave | | | | | |
| | Sandford Hill | 7.15709 | 2.71951 | 0.639 | -2.8726 | 17.1868 |
| | Caverne Marie- | 0.35896 | 3.17007 | 1.000 | -11.5061 | 12.2240 |
| | Jeanne | | | | | |
| | Trou Al'Wesse | -1.15623 | 5.07904 | 1.000 | -25.6529 | 23.3404 |
| | Trou Magrite | 5.03877 | 3.54500 | 1.000 | -8.1818 | 18.2593 |
| | Trou du Moulin | -4.13028 | 4.36332 | 1.000 | -25.2862 | 17.0256 |
| | Trou du Sureau | -0.05730 | 3.26330 | 1.000 | -12.1784 | 12.0638 |
| | Salzgitter- | 5.90467 | 2.28818 | 0.680 | -2.7940 | 14.6034 |
| | Lebenstedt | | | | | |
| | Raalte | 5.40385 | 2.46751 | 0.933 | -3.8603 | 14.6680 |
| Caverne | Brixham Cave | 14.48242* | 3.15649 | 0.023 | 1.2396 | 27.7252 |
| Marie- | Gully Cave | -12.32791 [*] | 2.81693 | 0.015 | -23.3310 | -1.3248 |
| Jeanne | Inchnadamph | -1.23424 | 4.01275 | 1.000 | -27.5173 | 25.0488 |
| Coanno | Bone Cave | - | | | | |
| | Kents Cavern | 3.99742 | 3.07061 | 1.000 | -7.7382 | 15.7331 |
| | Mammoth Cave | 12.98338 | 4.18363 | 0.381 | -5.9477 | 31.9144 |
| | Pin Hole Cave | 1.93642 | 3.98281 | 1.000 | -13.7918 | 17.6647 |
| | Robin Hood | 0.77519 | 4.67661 | 1.000 | -34.5629 | 36.1133 |
| | Cave | | | | | |
| | Sandford Hill | 6.79813 | 2.78362 | 0.787 | -3.7533 | 17.3495 |
| | Govet | -0.35896 | 3.17007 | 1.000 | -12.2240 | 11.5061 |
| | Trou Al'Wesse | -1.51519 | 5.11366 | 1.000 | -26.0472 | 23.0168 |
| | Trou Magrite | 4.67981 | 3.59442 | 1.000 | -8.8365 | 18.1961 |
| | Trou du Moulin | -4.48924 | 4.40356 | 1.000 | -25.7067 | 16.7282 |
| | Trou du Sureau | -0.41627 | 3.31692 | 1.000 | -12.8891 | 12.0566 |
| | Salzgitter- | 5.54571 | 2.36401 | 0.829 | -3.8959 | 14.9873 |
| | Lebenstedt | | | | | |
| | Raalte | 5.04488 | 2.53799 | 0.975 | -4.8528 | 14.9426 |
| Trou | Brixham Cave | 15.99762 | 5.07058 | 0.388 | -8.8763 | 40.8715 |
| Al'Wesse | Gully Cave | -10.81271 | 4.86646 | 0.833 | -35.5767 | 13.9513 |
| | Inchnadamph | 0.28095 | 5.64353 | 1.000 | -28.3493 | 28.9112 |
| | Bone Cave | | | | | |
| | Kents Cavern | 5.51262 | 5.01757 | 1.000 | -19.0727 | 30.0979 |
| | Mammoth Cave | 14.49857 | 5.76629 | 0.703 | -11.7629 | 40.7601 |
| | Pin Hole Cave | 3.45162 | 5.62229 | 1.000 | -21.6383 | 28.5416 |
| | Robin Hood | 2.29039 | 6.13335 | 1.000 | -30.3658 | 34.9466 |
| | Cave | | | | | |
| | Sandford Hill | 8.31332 | 4.84725 | 0.977 | -16.4048 | 33.0314 |
| | Goyet | 1.15623 | 5.07904 | 1.000 | -23.3404 | 25.6529 |
| | Caverne Marie- | 1.51519 | 5.11366 | 1.000 | -23.0168 | 26.0472 |
| | Jeanne | | | | | |
| | Trou Magrite | 6.19500 | 5.35417 | 1.000 | -18.3651 | 30.7551 |
| | Trou du Moulin | -2.97405 | 5.92778 | 1.000 | -30.1775 | 24.2294 |
| | Trou du Sureau | 1.09893 | 5.17197 | 1.000 | -23.4005 | 25.5983 |
| | Salzgitter- | 7.06090 | 4.61908 | 0.991 | -18.2048 | 32.3266 |
| | Lebenstedt | | | | | |
| | Raalte | 6.56008 | 4.71049 | 0.997 | -18.4489 | 31.5691 |
| Trou Magrite | Brixham Cave | 9.80262 | 3.53286 | 0.533 | -4.3888 | 23.9941 |

| | Gully Cave | -17.00771 [*] | 3.23308 | 0.001 | -29.4192 | -4.5962 |
|---------|-------------------------|------------------------|----------|-------|----------|---------|
| | Inchnadamph | -5.91405 | 4.31507 | 0.997 | -30.5366 | 18.7085 |
| | Bone Cave | | | | | |
| | Kents Cavern | -0.68238 | 3.45635 | 1.000 | -13.7543 | 12.3895 |
| | Mammoth Cave | 8.30357 | 4.47443 | 0.977 | -10.9802 | 27.5874 |
| | Pin Hole Cave | -2 74338 | 4 28725 | 1 000 | -19.3378 | 13 8510 |
| | Pobin Hood | -3 90461 | 4 93846 | 1.000 | -36 5010 | 28 6918 |
| | | 0.00401 | 4.00040 | 1.000 | 00.0010 | 20.0010 |
| | Cave Sondford Hill | 2 11832 | 3 20/10 | 1 000 | -0.0745 | 1/ 2111 |
| | | 5.02977 | 3.20410 | 1.000 | 19.2502 | 0 1010 |
| | Goyet | -5.03077 | 2.54500 | 1.000 | -10.2090 | 0.1010 |
| | Caverne Marie- | -4.07901 | 3.39442 | 1.000 | -10.1901 | 0.0303 |
| | | 6 10500 | E 25/17 | 1 000 | 20 7551 | 10 2651 |
| | | -0.19500 | 3.33417 | 1.000 | -30.7551 | 10.3031 |
| | | -9.16905 | 4.68071 | 0.947 | -30.4599 | 12.1218 |
| | Trou du Sureau | -5.09607 | 3.67691 | 1.000 | -18.8366 | 8.6444 |
| | Salzgitter- | 0.86590 | 2.84715 | 1.000 | -10.2536 | 11.9854 |
| | Dealta | 0 36508 | 2 00318 | 1 000 | _11 1515 | 11 8817 |
| Trou du | Rivhom Cours | 18 07167 | 1 353/6 | 0.103 | -2 783/ | 10 7268 |
| Moulin | | -7 83867 | 4.000+0 | 0.103 | -20 3058 | 13 718/ |
| WOUIIT | | -7.00007 | 5 00012 | 1.000 | -29.3930 | 20.4060 |
| | Inchnadamph | 3.25500 | 5.00912 | 1.000 | -23.9000 | 30.4900 |
| | Bone Cave | 9 49667 | 4 20160 | 0.026 | 12 7000 | 20 7722 |
| | Kents Cavern | 0.40007 | 4.29100 | 0.920 | -12.7999 | 29.1132 |
| | Iviammoth Cave | 6 42567 | 0.14703 | 0.270 | -0.2395 | 41.1047 |
| | Pin Hole Cave | 5.26442 | 4.90017 | 1.000 | -13.0440 | 20.4909 |
| | RODIN HOOD | 5.20445 | 5.55517 | 1.000 | -27.2090 | 37.7000 |
| | Sandford Hill | 11 28737 | 4 09118 | 0.578 | -10 1886 | 32 7634 |
| | Govet | 4 13028 | 4 36332 | 1 000 | -17 0256 | 25 2862 |
| | Caverne Marie- | 4 48924 | 4 40356 | 1 000 | -16 7282 | 25 7067 |
| | leanne | | | | | |
| | | 2 97405 | 5 92778 | 1 000 | -24 2294 | 30 1775 |
| | Trou Magrito | 9 16905 | 4 68071 | 0.947 | -12 1218 | 30 4599 |
| | | 4 07298 | 4.00071 | 1 000 | -17 1028 | 25 2/87 |
| | Sol=sitter | 10 03/05 | 3,81808 | 0.644 | -12 3023 | 32 4622 |
| | Salzyiller- | 10.00400 | 5.01000 | 0.044 | -12.0020 | 52.7022 |
| | Dealta | 0.53/12 | 3 02818 | 0 732 | -12/28/ | 31 /067 |
| Troudu | Radile Drivborn Covo | 14 90960* | 3.32010 | 0.732 | 1 5220 | 29.2754 |
| Surcou | Gully Cove | -11 01164* | 2 021/15 | 0.019 | -23 1507 | -0.6726 |
| Suleau | | 0.91709 | 4.09690 | 1.000 | -20.1007 | 24 9965 |
| | Bone Cave | -0.01790 | 4.00000 | 1.000 | -20.5225 | 24.0005 |
| | Konte Cave | 4 41369 | 3 16677 | 1 000 | -7 5637 | 16 3910 |
| | Mommeth Cove | 13 39964 | 4 25471 | 0.353 | -5 5592 | 32 3585 |
| | | 2 35260 | 4.057/1 | 1 000 | -13 5382 | 18 2/35 |
| | Pill Hole Cave | 1 101/6 | 4.00741 | 1.000 | -33 3084 | 35 6013 |
| | | 1.13140 | 7.77030 | 1.000 | 00.0004 | 00.0010 |
| | Sandford Hill | 7,21440 | 2,88935 | 0 751 | -3 6100 | 18 0388 |
| | Govet | 0.05730 | 3 26330 | 1 000 | -12 0638 | 12 1784 |
| | Caverne Marie | 0.41627 | 3 31692 | 1 000 | -12 0566 | 12 8801 |
| | Leanno | 0.71021 | 0.01002 | 1.000 | 12.0000 | 12.0001 |
| | | -1.09893 | 5,17197 | 1.000 | -25,5983 | 23,4005 |
| | Trou Magrita | 5 09607 | 3 67691 | 1 000 | -8 6444 | 18 8366 |
| | Trou du Moulin | -4 07298 | 4 47114 | 1 000 | -25 2487 | 17 1028 |
| | Salzaittor | 5 96197 | 2 48764 | 0.808 | -3 7241 | 15 6481 |
| | Labonstodt | 0.00107 | 2.10/04 | 0.000 | 0.7271 | 10.0401 |
| | Lebensleul | | | | | |

| | Raalte | 5.46115 | 2.65353 | 0.965 | -4.6970 | 15.6193 |
|-------------|----------------|------------------------|---------|-------|----------|---------|
| Salzgitter- | Brixham Cave | 8.93672 | 2.26932 | 0.214 | -3.8009 | 21.6743 |
| Lebenstedt | Gully Cave | -17.87362* | 1.76678 | 0.000 | -25.8432 | -9.9040 |
| | Inchnadamph | -6.77995 | 3.35985 | 0.843 | -45.4390 | 31.8791 |
| | Bone Cave | | | | | |
| | Kents Cavern | -1.54828 | 2.14827 | 1.000 | -10.3301 | 7.2335 |
| | Mammoth Cave | 7.43767 | 3.56219 | 0.875 | -11.8529 | 26.7282 |
| | Pin Hole Cave | -3.60928 | 3.32403 | 1.000 | -17.8603 | 10.6417 |
| | Robin Hood | -4.77052 | 4.13002 | 0.994 | -53.6238 | 44.0828 |
| | Cave | | | | | |
| | Sandford Hill | 1.25242 | 1.71317 | 1.000 | -5.0716 | 7.5765 |
| | Goyet | -5.90467 | 2.28818 | 0.680 | -14.6034 | 2.7940 |
| | Caverne Marie- | -5.54571 | 2.36401 | 0.829 | -14.9873 | 3.8959 |
| | Jeanne | | | | | |
| | Trou Al'Wesse | -7.06090 | 4.61908 | 0.991 | -32.3266 | 18.2048 |
| | Trou Magrite | -0.86590 | 2.84715 | 1.000 | -11.9854 | 10.2536 |
| | Trou du Moulin | -10.03495 | 3.81808 | 0.644 | -32.4622 | 12.3923 |
| | Trou du Sureau | -5.96197 | 2.48764 | 0.808 | -15.6481 | 3.7241 |
| | Raalte | -0.50083 | 1.27586 | 1.000 | -5.4701 | 4.4685 |
| Raalte | Brixham Cave | 9.43754 | 2.45004 | 0.188 | -2.9158 | 21.7908 |
| | Gully Cave | -17.37279 [*] | 1.99358 | 0.000 | -25.7209 | -9.0247 |
| | Inchnadamph | -6.27912 | 3.48445 | 0.907 | -40.6869 | 28.1286 |
| | Bone Cave | | | | | |
| | Kents Cavern | -1.04746 | 2.33836 | 1.000 | -10.2988 | 8.2039 |
| | Mammoth Cave | 7.93850 | 3.67995 | 0.857 | -11.0794 | 26.9564 |
| | Pin Hole Cave | -3.10846 | 3.44994 | 1.000 | -17.5522 | 11.3353 |
| | Robin Hood | -4.26969 | 4.23202 | 0.999 | -49.2032 | 40.6638 |
| | Cave | | | | | |
| | Sandford Hill | 1.75325 | 1.94623 | 1.000 | -5.4294 | 8.9359 |
| | Goyet | -5.40385 | 2.46751 | 0.933 | -14.6680 | 3.8603 |
| | Caverne Marie- | -5.04488 | 2.53799 | 0.975 | -14.9426 | 4.8528 |
| | Jeanne | | | | | |
| | Trou Al'Wesse | -6.56008 | 4.71049 | 0.997 | -31.5691 | 18.4489 |
| | Trou Magrite | -0.36508 | 2.99318 | 1.000 | -11.8817 | 11.1515 |
| | Trou du Moulin | -9.53412 | 3.92818 | 0.732 | -31.4967 | 12.4284 |
| | Trou du Sureau | -5.46115 | 2.65353 | 0.965 | -15.6193 | 4.6970 |
| | Salzgitter- | 0.50083 | 1.27586 | 1.000 | -4.4685 | 5.4701 |
| | Lebenstedt | | | | | |

4.3.3. Late Devensian/Weichselian Body Mass

Five countries provided average estimates of body mass from the late last cold stage: Britain, Belgium, Denmark and France (**Table 4.8**). To determine whether there was a statistically significant difference in the size of males and females when the average mass equation was used to estimate body mass, t-tests were applied to all Late Devensian/Weichselian sites with the exception of Trou des Nutons, where only females were identified. From t-tests (**Table 4.13**), Nørre Lyngby was the only site were a nonsignificant difference was observed otherwise, there was a significant difference between the body masses of males and females from all Late Devensian/Weichselian sites. However, small sample sizes were recorded for both the sexes at Nørre Lyngby, as well as from Gully Cave and Trou de Chaleux (**Table 4.8**). Equal variances were assumed from Levene's test which was non-significant for all sites apart from Nørre Lyngby and Laugerie Haute, where Levene's test was significant and equal variances were not assumed.

Table 4.13. Results of Levene's Test and Independent Samples T-Test for Late Devensian/Weichselian *Rangifer tarandus*. *R. t. tarandus* were tested to determine whether a significant difference was evident between the body masses of males and females at each site. Results were significant at p<0.05.

| Site | Sex | n | mean | SD | Levene's test | t-test |
|--------------|-----|----|--------|-------|----------------------------|----------------------------|
| Chelm's | Μ | 8 | 128.29 | 11.08 | F ₁₂ =1.632 | t ₁₂ =4.536 |
| Combe | F | 6 | 104.64 | 7.18 | p=0.226 | p=0.001 |
| Gully Cave | Μ | 3 | 124.54 | 4.55 | F₃=3.457 | t₃=6.193 |
| | F | 2 | 103.31 | 0.98 | p=0.160 | p=0.008 |
| Ossom's | Μ | 5 | 114.50 | 4.57 | F ₈ =1.017 | t ₈ =3.992 |
| Cave | F | 5 | 94.57 | 10.18 | p=0.343 | p=0.004 |
| Soldier's | Μ | 61 | 117.81 | 9.22 | F ₇₈ =0.017 | t ₇₈ =7.497 |
| Hole | F | 28 | 101.03 | 9.41 | p=0.897 | p=0.0001 |
| Trou de | Μ | 2 | 114.29 | 9.52 | F ₈ =0.354 | t ₈ =4.083 |
| Chaleux | F | 8 | 91.67 | 6.57 | p=0.569 | p=0.004 |
| Køge Bugt | Μ | 21 | 128.04 | 11.90 | F ₃₈ =0.626 | t ₃₈ =9.022 |
| | F | 19 | 92.08 | 13.31 | p=0.434 | p=0.0001 |
| Nørre Lyngby | Μ | 2 | 113.61 | 10.80 | F _{1.124} =16.067 | t _{1.124} =2.266 |
| | F | 3 | 95.78 | 3.27 | p=0.028 | p=0.242 |
| Abri de | Μ | 12 | 113.33 | 11.53 | F _{16.594} =5.165 | t _{16.594} =7.902 |
| Laugerie | F | 15 | 85.50 | 6.58 | p=0.032 | p=0.0001 |
| Haute | | | | | | |
| Abri de La | Μ | 34 | 120.53 | 7.925 | F ₁₁₉ =1.152 | t ₁₁₉ =15.240 |
| Madeleine | F | 87 | 94.83 | 8.49 | p=0.285 | p=0.0001 |

Body mass reconstructions from Britain (**Figure 4.11**) appeared to be consistent between the geographically proximal sites of Chelm's Combe, where males weighed 128.28 ± 9.27 kg and females weighed 104.64 ± 7.54 kg and at Gully Cave, where males weighed 124.54 kg and females weighed 103.31 kg. At Soldier's Hole, males were slightly lighter at 119.05 ± 2.75 kg and females weighed 101.03 ± 3.88 kg however, the lowest estimates of body mass for either males or females were reconstructed from Ossom's Cave, where males weighed 114.50 ± 5.68 kg and females weighed 94.57 ± 12.64 kg.

Average estimates of body mass were reconstructed from Belgium, Denmark and France, each represented two sites (**Figure 4.11**). From Belgium, males, with an average body mass of 114.29 kg, were only measured from Trou de Chaleux, while females were present at both Trou de Chaleux, weighing 91.67 ± 5.49 kg, and Trou des Nutons, weighing 87.79 ± 8.63 kg. From Denmark, the average body mass of males from Køge Bugt was 128.04 ± 5.42 kg, larger than the individuals from Nørre Lyngby where male average body mass was reconstructed at only 113.61 kg. However, the size of females

from Køge Bugt and Nørre Lyngby was more similar, weighing 92.09 ± 6.41 kg and 95.78 kg respectively. From France, *R. tarandus* were slightly lighter from Laugerie Haute, where males weighed 113.61 ± 2.77 kg and females weighed 85.49 ± 1.81 kg, than from La Madeleine, where males weighed 120.53 ± 7.33 kg and females weighed 94.83 ± 3.64 kg.



Figure 4.11. Average Estimated Body Mass of *Rangifer tarandus* from Late Devensian/Weichselian Sites. Body mass is reconstructed from the postcrania of Late Devensian/Weichselian *R. tarandus* from sites in Britain including Chelm's Combe (CC), Gully Cave (GC), Ossom's Cave (OC) and Soldier's Hole (SoH), sites in Belgium including Trou de Chaleux (TC) and Trou des Nutons (TN), sites in Denmark including Køge Bugt (KB) and Nørre Lyngby (NL) and sites in France including La Madeleine (LM) and Laugerie Haute (LH). Males are represented by a square and females are shown as a diamond. The 95% confidence interval is also presented. The legend gives an indication of the colours representing each country.

Comparisons were also made between the Late Devensian/Weichselian sites using a one-way ANOVA, to separately test the differences between male and female body mass reconstructions. The sites of Trou de Chaleux and Nørre Lyngby were not included in the analysis of males due to small sample sizes (n<2). Between the male populations from each site, the one-way ANOVA was significant ($F_{(6,131)}$ =5.327, p=0.0001) and therefore there was a significant difference in body mass. Levene's test for equal variance was non-significant ($F_{(6,131)}$ =1.880, p=0.089) and indicative of equal variances. Therefore, body masses could be further analysed using the *post hoc* test Tukey HSD to compare the differences between each site (**Table 4.11**). The results of this test are summarised below.

- There was a significant difference between the larger body masses of male populations at Køge Bugt and the smaller body masses of males at both Soldier's Hole and Laugerie Haute.
- There was a significant difference between the smaller body masses of male populations at Laugerie Haute and the larger body masses of males at both Chelm's Combe and Køge Bugt.
- There was no significant difference between all remaining combinations of sites.

Table 4.14. Results of Tukey HSD Test for Male *Rangifer tarandus* from Late Devensian/Weichselian Sites. *R. tarandus* were tested to determine whether a significant difference was evident between the body masses of males from different fossil sites. The mean difference is significant (*) at p<0.05.

| Site (I) | Site (J) | Mean | Std. | Sig. | 95% Coi | nfidence |
|------------|----------------|------------------------|---------|-------|--------------|----------|
| | | Difference | Error | | Inte | rvai |
| | | (I-J) | | | Lower | Upper |
| Oh alva'a | Culler Cours | 2 74167 | 6 46444 | 0.007 | Bound | 22 1005 |
| Cheim s | Guily Cave | 3.74107 | 0.40441 | 0.997 | -13.0172 | 20.000 |
| edmo | Ossom's Cave | 13.78100 | 0.44002 | 0.157 | -2.5206 | 30.0626 |
| | Soldier's Hole | 10.47191 | 3.01312 | 0.065 | -0.3482 | 21.2920 |
| | Køge Bugt | 0.24548 | 3.96719 | 1.000 | -11.6350 | 12.1259 |
| | Abri de | 14.95083 | 4.35830 | 0.014 | 1.8991 | 28.0026 |
| | Laugerie Haute | | | | | |
| | Abri de la | 7.75118 | 3.75213 | 0.379 | -3.4853 | 18.9876 |
| | Madeleine | | | | | |
| Gully Cave | Chelm's Combe | -3.74167 | 6.46441 | 0.997 | -23.1005 | 15.6172 |
| | Ossom's Cave | 10.03933 | 6.97329 | 0.779 | -10.8434 | 30.9221 |
| | Soldier's Hole | 6.73024 | 5.66122 | 0.897 | -10.2233 | 23.6838 |
| | Køge Bugt | -3.49619 | 5.89350 | 0.997 | -21.1453 | 14.1530 |
| | Abri de | 11.20917 | 6.16357 | 0.538 | -7.2488 | 29.6671 |
| | Laugerie Haute | | | | | |
| | Abri de la | 4.00951 | 5.75094 | 0.993 | -13.2127 | 21.2317 |
| | Madeleine | | | | | |
| Ossom's | Chelm's Combe | -13.78100 | 5.44352 | 0.157 | -30.0826 | 2.5206 |
| Cave | Gully Cave | -10.03933 | 6.97329 | 0.779 | -30.9221 | 10.8434 |
| | Soldier's Hole | -3.30909 | 4.46013 | 0.990 | -16.6657 | 10.0476 |
| | Køge Bugt | -13.53552 | 4.75149 | 0.074 | -27.7647 | 0.6937 |
| | Abri de | 1.16983 | 5.08261 | 1.000 | -14.0510 | 16.3906 |
| | Laugerie Haute | | | | | |
| | Abri de la | -6.02982 | 4.57347 | 0.842 | -19.7259 | 7.6663 |
| | Madeleine | | | | | |
| Soldier's | Chelm's Combe | -10.47191 | 3.61312 | 0.065 | -21.2920 | 0.3482 |
| Hole | Gully Cave | -6.73024 | 5.66122 | 0.897 | -23.6838 | 10.2233 |
| | Ossom's Cave | 3.30909 | 4.46013 | 0.990 | -10.0476 | 16.6657 |
| | Køge Bugt | -10.22643 [*] | 2.44937 | 0.001 | -17.5615 | -2.8914 |
| | Abri de | 4.47892 | 3.04231 | 0.761 | -4.6318 | 13.5897 |
| | Laugerie Haute | | | | | |
| | Abri de la | -2.72073 | 2.08311 | 0.848 | -8.9590 | 3.5175 |
| | Madeleine | | | | | |
| Køge Bugt | Chelm's Combe | -0.24548 | 3.96719 | 1.000 | -12.1259 | 11.6350 |
| | Gully Cave | 3.49619 | 5.89350 | 0.997 | -14.1530 | 21.1453 |
| | Ossom's Cave | 13.53552 | 4.75149 | 0.074 | -0.6937 | 27,7647 |
| | 0330113 0476 | | | 0.0.1 | 0.0007 | |

| | Soldier's Hole | 10.22643* | 2.44937 | 0.001 | 2.8914 | 17.5615 |
|------------|----------------|------------------------|---------|-------|----------|---------|
| | Abri de | 14.70536 [*] | 3.45537 | 0.001 | 4.3576 | 25.0531 |
| | Laugerie Haute | | | | | |
| | Abri de la | 7.50570 | 2.65015 | 0.077 | -0.4306 | 15.4420 |
| | Madeleine | | | | | |
| Abri de | Chelm's Combe | -14.95083 [*] | 4.35830 | 0.014 | -28.0026 | -1.8991 |
| Laugerie | Gully Cave | -11.20917 | 6.16357 | 0.538 | -29.6671 | 7.2488 |
| Haute | Ossom's Cave | -1.16983 | 5.08261 | 1.000 | -16.3906 | 14.0510 |
| | Soldier's Hole | -4.47892 | 3.04231 | 0.761 | -13.5897 | 4.6318 |
| | Køge Bugt | -14.70536 [*] | 3.45537 | 0.001 | -25.0531 | -4.3576 |
| | Abri de la | -7.19966 | 3.20617 | 0.279 | -16.8011 | 2.4018 |
| | Madeleine | | | | | |
| Abri de la | Chelm's Combe | -7.75118 | 3.75213 | 0.379 | -18.9876 | 3.4853 |
| Madeleine | Gully Cave | -4.00951 | 5.75094 | 0.993 | -21.2317 | 13.2127 |
| | Ossom's Cave | 6.02982 | 4.57347 | 0.842 | -7.6663 | 19.7259 |
| | Soldier's Hole | 2.72073 | 2.08311 | 0.848 | -3.5175 | 8.9590 |
| | Køge Bugt | -7.50570 | 2.65015 | 0.077 | -15.4420 | 0.4306 |
| | Abri de | 7.19966 | 3.20617 | 0.279 | -2.4018 | 16.8011 |
| | Laugerie Haute | | | | | |

Between the female populations from each site, which did not include the site of Gully Cave in the analysis due to the small sample size (n<2), the one-way ANOVA was also significant ($F_{(8,167)}$ =5.194, p=0.0001) indicating that there was a significant difference in body mass. Furthermore, Levene's test for equal variance was significant ($F_{(8,167)}$ =2.319, p=0.022) and assumed unequal variances. Therefore, the *post hoc* test Dunnett's T3 was used to compare the differences between each site (**Table 4.15**). The results of this test are summarised below.

- There was a significant difference between the smaller body masses of female populations at Laugerie Haute and the larger body masses at Chelm's Combe, Soldier's Hole and La Madeleine.
- There was no significant difference between all remaining combinations of sites.

Table 4.15. Results of Dunnett's T3 Test for Female *Rangifer tarandus* from Late Devensian/Weichselian Sites. *R. tarandus* were tested to determine whether a significant difference was evident between the body masses of males from different fossil sites. The mean difference is significant (*) at p<0.05.

| Site (I) | Site (J) | Mean Difference | Std. Error | Sig. | 95% Confidence Interval | |
|----------|--------------------|--------------------|---------------|-------|----------------------------|----------------|
| | | (I-J) | | | Lower Bound | Upper Bound |
| Chelm's | Ossom's Cave | 10.06967 | 5.41689 | 0.820 | -14.6185 | 34.7578 |
| Combe | Soldier's Hole | 3.61207 | 3.48486 | 0.999 | -10.8690 | 18.0932 |
| | Trou de Chaleux | 12.97417 | 3.74118 | 0.126 | -2.3033 | 28.2517 |
| | Trou des Nutons | 16.85167 | 4.68107 | 0.089 | -1.6511 | 35.3544 |
| | Køge Bugt | 12.55693 | 4.23419 | 0.213 | -3.2675 | 28.3814 |
| | Nørre Lyngby | 8.86500 | 3.48705 | 0.473 | -7.0581 | 24.7881 |

| | Abri de | 19.14900 [*] | 3.38964 | 0.009 | 4.6206 | 33.6774 |
|-----------|----------------|-----------------------|---------|-------|----------|---------|
| | Laugerie Haute | | | | | |
| | Abri de la | 9.81029 | 3.07104 | 0.256 | -5.0267 | 24.6472 |
| | Madeleine | | | | | |
| Ossom's | Chelm's Combe | -10.06967 | 5.41689 | 0.820 | -34.7578 | 14.6185 |
| Cave | Soldier's Hole | -6.45760 | 4.92771 | 0.978 | -31.2351 | 18.3199 |
| | Trou de | 2.90450 | 5.11219 | 1.000 | -21.6212 | 27.4302 |
| | Chaleux | | | | | |
| | Trou des | 6.78200 | 5.83528 | 0.997 | -18.1051 | 31.6691 |
| | Nutons | | | | | |
| | Køge Bugt | 2.48726 | 5.48329 | 1.000 | -21.4560 | 26.4305 |
| | Nørre Lyngby | -1.20467 | 4.92926 | 1.000 | -26.5613 | 24.1520 |
| | Abri de | 9.07933 | 4.86084 | 0.805 | -15.9743 | 34.1330 |
| | Laugerie Haute | | | | | |
| | Abri de la | -0.25938 | 4.64428 | 1.000 | -26.4175 | 25.8987 |
| | Madeleine | | | | | |
| Soldier's | Chelm's Combe | -3.61207 | 3.48486 | 0.999 | -18.0932 | 10.8690 |
| Hole | Ossom's Cave | 6.45760 | 4.92771 | 0.978 | -18.3199 | 31.2351 |
| | Trou de | 9.36210 | 2.98932 | 0.155 | -1.7403 | 20.4645 |
| | Chaleux | | | | | |
| | Trou des | 13.23960 | 4.10512 | 0.172 | -3.2866 | 29.7658 |
| | Nutons | | | | | |
| | Køge Bugt | 8.94486 | 3.58719 | 0.418 | -3.5128 | 21.4025 |
| | Nørre Lyngby | 5.25293 | 2.66442 | 0.767 | -6.7115 | 17.2174 |
| | Abri de | 15.53693 [*] | 2.53560 | 0.000 | 6.8514 | 24.2225 |
| | Laugerie Haute | | | | | |
| | Abri de la | 6.19822 | 2.09066 | 0.159 | -0.9768 | 13.3732 |
| | Madeleine | | | | | |
| Trou de | Chelm's Combe | -12.97417 | 3.74118 | 0.126 | -28.2517 | 2.3033 |
| Chaleux | Ossom's Cave | -2.90450 | 5.11219 | 1.000 | -27.4302 | 21.6212 |
| | Soldier's Hole | -9.36210 | 2.98932 | 0.155 | -20.4645 | 1.7403 |
| | Trou des | 3.87750 | 4.32484 | 1.000 | -13.2464 | 21.0014 |
| | Nutons | | | | | |
| | Køge Bugt | -0.41724 | 3.83669 | 1.000 | -14.0593 | 13.2248 |
| | Nørre Lyngby | -4.10917 | 2.99188 | 0.977 | -17.3809 | 9.1626 |
| | Abri de | 6.17483 | 2.87776 | 0.677 | -4.8042 | 17.1539 |
| | Laugerie Haute | | | | | |
| | Abri de la | -3.16388 | 2.49461 | 0.992 | -13.6226 | 7.2949 |
| | Madeleine | | | | | |
| Trou des | Chelm's Combe | -16.85167 | 4.68107 | 0.089 | -35.3544 | 1.6511 |
| Nutons | Ossom's Cave | -6.78200 | 5.83528 | 0.997 | -31.6691 | 18.1051 |
| | Soldier's Hole | -13.23960 | 4.10512 | 0.172 | -29.7658 | 3.2866 |
| | Trou de | -3.87750 | 4.32484 | 1.000 | -21.0014 | 13.2464 |
| | Chaleux | | | | | |
| | Køge Bugt | -4.29474 | 4.75775 | 1.000 | -21.9751 | 13.3856 |
| | Nørre Lyngby | -7.98667 | 4.10698 | 0.786 | -25.3591 | 9.3858 |
| | Abri de | 2.29733 | 4.02461 | 1.000 | -14.2170 | 18.8117 |
| | Laugerie Haute | | | | | |
| | Abri de la | -7.04138 | 3.76019 | 0.818 | -23.5532 | 9.4705 |
| | Madeleine | | | | | |
| Køge Bugt | Chelm's Combe | -12.55693 | 4.23419 | 0.213 | -28.3814 | 3.2675 |
| | Ossom's Cave | -2.48726 | 5.48329 | 1.000 | -26.4305 | 21.4560 |
| | Soldier's Hole | -8.94486 | 3.58719 | 0.418 | -21.4025 | 3.5128 |
| | Trou de | 0.41724 | 3.83669 | 1.000 | -13.2248 | 14.0593 |
| | Chaleux | | | | | |

| | Trou des | 4.29474 | 4.75775 | 1.000 | -13.3856 | 21.9751 |
|------------|----------------|-------------|---------|---------|----------|---------|
| | Nutons | | | | | |
| | Nørre Lyngby | -3.69193 | 3.58933 | 1.000 | -17.3153 | 9.9314 |
| | Abri de | 6.59207 | 3.49477 | 0.853 | -5.6723 | 18.8564 |
| | Laugerie Haute | | | | | |
| | Abri de la | -2.74664 | 3.18669 | 1.000 | -14.2367 | 8.7434 |
| | Madeleine | | | | | |
| Nørre | Chelm's Combe | -8.86500 | 3.48705 | 0.473 | -24.7881 | 7.0581 |
| Lyngby | Ossom's Cave | 1.20467 | 4.92926 | 1.000 | -24.1520 | 26.5613 |
| | Soldier's Hole | -5.25293 | 2.66442 | 0.767 | -17.2174 | 6.7115 |
| | Trou de | 4.10917 | 2.99188 | 0.977 | -9.1626 | 17.3809 |
| | Chaleux | | | | | |
| | Trou des | 7.98667 | 4.10698 | 0.786 | -9.3858 | 25.3591 |
| | Nutons | | | | | |
| | Køge Bugt | 3.69193 | 3.58933 | 1.000 | -9.9314 | 17.3153 |
| | Abri de | 10.28400 | 2.53862 | 0.107 | -1.9864 | 22.5544 |
| | Laugerie Haute | | | | | |
| | Abri de la | 0.94529 | 2.09431 | 1.000 | -13.9358 | 15.8263 |
| | Madeleine | | | | | |
| Abri de | Chelm's Combe | -19.14900* | 3.38964 | 0.009 | -33.6774 | -4.6206 |
| Laugerie | Ossom's Cave | -9.07933 | 4.86084 | 0.805 | -34.1330 | 15.9743 |
| Haute | Soldier's Hole | -15.53693* | 2.53560 | 0.000 | -24.2225 | -6.8514 |
| | Trou de | -6.17483 | 2.87776 | 0.677 | -17.1539 | 4.8042 |
| | Chaleux | | | | | |
| | Trou des | -2.29733 | 4.02461 | 1.000 | -18.8117 | 14.2170 |
| | Nutons | | | | | |
| | Køge Bugt | -6.59207 | 3.49477 | 0.853 | -18.8564 | 5.6723 |
| | Nørre Lyngby | -10.28400 | 2.53862 | 0.107 | -22.5544 | 1.9864 |
| | Abri de la | -9.33871* | 1.92777 | 0.002 | -16.2323 | -2.4452 |
| | Madeleine | | 0.07404 | | 040470 | 5 0007 |
| Abri de la | Chelm's Combe | -9.81029 | 3.07104 | 0.256 | -24.64/2 | 5.0267 |
| Madeleine | Ossom's Cave | 0.25938 | 4.64428 | 1.000 | -25.8987 | 26.4175 |
| | Soldier's Hole | -6.19822 | 2.09066 | 0.159 | -13.3732 | 0.9768 |
| | Trou de | 3.16388 | 2.49461 | 0.992 | -7.2949 | 13.6226 |
| | Chaleux | | 0 70040 | 0.040 | 0.4705 | 00 5500 |
| | Trou des | 7.04138 | 3.76019 | 0.818 | -9.4705 | 23.5532 |
| | Nutons | 0 7 4 0 0 4 | 0.40000 | 1 0 0 0 | 0.7404 | 44.0007 |
| | Køge Bugt | 2.74664 | 3.18669 | 1.000 | -8.7434 | 14.2367 |
| | Nørre Lyngby | -0.94529 | 2.09431 | 1.000 | -15.8263 | 13.9358 |
| | Abri de | 9.33871 | 1.92777 | 0.002 | 2.4452 | 16.2323 |
| | Laugerie Haute | | | | | |

4.3.4. Late Pleistocene Body Mass

Figure 4.12 compares the total average body masses reconstructed from the Early Devensian, Middle Devensian/Weichselian and Late Devensian/Weichselian specimens to the weights of modern *R. tarandus* subspecies. The Late Pleistocene *R. tarandus* were more consistent with the range of body sizes expressed by the European *R. t. tarandus* than either the smaller Svalbard *R. t. platyrhynchus* or heavier North America *R. t. caribou* or *R. t. groenlandicus*. Comparisons between modern *R. t. tarandus* and the Late Pleistocene stages were made using a one-way ANOVA, to separately test the

differences between male and female body mass reconstructions. Between the male populations from each site, the one-way ANOVA was non-significant ($F_{(3,40)}$ =1.402, p=0.256) and therefore there was no significant difference in body mass between the modern and Late Pleistocene individuals. Levene's test for equal variance was significant ($F_{(3,40)}$ =5.442, p=0.003) and indicative of unequal variances. Between the female populations from each site, the one-way ANOVA was also non-significant ($F_{(3,36)}$ =2.067, p=0.122) indicating that there was no significant difference in body masses. Levene's test for equal variance was also non-significant ($F_{(3,36)}$ =2.675, p=0.062) and assumed equal variances.



Figure 4.12. Average Estimated Body Masses of Modern and Late Pleistocene *Rangifer tarandus.* Body mass reconstructed from the postcrania of Late Pleistocene specimens from the Early Devensian, Middle Devensian/Weichselian and Late Devensian/Weichselian are compared to modern specimens from the *R. t. caribou* (*R.t.c.*), *R. t. groenlandicus* (*R.t.g.*), *R. t. tarandus* (*R.t.t.*) and *R. t. platyrhynchus* (*R.t.p.*) subspecies. Males are represented by a square and females are shown as a diamond. The 95% confidence interval is also presented.

From the Late Pleistocene, the total average body mass was established for the males and females from each of the three stages studied. During the Early Devensian, males weighed 128.80 ± 8.67 kg and females weighed 95.90 ± 5.19 kg, during the Middle Devensian/Weichselian, males weighed 118.56 ± 4.08 kg and females weighed 89.25 ± 3.11 kg, and during the Late Devensian/Weichselian, males weighed 119.58 ± 4.72 kg while females weighed 95.12 ± 4.53 kg. To ascertain whether there was a significant difference between the total average body mass of the Early, Middle and Late last cold stage populations, a one-way ANOVA was applied. Between the male populations from each stage, the results of this test were significant (F_(2,29)=3.703, p=0.037) and therefore there was a statistically significant difference in the body mass of these ages. Levene's test for equal variance was non-significant ($F_{(2,29)}=0.155$, p=0.857) and therefore indicative of equal variances. Therefore, body masses could be further analysed using the post hoc Tukey HSD which identified differences between the larger average body masses of the Early Devensian and smaller average body masses of the Middle Devensian/Weichselian (Table 4.16). There was no significant difference between the body masses of male populations from the Early Devensian and Late Devensian/Weichselian, as well as the Middle and Late Devensian/Weichselian. Between the female populations from each stage, the one-way ANOVA was significant $(F_{2,29}=4.306, p=0.023)$ and therefore there was a statistically significant difference in the body mass of these ages. Levene's test for equal variance was non-significant $(F_{(2,29)}=0.405, p=0.671)$ and therefore indicative of equal variances. Therefore, body masses could be further analysed using the post hoc Tukey HSD which identified differences between the larger average body masses of female populations from the Late Devensian/Weichselian and smaller average body masses of females from the Middle Devensian/Weichselian (Table 4.17). There was no significant difference between the body masses of female populations from the Early Devensian and either the Middle or Late Devensian/Weichselian.

Table 4.16. Results of Tukey HSD Test for Male Rangifer tarandus from the LatePleistocene. R. tarandus were tested to determine whether a significant difference wasevident between the body masses of males from different fossil sites. The meandifference is significant (*) at p<0.05.</td>

| Stage (I) | Stage (J) | Mean Difference | Std. Error | Sig. | 95% Cor Inte | nfidence rval |
|----------------------|-------------------------------------|--------------------|---------------|-------|-----------------|------------------|
| | | (I-J) | | | Lower Bound | Upper Bound |
| Early Devensian | Middle Devensian/ Weichselian | 10.24077* | 3.80581 | 0.031 | 0.8417 | 19.6398 |
| | Late Devensian/ Weichselian | 9.22080 | 4.19916 | 0.089 | -1.1497 | 19.5912 |
| Middle Devensian/ | Early Devensian | -10.24077* | 3.80581 | 0.031 | -19.6398 | -0.8417 |
| Weichselian | Late Devensian/ Weichselian | -1.01997 | 3.07347 | 0.941 | -8.6104 | 6.5704 |
| Late Devensian/ | Early Devensian | -9.22080 | 4.19916 | 0.089 | -19.5912 | 1.1497 |
| Weichselian | Middle Devensian/ Weichselian | 1.01997 | 3.07347 | 0.941 | -6.5704 | 8.6104 |

Table 4.17. Results of Tukey HSD Test for Female Rangifer tarandus from the LatePleistocene. R. tarandus were tested to determine whether a significant difference was
evident between the body masses of males from different fossil sites. The mean
difference is significant (*) at p<0.05.</td>

| Stage (I) | Stage (J) | Mean Difference | Std. Error | Sig. | 95% Cor Inte | nfidence rval |
|-------------|-------------|-----------------------|---------------|-------|-----------------|------------------|
| | | (I-J) | | | Lower | Upper |
| | | | | | Bound | Bound |
| Early | Middle | 6.64971 | 3.01057 | 0.087 | -0.7853 | 14.0848 |
| Devensian | Devensian/ | | | | | |
| | Weichselian | | | | | |
| | Late | 0.77772 | 3.24122 | 0.969 | -7.2269 | 8.7824 |
| | Devensian/ | | | | | |
| | Weichselian | | | | | |
| Middle | Early | -6.64971 | 3.01057 | 0.087 | -14.0848 | 0.7853 |
| Devensian/ | Devensian | | | | | |
| Weichselian | Late | -5.87199 [*] | 2.35833 | 0.048 | -11.6962 | -0.0477 |
| | Devensian/ | | | | | |
| | Weichselian | | | | | |
| Late | Early | -0.77772 | 3.24122 | 0.969 | -8.7824 | 7.2269 |
| Devensian/ | Devensian | | | | | |
| Weichselian | Middle | 5.87199 [*] | 2.35833 | 0.048 | 0.0477 | 11.6962 |
| | Devensian/ | | | | | |
| | Weichselian | | | | | |

4.4. Comparison of Late Pleistocene Body Mass

As body mass was reconstructed for both modern and Late Pleistocene specimens using a mass estimating equation, which operates as a scaling relationship rather than relying on comparisons to a standard modern population, it was possible to make direct comparisons between the modern *R. tarandus* datasets and the Late Pleistocene record. Having established the various factors which control body size in modern *R. tarandus*, in particular, the sensitivity of herds to changes in climate, vegetation and density, the implications of these were then addressed with reference to palaeoenvironmental and palaeoclimatic reconstructions of the Late Pleistocene, on both a spatial and temporal scale.

4.4.1. Sexual Dimorphism and the Mass Estimating Equation

Although the initial application of the mass estimating equation to Late Pleistocene specimens did not attempt to differentiate between sex (Collinge, 2001), the sexual dimorphism exhibited by *R. tarandus* has, for the first time, enabled reconstructions from both males and females from the fossil record (**Figure 4.9, 4.10 and 4.11**). It has been suggested that only late-fusing epiphyses, or better still fully fused elements, should be used to assign the sex of Late Pleistocene specimens in an attempt to avoid the blurring

effect created by intermediate subadult individuals (Weinstock, 2000a; 200b). However, reconstructions from skeletal elements of both modern and fossil specimens in this study successfully incorporated elements from both early and late-fusing epiphyses. While the fragmentary nature of fossil remains means that the exact age of an individual is not always identifiable, in collections of modern specimens, known age subadults where the unmeasured epiphysis may be unfused or fusing, were therefore included in the calculation of average estimated body mass. As such, it was important to test whether the inclusion of both adults and subadults affected the sexual dimorphism of body mass reconstructions. Results from Independent Sample t-tests completed on modern R. t. platyrhynchus, R. t. tarandus (Table 4.2) and Early, Middle and Late last cold stage specimens (Table 4.9, 4.10 and 4.13) show that whether sex was known or inferred, there was a significant difference between male and female body masses. The only instances where there was no significant difference were Late Pleistocene sites with smaller (and thus potentially less reliable) sample sizes (Table 4.10 and 4.13). Of course, sample size is an important aspect when detecting sexual dimorphism from fossil assemblages. Even where large numbers of R. tarandus have been identified, for example from the German site of Stellmoor, it is almost impossible to discern any sexual dimorphism from skeletal measurements without limiting the study to only fully fused elements (Weinstock 2000a; 2000b). However, this level of postcranial preservation is distinctly rare in the fossil record. In the context of this study, only the German site of Salzgitter-Lebenstedt and the French site of Abri de la Madeleine, represented a sufficiently large MNI whereby sexual dimorphism was consistently harder (but still possible) to recognise across multiple elements.

Nevertheless, there was a greater distinction between the average body masses of the heavier males and smaller females observed from the fossil record, compared to modern *R. tarandus*. For Late Pleistocene assemblages, the mean difference in the size of the two sexes was 34.33 kg for the Early Devensian sites, 29.24 kg for the Middle Devensian/Weichselian sites and 21.30 kg for the Late Devensian/Weichselian sites, while in modern populations, the difference was 21.51 kg for *R. t. tarandus* and only 5.94 kg for *R. t. platyrhynchus*. The temporal scale of Late Pleistocene assemblages could potentially account for this variation. *R. tarandus* body size can vary from cohort to cohort and, as opposed to the modern samples which were taken from known populations during a given year, fossil sites may represent multiple years and generations, as the number of depositional events responsible for fossil accumulation are usually unknown. A range of sizes may therefore be included in the average estimated body mass, although the 95% confidence levels of modern and fossil estimates were not dissimilar. Alternatively, this variability could also have resulted from a selection bias towards skeletal elements where sexual dimorphism was clearly observable in bivariate plots

and, therefore, the extremes of the body mass reconstructions dominated calculations. Nevertheless, assigning sex using the sexual dimorphism of subadult and adult skeletal elements is an effective method in determining the respective body masses of males and females for both modern and fossil *R. tarandus*.

4.4.2. Early, Middle and Late Last Cold Stage Body Mass

Despite the differences in the scale of sexual dimorphism identified between modern and fossil specimens, the size of Late Pleistocene *R. tarandus* was similar to body masses measured from the modern *R. t. tarandus* subspecies (**Figure 4.12**). Given the proximity of the extant subspecies to the distribution of Late Pleistocene fossil sites in western Europe, this is not unexpected. Modern populations of Scandinavian *R. t. tarandus* originated from two last glacial populations, both of which with a strong European presence (Flagstad and Røed, 2003). Nevertheless, there were significant differences in body mass both within and between the Early, Middle and Late last cold stage fossil sites studied.

For both males and females, the body masses reconstructed from the British sites of the Early Devensian were shown by one-way ANOVA to be similar across the respective sexes (Figure 4.9). The only site not included in these comparisons was the single male from Stump Cross Cavern. Although the average body mass of 119.06 kg from this individual was smaller than the total average from Early Devensian males of 128.80 ± 8.67 kg, the small sample size makes it harder to draw comparisons. Otherwise, the Early Devensian represents the largest estimate of male body mass reconstructed from Late Pleistocene *R. tarandus* (Figure 4.12). Notably, the three sites of Banwell Bone Cave, Isleworth and Windy Knoll, all reconstructed average body masses in excess of 130 kg (Figure 4.9). In modern R. t. tarandus, males this heavy were recorded primarily from the northern provinces of Finnmark and Norrbotten (Figure 4.2 and 4.3), which are both forest herds. As well as occupying areas of softer taiga snow cover which can be up to 65 cm deep (Nieminen and Helle, 1980), these herds are characterised by smaller group sizes, around 184 individuals in Norrbotten herds (The Sami Parliament, 2019); these are dependent on the forest year-round and are therefore essentially nonmigratory. Given the similarities in the modern specimens, which weighed 134.63 ± 4.80 kg from Finnmark 1869, 140.97 \pm 4.87 kg from Norrbotten 1909 and 135.62 \pm 6.53 kg from Norrbotten 1950, to body masses from Banwell Bone Cave, which weighed 131.49 ± 4.86 kg, Isleworth, which weighed 135.32±6.38kg, and Windy Knoll, which weighed 134.071±3.39kg, this could infer similar conditions within the *R. tarandus* herds and the palaeoclimate and palaeoenvironment of the British Early Devensian, MIS 5a.

However, longer legs and perhaps therefore larger body masses, are also an adaptive advantage for lowering energy expenditure in R. tarandus undergoing frequent migrations over long distances (Klein et al., 1987; Couturier et al., 2010), contradicting the lack of movement of the modern larger-bodied forest type. The seasonality of site occupations could provide important insights into the migrations of Early Devensian R. tarandus (see Chapter 6). Furthermore, the females from the Early Devensian sites, although consistent within Britain with an average of 95.90±5.19 kg, were smaller than Norrbotten females which weighed 107.54 ± 9.45 kg. This demonstrates the larger difference in the scale of sexual dimorphism observed from Late Pleistocene reconstructions of body mass. Instead, females were more similar to individuals from the mountain herds of Jämtland, which weighed 94.05±3.33 kg, and Lappland, where females weighed 95.91±5.13 kg. It is hard to determine from the fossil record whether *R. tarandus* were forest or mountain types, particularly given the inconsistencies that have been observed between different palaeoclimatic proxies from Early Devensian Britain. Nevertheless, following reconstructions for the presence of a relict cold boreal fauna in either temperate grassland or woodland conditions (Coope and Angus, 1975; Coope et al., 1997: Maddy et al., 1998; Currant and Jacobi, 2011), the variability in the body masses of males and females, when compared to modern *R. tarandus*, could reflect the different rates of response of each sex to the fluctuating warmer and colder episodes of the Early Devensian (Rassmussen et al., 2014).

Given the inferred island status of Britain during the Early Devensian (Currant and Jacobi, 2011), it would be interesting to compare the larger size of the British *R. tarandus* to contemporary sites from continental Europe. Unfortunately, no Early Weichselian sites were studied from Europe as part of this research. This was not the case, however, for either the mid or late last cold stage. Only the males from the Middle Devensian/Weichselian, which weighed 118.56 ± 4.08 kg, were significantly smaller than the Early Devensian specimens, although the average estimated body mass from Late Devensian/Weichselian males of 119.58 ± 4.72 kg was very similar to that of the middle part of the last cold stage (**Table 4.16**).

This decrease in male average body mass from the Early Devensian onwards is exemplified by reconstructions from individuals at Picken's Hole in Britain, which were reduced from 124.05±10.78 kg to 114.23 kg. Although the sample from the Middle Devensian (MIS 3) levels at this site was not large enough to include in a one-way ANOVA, it was representative of the similarities in the size of males and females from Britain (Gully Cave, Inchnadamph Bone Cave, Kents Cavern, Pin Hole Cave, Robin Hood Cave) and Belgium (Trou du Moulin, Trou Al'Wesse, Caverne Marie-Jeanne, Goyet (Troisième Caverne) (**Figure 4.10**). Furthermore, these sites all measured within

the 95% Confidence intervals of Swedish mountain R. t. tarandus from Jämtland 1950, which weighed 110.92 ± 5.01 kg for males and 94.05 ± 3.33 kg for females, Härjedalen 1950, which weighed 117.31 ± 4.12 kg for males and 100.23 ± 8.18 kg for females from and Lappland 1950, which weighed 117.85 ± 3.00 kg for males and 95.91 ± 5.13 kg for females. In these modern herds, groups of around 419 animals (The Sami Parliament, 2019) occupy regions of hard-packed tundra snow <50 cm deep (Nieminen and Helle, 1980), while also undertaking bi-annual migrations between mountain and forest habitats. The similarities between modern and Middle Devensian/Weichselian body masses could therefore imply that similar social, palaeoclimatic and palaeoenvironmental conditions prevailed in the past. However, there were also significant differences between the body masses of a number of Middle Devensian/Weichselian sites (Table 4.11 and 4.12).

The smallest estimates of body mass from males and females during the Middle Devensian were reconstructed from the British site of Brixham Cave (Figure 4.10). With males weighing 98.92±3.87 kg and females weighing 76.93±5.61 kg, body mass at this site was significantly smaller than *R. tarandus* from the remaining mid last cold stage sites, with the exception of Sandford Hill and Pin Hole Cave (Table 4.11). In modern R. t. tarandus, individuals of this size were observed from the wild mountain R. t. tarandus of Norway in the provinces of Buskerud and Hordaland (Figure 4.2). Similarities between the modern specimens, which weighed 94.43±3.09 kg for males and 77.39±1.43 kg for females from Buskerud 1970, and 93.34 ± 1.89 kg for males and 82.08 ± 1.43 kg for females from Hordaland 1970s, suggest that R. tarandus from Brixham Cave may be similar to the Hardangervidda herd found across both the modern Norwegian provinces. The Hardangervidda herd is characterised by a particularly large density of 0.74 to 2.34 individuals/km² (Skogland, 1989; Skogland, 1990), which could account for the smaller sizes of individuals at Brixham Cave. However, from recent studies of modern R. tarandus the effects of climate appear to have had a much greater influence on body size than density, with warmer and wetter conditions limiting the availability of lichen in favour of mosses or reducing access to low-lying vegetation under ice crusts (Vors and Boyce, 2009; Sandström et al., 2016; Vanneste et al., 2017; Bargmann et al., 2019). Therefore, the *R. tarandus* at Brixham Cave could further represent an interstadial period of the Middle Devensian, whereby warmer and wetter conditions resulted in smaller sized individuals.

Conversely, the male average body mass of 134.65 ± 6.38 kg reconstructed from the Belgian Middle Weichselian site of Trou Magrite was not only significantly larger than *R. tarandus* from Brixham Cave, Salzgitter-Lebenstedt, Sandford Hill, Pin Hole Cave and Raalte (**Table 4.11**), but was much more consistent with the size of forest *R. t. tarandus*

from Finnmark and Norrbotten, as well as the Early Devensian. This could therefore represent a switch towards a more boreal woodland environment in Belgium. However, the female average body mass of 86.73 ± 5.70 kg from Trou Magrite was much lower than either the modern or Early Devensian specimens. Instead, this overlapped the average body masses of Norwegian mountain *R. t. tarandus* from Hordaland 1970s of 82.08 ± 1.43 kg and from Oppland 2006 of 89.77 ± 2.22 kg. Again, the body sizes of both of these modern populations have been affected by higher density herds (Uboni *et al.*, 2016), although in Oppland, vegetation changes have also coincided with variations in body mass (Bignon-Lau *et al.*, 2017; Vanneste *et al.*, 2017). Sites including Sandford Hill, Mammoth Cave and Raalte also had similarly low female body masses (**Figure 4.10**), but unlike Trou Magrite, the males from these sites were more similar to the size of the Jämtland, Härjedalen and Lappland mountain specimens than any of the forest herds.

Nevertheless, the smaller body sizes of these Middle Devensian/Weichselian females clearly contributed to a total average estimated body mass of 89.25±3.11 kg. This was significantly smaller than the females from Late last cold stage sites which weighed 95.12 ± 4.53 kg, despite the fact that the only site for which female body mass was reconstructed from both the Middle and Late Devensian, that of the British Gully Cave, were very similar in size at 103.74 ± 3.74 kg and 103.31 kg respectively. Similarities were also observed between the size of Lateglacial Interstadial males and females from Britain (Soldier's Hole), Belgium (Trou de Chaleux, Trou des Nutons), Denmark (Nørre Lyngby) and France (Abri de la Madeleine) (Figure 4.11), which like many of the mid last cold stage sites, all measured within the 95% Confidence intervals of Swedish mountain R. t. tarandus from Jämtland 1950, Härjedalen 1950 and Lappland 1950. This could therefore be indicative of individuals present in larger group numbers, snow cover that was more hard-packed and migrational rangers that were longer. However, also within this range of body sizes were *R. tarandus* from the Younger Dryas assemblage at Ossom's Cave (Figure 4.11). As the Late cold stage stadial is characterised by lower temperatures and a re-expansion of open grasslands (Lang et al., 2010; Currant and Jacobi, 2011; Brooks and Langdon, 2014), body mass might be expected to vary from the preceding interstadial. However, significant differences between the body masses of Late Devensian/Weichselian sites have occurred irrespective of the rapidly oscillating stadial/interstadial conditions of the Lateglacial (Table 4.14 and 4.15) (Rassmussen et al., 2014).

The largest estimates of male average body mass from the Late Devensian/Weichselian were reconstructed from the Younger Dryas site of Chelm's Combe, where males weighed 128.28±9.27 kg, and the Lateglacial Interstadial site of Køge Bugt, where males

weighed 128.04 \pm 5.42 kg (**Figure 4.11**). The size of these males was similar to averages estimated from the Middle Weichselian sites of Trou du Sureau, where males weighed 127.42 \pm 9.33 kg, and Westeregeln, where males weighed 125.42 \pm 9.37 kg, all of which compared closely to the Lappland forest *R. t. tarandus* at 126.201 \pm 6.04 kg. Although herds from Lappland are not as small as those found in Finnmark or Norrbotten, this still implies the influence of smaller group sizes and softer and deeper snow cover. On the other hand, the smallest estimates of male average body mass from the Late Devensian/Weichselian and significantly different from both Chelm's Combe and Køge Bugt, was the Lateglacial Interstadial site of Abri de Laugerie Haute (**Table 4.14**). Males at Abri de Laugerie Haute weighed an average of 113.61 \pm 2.77 kg, while females weighed 85.49 \pm 1.81 kg. Such sizes were similar to the patterns previously observed from the Middle Devensian/Weichselian sites of Sandford Hill, Mammoth Cave and Raalte, whereby males were consistent with the body masses of Swedish mountain *R. t. tarandus* and females matched their Norwegian counterparts.

While population dynamics clearly play an important role in the body masses of modern populations of *R. tarandus*, variability between the Early, Middle and Late last cold stage animals (**Figure 4.12**) could also be part of wider trends in mammalian body size during the Late Pleistocene. The most notable of these were the size reductions which occurred in numerous localities at the Pleistocene-Holocene transition and affected species including, but not limited to: caballoid horses (*Equus* spp.) (Forstén, 1991; Forstén, 1993), wild boar (*Sus Scrofa*, Linnaeus, 1758) (Davis, 1981; Albarella *et al.*, 2013), wolves (*Canis lupus*, Linnaeus, 1758) (Flower, 2016), foxes (*Vulpes vulpes*. Linnaeus, 1758) (Davis, 1981) and aurochs (*Bos primigenius*, Bojanus, 1827) (Davis, 1981). Initially, this was considered to be driven by increasing temperatures at the end of the last glaciation, with species adapting their size to improve thermoregulation following biological rules such as Bergmann's Rule (Davis, 1981). However, the relationship is clearly more complex (Saarinen *et al.*, 2016), with changes in body size through time occurring in response to the interaction between climatic and environmental conditions, population densities and forage quality and availability.

Although Guthrie (1985) noted that *R. tarandus* is one such species for which size has decreased from the Pleistocene into the Holocene and the present day, with the exception of the smaller sized island subspecies *R. t. platyrhynchus*, average estimates of body mass from modern *R. t. tarandus* in this study are not dissimilar from those of Late Pleistocene individuals (**Figure 4.12**). Furthermore, the North American subspecies of *R. t. caribou* is considerably larger than both the modern subspecies *R. t. tarandus* and fossil specimens (**Figure 4.12**). However, despite the relative stability of *R. tarandus* size over time, the body masses of last cold stage *R. tarandus* were visibly larger in

animals from the Early Devensian than either the Middle or Late Devensian/Weichselian (Figure 4.12). A similar size difference was also recognised by Saarinen et al. (2016) when Early and Middle Devensian *R. tarandus* were compared. This appears to deviate from other patterns of body size in the Cervidae, which, in species such as red deer (Cervus elaphus, Linnaeus, 1758), typically increase during the higher productivity open environments that would have been evident during the Middle Devensian/Weichselian (Saarinen et al., 2016). Nevertheless, the presence of smaller-sized individuals in the open environments of the Late Pleistocene have been identified from Bison spp., E. ferus and C. lupus (Flower, 2016; Saarinen et al., 2016). From each of these species, it was apparent that decreasing sizes were probably influenced not just by the interaction between the climatic and environmental conditions, but also by competition for resources. This could take the form of either intraspecific competition, as population size and therefore density increases together with the productivity of environments (Saarinen et al., 2016), or interspecific competition (Flower, 2016), as the species diversity within an environment increases. As has already been demonstrated from the modern subspecies, herd species such as R. tarandus are particularly susceptible to the pressures of population density and forage availability. While it is difficult to calculate reliably the density of fossil populations (see Chapter 6), species diversity was certainly greater in the Middle and Late Devensian/Weichselian, compared to the Early Devensian. Therefore, it is highly likely that even when open and productive grasslands develop, the body sizes of *R. tarandus* will remain small.

The relationship between forage availability and competition has also been important in the development of body size gradients or clines. In modern populations, gradients have been observed along both south-north and west-east trajectories, with species such as S. scrofa and C. elaphus recording larger body masses in the most northern and inland parts of their ranges (Langvatn and Albon, 1986; Weinstock, 2000a; Albarella et al., 2013). This primarily reflects the areas where forage quality is higher, although as continentality results in increasingly harsh climatic conditions away from coastal regions, the cooler and drier inland environments are also subject to less intraspecific competition (Weinstock, 2000a). The effect is apparent from even small-scale transects, for example in Norway, increases in *C. elaphus* body mass are visible between the coastal to inland areas, while individuals that migrate between the two are also recorded as being larger (Langvatn and Albon, 1986). Despite the identification of clines in previous studies of body size in Late Pleistocene R. tarandus (Weinstock, 2000a), neither latitudinal or longitudinal gradients have been reconstructed from the modern or fossil specimens included in this study. However, this may be a product of the spatial distribution of samples from only western Europe and could be explored in more detail with further study.

4.4.3. Taphonomic Influences

Where significant differences in body mass appear to be site-specific rather than representative of either temporal or spatial patterns between Britain and western Europe, there may also be a taphonomic bias attached to reconstructions of body mass from Late Pleistocene sites. The demography of a site will vary substantially depending on whether the mortality profile was non-selective or selective. Non-selective assemblages are usually deposited synchronously and caused by catastrophic events (Steele, 2003) such as natural flooding (Kahlke and Gaudzinski, 2005), or are accumulated by ambush predators (Stiner, 1990). For sites of this nature, body mass estimates should be representative of the living herd structure and therefore the males and females present in a population at that time. Selective assemblages, however, can be dominated by either vulnerable juvenile and old individuals (Stiner, 1990) accumulated under attritional processes such as disease, malnutrition and cursorial predation (Steele, 2003), or prime age adults, a product of a higher risk and return selection strategy which requires a level of skill and technology unique to hominins (Steele, 2003). As such, average estimates of body mass from a selective assemblage might not be reflective of the actual size of individuals on the surrounding landscape, particularly if, for example, carcasses have been selected for butchery. Nevertheless, it is evident from the study of modern R. tarandus that factors including density, climate and vegetation have a significant influence on body mass, and as such, the interpretation size may be only be blurred by the taphonomy of a fossil assemblage.

4.4.4. Implications for Recent Decreases in Body Mass

The fact that all Late Pleistocene populations are well above 50 kg (**Figure 4.9, 4.10, 4.11**), which has been referred to as a critical lower threshold for *R. tarandus*, is nevertheless significant. Even from the modern study range of 1861-2006, only individuals from Svalbard in 1975 have recorded body masses approaching this size, although more recent populations from Norrbotten in northern Sweden are also at risk. In both populations, decreases in body size have coincided with climatic changes combined with a restricted access to forage. In Svalbard, *R. t. platyrhynchus* have responded to a warmer and wetter climatic regime whereby rain-on-snow trap winter forage under thick ice layers. For the Norrbotten *R. t. tarandus*, increasing forestry has resulted in new coniferous forest growth which is denser and less conducive to the growth of lichen, which is the preferred winter forage. While the Late Pleistocene *R. tarandus* populations would not have been affected by the levels of human impact experienced by modern herds, both climate and vegetation could have had a significant
influence on body size. As such, with average estimates of body mass in excess of 75 kg from Late Pleistocene females (**Figure 4.9, 4.10, 4.11**), females being preferentially affected by the problem of lower body mass (Albon *et al.*, 2016), this implies that perhaps Late Pleistocene winters were neither as warm nor as wet as the present day, with forage unrestricted by rain-on-snow events. This further highlights the seriousness of current changes in body mass. Destabilising mass starvations and the subsequent population crashes are only set to continue with warming Arctic temperatures, if the frequency of rain-on-snow events does not allow herds to build sufficient resilience to icier winters (Hansen *et al.*, 2019a). Furthermore, the continual expansion of infrastructure within Arctic regions has similarly concerning impacts on *R. tarandus* populations. It is therefore of critical importance to improve our understanding of the relationships between *R. tarandus* resilience and body size in future conversation programs.

4.5. Summary

- For both subadult and adult individuals, the average mass estimating equation
 was effective at distinguishing between the male and female *R. tarandus* whether
 sex was known or determined from the sexual dimorphism of skeletal
 measurements. However, the mean difference between the sexes was larger
 from Late Pleistocene assemblages. This could have resulted from a selection
 bias towards the extremes of sexual dimorphism.
- Following the reconstruction of body mass from modern Scandinavian *R. t. tarandus* from various localities and collection dates, the most influential factors affecting body size in wild and semi-domesticated herds were identified; these include the group size and density, forage availability, snow and ice cover and human activity.
- Where Late Pleistocene assemblages enabled the reconstruction of an average body mass for male and female *R. tarandus*, these showed good consistency with the range of sizes observed from modern *R. t. tarandus*. There was, however, variability both within and between the Early, Middle and Late Devensian/Weichselian.
- The largest estimates of male average body mass were reconstructed from Early Devensian *R. tarandus*, and were similar from all sites in Britain. The size of the Early Devensian individuals was most consistent with the body masses of modern forest *R. t. tarandus* herds where individuals are present in smaller group numbers, snow cover was deeper and migrational ranges were shorter.

- Despite significant differences between the average body masses of females reconstructed from the Middle and Late Devensian/Weichselian, the size of *R. tarandus* from both stages was more consistent with the size of modern mountain *R. t. tarandus* herds where individuals are present in larger group numbers, snow cover was more hard-packed and migrational rangers were longer.
- Where Late Pleistocene sites were studied across Britain and western Europe, there was no discernible spatial variation between reconstructions of either male or female body mass.
- Although human impacts in the form of the expansion of infrastructure and, in particular, forestry, would not have had an influence on Late Pleistocene *R. tarandus*, the taphonomy of a site and therefore any selection bias could have affected reconstructions of average body mass for males and females.
- The fact that no Late Pleistocene populations appear to have reached the critical threshold of 50 kg highlights the current and future vulnerability of *R. tarandus*. Nevertheless, in both Svalbard (*R. t. platyrhynchus*) and northern Sweden (*R. t. tarandus*), recent decreases in body mass have been observed in response to a reduced access to forage, either as a result of changing climatic regimes or increased human activity. The need to improve our understanding of the mechanisms affecting body size and *R. tarandus* resilience is therefore essential if future conservation programs are to be effective.

Chapter 5. Results: Late Pleistocene Seasonality of Site Occupations

The following chapter presents results for the age at death and season of death of *R. tarandus* from the Early Devensian, Middle Devensian/Weichselian and Late Devensian/Weichselian sites of Britain and western Europe. A total of 4,789 Late Pleistocene specimens was studied as part of this research, the full list of which is available as **Supplementary Data** (**SD 1-8**). However, sites were only included in this chapter where the dental, antler, cranial or postcranial remains were of sufficient number and quality, to enable reconstructions of the seasonality of *R. tarandus* site occupations. For the Early Devensian, results are presented from seven sites all located in Britain. For the Middle Devensian/Weichselian, 17 sites are used from Britain, Belgium and Germany. Finally, for the Late Devensian/Weichselian, nine sites encompassed Britain, Belgium, Denmark and France. In addition to the number of specimens measured, the maximum established minimum number of individuals (MNI) was reported for each site, together with the MNI from each of the ageing and sexing techniques which yielded slightly different results.

5.1. Early Devensian

5.1.1. Britain

5.1.1.1. Banwell Bone Cave

A total of 313 specimens was measured from Banwell Bone Cave, with a maximum estimated MNI of 18, here derived from the dentition (**Figure 5.1**). Most of these represented prime age adults, with nine individuals aged between 3-9 years and two older individuals >10 years old. However, evidence of seasonality was also observed from subadult *R. tarandus* less than three years old. Using a calving date of May (Gordon, 1990), the presence of individuals aged 16-18 and 29 months old respectively would correspond with site occupation between September and November. Evidence from a single animal aged between 5-10 months both overlaps and extends the period of occupation from October to March. In contrast to the predominant signature of autumnal presence of *R. tarandus*, two individuals were also present at the site that indicate deaths occurring during August (3 months old) and June (25 months old).

As unshed antlers and crania are a more reliable estimate of site occupation than shed antlers, an MNI of 11 was recorded from Banwell Bone Cave (**Figure 5.2**). The antler cycles from one calf, one subadult female, two adult females, one subadult male and three adult males with unshed antlers encompassed the period September to May but overlap during October and November. Antlerless crania were also evident from Banwell Bone Cave for adult females, subadult males and adult males. Each group was represented by only one individual and indicated a spread of seasons between December and September, although the respective cycles overlapped during June to August. Slightly more abundant were the shed antlers, dominated by 13 subadult females, with six adult females and four calves. The antler cycles of these individuals represent March to June, while the presence of both subadult and adult males are confined to November to April.

Estimated body mass and morphometric measurements are displayed in bivariate plots where a clear clustering and distinction in sexual dimorphism was observed (**Figures 5.3 and 5.4**). At Banwell Bone Cave, an MNI of 11 was established from the postcrania. Early-fusing skeletal elements at Banwell Bone Cave followed the pattern of the living herd structure, with a 1:1 ratio observed from individuals >0.5 years old from the proximal radii (**Figure 5.3**). In subadult individuals, a shift towards a predominance of females over males was again consistent with the living herd structure and observable from individuals >1 year old from the distal humeri ratio of 3:5 (**Figure 5.3**) and continued within individuals >2.5 years old with ratio of 3:4 from the proximal metacarpals (**Figure 5.3**), 1:2 from the distal tibiae and 1:4 from the proximal metatarsals (**Figure 5.4**). However, this shift did not continue into adulthood as a reversed ratio of males to females was observed from the proximal ulnae of 2:1 (**Figure 5.3**) and the calcanea of 5:4 (**Figure 5.4**), with both of these elements representing individuals >4 years old.



Figure 5.1. Dentition Ages from *Rangifer tarandus* at Banwell Bone Cave.



Figure 5.2. Rangifer tarandus Antlers at Banwell Bone Cave.



Figure 5.3. *Rangifer tarandus* Postcranial Bivariate Plots from Banwell Bone Cave Forelimbs. Sex ratios determined from morphometric measurements and estimated body mass plots presented from the (a) distal humerus, (b) proximal radius, (c) proximal ulna and (d) proximal metacarpal. Left elements represented by a circle, and right by a square. The unmeasured epiphyses of elements were recorded as fully fused (black), unfused (empty) or unknown (grey).



Figure 5.4. *Rangifer tarandus* Postcranial Bivariate Plots from Banwell Bone Cave Hindlimbs. Sex ratios determined from morphometric measurements and estimated body mass plots presented from the (a) distal tibia, (b) proximal metatarsal and (c) calcaneus. Left elements represented by a circle, and right by a square. The unmeasured epiphyses of elements were recorded as fully fused (black), unfused (empty) or unknown (grey).

5.1.1.2. Feltham

Although a total of 32 specimens was studied from Feltham, the only remains that were preserved in sufficient enough numbers to be used for reconstructions of seasonality were the antler bases (**Figure 5.5**). As there were no antlerless crania measured from the site, an estimated MNI of five was derived from the unshed antlers of adult males only, corresponding to a period in the autumn between September and November. Of the shed antlers, adult males were also the most numerous group preserved at Feltham, with ten individuals measured. Together with the shed antlers of two subadult males, shedding for these two sexes occurs during November to April, but overlap during November and December. Females were only recorded at Feltham from shed antler bases. One subadult and two adult females both overlapped and extended the shed antler cycles of the males at the site from March to June.



Figure 5.5. Rangifer tarandus Antlers at Feltham.

5.1.1.3. Isleworth

Of the 151 specimens measured at Isleworth, the maximum estimated MNI of 25 was derived from the unshed antler bases from two age-sex groups: the subadult and adult males (**Figure 5.6**). Although adult males were the more numerous, with a total of 20 individuals compared to the five subadult males, the presence of males from both age groups nevertheless corresponds to an autumnal occupation of Isleworth during September to November. This prevalence for males was echoed by the shed antlers, whereby the bases of 32 adult males and seven subadult males were preserved. The antler cycles for these two sexes was not as tightly constrained as for unshed antlers, but range from November to April, overlapping in November and December. Shed antlers for the one subadult and six adult females would have been dropped from March to June.

Males were also more abundant from the postcranial remains at Isleworth contributing to an MNI of six (**Figure 5.7**). The only exception to this pattern was observed from the distal humeri, which represent individuals >1 year old and ratio of 1:1 male to female *R. tarandus*. Otherwise, males outnumbered females 2:1 from the proximal radii for individuals >0.5 years old, 3:0 from the proximal metacarpals for individuals >2.5 years and 4:1 from the distal radii for individuals >4 years, a deviation from the living herd structure at all age ranges.



Figure 5.6. Rangifer tarandus Antlers at Isleworth.



Figure 5.7. Rangifer tarandus Postcranial Bivariate Plots from Isleworth Forelimbs. Sex ratios determined from morphometric measurements and estimated body mass plots presented from the (a) distal humerus, (b) proximal radius, (c) distal radius and (d) proximal metacarpal. Left elements represented by a circle, and right by a square. The unmeasured epiphyses of elements were recorded as fully fused (black), unfused (empty) or unknown (grey).

5.1.1.4. Picken's Hole (Unit 5)

At Picken's Hole, two chronologically distinct layers were studied as part of this research. From the Early Devensian layer at Picken's Hole, Unit 5, a total of 32 specimens was studied. An MNI of one adult female was recorded from the unshed antlers at the site (**Figure 5.8**). The antler cycle for this individual and the occupation of Picken's Hole by *R. tarandus* range from October to May. Shed antler bases were also present at the site for each age-sex group and with the exception of the four subadult females, each group was represented by only one individual. This covered a period between November and June. The maximum estimated MNI of four was established from the Picken's Hole postcrania (**Figure 5.9**). Unlike either the unshed or shed antlers, the ratio of males to females of 3:1 from the early-fusing proximal radii, and individuals >0.5 years old, was clearly weighted towards the presence of males in the assemblage. This pattern deviated from the living herd structure, as well as the 1:1 ratio observed from individuals >2.5 years old using the distal tibiae.



Figure 5.8. Rangifer tarandus Antlers at Picken's Hole (Unit 5).



Figure 5.9. *Rangifer tarandus* Postcranial Bivariate Plots from Picken's Hole (Unit 5). Sex ratios determined from morphometric measurements and estimated body mass plots presented from the (a) proximal radius and (b) distal tibia. Left elements represented by a circle, and right by a square. The unmeasured epiphyses of elements were recorded as fully fused (black), unfused (empty) or unknown (grey).

5.1.1.5. Stump Cross Cavern

A total of 18 specimens was measured from Stump Cross Cavern, although a maximum estimated MNI of only two was calculated on the basis of either the dental or postcranial remains (**Figures 5.10 and 5.11**). The two individuals derived from the dentition represent one prime age adult 3-5 years old and a single animal 27 months old (**Figure 5.10**), which would correlate to occupation of the site during August. The ratio of sexes present at the site was observed for an MNI of two, from the distal humeri, proximal radii and proximal metacarpals (**Figure 5.11**). Both the proximal radii and distal humeri provided evidence for the predominance of females through a 0:1 ratio of males to females for individuals >0.5 years old and >1 year old respectively. However, males were evident from Stump Cross Cavern from the 1:1 ratio of individuals >2.5 years old recorded from proximal metacarpals.



Figure 5.10. Dentition Ages from Rangifer tarandus at Stump Cross Cavern.



Figure 5.11. Rangifer tarandus Postcranial Bivariate Plots from Stump Cross Cavern. Sex ratios determined from morphometric measurements and estimated body mass plots presented from the (a) distal humerus, (b) proximal radius and (c) proximal metatarsal. Left elements represented by a circle, and right by a square. The unmeasured epiphyses of elements were recorded as fully fused (black), unfused (empty) or unknown (grey).

5.1.1.6. Tornewton Cave (Reindeer Stratum)

Of the 45 specimens measured from the Reindeer Stratum at Tornewton Cave, a maximum estimated MNI of 4 was established from the dentition of mostly adult animals split between two prime age individuals 3-5 years old and one older individual over 10 years in age (**Figure 5.12**). The only indication of season preserved from the dental remains was a single individual aged 29 months old, equivalent to occupation during October. Site occupation based on antler and cranial remains further overlapped and extended this seasonality from October to May, based on the MNI of two calves with unshed antlers (**Figure 5.13**). The shed antlers of two calves were also measured at Tornewton Cave, which together with 11 subadult and six adult females, represent the shedding stage of their respective antler cycles from March to June. The only evidence for the presence of male *R. tarandus* at Tornewton Cave was a single shed antler from a subadult. Shedding for this age-sex group occurs during November to April.



Figure 5.12. Dentition Ages from *Rangifer tarandus* at Tornewton Cave (Reindeer Stratum).



■ Unshed Antlers ■ Shed Antlers □ Antlerless Crania

Figure 5.13. Rangifer tarandus Antlers at Tornewton Cave (Reindeer Stratum).

5.1.1.7. Windy Knoll

At Windy Knoll, a total of 118 specimens encompassing *R. tarandus* dentition, antlers, crania and postcrania was studied from the site. The maximum estimated MNI of 14 was derived from the dentition (**Figure 5.14**). The youngest known age individual recorded from Windy Knoll was 3-5 months old. The corresponding season of occupation for this single individual of August to October coincided with that of one late summer individual during August (27 months) and two autumnal individuals from October (29 months). This period could be extended further through the winter, following the presence of one individual 5-10 months old and two individuals 18-21 months old, which represent the months October to March and November to February respectively. A single animal, 10-12 months, was the only indication of spring occupation from the Windy Knoll dentition, corresponding to March to May. Six prime aged adults ranging from 3-9 years in age were also identified at the site.

Unshed antlers and cranial remains of both sexes contributed to an MNI of four at Windy Knoll. This included the unshed antlers of two subadult and one adult female, which both retain their antlers between October and May (**Figure 5.15**). One adult male with unshed antlers was also observed from the site, which would correspond to site occupation more tightly constrained to the autumn from September to November. Although the antlerless crania of one adult male also contributed to the MNI, this stage of the antler cycle is observable for over half of the year, encompassing three of the four seasons between December and August. Nevertheless, the presence of unshed antlers and crania overlapped during October to December and the autumn and early winter. At Windy Knoll, shed antlers were only recognised for one adult female, for which antler shedding is confined to a two-month period during May and June.

With an MNI of three, the postcrania at Windy Knoll followed the living herd structure with the early-fusing distal humeri present in a 1:1 ratio of males to females for individuals >1 year old, before a 1:2 ratio developed in proximal metacarpals and calaenea, representing individuals greater than 2.5 years old and 4 years old respectively (**Figure 5.16**).



Figure 5.14. Dentition Ages from Rangifer tarandus at Windy Knoll.



Figure 5.15. Rangifer tarandus Antlers at Windy Knoll.





5.2. Middle Devensian/Weichselian

5.2.1. Britain

5.2.1.1. Brixham Cave

Of the 27 specimens studied from Brixham Cave, a maximum estimated MNI of four was generated from both the dental and postcranial remains measured from the site (**Figures 5.17 and 5.19**). From the dentition, two individuals were indicative of *R. tarandus* occupation at Brixham Cave (**Figure 5.17**). Starting in autumn with one individual 29 months old that was equivalent to the month of October, seasonality could be extended from November to February to include the winter months through the presence of one individual 18-21 months old. The remaining two animals were assigned to the prime adult age band at 3-9 years old.

R. tarandus antlers at Brixham Cave were rare, with an MNI of two derived from the presence of one calf with unshed antlers and the antlerless cranium of a single adult female (**Figure 5.18**). Together, the antler cycles of these two age-sex groups represent an entire year, from October to May and June to September for the calf and adult respectively. Shed antlers were also present at Brixham Cave with one individual each for subadult females, adult females and adult males. The shedding of antlers for these age-sex groups would occur in March to May for the females and November to December for the male.

The early-fusing distal humeri (>1 year olds) and proximal radii (>0.5 year olds) followed the living herd structure with a 1:1 ratio of males to females in younger individuals at Brixham Cave, but this was not apparent from the later-fusing elements (**Figure 5.19**). From the calcanea, which are representative of individuals >4 years old, instead of moving to the more female dominated structure of the living structure, a 1:1 ratio persisted. Furthermore, it is the males, unrepresented by the antler remains, that dominate the 4:0 ratio for individuals >2.5 years old from the distal tibiae, contributing to an MNI of five from the Brixham Cave postcrania.



Figure 5.17. Dentition Ages from *Rangifer tarandus* at Brixham Cave.



Figure 5.18. Rangifer tarandus Antlers at Brixham Cave.



Figure 5.19. *Rangifer tarandus* Postcranial Bivariate Plots from Brixham Cave. Sex ratios determined from morphometric measurements and estimated body mass plots presented from the (a) distal humerus, (b) proximal radius, (c) distal tibia and (d) calcaneus. Left elements represented by a circle, and right by a square. The unmeasured epiphyses of elements were recorded as fully fused (black), unfused (empty) or unknown (grey).

5.2.1.2. Church Hole Cave

A total of 27 specimens was measured from Church Hole Cave, with a maximum estimated MNI of five that was derived from the dentition (**Figure 5.20**). Although three of these individuals were adults 3-9 years in age, the season of occupation at Church Hole Cave could be placed between late summer to autumn from the remaining subadult teeth. One individual 27 months old corresponded to occupation during August, while an additional individual aged between 16-18 months extended this range to include September to November. In addition to contributing to an MNI of two from the antler remains present at the site (**Figure 5.21**), the antler cycle of one unshed subadult female overlapped with the seasonality outlined from the dentition, as antlers are retained in this sex between October and March. The antlerless cranium of one adult male was also included in the MNI, but represented a larger range in seasonal presence from December to August. The shed antlers recorded from Church Hole Cave included one subadult male and one adult male, that both display shedding from November to April, in addition to two calves, two subadult females and one female, for which antlers are dropped between March and May.



Figure 5.20. Dentition Ages from Rangifer tarandus at Church Hole Cave.



■ Unshed Antlers ■ Shed Antlers □ Antlerless Crania

Figure 5.21. Rangifer tarandus Antlers at Church Hole Cave.

5.2.1.3. Gully Cave

At Gully Cave, two chronologically distinct layers were studied as part of this research. A total of 25 specimens comprising *R. tarandus* dentition, antlers and postcrania was studied from the site's Middle Devensian layers. The maximum estimated MNI of four was derived from the dentition of subadults (**Figure 5.22**). The presence of one animal aged 26-27 months old, together with another individual 27 months old, correspond to the months of July and August and would be representative of summer occupation of the site. However, evidence for occupation during both autumn (October) and winter (October to March) was also present in the form of one 29 month old and one calf 5-10 months old. A single calf was also observed from the shed antlers recovered from the site (**Figure 5.23**). Antler shedding by calves is well constrained between May and June.

The postcrania at Gully Cave contributed to an MNI of three (**Figure 5.24**). Despite the difference between the ratio of male to female *R. tarandus* from early-fusing elements, females appear to dominate both the 0:1 ratio from distal humeri and individuals >1 year old, and the 1:2 ratio from proximal radii and individuals >0.5 years old. This latter ratio is more characteristic of the living herd structure for subadults and adults than calves. Conversely, the 1:1 ratio observed from the distal tibiae and individuals >2.5 years old was more representative of the living herd structure ratio for calves.



Figure 5.22. Dentition Ages from Rangifer tarandus at Gully Cave.



■ Shed Antlers □Antlerless Crania

Figure 5.23. Rangifer tarandus Antlers at Gully Cave.



T4-Bd Estimated Body Mass (kg)



5.2.1.4. Inchnadamph, Bone Cave

Specimens from two caves at Inchnadamph were studied as part of this research, both of which were representative of the Middle Devensian. At Bone Cave, a total of 14 specimens was studied. The maximum estimated MNI of three was derived entirely from the dentition of calves 0-3 months old (**Figure 5.25**). Using the birth date during May, this would correlate to individuals present at the site from birth until August. Shed antlers were also preserved at the Bone Cave in the form of one individual each from subadult males and females, and two adult females (**Figure 5.26**). The seasonality represented by this stage of the antler cycle would be March to May for the females and November to April for the male.



Figure 5.25. Dentition Ages from *Rangifer tarandus* at Inchnadamph, Bone Cave.



Figure 5.26. Rangifer tarandus Antlers at Inchnadamph, Bone Cave.

5.2.1.5. Inchnadamph, Reindeer Cave

At Reindeer Cave, the second cave studied from Inchnadamph, although a total of 696 specimens was measured from the site, the maximum estimated MNI was only four. This was derived from the dentition, which consisted of two individuals 0-3 months old and two individuals 3 months, corresponding to occupation of the site by *R. tarandus* calves in the spring and summer between May and August (**Figure 5.27**). Large numbers of antlers were also measured from Reindeer Cave, but only in their shed form (**Figure 5.28**). Although these animals cannot be used to reliably estimate MNI, the 82 calves, 201 subadult females and 68 adult females, are indicative of antler shedding between March and May. Therefore, evidence for seasonality from both the dentition and antlers supported occupation during the spring. The shed antlers of two subadult males were

also evident from the site, indicating a period of their antler cycle during November to April.



Figure 5.27. Dentition Ages from Rangifer tarandus at Inchnadamph, Reindeer Cave.



■Unshed Antlers ■Shed Antlers □Antlerless Crania

Figure 5.28. Rangifer tarandus Antlers at Inchnadamph, Reindeer Cave.

5.2.1.6. Kents Cavern

At Kents Cavern, dental, antler and postcranial remains totalling 203 specimens was measured from the site, with a maximum estimated MNI of 35 derived from the dentition (**Figure 5.29**). Most of these represented prime age adults, with 18 individuals aged between 3-9 years and three older individuals over 10 years in age. The remaining dentition at Kents Cavern belonged to subadult individuals, from which it was possible to assign *R. tarandus* occupation to all four seasons. The presence of one individual 26 months old and one individual 27 months old correspond to site occupation during the summer months in July and August. This seasonality could be extended to include autumn, from one animal 16-18 months old and two individuals 29 months old, which

correlated to *R. tarandus* presence at the site during September to November. Evidence for the winter months of October to February was observed from three calves 5-10 months old and one individual 18-21 months old. The only dentition to represent occupation of Kents Cavern during the spring, from March to May, came from two calves 10-12 months. This overlapped with one animal 12-15 months, extending seasonality into the summer months of May to August.

Unshed antlers amounting to an MNI of six, were representative of one calf, two subadult and three adult females (**Figure 5.30**). The antler cycles of these three age-sex groups all overlap, with each retaining their antlers between October to May. Shed antlers were also preserved at Kents Cavern from all five age-sex groups with the exception of calves. The shed antlers of males were more numerous at Kents Cavern, with six subadults and 19 adults corresponding to a period of the antler cycle during November to December. From the females, for which shedding would occur between March and June, one subadult and two adults were present.

An MNI of five was derived from the postcrania of Kents Cavern (**Figures 5.31 and 5.32**). While the ratio of males to females from the distal humeri and individuals >1 year old was biased towards females at 0:1, the proximal radii was instead weighed towards the presence of males, reversing the living herd structure in a ratio of 3:2 for individuals >0.5 years old (**Figure 5.31**). Males also appear more numerous from the distal tibia at Kents Cavern, with a ratio of 3:0 for individuals >2.5 years old (**Figure 5.32**). However, this ratio differs from that of the metapodials which are also representative of individuals >2.5 years old, but instead displayed a ratio of 1:1 (**Figures 5.31 and 5.32**). This 1:1 ratio was also observed from the calcanea and adults >4 years old (**Figure 5.32**).



Figure 5.29. Dentition Ages from *Rangifer tarandus* at Kents Cavern.



■Unshed Antlers ■Shed Antlers □Antlerless Crania

Figure 5.30. Rangifer tarandus Antlers at Kents Cavern.







Figure 5.32. *Rangifer tarandus* Postcranial Bivariate Plots from Kents Cavern Hindlimbs. Sex ratios determined from morphometric measurements and estimated body mass plots presented from the (a) distal tibia, (b) calcaneus, (c) proximal metatarsal. Left elements represented by a circle, and right by a square. The unmeasured epiphyses of elements were recorded as fully fused (black), unfused (empty) or unknown (grey).

5.2.1.7. Picken's Hole (Unit 3)

The second chronologically distinct layer studied from Picken's Hole, Unit 3, represented a total of 14 *R. tarandus* specimens from the Middle Devensian. From the dentition (**Figure 5.33**), the site's maximum estimated MNI of six represented seasonality focussed on both spring and late summer. This was evident from two individuals 10-12 months old and equivalent to the period of March to May, while a single animal 15 months old corresponded to occupation during August. Three adults were also recorded at Picken's Hole, one prime age individual 6-9 years old and two older individuals >10 years in age. Antlers were also present at Picken's Hole but were not numerous. An MNI of one adult female with unshed antlers was the only indication of *R. tarandus* presence at the site (**Figure 5.34**). As prime age females retain their antlers from October to May, this overlapped with the spring seasonality already outlined from the dentition at Picken's

Hole. The only shed antler from Picken's Hole belonged to a calf and correlated to a point in the antler cycle during May and June.



Figure 5.33. Dentition Ages from Rangifer tarandus at Picken's Hole (Unit 3).



■Unshed Antlers ■Shed Antlers □Antlerless Crania

Figure 5.34. Rangifer tarandus Antlers at Picken's Hole (Unit 3).

5.2.1.8. Pin Hole Cave

The 575 specimens measured from Pin Hole Cave represent dentition, antlers and postcrania, although it was the mandibles and isolated cheek teeth from which the maximum estimated MNI of 23 was derived (**Figure 5.35**). These mostly comprised of adults, with ten individuals in the 3-9 years prime age band and four older individuals >10 years old. Only one calf, aged 3-5 months, was evident from the Pin Hole Cave dentition and represented seasonal occupation between August and October. This seasonality, from late summer into autumn, was also supported by older subadults with one 15 months old and two 27 month olds from August, two 29 month olds from October, and one 16-18 month old encompassing the autumnal range from September to

November. The dentition at Pin Hole Cave also showed evidence for a spring occupation by *R. tarandus*, with two individuals aged between 21-24 months covering the period between March and May.

Despite an MNI of 15 from the unshed antlers present at Pin Hole Cave, the antler remains measured from the site were predominantly shed (**Figure 5.36**). The majority of these shed antlers belonged to subadult females and calves, with 116 and 67 individuals respectively. Together with 15 adult females, the antler cycles for shedding from the three age-sex groups overlap during March to June. The presence of 23 adult and nine subadult males also show overlap in their shedding phases between November and April. Nevertheless, it is the study of unshed antlers that provides a more reliable estimate of season of site occupation. The antlers of the one calf, six subadult and three adult females are retained from October to May, while the antlers of five adult males are only present between September to November.

At Pin Hole Cave, the MNI from postcranial remains was five (**Figure 5.37**). In earlyfusing elements, the ratio of males to females differed between the distal humeri and individuals >1 year old, where a 1:0 ratio was recorded, and the 2:1 ratio from individuals >0.5 years old from the proximal radii. However, both elements were weighted towards the presence of males, a departure from any stage of the living herd structure. The 1:3 distal tibiae ratio for individuals >2.5 years old was more consistent with the prevalence for females in the living structure for subadults and adults, but this did not extend into either the distal radii or the proximal ulna, both of which displayed a 1:1 ratio for adults >4 years old.



Figure 5.35. Dentition Ages from Rangifer tarandus at Pin Hole Cave.



■Unshed Antlers ■Shed Antlers □Antlerless Crania

Figure 5.36. Rangifer tarandus Antlers at Pin Hole Cave.



Figure 5.37. *Rangifer tarandus* Postcranial Bivariate Plots from Pin Hole Cave. Sex ratios determined from morphometric measurements and estimated body mass plots presented from the (a) distal humerus, (b) proximal radius, (c) distal radius, (d) proximal ulna and (e) distal tibia. Left elements represented by a circle, and right by a square. The unmeasured epiphyses of elements were recorded as fully fused (black), unfused (empty) or unknown (grey).

5.2.1.9. Robin Hood Cave

Although a total of 15 specimens was studied from Robin Hood Cave, the only indication of seasonality from the site was derived from the dentition, which also described the maximum estimated MNI of four (**Figure 5.38**). Two *R. tarandus* were assigned to the prime age band of 3-9 years old however, the remaining dentition, belonging to a single individual 15-16 months old and one 29 month old, corresponded to the months of August to October respectively and the occupation of Robin Hood Cave during late summer and autumn. No unshed antlers or cranial remains were measured from Robin Hood Cave, but shed antlers were present for one calf and three subadult females (**Figure 5.39**). The antler cycles for shedding in these two age-sex groups overlapped during March to June.



Figure 5.38. Dentition Ages from Rangifer tarandus at Robin Hood Cave.



Figure 5.39. Rangifer tarandus Antlers at Robin Hood Cave.

5.2.1.10. Sandford Hill

At Sandford Hill, a total of 596 specimens comprised of dentition, antlers, cranial and postcranial remains, was measured from the site. The most numerous elements recovered were the dentition, from which the maximum estimated MNI of 78 was derived (Figure 5.40). Sandford Hill teeth were dominated by 27 calves, 26 prime age adults 3-9 years old and 22 subadults 12-29 months old. Older adults greater than 10 years were also present but only three individuals. Both the calves and subadults represented similar seasonality from the site. Although one individual 0-3 months old corresponded to site occupation from birth in the spring until August, evidence for the presence of R. tarandus in August was also observed from four individuals 3 months old and two individuals 15 months old. This seasonality could further be extended into autumn from September to November, with four animals 27-28 months old (August to September), seven calves 4 months old (September), nine individuals 29 months old (October) and one animal 16-18 months (September to November). However, the majority of calves from Sandford Hill, 14 individuals in total, were 5-10 months old. Incorporating the winter months between October and March, this age range further overlaps with one calf 10-12 months old and five subadults 21-24 months old, to extend juvenile seasonality from February to May and into the spring.

Unshed antlers and cranial remains of both sexes contributed to a total MNI of 16 at Sandford Hill (**Figure 5.41**). This included the unshed antlers of seven calves, two subadult and five adult females, that would have occupied the site between October and May, while one adult male overlapped this presence during September to November. A single subadult female was the only individual for which an antlerless cranium was preserved, representing the period of new antler growth from June to September. Two shed antlers were also recorded for each of the age-sex groups: calves, subadult and adult females, corresponding with antler shedding during March to May. A single subadult male, that would drop its antlers from November to April, was also evident from the shed antlers at Sandford Hill.

An MNI of eight was recorded from the postcrania at Sandford Hill (**Figure 5.42**). This was derived from the calcanea whereby the ratio of 1:3 male to female adult *R. tarandus* >4 years old, was characteristic of the bias towards females at Sandford Hill that existed in both early-fusing distal humeri ratio of 1:4 and proximal radii ratio of 2:3, and late-fusing proximal ulnae ratio of 1:2. These skeletal elements therefore followed the living herd structure for subadults and adults. The only exception to this pattern was from the distal radii, whereby a ratio of 2:1 for individuals >4 years old was a reverse of living herd structure.



Figure 5.40. Dentition Ages from Rangifer tarandus at Sandford Hill.



■ Unshed Antlers ■ Shed Antlers □ Antlerless Crania

Figure 5.41. Rangifer tarandus Antlers at Sandford Hill.



Figure 5.42. Rangifer tarandus Postcranial Bivariate Plots from Sandford Hill. Sex ratios determined from morphometric measurements and estimated body mass plots presented from the (a) distal humerus, (b) proximal radius, (c) distal radius, (d) proximal ulna and (e) calcaneus. Left elements represented by a circle, and right by a square. The unmeasured epiphyses of elements were recorded as fully fused (black), unfused (empty) or unknown (grey).

5.2.1.11. Wookey Hole (Hyaena Den)

A total of 28 specimens was studied from the Hyaena Den at Wookey Hole, contributing to a maximum estimated MNI of eight. The site MNI was derived from the dental remains (**Figure 5.43**), that were comprised of three subadults and five adults in the 3-9 years old prime age band. Of the subadults, the seasonality represented by these individuals was focussed on summer to early autumn. A single animal 13 months old corresponded to occupation of the site during June, while one individual each aged 15-16 months old and 27 months old encompassed the period of August to September. The antlers at Wookey Hole belonged entirely to subadults and were divided between four females and one male (**Figure 5.44**). Although shed antlers could not be used to determine MNI, there was an overlap in the timing of shedding between the two sexes with males losing their antlers between November and April and females reaching this stage of their antler cycle from March to May.



Figure 5.43. Dentition Ages from Rangifer tarandus at Wookey Hole (Hyaena Den).



Figure 5.44. Rangifer tarandus Antlers at Wookey Hole (Hyaena Den).

5.2.2. Belgium

5.2.2.1. Goyet (Troisième Caverne)

From the Troisième Caverne at Goyet, a total of 345 specimens consisting of dentition, antlers and postcrania was studied from the site. The site's maximum estimated MNI of 31 was derived from the dentition of mostly prime age (3-9 years old) adults for which 17 animals were recorded (**Figure 5.45**). One older individual >10 years in age was also present at the site. The remaining dentition belonged to subadults or calves approaching 12 months old. The seasonality of these individuals began with one individual 27 months, and therefore representing August and late summer occupation, and ranged through to November with the presence of one individual 16-18 months old (September to November) and five individuals 29 months old (October). The occupation at Goyet could further be extended through the winter and spring, with two calves aged 5-10 months old spanning October to March, three calves 10-12 months old and one subadult 21-24 months old, encompassing the period of February to May.

Antlers were particularly abundant at Goyet in their shed form however, a total MNI of three was established from the unshed antler bases present (**Figure 5.46**). From the subadult females, adult females and adult males recorded, only one individual each was preserved still retaining their antlers, corresponding to a period between October to March for the females and overlapping with males in September to November. Of the shed antlers, subadult females were the most numerous with 77 individuals which would have been shed between March and June. Although seven calves and 14 adult females also share this seasonality for the shedding of their antlers, the three subadult and four adult males reach this period of their antler cycles between November and April.

The MNI of nine derived from the postcrania measured from Goyet generally followed the living herd structure, representing a 1:1 ratio in early-fusing elements such as the distal humeri and individuals >1 year old, before switching to a more female dominated 1:2 ratio from the distal tibiae and individuals >2.5 years old (**Figure 5.47**). This relationship also continued into individuals >4 years old, with a 0:1 ratio from the proximal tibiae and a 2:3 ratio from the distal radii. The only element to deviate from this pattern was the proximal metacarpal, whereby the ratio of 1:1 was more consistent with male and female calves than individuals >2.5 years old.


Figure 5.45. Dentition Ages from Rangifer tarandus at Goyet (Troisième Caverne).



■Unshed Antlers ■Shed Antlers □Antlerless Crania

Figure 5.46. Rangifer tarandus Antlers at Goyet (Troisième Caverne).



Figure 5.47. *Rangifer tarandus* Postcranial Bivariate Plots from Goyet (Troisième Caverne). Sex ratios determined from morphometric measurements and estimated body mass plots presented from the (a) distal humerus, (b) proximal radius, (c) distal radius, (d) proximal tibia and (e) distal tibia. Left elements represented by a circle, and right by a square. The unmeasured epiphyses of elements were recorded as fully fused (black), unfused (empty) or unknown (grey).

5.2.2.2. Caverne Marie-Jeanne

At Caverne Marie-Jeanne, a total of 51 specimens was studied encompassing dentition, antlers and postcrania from the site. Although the total MNI established from each of the ageing and sexing techniques was very similar, the maximum estimated MNI of seven was derived from the dentition (**Figure 5.48**). Adults were the most prevalent age group from the Caverne Marie-Jeanne dentition and could be divided into four individuals 3-9 years old and one individual >10 years old. The only indication for the season of occupation by *R. tarandus* at the site came from one calf aged 5-10 months old and one subadult 29 months old. Both of these individuals are indicative of occupation from October to March, but overlap during the autumn in October.

A total MNI of six was observed from the unshed antlers of all age-sex groups at Caverne Marie-Jeanne with the exception of subadult males (**Figure 5.49**). While the antler bases of one calf, one subadult female and one female correspond to site occupation during October to May, the two adult males recorded from the site would only retain their antlers between September and November. Antlers that had already been shed were only present for males, with the shedding cycles for one subadult and three adults coinciding during November to April.

From the postcranial MNI of six, males and females at Caverne Marie-Jeanne deviated from the living herd structure by displaying a 1:1 ratio from individuals >2.5 years old, represented by the proximal metacarpals and distal tibiae, in addition to the late-fusing calcanae and individuals >4 years old (**Figure 5.50**). This ratio is more typical of calves in the living herd structure. The only early-fusing element at Caverne Marie-Jeanne, the proximal radii, displayed a female weighted ratio of 1:5 that was more exaggerated than the typical living herd structure.



Figure 5.48. Dentition Ages from Rangifer tarandus at Caverne Marie-Jeanne.



■ Unshed Antlers ■ Shed Antlers □ Antlerless Crania

Figure 5.49. Rangifer tarandus Antlers at Caverne Marie-Jeanne.



Figure 5.50. *Rangifer tarandus* Postcranial Bivariate Plots from Caverne Marie-Jeanne. Sex ratios determined from morphometric measurements and estimated body mass plots presented from the (a) proximal radius, (b) proximal metacarpal, (c) distal tibia and (d) calcaneus. Left elements represented by a circle, and right by a square. The unmeasured epiphyses of elements were recorded as fully fused (black), unfused (empty) or unknown (grey).

5.2.2.3. Trou Magrite

Of the 116 specimens measured from the site of Trou Magrite, a maximum estimated MNI of 19 was derived from the dentition (**Figure 6.51**) and mostly comprised of prime aged adults 3-9 years old (13 individuals). *R. tarandus* site occupation was shown to encompass late summer and autumn from August to November, with three individuals 27 months old (August), two individuals 29 months old (October) and one animal 16-18 months old (September to November). There were no unshed antler bases or antlerless crania at Trou Magrite that could be indicative MNI (**Figure 6.52**), but shed antlers were present from all age-sex groups with the exception of calves. Shedding for both sexes occurs over relatively constrained timeframes, with the eight subadult and five females losing their antlers between March and May, and the three subadult and two adult males reaching this stage of the antler cycle between November and April.

An MNI of six was recognised from the postcranial elements studied from Trou Magrite (**Figure 6.53**). From the early-fusing distal humeri and individuals >1 year old, a 1:3 ratio of males to females showed a bias towards females at the site similar to that of the living structure for subadult and adult individuals. The proximal radii exaggerated this relationship further, in a 0:6 ratio that otherwise negated the presence of males at Trou Magrite. However, from both the proximal metacarpals and distal tibiae, elements that represent individuals >2.5 years old, the 1:1 ratio supported the presence of males yet was more consistent with the sex ratio of calves in the living herd structure.



Figure 5.51. Dentition Ages from *Rangifer tarandus* at Trou Magrite.



■Unshed Antlers ■Shed Antlers □Antlerless Crania

Figure 5.52. Rangifer tarandus Antlers at Trou Magrite.



Figure 5.53. *Rangifer tarandus* Postcranial Bivariate Plots from Trou Magrite. Sex ratios determined from morphometric measurements and estimated body mass plots presented from the (a) distal humerus, (b) proximal radius, (c) proximal metacarpal and (c) distal tibia. Left elements represented by a circle, and right by a square. The unmeasured epiphyses of elements were recorded as fully fused (black), unfused (empty) or unknown (grey).

5.2.2.4. Trou du Sureau

From a total of 145 specimens measured from Trou du Sureau, the maximum estimated MNI, here derived from the dentition, was 12 (**Figure 5.54**). Eight prime age adults 3-9 years old and one older animal >10 years old was observed from the Trou du Sureau dentition. Although one individual 21-29 months represented a range of seasons between February and October, seasonality could be more precisely assigned to late summer and autumn from one individual each 27 months old and 29 months old, corresponding to August and October respectively.

A total MNI of five was evident from the unshed antler bases and antlerless crania at the site (**Figure 5.55**). Of the unshed antlers, two belonged to subadult females and corresponded to site occupation during October to March, while a single adult male represented *R. tarandus* presence during September to November. Antlerless crania were also present from a subadult and an adult female, a state which occurs in both ages between June and September. The shed antlers from Trou du Sureau included three calves, 24 subadult females, eight adult females and one adult male, for which shedding occurs from March to June for the females and calves, and between November to December for the male.

The postcrania from Trou du Sureau represented a total MNI of six from the two elements whereby the ratio of males to females was sufficiently clear (**Figure 5.56**). From the proximal radii and individuals >0.5 years old, a ratio of 1:4 persisted. Although this differed from the 2:3 ratio of males to females observed from the proximal metacarpals and individuals >2.5 years old, both elements were representative of the female bias that develops in subadult and adult *R. tarandus*.



Figure 5.54. Dentition Ages from *Rangifer tarandus* at Trou du Sureau.



■ Unshed Antlers ■ Shed Antlers □ Antlerless Crania

Figure 5.55. Rangifer tarandus Antlers at Trou du Sureau.





5.2.3. Germany

5.2.3.1. Salzgitter-Lebenstedt

At Salzgitter-Lebenstedt, a total of 501 specimens encompassing *R. tarandus* dentition, antlers, crania and postcrania was studied from the site. From an MNI of 51, the dentition at Salzgitter-Lebenstedt was predominantly comprised of prime age adults (**Figure 5.57**), with very little distinction between the 21 individuals 3-5 years old and 19 individuals 6-9 years old. Three older individuals >10 years old were also evident from the site, while the remaining dentition belonged to subadults. The youngest individual recorded from Salzgitter-Lebenstedt was 3 months old, corresponding to occupation

during August. This late summer-early autumn presence by *R. tarandus* was confirmed by two individuals 15-16 months old (August to September) and two individuals 29 months old (October), representative of occupation from August to October. This could also be extended from October to March by one individual 5-10 months, while one individual 10-12 months old and one animal 21-24 months old overlap this winter range and even extend the seasonal range into spring from February to May.

The maximum estimated MNI of 58 for Salzgitter-Lebenstedt was taken from the unshed antler bases and cranial fragments (**Figure 5.58**). Most of the unshed antlers, 41 individuals in total, were subadult and adult males that would have retained their antlers between September and November. Less constrained was the antlerless cranium of a single subadult male, that represented a state which occurs from April to August. Females were also present at Salzgitter-Lebenstedt, with the unshed antlers of six calves, three subadult and eight adult females corresponding with October to May occupation. The antlerless crania from one subadult and one adult female further represent the period of antler growth between June and September that could extend the presence of *R. tarandus* females. Shed antlers were uncommon at Salzgitter-Lebenstedt. From one calf, two subadults and one adult female, antler shedding overlaps during March to June, while the two subadults and six adult males drop their antlers earlier in year between November and April.

The MNI from the postcrania at Salzgitter-Lebenstedt was 35 (**Figure 5.59**). The ratio of males to females for individuals >0.5 years old from proximal radii was 11:18, demonstrating a bias towards females consistent with the living herd structure for adults and subadults. The only element from which individuals were all adults >4 years was the proximal ulnae, where a 1:2 ratio of males to females followed the living herd structure for animals of this age (**Figure 5.59**). However, consistent with the predominantly male antler and cranial remains, the number of males from the postcrania at Salzgitter-Lebenstedt was often double than of females. This relationship was clearest from the proximal metatarsals (individuals >2.5 years old), where a 2:1 ratio persisted (**Figure 5.60**) and weakest from the 9:8 ratio from the distal radii (individuals >4 years old) (**Figure 5.59**). Nevertheless, the ratios from the forelimb elements (**Figure 5.59**) of 15:8 from the proximal humeri (individuals >1 year old) and 12:5 from the proximal metacarpals (individuals >2.5 years old), as well as the 17:7 from the proximal tibiae (individuals >2.5 years old), also demonstrated this male dominance.



Figure 5.57. Dentition Ages from Rangifer tarandus at Salzgitter-Lebenstedt.



■ Unshed Antlers ■ Shed Antlers □ Antlerless Crania

Figure 5.58. Rangifer tarandus Antlers at Salzgitter-Lebenstedt.



Figure 5.59. *Rangifer tarandus* Postcranial Bivariate Plots from Salzgitter-Lebenstedt Forelimbs. Sex ratios determined from morphometric measurements and estimated body mass plots presented from the (a) distal humerus, (b) proximal radius, (c) distal radius, (d) proximal ulna and (e) proximal metacarpal. Left elements represented by a circle, and right by a square. The unmeasured epiphyses of elements were recorded as fully fused (black), unfused (empty) or unknown (grey).



Figure 5.60. *Rangifer tarandus* Postcranial Bivariate Plots from Salzgitter-Lebenstedt Hindimbs. Sex ratios determined from morphometric measurements and estimated body mass plots presented from the (a) proximal tibia and (b) proximal metatarsal. Left elements represented by a circle, and right by a square. The unmeasured epiphyses of elements were recorded as fully fused (black), unfused (empty) or unknown (grey).

5.2.3.2. Westeregeln

In total, 32 specimens were studied from Westeregeln with a maximum estimated MNI of four derived from the dentition (**Figure 5.61**). The only indication for the season of site occupation from the teeth was from a single juvenile 27 months old that corresponded with the month of August and late summer. Otherwise, the remaining three individuals at Westeregeln were all prime age adults, 3-9 years old. From the antler and cranial remains (**Figure 5.62**), an MNI of one reflected an adult male with unshed antlers, a period which lasts from September to November for this age-sex group. Shed antlers were slightly more numerous from the site for both males and females. Antler shedding occurs earlier in males than it does in females, with the two subadults and one adult male losing their antlers from November to April, compared to March to June for the seven subadults and three adult females.

Postcranial remains were also studied from Westeregeln and generated an MNI of three (**Figure 5.63**). In a reverse of the living herd structure, the ratio of males to females from the distal humeri and individuals >1 year old was 2:1. This differed from the other elements measured at the site where a female bias of 0:1 was measured from the proximal radii and individuals >0.5 years old, while a 1:1 ratio more consistent with that of calves was recognised from the calcanea and adults >4 years old.



Figure 5.61. Dentition Ages from Rangifer tarandus at Westeregeln.



■ Unshed Antlers ■ Shed Antlers □ Antlerless Crania

Figure 5.62. Rangifer tarandus Antlers at Westeregeln.





5.3. Late Devensian/Weichselian

5.3.1. Britain

5.3.1.1. Chelm's Combe

Of the 37 specimens studied from Chelm's Combe, a maximum estimated MNI of seven was generated from the dentition (**Figure 5.64**). Three prime age adults 3-9 years old were present at Chelm's Combe, as well as one older individual >10 years old. The youngest individual recorded from the teeth at Chelm's Combe was one calf aged 10-12 months old. Together with one older subadult 21-24 months old, the two individuals corresponded to occupation of the site from the late winter (February) to spring (May). However, the presence of one individual 16-18 months old would instead correlate to September to November and an autumnal presence.

The total MNI from unshed antlers and antlerless crania at Chelm's Combe was five (**Figure 5.65**). From the unshed antlers, three calves and one subadult female would have retained their antlers from October to May. This overlapped with the wide range of seasons represented by the antlerless crania of one adult male, which having lost its antlers by December is antlerless until August. The shed antlers of one adult male and two adult females were also present at the site. For both sexes, shedding is a well constrained period of the antler cycle that occurs in November to December for males and May to June for females.

With an MNI of five, both males and females were also evident from the postcranial remains at Chelm's Combe, but alternated in the early-fusing elements between being dominated by males 3:0 from the distal humeri and individuals >1 year old, or by females 0:2 from the proximal radii and individuals >0.5 years (**Figure 5.66**). From the proximal metacarpals and distal tibiae, both of which represent individuals >2.5 years old, a 1:1 ratio of males to females was observed. None of these patterns were consistent with the living herd structure with the exception of the female weighted proximal radii.



Figure 5.64. Dentition Ages from Rangifer tarandus at Chelm's Combe.



■Unshed Antlers ■Shed Antlers □Antlerless Crania

Figure 5.65. Rangifer tarandus Antlers at Chelm's Combe.





5.3.1.2. Gully Cave

A total of nine specimens was studied from the Late Devensian material at Gully Cave. The maximum estimated MNI of three was derived from the dentition of one prime age adult 3-5 years old and two subadults (**Figure 5.67**). Together, the juvenile individuals at Gully Cave were representative of late summer to autumn occupation. One individual 27 months old corresponded to August, while a 16-18 month old was present between September and November. As there were no unshed antler bases or antlerless crania measured from Gully Cave (**Figure 5.68**), a total MNI could not be derived from the antler and cranial remains. However, shed antlers from one adult female and one subadult male were recorded from the site. Shedding for these two sexes occurs in November to April for the male and May to June for the female. Although the antlers could not confirm which of the sexes were present at Gully Cave, an MNI of two was recognised from the postcrania (**Figure 5.69**). A 2:0 ratio of males to females was evident from the proximal radii and individuals >0.5 years old at the site. This bias towards males is not typical of the living herd structure.



Figure 5.67. Dentition Ages from Rangifer tarandus at Gully Cave.



Figure 5.68. Rangifer tarandus Antlers at Gully Cave.



Figure 5.69. *Rangifer tarandus* Postcranial Bivariate Plots from Gully Cave. Sex ratios determined from morphometric measurements and estimated body mass plots presented from the (a) proximal radius. Left elements represented by a circle, and right by a square. The unmeasured epiphyses of elements were recorded as fully fused (black), unfused (empty) or unknown (grey).

5.3.1.3. Ossom's Cave

A total of 33 specimens was studied from Ossom's Cave, with a maximum estimated MNI of six derived from the dentition (**Figure 5.70**). Only two of these individuals were prime age adults 6-9 years old, while the remaining dentition belonged to subadults. The presence of two individuals aged 10-12 months old and one individual 12-15 months old correspond to occupation during spring to summer, from the months of March to May and May to August respectively. A single animal 16-18 months old was also recorded from Ossom's Cave, correlating to autumn occupation from September to November. Either autumn or spring seasonality could be further supported by the MNI of two derived

from the unshed antlers (**Figure 5.71**). Belonging to a single calf and adult female, both of these individuals retain their antlers from October to May.

A total MNI of three was evident from the postcrania at Ossom's Cave (**Figure 5.72**). Although the early-fusing distal humeri (individuals >1 year old) and proximal radii (individuals >0.5 years old) displayed a 1:1 ratio of males to females characteristic of the living herd structure in calves, the male bias of 2:0 observed from the distal tibiae was a reversal of the expected female dominance of the living herd structure for subadult and adult individuals >2.5 years old.



Figure 5.70. Dentition Ages from Rangifer tarandus at Ossom's Cave.



■ Unshed Antlers ■ Shed Antlers □ Antlerless Crania

Figure 5.71. Rangifer tarandus Antlers at Ossom's Cave.





5.3.1.4. Soldier's Hole

At Soldier's Hole, a total of 98 specimens encompassing *R. tarandus* dentition, antlers and postcrania was studied from the site. The maximum estimated MNI of 10 was derived from the dentition of entirely adult individuals, that was divided between eight prime age individuals 3-9 years old and two individuals >10 years old (**Figure 5.73**). As there were no antlerless crania measured from Soldier's Hole, an estimated MNI of two was singularly derived from the unshed antlers of subadult females (**Figure 5.74**). As subadult females retain their antlers between October and March, site occupation occurred during autumn to winter. Shed antlers were also present from Soldier's Hole for subadult and adult males and females. Shedding occurs separately between the sexes, with the single subadult and adult males dropping their antlers from November to April, while the one subadult and one adult females reach this stage of their antler cycle from March to June. A total MNI of six was derived from the postcrania at Soldier's Hole (**Figures 5.75 and 5.76**). The early-fusing proximal radii represented the living herd structure for calves >0.5 years old, with a 1:1 ratio of males to females that was also evident from later-fusing elements at Soldier's Hole including the proximal metacarpals and individuals >2.5 years, as well as the proximal tibiae and adult individuals >4 years old (**Figures 5.75 and 5.76**). A female-dominated ratio of 1:2 was observed from the distal humeri (individuals >1 year old) and proximal metatarsals (individuals >2.5 years old) that was characteristic of the living herd structure for subadults and adults, while the 2:3 ratio from calcanea and adults >4 years old remained weighted towards females (**Figures 5.75 and 5.76**). The only element for which males outnumbered females was the distal radius and individuals >4 years old, where a 4:1 ratio persisted in a exaggerated reversal of the living herd structure (**Figure 5.75**).



Figure 5.73. Dentition Ages from *Rangifer tarandus* at Soldier's Hole Cave.



Figure 5.74. Rangifer tarandus Antlers at Soldier's Hole Cave.







Figure 5.76. *Rangifer tarandus* Postcranial Bivariate Plots from Soldier's Hole Hindlimbs. Sex ratios determined from morphometric measurements and estimated body mass plots presented from the (a) proximal tibia, (b) calcaneus, (c) proximal metatarsal. Left elements represented by a circle, and right by a square. The unmeasured epiphyses of elements were recorded as fully fused (black), unfused (empty) or unknown (grey).

5.3.2. Belgium

5.3.2.1. Trou des Nutons

A total of 133 specimens was measured from Trou des Nutons. The dentition at the site represented two prime age adults 3-5 years old that could not be used to directly infer the season of occupation (**Figure 5.77**). From the antlers, only females and calves were recorded from Trou des Nutons, with the most abundant being those antlers that had already been shed (**Figure 5.78**). Shedding for the seven calves, 41 subadult females and 17 adult females is confined to March to June. Two unshed antlers were also present from a calf and one subadult female. The overlap in the antler cycle of these two age groups meant that *R. tarandus* presence at the site was between October and May. From Trou des Nutons, the maximum estimated MNI of three was derived from the postcrania (**Figure 5.79**). Similar to the antlers at the site, a clear bias towards female individuals

was also observed from the ratio of 0:3 males to females from the proximal metacarpals and individuals >2.5 years old. Although the living herd structure for subadults and adults is weighted towards females, this was exaggerated at Trou des Nutons.



Figure 5.77. Dentition Ages from Rangifer tarandus at Trou des Nutons.



Figure 5.78. Rangifer tarandus Antlers at Trou des Nutons.

(a) Proximal Metacarpal



Figure 5.79. *Rangifer tarandus* Postcranial Bivariate Plots from Trou des Nutons. Sex ratios determined from morphometric measurements and estimated body mass plots presented from the (a) proximal metacarpal. Left elements represented by a circle, and right by a square. The unmeasured epiphyses of elements were recorded as fully fused (black), unfused (empty) or unknown (grey).

5.3.3. Denmark

5.3.3.1. Køge Bugt

At Køge Bugt, a total of 50 specimens encompassing *R. tarandus* dentition, antlers, crania, and postcrania was studied from the site. Only two individuals were recorded from the mandibular dentition at Køge Bugt, one prime age adult 6-9 years old and one subadult 27-29 months old (**Figure 5.80**). The age range of this subadult would correspond to occupation of the site by *R. tarandus* from late summer (August) to autumn (October). Antlers at Køge Bugt were slightly more numerous, with an MNI of four (**Figure 5.81**). This was derived from the unshed antler bases of one adult female and one adult male, as well as the antlerless crania of one subadult and one adult male. As antlers are retained in adults between October and May for the females and from September to November for males, the antler cycles of the two sexes would overlap during autumn. The presence of antlerless crania from males would therefore extend the autumn site occupation either into December or August. Shed antlers were only measured at Køge Bugt from subadults. Shedding occurs for these two sexes from March to June for one female and November to April for two males.

The maximum estimated MNI of eight from Køge Bugt was derived from the postcrania (**Figures 5.82 and 5.83**). The only element for which the living herd structure was reversed and males outnumbered females 5:3 was the proximal metacarpals and individuals >2.5 years old. Otherwise, the postcrania at Køge Bugt demonstrated ratios of 1:1 from the early-fusing distal humeri and individuals >1 year old and proximal radii

and individuals >0.5 years old (**Figure 5.82**). This ratio was also observed from the latefusing proximal tibiae which is representative of adults >4 years old (**Figure 5.83**). From the remaining distal tibiae and proximal metatarsals (**Figure 5.83**), a 1:2 ratio of males to females persisted that was characteristic of the living herd structure for the subadults and adults these individuals >2.5 years old represent.



Figure 5.80. Dentition Ages from Rangifer tarandus at Køge Bugt.



■Unshed Antlers ■Shed Antlers □Antlerless Crania

Figure 5.81. Rangifer tarandus Antlers at Køge Bugt.







Figure 5.83. Rangifer tarandus Postcranial Bivariate Plots from Køge Bugt Hindlimbs. Sex ratios determined from morphometric measurements and estimated body mass plots presented from the (a) proximal tibia, (b) distal tibia and (c) proximal metatarsal. Left elements represented by a circle, and right by a square. The unmeasured epiphyses of elements were recorded as fully fused (black), unfused (empty) or unknown (grey).

5.3.3.2. Slotseng

Although a total of 12 specimens was studied from Slotseng, the only remains that could be used for reconstructions of seasonality were the antler bases and crania (**Figure 5.84**). A maximum estimated MNI of five was derived from the unshed antlers of one subadult female, one subadult male, two adult males and the antlerless crania of a single adult female. For individuals with unshed antlers, the antler cycles of the two sexes overlap in autumn with the two males representing September to November and the subadult female corresponding to October to March. Furthermore, the presence of the female's antlerless cranium would indicate *R. tarandus* occupation during June to September, extending seasonality towards the late summer-early autumn. Shed antlers were also recorded for the site from one subadult female that would have displayed

shedding from March to May, and one subadult and one adult male that both lose their antlers earlier during November to April.



Figure 5.84. Rangifer tarandus Antlers at Slotseng.

5.3.4. France

5.3.4.1. Abri de Laugerie Haute

A total of 32 specimens was studied from Abri de Laugerie Haute. From the unshed antlers of one adult male, the seasonal presence of *R. tarandus* at Laugerie Haute correlated to between September to November when males retain their antlers (**Figure 5.85**). Female antlers were also recorded from the site from one subadult and one adult but the antlers had already been shed, a process which occurs from March to June. The maximum estimated MNI of five was derived from the postcrania at Laugerie Haute (**Figure 5.86**). From the skeletal elements measured, the living herd structure for subadults and adults was followed and even exaggerated with a ratio of 0:1 from the distal humeri and individuals >1 year old, 1:3 from the distal radii and 1:4 from the calcanea, both of which represent individuals >4 years old. This differed from the pattern derived from unshed antlers, where no females were present from the Laugerie Haute assemblage.



Figure 5.85. Rangifer tarandus Antlers at Abri de Laugerie Haute.



Figure 5.86. Rangifer tarandus Postcranial Bivariate Plots from Abri de Laugerie Haute. Sex ratios determined from morphometric measurements and estimated body mass plots presented from the (a) distal humerus, (b) distal radius and (c) calcaneus. Left elements represented by a circle, and right by a square. The unmeasured epiphyses of elements were recorded as fully fused (black), unfused (empty) or unknown (grey).

5.3.4.2. Abri de la Madeleine

From the 108 specimens studied from Abri de la Madeleine, a maximum estimated MNI of 12 was derived from the dental remains (**Figure 5.87**). Adult dentition at the site could be divided into prime age individuals, for which four animals 3-9 years old were present, as well as one older individual >10 years old. No calves were recorded from La Madeleine and therefore season of site occupation was based on juveniles 12-29 months old. This seasonality primarily ranged from August to October and the late summer to autumn, here discerned from two individuals 27 months old (August), three individuals 29 months old (October) and one animal 27-29 months old. The presence of one individual 21-24 months would correspond to occupation from February in the winter to May in the spring.

The unshed antlers were used to establish an MNI of five from La Madeleine (**Figure 5.88**). These individuals mostly belonged to four adult males that would retain their antlers between September to November. One calf was also present with unshed antlers, a state observable between October and May. Shed antlers at the site were only preserved for males, one subadult and four adults, that both drop their antlers from November to April.

The only postcranial element from which a clear distinction between males and females could be observed was the calcanea and an MNI of six was therefore derived from La Madeleine (**Figure 5.89**). The 1:2 ratio of males to females generated for adult individuals >4 years old was consistent with the living herd structure for animals of this age.



Figure 5.87. Dentition Ages from Rangifer tarandus at Abri de La Madeleine.



Figure 5.88. Rangifer tarandus Antlers at Abri de La Madeleine.



Figure 5.89. *Rangifer tarandus* Postcranial Bivariate Plots from Abri de La Madeleine. Sex ratios determined from morphometric measurements and estimated body mass plots presented from the (a) calcaneus. Left elements represented by a circle, and right by a square. The unmeasured epiphyses of elements were recorded as fully fused (black), unfused (empty) or unknown (grey).

5.4. Summary of Season of Death

In order to summarise the evidence for the season of death represented at each site, **Figures 5.90-5.94** present the results of the direct ageing and sexing techniques applied to *R. tarandus* fossils from Britain and western Europe (Belgium, Denmark, France, and Germany) during the Early Devensian, Middle Devensian/Weichselian and Late Devensian/Weichselian. The most consistently abundant remains preserved from *R. tarandus* assemblages were the dentition, which outnumbered antlers, crania and postcrania.

From the British Early Devensian (Figure 5.90), Stump Cross Cavern represented both the most northerly site, located at 54°N, as well as the clearest evidence for season of death. Derived from subadult dentition aged to the month of August, a late summer occupation was evident from Stump Cross Cavern. This seasonality differed from that of sites in the south of Britain, between 50-51°N, where season of death was more indicative of the presence of *R. tarandus* during the autumn and winter. This was recognisable from the similar patterns of male and female antlers preserved at the River Thames sites of Isleworth and Feltham. At Picken's Hole (Unit 5) and Tornewton Cave (Reindeer Stratum) in southwest Britain, subadult dentition at Tornewton Cave further confirmed autumnal occupation in October, while the presence of the antlers of calves, females and males extended this occupation through winter and potentially as late as April and therefore spring at both sites. However, despite the difference in latitude between Windy Knoll at 53°N and Banwell Bone Cave at 51°N, the larger assemblages from both sites could potentially represent occupation throughout the whole year, as seen from the variable presence of antlers and dentition from calves and subadults, females and males.

From the Middle Devensian/Weichselian, the season of death was derived for R. tarandus from both British (Figure 5.91) and European (Figure 5.92) assemblages. The clearest patterns of seasonality from the British Middle Devensian (Figure 5.91) were observed from the two caves at Inchnadamph, also the most northerly sites studied at 58°N. The similar preservation of calf, male and female antlers, in addition to the dentition of calves, represented site occupation during the spring and summer from May to August at both Reindeer Cave and Bone Cave. Of the three sites studied from 53°N, only Robin Hood Cave preserved a clear pattern of seasonal occupation from the antlers of calves and females and dentition of subadults, that indicated *R. tarandus* presence from August to September and so the late summer-early autumn. On the other hand, the variable presence of antlers and dentition from calves and subadults, females and males at both Church Hole Cave and Pin Hole Cave, potentially represented site occupation throughout the whole year. This was a pattern recognised from several Middle Devensian sites in Britain located at 50-51°N. Sites including Sandford Hill, Picken's Hole (Unit 3), Gully Cave, Kents Cavern and Brixham Cave all represented multiple seasons of occupation from the variable presence of antlers and dentition. Wookey Hole (Hyaena Den) was the only site at this latitude for which the antlers of males and females, as well as the dentition of subadults, corresponded to a clear season of death in the summer and early autumn from June, August and September.

| Latitude | Sites | Ageing/Sexing | | Season of Death | | | | | | | | | | | |
|----------|--------------------------------|----------------------|----------------------------|-----------------|---|---|---|---|---|---|---|---|---|---|---|
| | | Tech | Technique | | F | м | Α | М | J | J | Α | S | 0 | Ν | D |
| 54°N | Stump Cross Cavern | Dentition | Subadults | | | | | | | | | | | | |
| 53°N | Windy Knoll | Dentition | Calves Subadults | | | | | | | | - | | | | |
| | | Antlers | Females Males | | | | | | _ | | | | _ | | |
| 51°N | Isleworth | Antlers | Females Males | | | | | | | | | | | | |
| | Feltham | Antlers | Females Males | | | | | | | | 2 | | | | |
| | Banwell Bone Cave | Dentition | Calves Subadults | | _ | _ | , | , | _ | | | | _ | | |
| | | Antlers | Calves Females Males | | _ | | | | _ | | | | | _ | |
| | Picken's Hole (Unit 5) | Antlers | Calves Females Males | | | | | | _ | | |] | | | |
| 50°N | Tornewton Cave (Reindeer | Dentition Antlers | Subadults Calves | | | | | | | | | | _ | | |
| | Stratum) | | Females Males | | | | | | _ | | | | | | |

Figure 5.90. Summary of *Rangifer tarandus* Season of Death from Early Devensian Sites. Season of death was determined for each site from dentition, unshed antlers and antlerless crania (black lines) which indicate actual site occupation, while shed antlers (grey lines) are more susceptible to post-depositional transport.

| Latitudo | Sites | Ageing/Sexing Technique | | Season of Death | | | | | | | | | | | |
|----------|---------------------------|----------------------------|----------------------------|-----------------|---|----|---|----|----|---|---|---|---|---|---|
| Latitude | Ones | | | J | F | м | Α | М | J | J | Α | S | 0 | N | D |
| 58°N | Inchnadamph Bone Cave | Dentition | Calves | | | | | | | | | C | | | |
| | | Antlers | Females Males | | | | | c. | | | | | | | |
| | Inchnadamph Reindeer | Dentition | Calves | | | | | _ | | | | | | | |
| | Cave | Antlers | Calves Females Males | | | | | | | | | | | | |
| 53°N | Church Hole Cave | Dentition | Subadults | | | | | | | | _ | | | | |
| | | Antlers | Calves Females Males | | | | | _ | | | | | _ | | |
| | Pin Hole Cave | Dentition | Calves Subadults | | | | | | | | = | | | | |
| | | Antlers | Calves Females Males | | | | | | | | | - | _ | _ | |
| | Robin Hood Cave | Dentition | Subadults | | | | | | | | _ | | | | |
| | | Antlers | Calves Females | | | | | _ | | | | | | | |
| 51°N | Sandford Hill | Dentition | Calves Subadults | | | | _ | | | | _ | | | | |
| | | Antlers | Calves Females Malos | _ | _ | | | _ | | _ | | | _ | _ | _ |
| | Picken's Hole (Unit 3) | Dentition | Calves Subadults | | | | | | | | | | | | |
| | | Antlers | Calves Females | - | | | | _ | | | | | _ | | |
| | Gully Cave | Dentition | Calves Subadults | | | | | | | | | | _ | | |
| | | Antlers | Calves | | | | | _ | | | | | | | |
| | Wookey Hole (Hyaena | Dentition | Subadults | | | | | | 8 | | _ | | | | |
| | Den) | Antlers | Females Males | | | | | | | | | | | | |
| 50°N | Kents Cavern | Dentition | Calves Subadults | | _ | | | _ | R: | | | | _ | | |
| | | Antlers | Calves Females Males | | | | | | | | | | = | | |
| | Brixham | Dentition | Subadults | | _ | U. | | | | | | | _ | _ | |
| | Cave | Antlers | Calves Females Males | | | | | | | _ | | | | | |

Figure 5.91. Summary of *Rangifer tarandus* Season of Death from Middle Devensian Sites. Season of death was determined for each site from dentition, unshed antlers and antlerless crania (black lines) which indicate actual site occupation, while shed antlers (grey lines) are more susceptible to post-depositional transport.

In Europe (**Figure 5.92**), the German site of Salzgitter-Lebenstedt at 52°N, in addition to the Belgian sites of Goyet (Troisième Caverne), Trou du Sureau and Caverne Marie-Jeanne at 50°N, were the only Middle Weichselian sites for which the season of death could potentially represent seasonality throughout the whole year. This was mostly derived from the variable presence of antlers and dentition from calves and subadults, females and males. At the German site of Westeregeln at 51°N, the calf and subadult dentition present in August suggested late summer seasonality that could be further extended into autumn, from September to October, by male and female antlers. From the remaining Belgian site of Trou Magrite at 50°N, the male and female antlers and subadult dentition represented site occupation from August to November and therefore late summer to autumn.

| Latitude | Sites | Ageing/Sexing Technique | | Season of Death | | | | | | | | | | | |
|----------|--------------------------------|----------------------------|----------------------------|-----------------|---|---|---|---|---|---|---|---|---|-----|----|
| Lutitudo | | | | J | F | М | Α | M | J | J | Α | S | 0 | Ν | D |
| 52°N | Salzgitter- Lebenstedt | Dentition C S | Calves Subadults | | | _ | _ | _ | | | | | _ | i j | |
| | | Antlers C F N | calves Temales Nales | | | | _ | | | | | | | - | |
| 51°N | Westeregeln | Dentition S | Subadults | | | | | | | | | | | | |
| | | Antlers F N | emales lales | | | | | | | | | | | | |
| 50°N | Goyet (Troisème Caverne) | Dentition C S | Calves Subadults | | | _ | | _ | | | | | | _ | C. |
| | , | Antlers C F N | alves emales lales | | | | | | _ | | | | | | |
| | Trou du Sureau | Dentition S | Subadults | Ĩ | | | | | | | | | | | i. |
| | | Antlers C F N | Calves Temales Nales | | | | | | _ | | | | | | |
| | Trou Magrite | Dentition S | Subadults | | | | | | | | | | | | Ľ |
| | | Antlers F N | emales lales | | | | | | | | | | | | |
| | Caverne Marie-Jeanne | Dentition C S | Calves Subadults | | | | | | | | | | | L. | |
| | | Antlers C F N | alves emales Iales | | | | _ | | | | | | | | |

Figure 5.92. Summary of *Rangifer tarandus* Season of Death from Middle Weichselian Sites. Season of death was determined for each site from dentition, unshed antlers and antlerless crania (black lines) which indicate actual site occupation, while shed antlers (grey lines) are more susceptible to post-depositional transport.
R. tarandus season of death was also established for sites in Britain (**Figure 5.93**) and Europe (**Figure 5.94**) from the Late Devensian/Weichselian. In Britain (**Figure 5.93**), the most northerly site studied was Ossom's Cave at 53°N, where the seasonality of site occupations from female and calf antlers, as well as the calf and subadult dentition ages, could potentially represent the presence of *R. tarandus* throughout the whole year. Further south in Britain, at 51°N, multiple seasons of occupation were also evident from the site of Chelm's Combe, where antlers and dentition from calves and subadults, females and males, were present potentially throughout the year. Also located in southwest Britain were Gully Cave and Soldier's Hole. At Gully Cave, the dentition of subadults and antlers of both sexes corresponded with seasonality during the late summer and autumn from August to November, while at Soldier's Hole, male and female antlers indicated an autumn to winter site occupation from October to February.

| Latitude | Sites | Ageing/Sexing Technique | | Season of Death | | | | | | | | | | | | | |
|----------|------------------|--|----------------------------|-----------------|---|---|---|---|---|---|---|----|---|---|---|---|---|
| | | | | J | F | : | М | Α | | M | J | J | Α | S | 0 | N | D |
| 53°N | Ossom's Cave | Dentition Calves Subadults Antlers Calves Females | | | | - | | | | | | | | | | | |
| | | | | | | | | | | | | | | | _ | | |
| 51°N | Chelm's Combe | Dentition Calves Subadults | | | _ | - | _ | _ | | = | | | | _ | | | |
| | | Antlers | Calves Females Males | | | - | | | _ | | | | | - | _ | | |
| | Soldier's Hole | Antlers Females Males | | | | - | | | | | | ¢. | | | - | | _ |
| | Gully Cave | Dentition Subadults | | | | | | | | | | | - | | | | • |
| | | Antlers | Females Males | | | | | | | | | | | | | | |

Figure 5.93. Summary of *Rangifer tarandus* Season of Death from Late Devensian Sites. Season of death was determined for each site from dentition, unshed antlers and antlerless crania (black lines) which indicate actual site occupation, while shed antlers (grey lines) are more susceptible to post-depositional transport.

In Europe (**Figure 5.94**), the highest latitude sites were located in Denmark at 55°N. Evidence for the season of death of *R. tarandus* from Slotseng relied solely on the antlers of males and females and represented site occupation from summer to winter. The second Danish site from which *R. tarandus* were studied was Køge Bugt. Male and female antlers, together with subadult dentition, potentially represented a full year of occupation at Køge Bugt. Further south in Europe at 50°N, the antlers of females and calves from Trou des Nutons in Belgium, corresponded to an autumn to winter seasonality from October to May. The remaining Late Weichselian sites were both

located in southwest France at 44°N. At Abri de Laugerie Haute, antlers were present for males and females corresponding to an autumnal season of occupation from September and October. However, at Abri de la Madeleine, subadult dentition, as well as the antlers of calves and males, contributed to reconstructions of the season of death that potentially represented occupation throughout the whole year.

| Latitude | Sites Agein Tecl | | g/Sexing | Season of Death | | | | | | | | | | | | |
|----------|---------------------------|--------------------------|-------------------|-----------------|---|---|----------------|---|---|---|---|---|---|---|----|---|
| | | | hnique | J | F | M | ۱ _۱ | Α | м | J | J | Α | S | ο | Ν | D |
| 55°N | Køge Bugt | Dentition Subadults | | | | | | | | | | | | | I. | |
| | | Antlers Females Males | | | | | | | | | | | | | | |
| | Slotseng | Antlers | Females Males | | | _ | _ | | | | | | - | | | |
| 50°N | Trou des Nutons | Antlers | Calves Females | | | | | | | | | | | | | |
| 44°N | Abri de Laugerie Haute | Antlers | Females Males | | | _ | _ | | | | | | | | 6 | |
| | Abri de la Madeleine | Dentition Subadults | | | | | _ | | | | | _ | | | I. | |
| | | Antlers | Calves Males | | | | | | | | | | - | | _ | |

Figure 5.94. Summary of *Rangifer tarandus* Season of Death from Late Weichselian Sites. Season of death was determined for each site from dentition, unshed antlers and antlerless crania (black lines) which indicate actual site occupation, while shed antlers (grey lines) are more susceptible to post-depositional transport.

Chapter 6. Seasonality and Migrations of Late Pleistocene *Rangifer tarandus*

The following chapter discusses the seasonality of site occupations by *Rangifer tarandus* at Early, Middle and Late last cold stage sites from across Britain and western Europe. This discussion is based on age at death and season of death data derived from dental, antler, cranial and postcranial *R. tarandus* remains. Where seasonal movements have been identified the potential migrational pathways have been hypothesised.

6.1. Early Devensian

Only material from British sites was studied from the Early Devensian. Despite being strong swimmers, capable of crossing lakes and large rivers 6.5 km or wider at a constant speed of 6.5 km/hr (Kelsall, 1968; Burch, 1972), it is unlikely that the British Early Devensian *R. tarandus* had free access into continental Europe at this time, because of Britain's presumed island status (Currant and Jacobi, 2011). Therefore, it is assumed that the migrational ranges of *R. tarandus* would have been limited to movements exclusively within Britain. **Figure 6.1** outlines the seasonality of *R. tarandus* site occupations reconstructed from Early Devensian assemblages. These appear to represent the presence of migratory rather than sedentary herds in Britain, following the north-south trajectory exemplified by modern *R. tarandus* that move between northern summer tundra and southern winter taiga environments (Skogland, 1980; Tablado *et al.*, 2014).

Records for summer occupations were evident from Stump Cross Cavern and Windy Knoll, both located above 53°N (**Figure 6.1**). While only tentative interpretations could be made from Stump Cross Cavern, where an MNI of two was established, the combination of subadult dentition from August and a living herd structure of males to females in the postcrania of individuals >2.5 years old, corresponds to the aggregations associated with summer grazing. The upland environment of the Yorkshire Dales where Stump Cross Cavern is located, would provide ample opportunities for *R. tarandus* to utilise the high and open topography, which is similar to the summer grazing pastures of modern *R. tarandus* (Bergerud and Luttich, 2003). Today, *R. tarandus* demonstrate high levels of site fidelity to such areas in the summer, as the windy ridges reduce the risk of harassment from insects and predators, in turn allowing individuals to prioritise grazing



Figure 6.1. Summary of British Early Devensian Seasonality of Site Occupations. Sites studied include Stump Cross Cavern (STC), Windy Knoll (WK), Isleworth (I), Feltham (F), Picken's Hole (PicH), Banwell Bone Cave (BBC) and Tornewton Cave (TC).

in anticipation of the oncoming winter (Schaefer *et al.*, 2000; Weladji *et al.*, 2003; Body *et al.*, 2014; Tablado *et al.*, 2014; Lafontaine *et al.*, 2017). Although the small number of *R. tarandus* preserved at Stump Cross Cavern does not necessarily reflect the annual use of the area surrounding the site, as July and August represent periods of maximum herd dispersal (Burch, 1972), the precise location of individuals may have changed year-on-year around this natural pitfall trap (Collins, 1959).

At Windy Knoll, the more abundant remains preserved at the site potentially represented the presence of *R. tarandus* not only during the summer, but throughout the whole year. However, in both calves and subadults, the monthly precision of dentition ages was focussed on the period from August to October, with individuals aged to 3-5, 27 and 29 months old. Although this late summer to autumn occupation could be further extended into the winter as late as March, with the presence of 5-10 month and 18-21 month olds,

the overlap in October with the antler cycles of unshed subadult females and adult males would support the autumn occupation of Windy Knoll. Similarly, both the dentition from a 12-15 month old and antlerless cranium of an adult male could represent the presence of animals during spring or summer, but the overlap during August would more likely support seasonality during the late summer. While the high and open topography of Windy Knoll in the Peak District would provide good summer grazing for *R. tarandus*, the late summer to autumn seasonality expressed at the site could represent the autumn migration (Figure 6.1). As the entire herd moves towards the location of the winter grazing grounds, the living herd structure observed in the early- and late-fusing postcrania at Windy Knoll represent an aggregation which was not vastly sexually segregated. The position of Windy Knoll above Winnats Pass, a steep-sided limestone valley, was suggested by Dawkins (1875) to form part of a migration route for herbivores between the high ground of the surrounding Peak District and the open plains of Lancashire and Cheshire. Although modern *R. tarandus* are capable of using a range of topographies during migrations, rather than detour around areas of higher ground, large aggregations will often use routes through mountain passes such as those near Windy Knoll (Burch, 1972). Individual movements during migrations are relatively quick at 25-30km/day (Kelsall, 1968; Skoog, 1968) however, the duration of herd migrations last for several months (Birtton et al., 2009), which may explain the extended period of occupation at Windy Knoll.

In contrast, the Early Devensian sites in southern Britain around 50-51°N (**Figure 6.1**) suggest a different pattern of seasonality, as exemplified from two fluvial sites from the Middle Thames Valley, Isleworth and Feltham, located within 10 km of each other. Both sites contained indicators for occupation from September to November in the form of subadult and adult male unshed antlers. A total of 25 males was identified at Isleworth, while at Feltham five individuals were measured. This autumn seasonality coincides with the breeding season, known as the rut, which occurs over 3-4 weeks generally in the same annual location (Weinstock, 2000a; Body *et al.*, 2014). The aggregations formed during this period are characterised by fewer males and multiple female and calf pairs (L'Italien *et al.*, 2012), as individual adult males gather harems of females (Holand, 2006). This is reflected in a ratio of 1:2 or 1:3 males to females for a living population on entering the rut (Weinstock, 2000a). However, in addition to the predominance of male antlers at the site, a reversal of the living structure was identified from the postcrania at Isleworth. Ratios of 3:0 and 2:1 males to females were derived from subadult individuals >2.5 years old (proximal metacarpals) and adults >4 years old (distal radii) respectively.

As such, rather than the location of the rut, the bias towards male remains expressed at both sites could reflect the starvation of adult males during the late autumn and early winter, as a result of the high energy demands exerted during the breeding season. The combination of fighting, challenging males in violent displays whist continuing to herd females into harems, greatly depletes the energy reserves of prime-age males (Weinstock, 2000b; Holand, 2006). As younger subadult males tend to sustain negligible losses by prioritising feeding at this time (Weinstock, 2000a), the larger quantities of adult males at both Isleworth and Feltham would support this late autumn to early winter seasonality. Furthermore, although shed antlers provide a much less reliable indication of occupation due to their vulnerability to post-depositional transport (Spiess, 1979), especially in the fluvial gravels of the River Thames sites, the large volume of shed antlers at Isleworth could also be used to confirm the winter occupation. The shedding cycles for the 39 subadult and adult male shed antler sets at Isleworth overlap during November and December in the early winter. While not as numerous, this pattern of subadult and adult males was also observed at Feltham for 12 shed antler sets. It is therefore evident that following the dispersal of the rut aggregation into smaller bands, males used this area of the Middle Thames Valley as a winter grazing range.

Similar to the assemblage at Windy Knoll, the more abundant remains preserved at Banwell Bone Cave, in the Mendip Hills in Somerset, potentially represented *R. tarandus* presence throughout the whole year in southwest Britain. However, at Banwell Bone Cave, evidence for seasonal occupation was strongly focussed towards late autumn and specifically October (**Figure 6.1**). The overlap of the unshed antler cycles of all ages and sexes during this month was supported further by dentition classes of 5-10, 16-18 and 29 months old. A reversed living herd ratio of 2:1 males to females was also observed from adult individuals >4 years old (proximal ulna) at the site. Like the *R. tarandus* in the Middle Thames Valley, this could reflect the high energy demands and subsequent male mortality observed during the late autumn to early winter and associated with rut.

The clear seasonality signal at Banwell Bone Cave may be strongly due to the floodwater origins of the assemblage (Currant, 2004). A flood event occurring at Banwell Bone Cave after the rut and during late autumn-early winter would account for the distinctive demography seen at the site. By this time, the large rut aggregation would have broken into smaller groups, allowing for individuals grazing on winter pastures to be incorporated into the assemblage. In addition to the natural living herd structure pattern, increased male mortality during this season would have led to a large number of adult male carcasses being washed in the cave at this time. Nevertheless, questions remain as to whether flood processes in the vicinity of the site were a single or multi seasonal event (Lubinski, 2013) and the extent to which the site acted as a natural pitfall trap throughout the year. Despite the presence of 23 shed antlers from calves, subadult and adult females suggesting a spring occupation from May to June, the risk of post-depositional

transport makes them a less reliable indicator of seasonality (Spiess, 1979). This also applies to the shed adult and subadult male antlers, which would otherwise confirm the late autumn-early winter occupation suggested here. Nevertheless, two individuals were recognised on the basis of dentition, aged 3 and 25 months old, along with antlerless subadult male and adult male and female crania, indicating occupation during the months of June to August. Although this could suggest summer occupation, these animals are here regarded as outliers.

Smaller assemblages were also studied from southwest Britain and the sites of Picken's Hole (Unit 5) and Tornewton Cave. At Picken's Hole, in the Mendip Hills in Somerset, one unshed antler from an adult female provided the only direct indication of seasonality during October to May, when these individuals are found with fully grown antlers still attached. Like the Middle Thames Valley sites, as well as Banwell Bone Cave which is less than 10 km north of Picken's Hole, the 3:1 ratio of males to females show a reversal of the living herd structure. Although this was observed from the early-fusing proximal radii and can therefore only confidently represent subadult individuals >0.5 years old, the higher male mortality would correspond to the late autumn-early winter occupation of Picken's Hole. However, unlike other sites in southern Britain, Unit 5 at Picken's Hole was thought to have been accumulated by wolves (Canis lupus, Linnaeus, 1758) transporting partial carcasses and antlers to the cave (Scott, 2018). As cursorial or pursuit predators, C. lupus typically select the more vulnerable young and old members of a herd (Steele, 2003), but are capable of hunting adults (Nybakk et al., 2002). As such, the selective predation of males would suggest that they were perhaps more abundant on the surrounding landscape, which would correspond with late autumn-early winter when the herd disperses for winter grazing and male mortality increases. A similar taphonomic origin is also inferred from the Reindeer Stratum at the site of Tornewton, in south Devon (Scott, 1986). The remains at Tornewton also support the autumn and winter occupation of sites in southern Britain (Figure 6.1). This was inferred from the unshed antlers of a calf, which are retained between October and May, together with an individual 29 months old from October. A total of 19 shed antlers from calves, subadult and adult females were also identified at the site and suggest a spring occupation from May to June. However, given the preference of C. lupus for collecting and chewing antlers (Scott, 2018), it is uncertain based on these remains whether the seasonality at Tornewton extended from autumn into spring, or if antlers were brought from elsewhere.

From the British Early Devensian sites studied, there was a distinct absence of robust evidence for spring occupation (**Figure 6.1**). This season is most clearly identifiable from the fossil record by the sexually segregated aggregations that form during calving (Aaris-Sørensen *et al.*, 2007), which the predominance of males within all the Early Devensian

sites would similarly not support. Nevertheless, although none of the sites represent spring, the geographical separation between summer and wintering sites supports the migratory behaviour of *R. tarandus*. While it is not possible to determine precise centres and directions of migrations from the seasonality of site occupations, if the Early Devensian *R. tarandus* did range from the south of Britain to at least North Yorkshire, then herds could be moving distances of up to 500 km. Applying an average migrational rate of 25-30 km/day from modern *R. tarandus* (Kelsall, 1968; Skoog, 1968), this would represent 2-3 weeks of movement.

6.2. Middle Devensian/Weichselian

From the British Middle Devensian, the most northerly site from which *R. tarandus* were studied was the two caves at Inchnadamph, 58°N in the Scottish Highlands. Although the assemblage at Bone Cave was smaller than that from Reindeer Cave, identical patterns of seasonality were recognised from both sites (Figure 6.2). Most notably, these were dominated by the remains of shed antlers. From Reindeer Cave alone, 82 calves, 202 subadult females and 68 adult females were recorded from the site. While shed antlers can be subject to post-depositional transport, antlers preserved in such volumes could be used to infer the presence of *R. tarandus* in the surrounding area. The antlers of females and calves are shed from May to June to coincide with the calving period during the spring. This represents a period when aggregations express a high degree of sexual segregation, as well as site fidelity, meaning that sites are returned to over many generations (Schaefer et al., 2000). This would further account for the large numbers of shed antlers preserved and the relative absence of adult males; only a small number of subadult males were identified from Reindeer Cave in the form of shed antlers. Furthermore, the only dentition preserved at either cave belonged to calves aged 0-3 months old. These new born individuals would correspond to the site occupation from May to August, supporting the interpretation that the limestone ridges surrounding Inchnadamph represented not only spring calving grounds, but also part of the summer grazing grounds (Figure 6.2), although as a period of greater dispersal (Burch, 1972) there was less evidence to support this season. Such high and open topography would provide relatively safer environments for mothers and their young calves from the risk of predators and insect harassment (Bergerud and Luttich, 2003; Weladji et al., 2003; Tablado et al., 2014). Evidence for gnawing on the shed antlers suggest that predators including V. lagopus and L. lynx (Murray et al., 1993) were responsible for the assemblages at Inchnadamph. Nevertheless, this spring to summer northern range for Middle Devensian *R. tarandus* would imply that animals occupied a migrational niche.



Figure 6.2. Summary of British and European Middle Devensian/Weichselian Seasonality of Site Occupations. Sites studied include Inchnadamph Bone Cave (In-B), Inchnadamph Reindeer Cave (In-R), Church Hole Cave (CHC), Pin Hole Cave (PHC), Robin Hood Cave (RHC), Sandford Hill (SH), Picken's Hole (PicH), Gully Cave (GC), Wookey Hole (WH), Kents Cavern (KC), Brixham Cave (BC), Salzgitter-Lebenstedt (SL), Westeregeln (W), Ellewoutsdijk (E), Goyet Troisième Caverne (G3e), Trou du Sureau (TS), Trou Magrite (TMa), Caverne Marie-Jeanne (CMJ).

Further south at 53°N, three caves were studied from the Creswell Crags fluvial gorge in Derbyshire: Pin Hole Cave, Church Hole Cave and Robin Hood Cave. Each of these sites represented the presence of *R. tarandus* during the late summer and autumn (**Figure 6.2**), from the dentition of subadults 15-18 months old and 27-29 months which correspond to site occupation from August to November. At Pin Hole Cave, which was the most abundant assemblage of the three, a calf 3-5 months old would also support this range, together with the unshed antlers of calves, subadult and adult females and adult males, which overlap in their respective antler cycles during October. The unshed antlers of a subadult female and antlerless crania of an adult male was also identified at Church Hole Cave, further confirming this seasonality. However, at Pin Hole Cave,

dentition aged to 21-24 months old also implied the presence of subadult individuals between February and May. Together with shed antlers from 67 calves and 116 subadult females, which can be dropped as early as March but are typically lost between May to June, this could also suggest a spring occupation (Figure 6.2). Although not as numerous, antlers belonging to these two groups were also present at Church Hole Cave and Robin Hood Cave. However, unlike at Inchnadamph, the absence of the dentition of any new born calves 0-3 months old, as well as the shed antlers of adult females, would imply that the Creswell Crags R. tarandus were separate from the main spring calving aggregation. Instead of mother and calf pairs, subadult, prime age and old individuals were present at the three sites. With no evidence for either summer or winter grazing grounds, the area was therefore potentially occupied as part of autumn and spring migrational routes between southern and northern regions. The 1:1 ratio of males to females from adult individuals >4 years old (ulnae and distal radii) also deviated from the living herd structure. As migrations towards spring calving grounds are led by pregnant females, with the males, non-pregnant females and yearlings lagging behind this movement, this could therefore be indicative of a more marginal group of individuals that was not yet sexually active in the autumn rut and subsequent spring calving, migrating either through or near the gorge and being hunted by primarily spotted hyaena (Crocuta crocuta, Erxleben, 1777).

Following the pattern observed from Early Devensian *R. tarandus*, moving to southwest Britain and 50-51°N, an autumn or winter occupation might be expected. At both Brixham Cave on the south Devon coast and Sandford Hill in the Mendip Hills in Somerset this was apparently the case (Figure 6.2), although the evidence for season of death at these two caves potentially provided a continuous signal for occupation during late summer, autumn, winter and spring. At Sandford Hill, ratios from both early-fusing elements (distal humeri) and adult individuals >4 years old (calcanea) were strongly biased towards females by 1:4 and 1:3 males to females respectively. Similar numbers of unshed antlers from calves and adult females, as well as the dentition of 27 calves and 26 prime age adults, therefore suggest the presence of mother and calf pairs at Sandford Hill. Despite the highly sexually-segregated nature of this assemblage, the lack of either neonatal individuals or the presence of numerous shed antlers would rule this out as a calving ground. Dentition from calves 3-4 month olds and subadults 15-18 and 27-29 months old represent occupation from August to October and therefore late summer and autumn. This also overlapped the seasonality suggested by the unshed antlers of calves, females and an adult male, as well as the antlerless crania of a subadult female. However, dentition 5-10 months old, 10-12 months old and 21-24 months would extend occupation from October to March as *R. tarandus* used the surrounding Somerset Levels for winter grazing. Compared to other seasons, annual site use of winter grazing grounds may be 226

somewhat varied (Schaefer *et al.*, 2000). Nevertheless, as calves remain with their mothers throughout the first winter despite weaning within 3 months of birth (Holand *et al*, 2012), both are particularly vulnerable to predation at this time by *C. lupus* and *C. crocuta*, also reported from the Sandford Hill assemblage (Bergerud, 1980; Weinstock, 2000a).

Conversely, at the Brixham Cave fissure, the presence of a 1:1 ratio of males to females from individuals >4 years old (calcanea) at Brixham Cave, diverged from the typical living herd structure and suggested the presence of a more marginal group. This was further supported by the dominance of males in the 4:1 ratio from the distal tibiae and individuals >2.5 years old. The dentition of subadult and adult individuals 29 months old and 18-21 months would correspond to October to February. Combined with the unshed antlers of a calf and the antlerless crania of an adult female, this would confine site occupation to the autumn and winter from September to February. During the winter grazing, subadults and males are forced to occupy the margins of grazing areas, which could represent the occupations at Brixham Cave. If subadults and males were more abundant on the surrounding landscape, they would certainly have dominated the diet of the prevailing large carnivores at the cave.

The presence of *R. tarandus* in southwest Britain during the summer and autumn was also evident from Gully Cave in Ebbor Gorge, which like Sandford Hill is part of the Mendip Hills in Somerset (Figure 6.2). The dentition of subadults 27 and 29 months old corresponds to occupation from August to October, while the 1:1 ratio of males to females from the distal tibiae and individuals >2.5 years old demonstrated a more marginal group of subadults similar to the Brixham Cave assemblage. The presence of a calf 5-10 months old might also imply the movement of *R. tarandus* onto the Somerset Levels for winter grazing between October and March. However, one subadult individual was also aged to 26-27 months old. Encompassing July to August, this potentially represented a longer summer occupation than any of the previous sites from southwest Britain. A similar pattern of earlier summer presence was also observed from the nearby Wookey Hole Hyaena Den (Figure 6.2), where dentition from individuals 13 months old, 15-16 months old and 27 months old implied an occupation from June to September. As such, in addition to moving to southern Britain for lower latitude autumn and winter ranges, perhaps R. tarandus were also exploiting summer grazing pastures on the high outcrops of the Mendip Hills.

Another assemblage to deviate from this pattern of seasonal occupation was that from Unit 3 at the site of Picken's Hole. Similar to other sites in southern Britain, the only unshed antlers identified from the site belonged to an adult female which retain their antlers from October to May. However, from the dentition ages, it is the spring and summer which were represented at the site (**Figure 6.2**), as animals 10-12 months old and 15 months old correspond to a May to August occupation. It is important to consider that the collection at Picken's Hole was not large and therefore the evidence for this season was not robust, but the absence of a clear autumn and winter signal is an interesting difference. Furthermore, this seasonality appeared to differ from that of the older, Early Devensian Unit 5 at Picken's Hole, where an autumn/winter occupation was evident. As such, this could represent a shift in the ranges of British *R. tarandus* from the Early Devensian, when Britain was isolated, to the Middle Devensian, when lower sea levels resulted in a reconnection to continental Europe (Cutler *et al.*, 2003; Currant and Jacobi, 2011).

A change in the occupation of southwest Britain would have significant implications for the interpretation of seasonality at Kents Cavern on the south coast of Devon. At this site, R. tarandus potentially provided a continuous signal for occupation during spring, summer, autumn and winter (Figure 6.2). This was evident from the presence of dentition from individuals 5-15 months old and 16-21 months old, encompassing October to August and September to February respectively, as well as the unshed antlers of calves, subadult and adult females, which retain their antlers from October to May. Although the presence of a 1:1 ratio of males to females from individuals >4 years (proximal calcanea) at Kents Cavern diverged from the typical living herd structure towards a group of subadults, the shift in the ratios of early-fusing (proximal radii) and >2.5 years old (distal tibiae) individuals towards a 3:2 and 3:0 male dominated ratio, would support the reliability of the 19 shed antlers of adult males to imply presence from November to December. As subadults and males are forced to occupy the margins of winter grazing areas, this could represent part of the occupations at Kents Cavern. However, like Gully Cave and Picken's Hole, the dentition of subadults at Kents Cavern also included individuals 26 and 27 months old and therefore supported their presence earlier in the summer from July to August. While the absence of calves younger than 5 months old implied that the area surrounding Kents Cavern was probably not part of the summer grazing grounds of mothers and calves, dentition from 5-10 month olds and 10-12 month olds would correlate with 10 month old calves moving here in March as antagonistic relationships began to develop with their mothers.

As an assemblage, Kents Cavern represents a long period of accumulation; therefore, it is possible that the multiple seasons of occupation preserved at the site might reflect animals that were not contemporaries. Nevertheless, if *R. tarandus* were occupying the area surrounding Kents Cavern throughout the whole year, this could be interpreted as either the presence of a more sedentary herd, moving only small distances in order to preserve the productivity of grazing pastures, or the different migrational patterns of

separate herds using the south of Britain for both winter and summer ranges. If the latter were the case and herds moved between autumn/winter ranges in south Devon and spring/summer ranges in northern Scotland, it would take *R. tarandus* between 5-6 weeks to migrate this distance when an average migrational rate of 25-30 km/day from modern *R. tarandus* was applied (Kelsall, 1968; Skoog, 1968). Although it is not possible to directly reconstruct the locations Late Pleistocene *R. tarandus* were moving from the seasonality of site occupations, techniques such as strontium isotope analysis (see Chapter 8) will provide further insight into the centres and directions of migrations. This could be particularly insightful given the exposure of the landbridge between Britain and continental Europe during the Middle Devensian/Weichselian.

In mainland Europe, R. tarandus nevertheless continued to show the seasonal occupation of open-air sites at Westeregeln and Salzgitter-Lebenstedt at 51-52°N in Germany (Figure 6.2). At Westeregeln, dentition aged to 27 months would correspond to August and late summer, while the unshed antlers of adult males extended this occupation into the autumn. The presence of a 1:1 ratio of males to females from individuals >4 years (proximal calcanea) diverged from the typical living structure towards a group of subadults and presumably males, given the 2:1 ratio evident from the early-fusing distal humeri. A total of only four individuals was identified at Westeregeln making this a relatively small assemblage. However, the late summer to autumn seasonality of the site was similar to that of the 58 individuals at the nearby Salzgitter-Lebenstedt (Figure 6.2). As opposed to the C. crocuta-accumulated assemblage at Westeregeln (Diedrich, 2012), Neanderthal hunters at Salzgitter-Lebdenstedt are thought to have driven *R. tarandus* towards tributaries of the River Fuhse valley, resulting in the non-selective killing of these individuals (Gaudzinski and Roebroeks, 2000; White et al., 2016). Despite the dentition at the site being weighted towards the 40 prime age adults, juvenile individuals aged to 3 months old, 15-16 months old and 29 months old, would place site occupation between August and October. The unshed antlers of 27 adult and 14 subadult males that also dominated the assemblage would further correspond to the period between September to November, when these individuals have their antlers attached. Although less numerous, this autumnal presence would also be confirmed by the unshed antlers and antlerless crania from subadult and adult females. Large aggregations formed during the autumn are associated with the rut. However, the rut itself is characterised by fewer males compared to the females they will attempt to herd into harems (Holand, 2006; L'Italien et al., 2012), something not visible from the unshed antlers of predominantly males at Salzgitter-Lebenstedt. Furthermore, males continued to dominate the assemblage in both the early-fusing and later-fusing elements of the postcrania. Rather than the location of the rut, the site could be part of a migration route between summer and winter grazing pastures. However, the identification of 229

calves' and subadults' dentition, 5-10 months old, 10-12 months old and 21-24 months old, would extend the occupation at Salzgitter-Lebenstedt through the winter to overlap in February and March. The area surrounding Salzgitter-Lebenstedt may therefore have also been part of winter grazing grounds, although with humans having conducted extensive hunting during the autumn, there is comparatively less evidence for this season at the site. Nevertheless, *R. tarandus* in Germany do appear to have been migratory.

Middle Weichselian R. tarandus were also studied from four cave sites in the Ardennes in southwest Belgium at 50°N, located on the valley sides of tributaries of the River Meuse. The seasonality from these sites indicate that the area was potentially occupied during spring, summer, autumn and winter, something which could be indicative of a more sedentary niche being occupied at this time (Figure 6.2). This was clearly reflected by the *R. tarandus* from Goyet's Troisième Caverne (Figure 6.2). Dentition ages indicating occupation from August to October, and therefore late summer and autumn, were evident from individuals 16-18 months old, 27 months old and 28-29 months old, as well as the unshed antlers of adult males and subadult and adult females. The presence of calves and subadults 5-10 months old, 10-12 months and 21-24 months old also had the potential to extend this occupation from October to May, although these annually-recurring dentition ages overlap during March and late winter. In the postcrania at Goyet, the living herd structure was supported by the 1:1 ratio in early-fusing elements (distal humeri) and the 1:2 ratio in individuals >2.5 years old (distal tibiae). As the living structure of a herd described observations following annual calving when the main herd joins together (Steele, 2005), the assemblage at Govet could therefore be representative of such large aggregations, which from the dentition and antler reconstructions of seasonality are more likely to be the autumn rut. However, the prevalence of shed antlers at Goyet could also provide evidence for another female-dominated aggregation, calving. Although shed antlers can be an unreliable indicator for animal seasonality, the shedding of antlers from 77 subadult females and 14 adult females would occur from March to June, therefore supporting a spring occupation. If this was the case, the significantly lower number of adult females and calves at the site might imply that the subadults at Goyet were lagging behind the movement of pregnant females to the calving grounds themselves, which was evidently not located at Goyet. Therefore, it is unlikely that R tarandus in the surrounding area were completely sedentary.

At both Trou du Sureau and Trou Magrite, similar patterns of late summer and autumn occupations were also observed (**Figure 6.2**). Dentition was identified from individuals 16-18 months old at Trou Magrite and 27 months old and 29 months old at both sites, indicating occupation during August and October. Together with the unshed antlers of

subadult females and adult males at Trou du Sureau, as well as the antlerless crania of subadult and adult females at this site, these would overlap during September, confirming an autumnal occupation. Both sites also represented a living herd structure that was weighted towards females. Although these were mainly generated from earlyfusing elements such as the distal humeri and proximal radii, ratios of 1:3, 0:6 and 1:4 were observed from these elements. Combined with the dentition ages, this is likely to represent the autumn rut aggregation. However, at Trou du Sureau, like Goyet, the female-dominated assemblage was further supported by the shed antlers of 24 subadult females. Therefore, although there was little evidence for a winter occupation, the seasonality at Trou du Sureau could potentially have extended to the spring. The living structure at Goyel, Trou du Sureau and Trou Magrite is also typical of assemblages formed by non-selective or catastrophic processes such as ambush predators (Stiner, 1990). Within the Belgian Middle Weichselian sites, this is particularly significant given the abundance of Middle and Upper Palaeolithic technology associated with this landscape. It is therefore possible that hunters in Belgium used the Meuse river valley and its tributaries in a similarly planned manner to those at Salzgitter-Lebenstedt, exploiting *R. tarandus* migrating along these river valleys between their summer and winter grazing pastures. Although both Salzgitter-Lebenstedt and the Troisième Caverne at Goyet are Mousterian sites, while Trou du Sureau and Trou Magrite represent the Aurignacian, the hunting practices of the two cultures are not thought to have varied greatly (White et al., 2016).

The only evidence for late autumn and winter seasonal occupation in Belgium was observed from Caverne Marie-Jeanne (Figure 6.2). This was evident from the dentition of individuals 5-10 months old and 29 months old, which correspond to occupation between October and March. Although the seasonality suggested by the unshed antlers of the calves, subadult and adult females and males present at the site ranged from September to April, these nevertheless overlapped with the period of occupation from the dentition ages. The 1:1 ratio of males to females >2.5 years old (distal tibiae) further suggested that the *R. tarandus* occupied Caverne Marie-Jeanne only after the rut. During the breeding season, aggregations are dominated by females in ratios of 1:2 or 1:3 males to females, as individual adult males form harems (Weinstock, 2000b; Holand, 2006; L'Italien et al., 2012). As this female weighted ratio was not observed at Cavern Marie-Jeanne, the site probably represented winter grazing areas for *R. tarandus* instead. However, what was particularly unique about the postcrania studied at Caverne Marie-Jeanne was that 20.6% of elements displayed cut marks, the largest percentage observed from any of the Middle Weichselian sites, although these only reflect the material suitable for the parameters of this study. These included radii, metacarpals and tibia of both sexes. A site associated with Mousterian technologies, Caverne MarieJeanne could therefore represent the seasonal exploitation of *R. tarandus* by humans, similar to the autumn exploitation suggested for other Belgian sites.

Similarities between the Belgian Middle Weichselian sites further extended to the large numbers of shed antlers preserved, indeed only shed antlers were present from Trou Magrite. Nevertheless, the vulnerability of shed antlers to post-depositional transport means that their taphonomic origins must be fully considered before patterns of seasonality can be inferred (Spiess, 1979). While carnivores, such as C. crocuta and C. lupus, collect shed antlers (Tejero, 2014; Scott, 2018), evidence of gnawing was not extensive among the Belgian remains. However, small, thin antlers from young and female *R. tarandus* similar to the subadult females which dominated the Belgian Middle Weichselian (Figure 6.3), have also been preserved at Westeregeln in central Germany. Unfortunately, only a small subset of the Westeregeln Middle Weichselian assemblage was included in this study, for which this volume of antlers was not evident. Nevertheless, the shed antlers of subadult females from Westeregeln were not only the most abundant age-sex group identified, but visually resembled the Belgian remains (Figure 6.3). Despite the minimal cut marks found on large collections of antlers at Westeregeln, these have been suggested to be antler stores of Magdalenian origin (Diedrich, 2012). This is something practiced by modern Sami *R. tarandus* herders, who store antlers away from their main settlements (Bleicher, 1993). The four cave sites from southern Belgium could therefore represent a series of these antler stores. Although only Goyet represented Magdalenian technologies (Germonpre, 1997), the movement during the Early Aurignacian towards the production of antler points instead of lithic alternatives may be significant (Tejero, 2014). Evidence for Aurignacian technologies was present at Trou du Sureau and Trou Magrite (Gautier et al., 1997; Goubel et al., 2012). As such, the storing of antlers could be an important component for the production of weapons at these sites, particularly as the complete mineralisation of shed antlers would make them preferable for working (Tejero, 2014).

Another potential location for an antler store similar to those suggested in Belgium and Germany, is the Middle Devensian site of Pin Hole Cave in Britain. Shed antlers at this site number 230 individuals, most of which belonged to subadult females similar in size and levels of human and carnivore alterations to the identified antler stores. However, at Pin Hole Cave, the antlers are associated with Mousterian levels (Currant and Jacobi, 2011), a period in which antler exploitation was not thought to have occurred (Tejero, 2014). However, Mousterian technologies were also present at Goyet and therefore antler storage could still have been possible from the Late Middle Palaeolithic. This might also account for the lack of direct evidence for calving grounds surrounding Pin Hole Cave, if the shed antlers had been transported from elsewhere with the intent of storage.

Of course, with a total of 357 individuals, the most abundant shed antler remains from the British Middle Devensian were located at Inchnadamph. However, as the integrity of Palaeolithic artefacts from this site are unreliable (Saville, 2005) and the evidence of gnawing on these remains is certainly more prevalent than at Pin Hole Cave, it is perhaps more likely that the assemblage is carnivore-derived.



Figure 6.3. Abundant Subadult Antler Remains. Large numbers of subadult and adult female shed antlers, similar to the example here from Goyet Troisième Caverne (left) and Westergeln (right), dominated assemblages from the Middle Devensian/Weichselian.

6.3. Late Devensian/Weichselian

Similar to the seasonality expressed during the British Early and Middle Devensian, Lateglacial Interstadial R. tarandus appeared to represent migrational populations moving along north-south trajectories within Britain (Figure 6.4). In southern Britain at 51°N, evidence for winter occupations was present at Soldier's Hole and Gully Cave, both located in the Mendip Hills in Somerset. Although the dentition of fully mature adults could not be used to directly assign the season of occupation to the rock shelter of Soldier's Hole in Cheddar Gorge, unshed antlers of subadult females indicated the presence of *R. tarandus* potentially from October to February and therefore a late autumn to winter occupation. However, despite following the 1:1 living structure ratio in earlyfusing elements, in adults >4 years old, both female-dominated ratios of 2:3 from the calcanea and male-dominated ratios of 4:1 generated from the distal radii, were present in the assemblage. This variability in the sexes would correspond to both the late autumn when the female dominated rut is disbanding and the early winter period when males are susceptible to starvation. Furthermore, the separation of adult individuals during grazing periods into males and females, and solitary mature males (Main et al., 1996), could represent the differential use of the area by each group. Nevertheless, the flat plain of the Somerset Levels that surround Cheddar Gorge and Soldier's Hole could have

provided the winter grazing pastures for *R. tarandus*. The absence of calves at Soldier's Hole might also be a product of more selective accumulation at the site. The assemblage at Soldier's Hole contains the remains of several predators including *C. lupus* (Jackson, 1931), which are present in the most abundant *R. tarandus* layers from site. Although *C. lupus* have been shown to hunt the adult individuals which characterise Solder's Hole (Nybakk *et al.*, 2002), evidence for Magdalenian type flint technology was also present at the site (Parry, 1931). Assemblages dominated by prime-age animals are typically reflective of a level of focus, skill and technology unique to humans (Steele, 2003). Nevertheless, as there was an absence of either evidence for cut marks or gnawing on the fossils at Soldier's Hole, it is difficult to confidently assign the accumulation to one or other of these predators.



Figure 6.4. Summary of British and European Late Devensian/Weichselian Seasonality of Site Occupations. Sites studied include Ossom's Cave (OC), Chelm's Combe (CC), Soldier's Hole (SoH), Gully Cave (GC), Køge Bugt (KB), Slotseng (SL), Trou des Nutons (TN), Abri de Laugerie Haute (LH), Abri de la Madeleine (LM).

Another Lateglacial Interstadial site located in southwest Britain was Gully Cave in Ebbor Gorge. However, R. tarandus presence was slightly earlier in the year at this site than at Soldier's Hole (Figure 6.4), with dentition aged to 27 months old and 16-18 months old corresponding to a range from August in the late summer to November in the autumn. It is unlikely that this represents the rut aggregation, as the 2:0 ratio from proximal radii indicated that males, rather than females, were more prevalent in individuals >0.5 years old. While this is an early-fusing element and therefore not always representative of the adults in an assemblage, at least one of the bones was a fully-fused adult. As such, the reversal of the living herd structure would be more indicative of a male dominated group of *R. tarandus* moving further south for autumn and winter grazing ranges. In their early years, subadult males will tend to prioritise feeding over challenging mature males in the rut, where the risks are high, and are therefore likely to be separate from the main group during this time (Weinstock, 2000a; Holand, 2006). Nevertheless, this seasonality is similar to the pattern expressed at Gully Cave by the Middle Devensian R. tarandus, showing a continuation in the use of the site from late summer to autumn. However, during the Middle Devensian, it was also possible that a longer period of summer occupation was evident at the site. The summer grazing is particularly important for R. tarandus as the higher nutrient content of forage supports the recovery of females from the pressures of reproduction (Heggberget et al, 2002) and facilitates the growth of calves (Adamczewski et al. 1987), so that both may avoid winter starvation (Fauchald et al., 2004). An early movement to lower latitude ranges could therefore have significant implications for the quality of vegetation during the Middle and Late Devensian.

Located within Cheddar Gorge, but dated to the Younger Dryas, is the rock shelter of Chelm's Combe. Here, calves and subadults with dentition ages of 10-12 months and 21-22 months indicated occupation during late winter and earlier spring from February to May, but overlapped during March. This corresponded with the record for male skulls without antlers and calf and subadult female unshed antlers, both observable in *R. tarandus* from December to March. The dentition from one 16-18 month old present from September to November was also recognised at Chelm's Combe, but this was probably more consistent with the early winter, rather than autumn occupation of the site. The 1:1 ratio of males to females >2.5 years old (proximal metacarpals) suggested that while site occupation may have extended from winter into early spring, this was not a calving site but a more marginal population of males and females. It is likely that the yearling *R. tarandus* represented at Chelm's Combe had developed antagonistic relations with their mothers and left them to join subadult groups (Hirotoni, 1990). However, some yearlings will remain with their mothers for slightly longer, leaving only with the spring migration to calving sites (Takken Beijerbergen, 2017). Despite the temporal differences between the

Late Devensian sites in southwest Britain, the Mendip Hills appear to have been used consistently as an autumn and winter range for *R. tarandus* (**Figure 6.4**).

At the second Younger Dryas site, the more northerly Ossom's Cave in Staffordshire at 53°N, individuals with dentition ages of 10-12 months, together with the unshed antlers of females and calves, suggested the seasonal occupation of Ossom's Cave between March and June. Once again, the absence of neonatal individuals combined with a ratio of 2:0 males to females >2.5 years old (distal tibiae), implied that Ossom's Cave was not specifically a calving site although this was potentially nearby. R. tarandus express a preference for high open topography during calving in an attempt to lower the risk of predation at this vulnerable time (Bergerud and Luttich, 2003). The surrounding Peak District at Ossom's Cave could therefore have provided many potential sites for pregnant females to calve. At Ossom's Cave, dentition from an individual 12-15 months old also had the potential to extend site occupation from May to August, indicating both spring and tentatively summer occupation. This was the only Late Devensian site to indicate any evidence for summer seasonality, although a single dentition age must be treated with caution. Furthermore, given the strong signal for spring occupation already observed from Ossom's Cave, the 12-15 month old probably represented an animal closer to 12 months in age, with individuals instead moving further north for summer grazing grounds.

As such, the Manifold Valley, where Ossom's Cave is located, potentially represented a similar route through the Peak District between summer and winter pastures as Winnats Pass did during the Early Devensian. Large aggregations of *R. tarandus* prefer to travel through areas of lower topographic resistance but precise routes can change very suddenly, explaining this variability over time (Burch, 1972). Furthermore, the annual movement of potentially large numbers of animals would have provided ample opportunities for both humans and C. lupus, which have been attributed to the accumulation of this site (Scott, 1986; O'Connor and Jacobi, 2015), to hunt R. tarandus. By applying an average daily movement rate from modern *R. tarandus* of 25-30 km/day (Kelsall, 1968; Skoog, 1968), it would take 8-10 days for herds to travel the 260 km distance between the suggested winter occupation at Chelm's Combe and the spring occupation at Ossom's Cave during the Younger Dryas. This is consistent with the migrations of Late Weichselian R. tarandus in France suggested by Gordon (1988), which will be discussed further in relation to the French sites included in this study. However, without the study of additional sites at higher latitudes, it is unknown whether this movement was also undertaken by Lateglacial Interstadial R. tarandus. This demonstrates the limitations associated with the spatial distribution of fossil sites, a problem that extends throughout the last cold stage.

As was apparent during the Middle Devensian/Weichselian, the potential also existed for R. tarandus to move across the landbridge between Britain and continental Europe during the Late Devensian/Weichselian (Cutler et al., 2003; Current and Jacobi, 2011), although the Late Devensian *R. tarandus* appeared to moved only within Britain (Figure 6.4). The Lateglacial Interstadial R. tarandus in western Europe also occupied a migrational niche (Figure 6.4). At 50°N, the seasonality of *R. tarandus* from Trou des Nutons represented occupation of southern Belgium during the late winter and spring (Figure 6.4). The site was particularly notable for the predominance of females at the site. In addition to the 0:3 ratio of males to females identified from metacarpals >2.5 years old, the strong presence of females was further supported by both the unshed and shed antler remains of adult females, subadult females and calves. Although dentition ages from the site could not provide any insight into seasonality due to the preservation of only two individuals 3-5 years in age, the respective antler cycles suggested occupation at Trou des Nutons between February to June. This therefore suggests that either the upland area surrounding Trou des Nutons was representative of a R. tarandus calving site or the River Lesse Valley provided an important migration route towards calving grounds. Although no neonatal individuals were recognised from the site, which might otherwise be indicative of a calving site, the absence of males from Trou des Nutons was particularly significant.

The spring calving forms a highly sexually-segregated aggregation composed of females and calves (Aaris-Sørensen et al., 2007), as yearlings develop antagonistic relations with their mothers by the time pregnant females begin the movement towards calving sites (Hirotoni, 1990). However, compared to their male counterparts, subadult females tend to rely on their mothers for longer (Kojola, 1997), something that could account for the abundance of these individuals at Trou des Nutons. Another characteristic of calving sites are the shed antlers of females and calves. As has already been recognised from both the British and Belgian Middle Devensian/Weichselian sites studied, the large number of shed antler remains, belonging particularly to subadult females, could have been transported to the cave by a number of means. More than 40 shed antlers from subadult females were identified at Trou des Nutons, a site associated with evidence for Magdalenian technologies and human hunting (Charles, 1996). Trou des Nutons could therefore represent another example of an antler store and a continuation of this behaviour from the Middle Devensian/Weichselian. Although Gordon (1988) suggested that caching was unlikely to be a trait amongst Late Weichselian humans that followed the movements of *R. tarandus*, the seasonality of *R. tarandus* site occupations at Trou des Nutons would more likely support the seasonal exploitation of this resource.

In contrast to the northwards trajectory of spring and summer migrations suggested for the British Younger Dryas R. tarandus, the winter to spring occupation of Trou des Nutons could therefore provide a more southern spring and summer range for the Lateglacial Interstadial R. tarandus occupying southern Britain during the autumn and winter. Although previous Lateglacial Interstadial studies of Belgian R. tarandus from the site of Remouchamps have suggested that herds were in fact moving northwards from winter pastures in the Paris Basin to calving grounds in Belgium, more southerly spring and summer ranges in the Pyrenees have been suggested for sites in the Dordogne in southwest France at 44°N (Gordon, 1988). Two sites from this region were also studied during this research. Both Abri de Laugerie Haute and Abri de la Madeleine are rock shelters located on the valley side of the River Vézère in the Dordogne. At Laugerie Haute, the exaggerated living herd structure of 1:3 observed in the distal radii and 1:4 in the calcanea, and therefore adults >4 years old, suggested that females dominated the area surrounding the site. Although this could correspond with either the autumn rut or spring calving, when females outnumber males in large aggregations, the presence of the unshed antlers of adult males would correspond to the period between September to November and the autumn rut (Figure 6.4).

At la Madeleine, dentition aged to 27 and 29 months old, together with the antler cycles for the unshed antlers of adult males, represent site occupation from August and October. In addition to a late summer to autumn season of occupation, the unshed antlers of a calf, as well as subadults dentition aged to 21-24 months old, would further support the animal's presence between February to May and the late winter to spring. As such, this could imply site occupation throughout the whole year, or at least during the two phases of migration during autumn and spring. However, it is more likely that the assemblage represents an extension of the seasonality from the autumn migration into winter (Figure 6.4). The living herd structure ratio of 1:2 recognised from adult individuals >4 years old (calcanea) was representative of a large aggregation more similar to the autumn migration and the rut, than the spring when sexual segregation is more evident. Certainly, if large aggregations of *R. tarandus* were moving along the Vézère river valley as both sites seem to suggest, they would be easily accessible for Magdalenian humans to hunt. Without a wider range of sites, it is also difficult to assess the migrational pathways of these animals towards spring and summer grazing pastures. However, if movements were made as far north as Belgium, it would only take 4 weeks for R. tarandus to cover this distance at an average rate of 25-30 km/day (Kelsall, 1968; Skoog, 1968), something which is not uncommon when compared to the 6 week and 800 km long migrations undertaken by some modern populations (Kelsall, 1968).

Even further north in Europe at 55°N in Denmark, the lower sea level during the Late Weichselian would also have meant that the Lateglacial Interstadial R. tarandus could have moved freely between islands (Aaris-Sørensen, 2009). At the Slotseng kettle hole on the main island of Jutland, only antlers and crania were preserved however, the antler cycles for subadult females and subadult and adult males, all with unshed antlers, would overlap during September and October. Together with the antlerless crania of an adult female, which remain in this state from June to September, this would confirm the use of the Slotseng watering hole during the autumn (Figure 6.4). Shed antlers were also identified at Slotseng, but like the unshed forms, these were not numerous and therefore less likely to be indicative of site occupation by R. tarandus than post-depositional transport by the humans that were evidently present in the area and working antlers (Aaris-Sørensen et al., 2007). Further west off the island of Zealand, R. tarandus from the Køge Bugt bay also represented occupation during the autumn (Figure 6.4). Subadult dentition aged to 27-29 months old, combined with the unshed antlers of adult males and females, supported site occupation from September to November. In subadult and adult males, the antierless crania identified at Køge Bugt could have been present as early as December or as late as August. This would therefore extend occupation at the site either into the late summer or early winter. In the postcrania, despite following the 1:1 living herd structure ratio in the early-fusing elements, for individuals >2.5 years old, both female dominated ratios of 1:2 from the distal tibiae and male dominated ratios of 5:3 generated from the metacarpals were present in the assemblage. This variability in the presence of the sexes most likely represents the inconsistent preservation of individual postcranial elements which occurs naturally at fossil sites and, as such, seasonal occupation could not be directly assigned from the postcrania at Køge Bugt. Nevertheless, if *R. tarandus* herds were traveling through both Køge Bugt and Slotseng during the autumn and perhaps into the early winter, given the connectivity afforded by lower sea levels and exposed landbridges (Aaris-Sørensen, 2009), it would have been possible for herds to have migrated north for spring and summer pastures in either higher latitude sites within Denmark or Sweden.

6.4. Body Mass and Migrational Range

From the Early Devensian, Middle Devensian/Weichselian and Late Devensian/Weichselian sites, comparisons could also be drawn between the differences in body mass and the variability in the migrational ranges of *R. tarandus*. For modern herds undergoing regular migrations over long distances, energy expenditure is proportionally higher for individuals with shorter legs, so animals with longer leg lengths should be selectively advantaged (Klein *et al.*, 1987; Couturier *et al.*, 2010). The

presence of larger males >130 kg at the Early Devensian sites of Banwell Bone Cave, Isleworth and Windy Knoll (see Chapter 4), could reflect longer leg lengths within the *R. tarandus* and therefore greater migrational distances as *R. tarandus* moved throughout Britain (**Figure 6.1**). However, the relationship between body size and migrational range is clearly complex.

During the Late Devensian, *R. tarandus* appear to have undertaken similar migrations to the Early Devensian herds, remaining primarily within Britain despite the presence of the connecting landbridge between Britain and continental Europe enabling more widespread movements. The primary difference between the two periods was the smaller body sizes reconstructed from Late Devensian/Weichselian sites. A similar disparity was observed between the two units studied at Picken's Hole, where body mass decreased from the Early (124 kg) to Middle (114 kg) Devensian. Although the seasonality at this site varied from autumn/winter in the Early Devensian to spring/summer in the Middle Devensian, R. tarandus nevertheless continued to move away from the site for portions of the year. Conversely, both the average body masses (103 kg) and seasonality (late summer/autumn) were consistent between the Middle and Late Devensian *R. tarandus* at Gully Cave. Generally, the body masses from a number of Middle and Late Devensian/Weichselian *R. tarandus* could be compared, varying only at the site level between those that more closely resembled the modern forest or mountain types (see Chapter 4). However, while the Late Devensian/Weichselian R. tarandus do appear to be migrational (Figure 6.4), some Middle Devensian/Weichselian sites represented multiple seasons of occupation (Figure 6.2) that could instead imply either the presence of more sedentary herds or multiple directions of movement.

This suggests that alternative factors such as population density, snow cover and vegetation quality potentially had a greater influence on body mass during the Late Pleistocene than the total range of *R. tarandus* migrations. While the diet of Late Pleistocene *R. tarandus* will be explored further through the application of dental microwear analysis (see Chapter 7), the MNI from each site (**Table 6.1**) could provide an indication of the population density. The sites of Sandford Hill and Salzgitter-Lebenstedt recorded the highest MNI, with 78 and 58 individuals respectively. This would support the presence of higher density herds of *R. tarandus* consistent with the smaller body masses of males (107-110 kg) and females (84-85 kg) reconstructed from the two sites. However, similar body masses were also reconstructed from the site of Laugerie Haute where the MNI was only five. As Laugerie Haute is located in an area of the Dordogne where numerous *R. tarandus* have been collected, presumably the density is higher than the smaller MNI would suggest. Therefore, both the regularity of depositional events, as well as the site taphonomy, could influence the reliability of the MNI when it

is used in this way. Nevertheless, the density dependence of *R. tarandus* is still an important influence of body mass, perhaps more so than migrational range.

| Early | | Middle | Late | | | | |
|-----------------------------------|-----|------------------------------|------|---------------------------|--------|--|--|
| Devensian | | Devensian/Weichse | lian | Devensian/Weich | selian | | |
| Site | MNI | Site | MNI | Site | MNI | | |
| Isleworth | 25 | Sandford Hill | 78 | Abri de la Madeleine | 12 | | |
| Banwell Bone Cave | 18 | Salzgitter-Lebenstedt | 58 | Soldier's Hole | 10 | | |
| Windy Knoll | 14 | Kents Cavern | 35 | Chelm's Combe | 7 | | |
| Feltham | 5 | Goyet (Troisième Caverne) | 31 | Køge Bugt | 8 | | |
| Picken's Hole (Unit 5) | 4 | Pin Hole Cave | 23 | Ossom's Cave | 6 | | |
| Tornewton Cave (Reindeer Stratum) | 4 | Trou Magrite | 19 | Slotseng | 5 | | |
| Stump Cross Cavern | 2 | Trou du Sureau | 12 | Abri de Laugerie Haute | 5 | | |
| | | Wookey Hole (Hvaena Den) | 8 | Gully Cave | 3 | | |
| | | Caverne Marie- Jeanne | 7 | Trou des Nutons | 3 | | |
| | | Picken's Hole (Unit 3) | 6 | | | | |
| | | Church Hole Cave | 5 | | | | |
| | | Brixham Cave | 4 | | | | |
| | | Gully Cave | 4 | | | | |
| | | Inchnadamph Reindeer Cave | 4 | | | | |
| | | Robin Hood Cave | 4 | | | | |
| | | Westeregeln | 4 | | | | |
| | | Ellewoutsdijk | 4 | | | | |
| | | Inchnadamph Bone Cave | 3 | | | | |

Table 6.1. Minimum Number of Individuals. Ageing and sexing techniques were used to determine the minimum number of individuals (MNI) for each site studied.

6.5. Summary

- The seasonality of site occupations was used to identify the migrational behaviour and patterns of Late Pleistocene *R. tarandus.*
- From the Early Devensian, *R. tarandus* seasonality represented migrational herds potentially moving along a north-south trajectory throughout Britain, which was isolated from continental Europe at the time. From autumn/winter ranges in the south of Britain, *R. tarandus* appeared to move to spring/summer ranges further north.
- During the Middle Devensian/Weichselian, the landbridge connecting Britain to continental Europe enabled seasonal movements both on a north-south trajectory within Britain, as well as from autumn/winter ranges in the east to spring/summer ranges in the west. However, the reconstruction of multiple seasons of occupation from sites in southwest Britain and Belgium, could also be used to infer the presence of more sedentary individuals.
- With the connecting landbridge still apparent during the Late Devensian/Weichselian, *R. tarandus* continued to move within Britain following a north-south trajectory also recognisable from the European sites studied.
- The variability in body sizes of *R. tarandus* with both similar and differing migrational ranges, suggest that alternative factors such as population density, snow cover and vegetation quality had a greater influence on body mass during the Late Pleistocene than the total range of *R. tarandus* migrations.

The following chapter reconstructs the paleodiet of *Rangifer tarandus* from Early and Middle Devensian sites in Britain, using dental microwear analysis (DMA). The chapter outlines the technique and application of DMA in studies of palaeodiet. In addition, a new training set is presented composed of modern *R. tarandus* specimens from European and North American subspecies, against which comparisons of Late Pleistocene *R. tarandus* can be made. Given the importance of seasonality to *R. tarandus* diets in the present day, where possible, DMA was conducted on fossil specimens with a known season of death to determine whether seasonal grazing, browsing or mixed feeding niches were occupied.

7.1. Introduction to Studying Diet in Rangifer tarandus

Reconstructions of the seasonality of R. tarandus site occupations, and potentially mobility, have recognised both temporal and spatial differences between Early, Middle and Late Devensian fossil sites in Britain (see Chapter 6). However, one of the most important influences on *R. tarandus* migrations is forage. At high latitudes, strong seasonality and the short length of the growing season affect resource availability to such an extent, that migrations occur in response to the reduced forage quality and access during the winter months (Heggberget et al., 2002: Tablado et al., 2014). In winter, lichen tends to dominate most *R. tarandus* diets, the high carbohydrate and low protein content providing a source of energy otherwise unexploited by other northern ungulates (Heggberget et al., 2002; Leader-Williams, 1988). Although not weaned until the autumn (Holand et al., 2012), calves begin to forage only days after birth, developing an important digestive capacity for lichens in preparation for their first winter (Bergerud, 1972). As summer approaches and the snowline recedes, nutrient-rich vascular plants such as shrubs and graminoids increasingly become a more significant part of the R. tarandus diet (Leader-Williams, 1988; Heggberget et al., 2002). While the distance between the summer and winter pastures of migrational R. tarandus may vary between 100-1000 km², even sedentary herds demonstrate some degree of nomadism within their home ranges in order to avoid resource depletion (Tyler and Øritsland, 1989). Therefore, in order to gain insight into the palaeoenvironments that could have influenced the movements of Late Pleistocene populations, the palaeodiet of fossil R. tarandus was reconstructed using DMA.

Several studies have demonstrated the effectiveness of DMA, recognising changes in the diets of modern and fossil *R. tarandus* specimens in regards to resource partitioning (Rivals *et al.*, 2010; Rivals and Lister, 2016), latitudinal gradients (Rivals and Semprebon, 2017), climatic transitions (from glacial to interglacial and stadial to interstadial) (Rivals and Solounias, 2007; Rivals *et al.*, 2020) and seasonality (Rivals and Solounias, 2007). The method operates on the principle that the abrasive (tooth on food) and attritive (tooth-on-tooth) nature of different diets, determine the microscopic patterns of dental wear identifiable on the enamel surfaces of teeth (Green and Croft, 2018). Through the development of modern training sets and comparative databases, the variations in microwear features, which include pits, scratches and gouges, can be used to differentiate between a browsing diet, more than 90% of which consists of leaves, twigs, buds, flowers and fruits, a grazing diet, more than 90% of which is grasses, and a mixed-feeding diet comprised of leaves, twigs, buds and grasses (Green and Croft, 2018). The turnover of these features is rapid, therefore dental microwear analysis provides a record of the diet of an individual in the days leading up to death (Grine, 1986).

The high temporal resolution of this technique means that DMA can also be used to study the seasonality of diets. Merceron *et al.* (2004) were the first to demonstrate visible shifts in the dental microwear of modern roe deer (*Capreolus capreolus*, Linnaeus, 1758) with a known season of death, as a spring/summer diet dominated by soft green leaves was replaced by dead leaves, acorns and ivy in the autumn/winter. Following this, Rivals and Solounias (2007) recognised cyclical variations in the dental microwear signal of modern *R. t. groenlandicus* from the Canadian Kaminuriak population. Because DMA was conducted on individuals for which both the month of death (June, September, November or April), and more unusually, the stomach contents and diet, were recorded (Miller, 1974b; 1976), it could be confidently assumed that observable increases in the average number of pits reflected the annual cycling of *R. t. groenlandicus* from willow and sedges (June and September) to lichens and fungi (November and April) (Rivals and Solounias, 2007).

The potential therefore exists to implement this approach in Late Pleistocene *R. tarandus*, where season of death could be determined from the dental eruption and wear age of a specimen. Previously, the only fossil studies to have combined the seasonality derived from tooth ages with dental microwear have focused on constraining the duration of human occupation and hunting episodes from red deer (*Cervus elaphus*, Linnaeus, 1758) and horse (*Equus ferus*, Boddaert, 1785) (Sánchez-Hernández *et al.*, 2014; 2016). However, the monthly precision afforded by the ageing of dental eruption and wear (see Chapter 3), would enable seasonal patterns in *R. tarandus* diet to be inferred from the DMA of Late Pleistocene, as well as modern, specimens. Given the importance of

seasonality in *R. tarandus* diets in the present day, this new approach is a particularly significant advance which will provide greater insights into not only diet, but also how this relates to the palaeoenvironment, body condition and migrations of *R. tarandus*.

R. tarandus from three fossil sites were examined using the dental microwear technique to reconstruct palaeodiet (**Table 7.1**). These were the Early Devensian site of Windy Knoll and the two Middle Devensian sites of Kents Cavern and Pin Hole Cave. From the ageing and sexing of individual *R. tarandus* specimens, each site showed multiple signals for the season of occupation (see Chapter 6). Evidence for the presence of *R. tarandus* represented summer and autumn at Windy Knoll, autumn and spring at Pin Hole Cave and spring, summer, autumn and winter at Kents Cavern. Unfortunately, not all of the fossil samples were young enough to be aged with monthly precision (**Table 7.1**); nevertheless, where variability between diets was observed, it was hypothesised that this could provide insight into the seasonal availability of particular types of forage at the respective sites.

Table 7.1. Summary of Late Pleistocene Dental Microwear Samples. Specimens from
the Early Devensian (Windy Knoll) and Middle Devensian (Kents Cavern, Pin Hole
Cave) were selected for dental microwear analysis. For juveniles, month of death could
be inferred from the tooth eruption and wear age.

| Site | Sample | Tooth eruption/ wear Age | Month of Death |
|---------------|---------------|-----------------------------|----------------|
| Kents Cavern | NHMUK PV | 29 months | October |
| | OR16741 | | |
| | NHMUK PV | 3-5 years | - |
| | M706 | | |
| | NHMUK PV | 6-9 years | - |
| | M104644 | | |
| Pin Hole Cave | LL.15954.1021 | 22 months | March |
| | LL.15954.998 | 29 months | October |
| Windy Knoll | P.2423 | 27 months | August |
| | P.2425d | 17-22 months | October-March |

In order to determine the diet of fossil *R. tarandus*, it was necessary to compare patterns of dental microwear in the Late Pleistocene specimens with those of modern specimens. However, in addition to seasonal shifts in diet, modern *R. tarandus* display variability between populations both in terms of the availability of plant species and the capability of individuals to digest them (Heggberget *et al.*, 2002). Due to the scarcity of museum specimens for which the specific diet of the individual is known (Green and Croft, 2018), for example from the measurement of rumen contents (Miller, 1974b; 1976), a modern training set was developed based on *R. tarandus* specimens where collection location, and ideally season of death, was known (**Table 7.2**). This included individuals which

inhabit forest, mountain and high Arctic island environments from the North American subspecies *R. t. caribou*, *R. t. groenlandicus* and *R. t. pearyi*, as well as the European subspecies *R. t. tarandus* and *R. t. platyrhynchus*. Given the geographical and genetic proximity of *R. t. tarandus* to western European fossil sites (Flagstad and Røed, 2003), it was essential to include individuals from this subspecies instead of relying solely on comparisons with North American specimens, as has been the standard practice in past studies of fossil *R. tarandus* (Rivals and Solounias, 2007; Rivals and Semprebon, 2017; Rivals *et al.*, 2020). Published literature was used to establish the seasonality of diets in the modern populations, from which the palaeodiet of *R. tarandus* was subsequently inferred.

Table 7.2. Summary of Modern Dental Microwear Samples. Specimens from bothEuropean and North American *R. tarandus* subspecies were selected for dentalmicrowear analysis only when collection location was known. The presence of acollection date also enabled month of death to included. * Indicates samples for whichmonth of death was based on the male antler cycle for unshed antlers.

| Subspecies | Country | Locality | Sample | Month of |
|-------------------|----------|--------------|----------|------------|
| - | - | - | - | Death |
| R.t.caribou | Canada | Newfoundland | 122389 | September- |
| | | | | November* |
| | | | 14240 | January |
| R.t.groenlandicus | Canada | Nunavut | 22937 | November |
| | | Territory | 19501 | January |
| R.t.tarandus | Norway | Buskerud | B1861 | December |
| | | Finnmark | B.M.1569 | - |
| | | Hordaland | B.2383 | November |
| | | | B.2588 | August |
| | Sweden | Härjedalen | AJN:4505 | - |
| | | Lappland | AJN:4084 | - |
| | | Norrbotten | A614677 | December |
| R.t.pearyi | Canada | Nunavut | 29980 | March |
| | | Territory | 27946 | October |
| R.t.platyrhynchus | Svalbard | Spitsbergen | B.696 | August |
| | | | A633003 | November |

7.2. Methods for Reconstructing Diet

Although reconstructions of fossil palaeodiets can be achieved through the analysis of δ^{13} C and δ^{15} N from either the bone or tooth collagen of *R. tarandus* (Drucker *et al.*, 2001; Drucker *et al.*, 2011; Rivals *et al.*, 2020), the application of DMA is both more cost effective and an entirely non-invasive technique. The technique of DMA was first developed in the 1970s on primates, with two-dimensional images taken by scanning electron microscopes (Rensberger, 1978; Walker *et al.*, 1978; Grine, 1977). Following many years of methodological inconsistencies between researchers (Calandra and

Merceron, 2016), Solounias and Semprebon (2002) demonstrated the effectiveness of using stereoscopic light microscopes at low magnification to count microwear features on the casts of teeth, standardising the method, as well as expanding the scope of application to include a range of species (Solounias and Semprebon, 2002). However, the subjective nature of this method has led researchers in recent years to develop software for the three-dimensional image analysis of surface texture (Ungar *et al.*, 2003, Scott *et al.*, 2005), with the aim of improving the accuracy and repeatability of the method (Scott *et al.*, 2005; DeSantis *et al.*, 2013). Dental microwear texture analysis (DMTA) quantifies the texture (roughness) across the whole of a tooth's surface (Calandra and Merceron, 2016). Not only is the process automated, but the resolution of three-dimensional images enables a greater sensitivity to finer scale textures on the enamel surface of teeth than traditional DMA (Mihlbachler *et al.*, 2019).

DMTA has been successfully applied to modern *R. tarandus* (Bignon-Lau *et al.*, 2017); however, despite advances towards these automatic quantifications (Calandra and Merceron, 2016), analysis of diet still primarily follows user identification techniques such as DMA (Rivals and Solounias, 2007; Rivals *et al.*, 2010; Rivals and Lister, 2016; Rivals and Semprebon, 2017; Rivals *et al.*, 2020). Where the results of the two approaches have been directly compared (Mihlbachler *et al.*, 2012; 2019), individual variability in the precision and repeatability of methods have not significantly restricted the ability of either technique to discriminate between the different diets of individuals. Nevertheless, in order to avoid any potential observer errors in the application of traditional DMA in this research, a modern training set of *R. tarandus* was collected for the purpose of this study, while all final counts of microwear features were made by one well trained and experienced observer (Dr Spyridoula Pappa of the Natural History Museum, London).

In many studies of dental microwear, reconstructions of *R. tarandus* diet have also considered the mesowear of teeth (Rivals *et al.*, 2010; Rivals and Lister, 2016; Rivals and Semprebon, 2017; Rivals *et al.*, 2020). Mesowear refers to the sharpness or relief of the apices of a tooth's cusps, which vary with the attritive or abrasive nature of a browsing (sharp cusps) or grazing (rounded and blunt cusps) diet (Fortelius and Solounias, 2000; Mihlbachler *et al.*, 2011). However, compared to the 'last supper' signal of dental microwear (Grine, 1986), mesowear only represents the diet of individuals from the months or even years leading up to death (Sanchez-Hernandez *et al.*, 2016; Rivals and Semprebon, 2017; Green and Croft, 2018). Therefore, in this initial study focusing on the seasonality of diets in *R. tarandus*, only the higher temporal resolution technique of dental microwear analysis was applied, although future work on these samples should endeavour to combine the two methods.

7.2.1. Dental Microwear Analysis

DMA requires the moulding of tooth samples from both modern and fossil R. tarandus specimens, in order to make the casts from which microwear features are counted. Although Xafis et al. (2017) has recently demonstrated the strength of both premolars and molars in distinguishing between the dental microwear patterns generated by different diets, analysis is typically completed on the mandibular second molar (M₂) (Rivals and Solounias, 2007; Rivals and Lister, 2016; Rivals and Semprebon, 2017; Rivals et al., 2020). Only teeth already in wear and with undamaged occlusal surfaces were selected for analysis. Moulds were then taken following methodology developed from Solounias and Semprebon (2002) by Pappa (2016), in conjunction with the Palaeontology Conservation Unit of the Natural History Museum, London. The tooth's occlusal surface was cleaned first with acetone and then 96% ethanol. A mould of the sample area was then taken using evenly spread polyvinylsiloxane dental impression material applied with a dispersing gun (Figure 7.1) and stabilized with dental putty. This combined technique ensures sampling is both non-invasive and leaves no residue on the tooth once dental putty sets and the mould can be carefully removed. Casts of the tooth specimens were then made using an epoxy resin. Microwear features were counted under a stereoscopic light microscope with magnification 35x from two separate square areas 0.16 mm² on either the buccal or lingual protoconid enamel cusp (Figure 7.1) (Rivals and Solounias, 2007; Rivals and Lister, 2016; Rivals and Semprebon, 2017; Rivals et al., 2020).

Definitions of the dental microwear features by Solounias and Semprebon (2002) and Semprebon *et al.* (2004) counted in this research are summarised below.

- Pits, which are circular, are similar in both width and depth and can be divided into small pits and large pits. Large pits are twice the size of small pits and are recognisable by less regular outlines, as well as reduced refractivity.
- Gouges, compared to large pits, are 2-3 times larger and deeper, have irregular outlines and low refractivity.
- Scratches, which are elongated in shape with parallel sides, can be divided into the narrow and shallow fine scratches and the wide and deep coarse scratches. These are further differentiated by the higher refractivity of coarse scratches.
- Cross scratches are not parallel to the majority of scratches.
- The scratch width score (SWS) is a three-point scale used to further describe the texture of scratches present on a sample as predominantly fine scratches (0), a mix of fine and coarse scratches (1), or predominantly coarse scratches (2).



Figure 7.1. Dental Microwear Analysis Sampling Location. Moulds were taken using polyvinylsiloxane dental impression material from the occlusal surface of the protoconid of the lower M_2 of *R. tarandus* specimens. The tooth schematic shows the left tooth.

In order to determine the grazing, browsing or mixed diet of *R. tarandus* specimens, the counts of microwear features were compared to databases of extant species (Solounias and Semprebon, 2002; Rivals *et al.*, 2010). In grazing herbivores, increased levels of abrasion (food on tooth) are reflected in high numbers of scratches and low numbers of pits (Rivals *et al.*, 2007; Rivals and Semprebon, 2011), while in browsing herbivores, lower levels of abrasion and therefore higher attritive wear (tooth on tooth), are reflected in low numbers of scratches and varying numbers of pits (Rivals *et al.*, 2007; Rivals and varying numbers of pits (Rivals *et al.*, 2007; Rivals and Semprebon, 2011). The microwear profile of a mixed diet falls between that of the browsing and grazing signals. Nevertheless, it is possible to identify a mixed feeding signal from the percentage of individuals with a low scratch count (0-17 scratches) (Semprebon and Rivals, 2007). In browsers, 72.73-100% of individuals have a low scratch count, and in mixed feeders, 20.93-70% of individuals have a low scratch count (Semprebon and Rivals, 2007).

For *R. tarandus* in particular, lichen accounts for a significant component of the diet of many modern *R. tarandus* populations (Bergerud, 1972; Gaare and Skogland, 1975; Boertje, 1984; Skogland, 1984). Rivals and Semprebon (2017) have demonstrated from

modern Canadian *R. tarandus*, that the lichen microwear signal is characterised by high numbers of pits and gouges. Although it is not yet possible to differentiate between the different types of lichen (terrestrial and arboreal) consumed seasonally by *R. tarandus* (Rivals and Semprebon, 2017), the potential of this technique in widening our understanding of Late Pleistocene diets is significant.

7.3. Results of Dental Microwear Analysis

7.3.1. Modern and Late Pleistocene Dental Microwear Features

Results of DMA for the 15 modern teeth studied as part of the investigation into *R. tarandus* diet, are summarised in **Table 7.3**. Raw feature counts for each of the specimens are available as **Supplementary Data** (**SD 11**).

Table 7.3. Summary of Modern *Rangifer tarandus* Microwear Data. N = Number of individuals, NP = Average number of pits, NS = Average number of scratches, %LP = Percentage of individuals with large pits, %XS = Percentage of individuals with cross scratches, %G = Percentage of individuals with Gouges, %0-17 = Percentage of individuals with low numbers of scratches (0-17 scratches). (f) Indicates *Rangifer t. tarandus* occupying forest rather than mountain habitats.

| Subspecies | Locality | Ν | NP | NS | %LP | %XS | SWS | %G | % |
|---------------|----------------|---|-------|-------|-----|-----|-----|-----|------|
| | | | | | | | | | 0-17 |
| R.t.caribou | Newfoundland | 2 | 39.00 | 12.25 | 100 | 50 | 0 | 100 | 100 |
| R.t. | Nunavut | 2 | 33.75 | 15.50 | 100 | 100 | 0 | 100 | 100 |
| groenlandicus | Territory | | | | | | | | |
| R.t.tarandus | Buskerud | 1 | 39.50 | 13.50 | 100 | 100 | 0 | 100 | 100 |
| | Finnmark (f) | 1 | 29.00 | 14.00 | 100 | 100 | 0 | 100 | 100 |
| | Härjedalen | 1 | 38.00 | 15.50 | 100 | 100 | 0 | 100 | 100 |
| | Hordaland | 2 | 37.75 | 11.50 | 100 | 100 | 0 | 100 | 100 |
| | Lappland | 1 | 38.50 | 12.00 | 100 | 0 | 0 | 100 | 100 |
| | Norrbotten (f) | 1 | 26.50 | 11.50 | 100 | 100 | 0 | 0 | 100 |
| R.t.pearyi | Nunavut | 2 | 36.25 | 17.75 | 100 | 100 | 0 | 50 | 50 |
| | Territory | | | | | | | | |
| R.t. | Svalbard | 2 | 33.50 | 11.75 | 100 | 100 | 0 | 100 | 100 |
| platyrhynchus | | | | | | | | | |

From the modern subspecies (**Table 7.3**), a SWS of 0 for all individuals indicated that *R. tarandus* teeth were characterised by predominantly fine scratches. Large pits were also evident from 100% of the individuals studied from each subspecies. Although both cross scratches and gouges were present in 100% of the *R. t. groenlandicus* from Nunavut Territory, R. *t. tarandus* from Buskerud, Finnmark, Härjedalen and Hordaland, as well as the *R. t. platyrhynchus* from Svalbard, variability was observed in both of these microwear features. The percentage of individuals with cross scratches was only 50% in the *R. t. caribou* from Newfoundland, while no cross scratches were recorded from the Lappland *R. t. tarandus*. Furthermore, none of the *R. t. tarandus* from Norrbotten showed

gouges, while only 50% of the Nunavut Territory *R. t. pearyi* individuals recorded this feature. There was additional variability within the microwear of *R. t. pearyi* from Nunavut Territory, which was the only subspecies where the percentage of individuals with between 0-17 scratches was 50% and not 100%. The low number of scratches was confirmed in the raw scratches per individual (**Figure 7.2**). Scratch count was equal to or below 17 at all localities with the exception of the Nunavut Territory *R. t. pearyi*, although the largest scratch count from this subspecies was only 18.5, not far outside the 0-17 range. For the remaining localities, 72.73-100% of individuals demonstrated a scratch count of 0-17.



Figure 7.2. Raw Scratches per Individual. Raw scratch counts are presented for both modern and Late Pleistocene *R. tarandus* tooth specimens. The subspecies *R. t. tarandus* can be divided into localities in mountain (m) or forest (f) regions. The dashed line at 17 scratches marks the upper boundary for a low number of scratches.

Figure 7.3 shows the average number of scratches versus the average number of pits from the modern *R. tarandus* compared to the modern databases of browsing and grazing species. While *R. t. pearyi* plotted outside either the browsing or grazing ellipses, the overlap of the standard error of the mean for this subspecies with the 95% confidence ellipse for browsers, suggest a browsing to mixed feeding diet. Otherwise, the remaining modern and fossil localities all plotted within the 95% confidence ellipses for the diets of extant leaf-browsing species. As such, there were only small variations in the number of pits and scratches between the majority of *R. tarandus* specimens from both the North American and European subspecies. Individuals with the highest average number of pits were recorded from *R. t. caribou* and the mountain *R. t. tarandus*. As such, there was a notable difference in the average number of pits between the *R. t. tarandus* occupying mountain and forest ranges, as forest *R. t. tarandus* recorded the lowest average number

of pits. Both *R. t. platyrhynchus* and *R. t. groenlandicus* plotted between the two *R. t. tarandus* types in terms of the average number of pits however, relatively more scratches were counted from *R. t. groenlandicus*.



Average Number of Scratches

Figure 7.3. Bivariate Plots for Modern and Late Pleistocene *Rangifer tarandus*. The average number of scratches versus the average number of pits from (a) modern *R. tarandus* subspecies are compared to (b) the Late Pleistocene fossil sites of Kents Cavern (KC), Pin Hole Cave (PHC) and Windy Knoll (WK). The subspecies *R. t. tarandus* can be divided into localities in mountain (m) or forest (f) regions. The 95% confidence ellipses correspond to feature counts from databases of extant browsers and grazers (Solounias and Semprebon, 2002; Rivals *et al.*, 2010). The standard error of the mean is also presented.

Results of DMA for the seven Late Pleistocene teeth studied as part of the investigation into *R. tarandus* diet, are summarised in **Table 7.4**. Raw feature counts for each of the specimens are available as **Supplementary Data** (**SD 11**). From the fossil sites (**Table**
7.4), R. tarandus teeth were also characterised by predominantly fine scratches as all individuals recorded a SWS of 0. Large pits and gouges were also present in 100% of the individuals studied from the three sites. The percentage of individuals with between 0-17 scratches was 100% from Kents Cavern, Pin Hole Cave and Windy Knoll (Table 7.4) and was confirmed in the low number of raw scratches per individual (Figure 7.2). However, there was variability between the sites in the percentage of individuals with cross scratches, which were present in 100% of individuals at Kents Cavern, 50% of individuals at Windy Knoll and 0% of individuals at Pin Hole Cave (**Table 7.4**). Compared to the average number of scratches versus the average number of pits from modern individuals (Figure 7.3), less pits were counted from the Late Pleistocene specimens, although all three fossil sites plotted within the 95% confidence ellipses for the diets of extant leaf-browsing species. Similarities were observed between the average number of pits and scratches measured from modern R. t. tarandus occupying forests and the Kents Cavern and Windy Knoll fossil specimens. Of the three fossil sites studied, the standard error of the mean was largest from Pin Hole Cave and overlapped with the average number of pits and scratches from both forest R. t. tarandus, as well as R. t. platyrhynchus.

| Percentage of individuals with low numbers of scratches (0-17 scratches). | | | | | | | | | |
|---|------------------|---|-------|-------|-----|-----|-----|-----|------------|
| Stage | Locality | Ν | NP | NS | %LP | %XS | SWS | %G | %0- |
| | | | | | | | | | 17 |
| Early | Windy Knoll | 2 | 26.25 | 11.00 | 100 | 50 | 0 | 100 | 100 |
| Middle | Kents Cavern | 3 | 27.17 | 14.17 | 100 | 100 | 0 | 100 | 100 |
| | Pin Hole Cave | 2 | 29.50 | 11.00 | 100 | 0 | 0 | 100 | 100 |

Number of individuals, NP = Average number of pits, NS = Average number of scratches, %LP = Percentage of individuals with large pits, %XS = Percentage of individuals with cross scratches, %G = Percentage of individuals with Gouges, %0-17 = Percentage of individuals with low numbers of scratches (0-17 scratches).

Table 7.4. Summary of Late Pleistocene Rangifer tarandus Microwear Data. N =

7.3.2. Seasonal Variability in Pit and Scratch Counts

Figure 7.4 shows the variability in the number of scratches and pits from specimens where season of death was known. From the modern subspecies, a decrease in the number of scratches and increase in the number of pits was observed between the autumn and winter samples from both the Newfoundland *R. t. caribou* and Nunavut Territory *R. t. groenlandicus*. Similarly, there was a decrease in the number of scratches and increase in number of pits recorded in samples from the autumn to the spring from the Nunavut Territory *R. t. pearyi*. However, where specimens were representative of summer and autumn, individuals from different localities and subspecies show different

shifts in pit and scratch counts. For the Svalbard *R. t. platyrhynchus*, there was a small increase in both the number of pits and scratches from summer to autumn, while for the Hordaland mountain *R. t. tarandus*, there was a decrease in the number of pits but little or no change in the number of scratches. One of the most notable differences in the seasonal microwear signal from Newfoundland *R. t. caribou*, when compared to other modern subspecies, was the relatively large difference in the number of pits counted from each season. The only other specimens to demonstrate this level of seasonal variability were from the fossil sites of Pin Hole Cave and Kents Cavern.



Number of Scratches

Figure 7.4. Seasonal Variability in the Number of Scratches versus the Number Pits from Modern and Late Pleistocene *Rangifer tarandus*. Month of death and therefore season was determined either from the known age at death of modern specimens (B-Buskerud, H-Hordaland, NL-Newfoundland NU-Nunavut Territory, S-Svalbard), or inferred from the eruption and wear age of fossil specimens (KC-Kents Cavern, PHC-Pin Hole Cave, WK-Windy Knoll). The subspecies *R. t. tarandus* can be divided into localities in mountain (m) or forest (f) regions. The legend gives an indication of the colour used to distinguish each season and the shape representing each subspecies. Lines are used to link localities where multiple seasons are represented.

From the fossil *R. tarandus*, only the specimens from Pin Hole Cave represented dental microwear from two distinct seasons, for which there was a decrease in the number of scratches and increase in number of pits observed from the autumn to the spring microwear signal. At both Kents Cavern and Windy Knoll, season of death could only be inferred from one specimen each. Although at Kents Cavern there was a large decrease in the number of scratches and increase in the number of pits from the autumnal specimen to the specimens for which season was unknown, at Windy Knoll, the decrease in the number of scratches from the summer specimen to the specimen for which season of death was unknown was minimal.

In this preliminary study of palaeodiet, small samples sizes meant that it was not possible to test whether there was a statistically significant difference in the number of scratches or pits between the seasonal diets of either the modern or fossil specimens. However, the potential that this technique has demonstrated for identifying the seasonality of *R*. *tarandus* palaeodiet, strongly justifies the need for future research in order to improve the robustness of the interpretations discussed in the following sections.

7.4. Diet in Modern and Late Pleistocene Rangifer tarandus

7.4.1. Variability in the Diets of Modern *Rangifer tarandus* Subspecies

The reconstruction of dental microwear from modern R. tarandus was characteristic of the dietary signal expressed by both extant leaf-dominated browsers and browsedominated mixed-feeders (Figure 7.3). The high average number of pits, combined with the presence of large pits, gouges and a low number of mostly fine scratches, suggest a highly attritive diet indicative of open country animals feeding mostly on low lying plants and the leaves, twigs, buds and flowers of dicotyledons (Table 7.3, Figure 7.3) (Rivals and Semprebon, 2011). Previous studies of dental microwear in modern R. t. caribou, R. t. groenlandicus and R. t. pearyi have demonstrated the occupation of similar dietary niches by extant *R. tarandus* populations, albeit over a much wider dietary range (Figure 7.5). Although this could reflect genuine differences in the diets of individuals from separate populations, it also highlights the importance of compiling large and robust databases of species-specific comparative material, in the analysis of patterns of dental microwear. For *R. tarandus* in particular, the high number of pits and gouges measured in this study (**Table 7.3**) was also consistent with the microwear signal of a diet high in the consumption of lichen (Rivals and Semprebon, 2017), as the inclusion of angular and abrasive dust and grit particles, especially in terrestrial lichen, abrade the tooth surface (Rivals et al., 2010). Nevertheless, for R. tarandus, which are greatly influenced by the strong seasonality of Arctic environments, it was also possible to observe seasonal patterns in the dental microwear signal as the number of pits increased from the summer/autumn to the winter/spring (Figure 7.4). This was similar to the yearly changes in pits recognised by Rivals and Solounias (2007) in the Canadian Kaminuriak R. t. groenlandicus population, which was attributed to the fluctuation between a diet of mostly willow and sedges in the summer to lichens and fungi in the winter (Miller, 1974b; Rivals and Solounias, 2007). The variability in the diets and microwear signal of the subspecies included in this study have been summarised in Table 7.5.



Figure 7.5. Comparison of Modern *Rangifer tarandus* Training Sets. The average number of scratches versus the average number of pits are compared for training sets of modern *R. tarandus* dental microwear subspecies developed by this research (green) and by Rivals and Solounias, 2007 (grey) and Rivals and Semprebon, 2017 (grey). The legend gives an indication of the shape representing each subspecies.

The R. t. pearyi from Nunavut Territory in Canada represented the highest average number of scratches recorded from this study, placing the specimens in a browsedominated mixed-feeding niche (Figure 7.2, Figure 7.3). Most populations of R. t. pearyi live on islands in the Canadian Arctic Archipelago (Petersen et al., 2010) where more abrasive plants such as willow, sedges and grasses form an important component of the diet (Parker and Ross 1976, Larter and Nagy 2004). This is due to the reduced availability of the more attritive lichen on Arctic Islands (Larter and Nagy 1997, Miller 1998), which as the preferred forage of R. tarandus are often overgrazed in these confined environments (Reimers, 1982; Hansen et al., 2010; Schaefer et al., 2016). This reduced intake of lichen would also correspond to the lower percentage of individuals with gouges from the R. t. pearyi studied (Table 7.3), a key component of the dental microwear lichen signal (Rivals and Semprebon, 2017). Although graminoids, and particularly sedges, are a dietary constant throughout the year, the only period during which sedges represented less than 20% of the diet in faecal samples of the Banks Island R. t. pearyi of Nunavut Territory, was April to July (Larter and Nagy, 1997). This decrease in the consumption of sedges coincides with the increase in the number of pits and decrease in the number of scratches observed from the autumn to the spring microwear signal in this study (Figure 7.4). The spring diet of Nunavut Territory R. t. pearyi is also composed of legumes, Saxifrageceae (rockfoils) and Rosaceae (Dryas octopetala), while the inclusion of

deciduous shrubs (willow) and grasses during the autumn would correspond to the lower number of pits observed (Larter and Nagy, 1997).

Table 7.5. Summary of the Diets and Dental Microwear Signals of Modern Rangifer tarandus. Patterns of dental microwear describe relative changes in the average number of pits and scratches observed in this study. Dental microwear also varied seasonally with an increase in the number of pits from summer/autumn to winter/spring. Diet in modern *R. tarandus* subspecies is based on studies of *R. t. caribou* (Bergerud, 1972; Schaefer *et al.*, 2016), *R. t. groenlandicus* (Rickbeil *et al.*, 2017), *R. t. pearyi* (Larter and Nagy, 1997), *R. t. platyrhynchus* (Staaland *et al.*, 1983) and *R. t. tarandus* (Gaare and Skogland, 1975; Skogland, 1984; Mathiesen *et al.*, 2000). The subspecies *R. t. tarandus* can be divided into localities in mountain (m) or forest (f) regions.

| Subspecies | Dental Microwear | Diet Composition | Seasonal Variability |
|-------------------------|--|---|--|
| R.t.caribou | Highest number of pits, average number of scratches | 24-56% lichen graminoids evergreen leaves forbs fungi | Small increase in lichen, decrease in diversity of plant species |
| R.t.groenlandicus | Average number of pits higher number of scratches | lichens | Increase in lichen |
| R.t.pearyi | Average number of pits, highest number of scratches, less gouges | >20% graminoids Saxifrageceae Deciduous shrubs Rosaceae | Decrease in graminoids (sedge) and deciduous shrubs (willow), increase in Saxifrageceae |
| R.t.platyrhynchus | Average number of pits and scratches | 12-42% graminoids woody species mosses forbs fungi lichens | Decrease in graminoids, increase in mosses and woody species |
| <i>R.t.tarandus</i> (m) | High number of pits, average number of scratches | 25-62% lichen 28-49% graminoids deciduous shrubs woody species fungi mosses forbs | Increase in lichen, decrease in graminoids and deciduous shrubs |
| R.t.tarandus (f) | Lowest number of pits, average number of scratches, less gouges | 14-26% lichen graminoids deciduous shrubs fungi forbs | Small increase in lichen, decrease in diversity of plant species |

Specimens from the subspecies *R. t. groenlandicus* were also measured from Nunavut Territory. Despite plotting within the browsing ellipses in terms of the average number of pits and scratches (**Figure 7.3**), the number of scratches counted from *R. t. groenlandicus* was approaching a similar microwear signal to the samples of *R. t. pearyi*

from Nunavut Territory (**Table 7.2**) and therefore a browse-dominated to mixed-feeding diet. This was consistent with the dietary ranges of the two subspecies recognised in previous studies of *R. tarandus* diet (**Figure 7.5**). Unfortunately, no percentage breakdown was available for the diet of Nunavut Territory *R. t. groenlandicus* however, with lichen consumption increasing during the winter despite its availability throughout the year, their diet is nevertheless seasonal (Rickbeil *et al.*, 2017). As such, this would correspond to the increase in the number of pits from autumn to winter observed in the dental microwear signal (**Figure 7.4**).

The remaining R. tarandus subspecies represented a leaf-dominated browsing niche (Figure 7.3). Within this niche, there was a clear separation between the lowest average number of pits counted from the R. t. tarandus occupying forest regions in Norrbotten, northern Sweden, and Finnmark, northern Norway, and the highest average number of pits counted from the Canadian Newfoundland R. t. caribou and the R. t. tarandus occupying mountain regions from Buskerud and Hordaland in Norway and Lappland and Härjedalen in Sweden (**Figure 7.3**). Belonging to semi-domesticated herds, populations of forest R. t. tarandus are relatively sedentary compared to mountain herds from the same subspecies, moving exclusively within the open coniferous boreal forests (Bårdsen et al., 2017). Mat-forming lichen growing on the forest floor is therefore an important resource throughout the year, but particularly during the winter (Gaare, 1997; Mathiesen et al., 2000; Sakkinen et al., 2001; Inga, 2007; Sandström et al., 2016). In Finnmark, lichen measured from the rumen of *R. t. tarandus* rose from 14% in the autumn to 26% in the winter (Mathiesen et al., 2000). Although it is reported that up to 80% of the winter diet of *R. tarandus* could be composed of lichens (Gaare, 1997; Heggberget et al., 2002), lichen consumption is typically lower than this at 56-62% in the mountain R. t. tarandus from Hardangervidda (representative of Buskerud and Hordaland) in Norway (Gaare and Skogland, 1975; Skogland, 1984) and between 50-56% in Newfoundland R. t. caribou (Bergerud, 1972; Schaefer et al., 2016). Nevertheless, this is still double the winter lichen levels consumed in Finnmark. Instead, the Finnmark winter diet is much more consistent with the values of lichen consumption observed from the summer diets of both mountain R. t. tarandus from Hardangervidda, where lichen intake was 25% (Gaare and Skogland, 1975), and the Newfoundland R. t. caribou, where lichen intake was 24% (Bergerud, 1972). The lower proportion of lichen consumed by the Finnmark R. t. tarandus could therefore explain the lower average number of pits observed in the dental microwear of forest R. t. tarandus, compared to either the mountain R. t. tarandus or Newfoundland *R. t. caribou* (Figures 7.3).

As the forest *R. t. tarandus* from Norrbotten represented the winter diet, the microwear signal characterised by a relatively low number of pits and no gouges (**Table 7.3, Figure**

7.3) could therefore be similar to the low lichen intake of winter diets from the province of Finnmark. One of the most important influences on the quality of winter grazing is snow cover (Inga, 2007). Although open coniferous forests should provide the ground with some shelter, the deeper winter snow cover of boreal environments (50-80 cm) could result in lower proportions of terrestrial lichen being consumed (Miller, 1976; Nieminen and Helle, 1980; Inga, 2007), as R. tarandus must dig through the snow to establish feeding craters (Heggberget et al., 2002). In Newfoundland R. t. caribou, arboreal lichen becomes increasingly important as snow depth increases (Bergerud, 1972). This is also an important resource for mountain R. t. tarandus (Gaare, 1997), however, in Finnmark, R. t. tarandus appear to survive winter average snow depths of 51.50 cm by diversifying the number of plant genera ingested to 37 species, rather than rely on different types of lichen (Mathiesen et al., 2000; Kohler et al., 2006). The fact that both the forest R. t. tarandus from Europe and woodland R. t. caribou from North America occupy similar open coniferous stands (Schaefer et al., 2016; Bårdsen et al., 2017) and yet their pit counts differ, implies that lichen quantity is more important for the dental microwear signal than whether the terrestrial or arboreal form is being ingested. This differs from the suggestion by Rivals and Semprebon (2017) that variability in the microwear signal of *R. tarandus* could be due to the consumption of the different forms of lichen. Nevertheless, the identification of terrestrial versus arboreal lichen from either the rumen or faeces, may limit our ability to constrain this variable in studies of microwear.

Although the forest R. t. tarandus from Norrbotten only represented a winter signal for the subspecies, seasonal patterns in the dental microwear were evident from both the *R. t. caribou* and mountain *R. t. tarandus* (Figure 7.4). Despite the seasonal fluctuation in the lichen consumed by the Newfoundland R. t. caribou, from 24% in summer diets to 56% in winter diets (Bergerud, 1972), the relatively large increase in the number of pits from the autumn to winter in microwear signal (Figure 7.4) corresponds with only a small increase in dietary lichen, from 40% in the autumn to 56% in the winter (Bergerud, 1972). Instead, the primary difference between the two season is in the variety of plants consumed. During the autumn, the rumen contents of Newfoundland R. t. caribou included 40% lichens, 10% graminoids, 12% forbs, 12% fungi, 12% evergreen leaves as well as deciduous shrubs (willow) and mosses, while in the winter, diet is dominated by 56% lichens and 23% evergreen leaves (Bergerud, 1972). As the seasonal movements of Newfoundland R. t. caribou are comparatively small (Mahoney and Schaefer, 2002; Mahoney and Virgil, 2003), the reliance on a greater diversity of plant species during the autumn could therefore correspond to the decrease in the number of pits generated on the surface of the tooth.

On the other hand, the migratory R. t. tarandus from mountainous regions represented the only modern subspecies in this study to yield both a summer and winter microwear signal (Figure 7.4). Due to the timing of migrations in the Norwegian Hardangervidda herds, which include the provinces of Buskerud and Hordaland in their ranges, the autumn sample collected during November from Hordaland would already represent the winter diet (Gaare and Skogland, 1975). As such, the increase in the number of pits from summer to winter in Hordaland, was also observed from the proximal province of Buskerud, with only the number of scratches characterising regional differences. This corresponds with a shift in the importance of lichen, which contributes to only 16-25% of the summer diet, but 56-62% of the winter diet in Hardangervidda mountain R. t. tarandus (Gaare and Skogland, 1975; Skogland, 1984). The summer diet of mountain *R. tarandus* is also more diverse, as most plants are digestible, appetite increases to take advantage of the more nutritious new growth forage which is high in protein and therefore important for regaining body condition in preparation for the following winter (Bergerud, 1972; Mathiesen et al., 2000). In Hardangervidda mountain R. t. tarandus, this includes an increase in graminoids (grasses, sedges) from 28% to 45-49%, in addition to the ingestion of more deciduous shrubs (willow), woody species, fungi, mosses and forbs (Gaare and Skogland, 1975; Skogland, 1984).

The summer microwear signal from the Hordaland mountain R. t. tarandus was also similar to the number of pits and scratches counted from Svalbard R. t. platyrhynchus during both the summer and autumn (Figure 7.4). The similarities between the two diets is interesting, as while highly attritive, lichen is a much less important part of the summer diet of R. t. tarandus (16-25%) and it is almost completely removed from the diet of Svalbard R. t. platyrhynchus (Reimers, 1982; Staaland et al., 1983). Although primarily sedentary herds relying on only a few km² (Staaland et al., 1983), while lichen is available, R. t. platyrhynchus will risk higher mortality migration routes across open sea, thin ice or glaciers, in order to selectively forage for this resource (Skogland, 1984; Hansen et al., 2010). However, the lack of predators on Svalbard has enabled populations to reach carrying capacity and overgraze the preferred terrestrial lichens (Reimers, 1982; Staaland et al., 1983; Staaland et al., 1991; Hansen et al., 2010). Unless new lichen pastures become available to migrate to (Hansen et al., 2010), R. t. platyrhynchus have substituted the lichen in their diet for mosses and graminoids (Reimers, 1982; Staaland et al., 1983; Skogland, 1986). The summer diet is composed of 42% graminoids (grasses, sedges), 21% forbs, 23% woody species and mosses, while in winter, 50% of the diet is woody species, 25% is mosses, 12% is graminoids (grasses, sedges) and 2% is lichen (Staaland et al., 1983). Therefore, despite the differences in lichen availability, the summer diets of both R. t. tarandus and R. t. platyrhynchus are both characterised by an increase in the consumption of graminoids to represent more 260

than 40% of forage. As such, the relatively high number of pits and gouges recorded from the seasonal diets of both subspecies (**Table 7.3**, **Figure 7.4**), must be tied not only to the quantity of lichen consumed, but the graminoids as well. However, as the individuals studied from Svalbard represented the summer and autumn, it was not possible to observe whether changes in the winter/spring diet of *R. t. platyrhynchus* were reflected in the dental microwear signal, as was evident from other *R. tarandus* subspecies.

7.4.2. Variability in the Diets of Late Pleistocene Rangifer tarandus

At the Early Devensian site of Windy Knoll, as well as the two Middle Devensian sites of Kents Cavern and Pin Hole Cave, the average number of pits reconstructed from the dental microwear of the fossil teeth was lower than those of most modern R. tarandus populations (Figures 7.3). This was similar to the pattern recognised by Rivals and Solounias (2007), whereby average pit counts from fossil *R. tarandus* were lower than the modern training set composed of R. t. groenlandicus. However, in addition to the North American subspecies, the training set developed for the purpose of this research included for the first-time individuals from the European subspecies R. t. tarandus and R. t. platyrhynchus.(Rivals and Solounias, 2007; Rivals and Semprebon, 2017; Rivals et al., 2020). This approach was particularly significant in the study of British Devensian R. tarandus, as the lower average number of pits observed from the three Late Pleistocene was similar to that of the European forest dwelling R. t. tarandus from Norrbotten and Finnmark (Figures 7.3). This overlap enables a much more detailed interpretation of R. tarandus palaeodiet, particularly as the seasonal increase in the number of pits from the summer/autumn to the winter/spring observed from the dental microwear signal of Late Pleistocene specimens, was consistent with the seasonality expressed in modern R. tarandus (Figure 7.4).

At Pin Hole Cave, *R. tarandus* appeared to occupy a leaf-dominated browsing niche (**Figure 7.3**). Two seasons were directly identified from the tooth eruption and wear ages of individuals included in this analysis. From autumn to spring there was an increase in the number of pits and decrease in the number of scratches counted. In modern *R. tarandus*, this shift in the microwear signal is characteristic of the rising lichen content and the reduced number of graminoids that are consumed in the winter/spring diets. However, the lower overall pit count from Pin Hole Cave suggests greater similarity to the diets of forest *R. t. tarandus*, which move only small distances and occupy boreal open coniferous forests where snow cover is deeper. As such, both lichen and graminoids may represent a much less significant component of the diet, which is instead supplemented by a variety of plant species. As the spring Pin Hole Cave specimen $\frac{261}{261}$

corresponded to March, when snow still covers the ground and lichen consumption remains high, new growth evergreen leaves may also have been more available at the site (Bergerud, 1972). In the autumn, diets of forest *R. t. tarandus* in Norrbotten are also characterised by fungi, either exposed above the snow or frozen below (Inga, 2007), forbs, evergreen leaves and deciduous shrubs (willow). Evidence for the seasonality of site occupation at Pin Hole Cave also converged on the autumn and spring. As such, differences between the seasonal microwear signals could be used to imply that Pin Hole Cave was part of a larger migratory route, with microwear reflecting the diets consumed by *R. tarandus* either in the surrounding area or further along both the autumn and spring migration routes. Nevertheless, due to the long period of accumulation at Pin Hole Cave, 55-44 Ka ¹⁴C years BP (Higham et al., 2006; Jacobi et al., 2006), it is important to consider that the two seasons sampled could represent individuals which are temporally representative of different stadials/interstadials distinct and with different palaeoenvironmental characteristics.

At Windy Knoll, a leaf-dominated browsing niche was also occupied by R. tarandus (Figure 7.3). Although the season of death was only known from one of the specimens studied, the low number of pits counted from the individual representative of the summer at Windy Knoll was comparable to the microwear signal from the autumn specimen at Pin Hole Cave (Figure 7.4). As the seasonal pattern of dental microwear in *R. tarandus* is characterised by an increase in the number of pits from the summer/autumn to the winter/spring, this could imply that similarities existed between the diets and surrounding environment of Derbyshire during the summer and autumn of both the Early and Middle Devensian. This further corresponds to similarities in the seasonality of site occupations at the two sites, both of which potentially represented separate routes through the Peak District as part of the autumn migration (see Chapter 6). A summer diet at Windy Knoll might therefore be characterised by an increase in graminoids, as well as a diverse range of deciduous shrubs, lichen, mushrooms and mosses, consistent with the diet of the modern forest R. t. tarandus subspecies this sample overlaps with. Assuming that seasonal variability in diets and dental microwear was in fact evident from Windy Knoll, it might further be hypothesised that the specimen for which season of death was unknown could represent either the summer or autumn diet, due to the similar number of pit and scratch counts to the summer specimen. This would correlate well with the late summer to autumn occupation reconstructed from the site of Windy Knoll.

The second Middle Devensian site to be studied, Kents Cavern, also reflected an autumn diet. However, compared to Pin Hole Cave, the relatively high number of scratches from the Kents Cavern autumn specimen placed the *R. tarandus* from this site towards a browse-dominated to mixed-feeding niche (**Figure 7.4**). Although individuals from the

two sites are not necessarily contemporaries, this does imply that there may have been a latitudinal difference in the diets between the more southerly site of Kents Cavern, at 50°N, and the more northerly site of Pin Hole Cave, 53°N. Rivals and Semprebon (2017) suggested that lichen consumption in modern and fossil *R. tarandus* increased at higher latitudes. However, it is the number of scratches which vary between the two sites, while the number of pits, which are thought to be characteristic of lichen (Rivals and Semprebon, 2017), remain relatively constant. Latitudinal differences in the diet of British R. tarandus therefore reflect a shift towards more grazing at Kents Cavern rather than increased lichen consumption at Pin Hole Cave. Nevertheless, the relatively small latitudinal change observed between the two sites in Britain, compared to the north-south European transect studied by Rivals and Semprebon (2017), could imply that latitude alone was not responsible for variability in the diets of *R. tarandus*. Instead, the influence of more stadial conditions during the accumulation of the Pin Hole Cave R. tarandus, might have restricted the diet of *R. tarandus* towards a browsing niche, while a more interstadial environment during the accumulation of *R. tarandus* at Kents Cavern, could have increased the mixed feeding opportunities.

The dental microwear of two additional specimens with unknown season of death were also measured from Kents Cavern (Figure 7.4). Compared to the specimen from autumn, the increase in the number of pits and decrease in the number of scratches in the two unknown specimens, indicate a difference in the diet of R. tarandus at Kents Cavern. However, unlike at Pin Hole Cave, evidence for the seasonality of site occupation at Kents Cavern represents all four seasons, meaning that it is less clear whether or not Kents Cavern was part of a seasonal migratory route. Fortunately, the analysis of strontium isotopes from the sites of Kents Cavern and Pin Hole Cave will provide further insights into the movements of Middle Devensian R. tarandus, which could have implications for the interpretation of seasonal dietary signals (see Chapter 8). If R. tarandus occupied a more sedentary niche, the Kents Cavern specimens could be similar to modern forest subspecies, occupying boreal open coniferous forests with deeper snow cover and varying forage over smaller distances. The low overall number of pits would imply that lichen was relatively less important to individuals at Kents Cavern and a more diverse range of plant species were instead selected. Nevertheless, variability between the autumn and unknown specimens could still be driven by the consumption of lichen and graminoids, the latter being more abundant in summer and autumn diets. A larger number of pits from the unknown specimens would therefore correlate to a winter or spring diet. However, due to the long period of accumulation at Kents Cavern, 54-26 ka ¹⁴C years BP (Higham *et al.*, 2011), the samples could be temporally distinct and therefore representative of different stadials/interstadials with different palaeoenvironmental characteristics.

The dietary niches of the Kents Cavern, Pin Hole Cave and Windy Knoll R. tarandus could also be compared to studies of diet from other fossil sites in western Europe (Figure 7.6). Kents Cavern was the only site included in this research for which DMA had previously been conducted by Rivals and Lister (2016) and Rivals and Semprebon (2017), who also identified a leaf-dominated browsing to browse-dominated mixedfeeding niche at the site. From the study of additional Middle Devensian/Weichselian sites, Rivals and Semprebon (2017) further recognised a distinction between the browsedominated diet's at sites in northern Europe, including Salzgitter-Lebenstedt in Germany, Brown Bank in the North Sea and Kents Cavern in Britain, and the graze-dominated mixed feeders present at the French site of Portel-Ouest in southern Europe. This pattern was also confirmed by the predominantly browsing diets visible at the sites of Kents Cavern and Pin Hole Cave in this research. Similar work by Rivals et al. (2020) found that Younger Dryas (GS-1) R. tarandus from Stellmoor and Meiendorf also occupied a leaf-dominated browsing niche, while individuals from the Last Glacial interstadial (GI-1e) at Verberie, Stellmoor and Meiendorf were mixed-feeders. Combined with the Early Devensian specimens from Windy Knoll which also displayed leaf-dominated browsing, within northern Europe, R. tarandus have only deviated from browse-dominated diets during GI-1e. Otherwise, a diverse range of forage has continuously been exploited with only smalls shifts in regional and seasonal variability.



Figure 7.6. Comparison of Late Pleistocene Rangifer tarandus Studies of Diet. The average number of scratches versus the average number of pits are compared for Early (WK-Windy Knoll), Middle (KC-Kents Cavern, PHC-Pin Hole Cave, S-L-Salzgitter-Lebenstedt, BB-Brown Bank, P-O-Portel-Ouest) and Late (S-Stellmoor, M-Meiendorf, V-Verberie) Devensian/Weichselian sites studied by this research (green) and by Rivals and Solounias (2007), Rivals *et al.* (2010), Rivals and Lister (2016), Rivals and Semprebon (2017) and Rivals *et al.* (2020) (all grey). The legend gives an indication of the shape representing each stage.

7.5. Summary

- Reconstructions of the modern and fossil diets of *R. tarandus* were characteristic of leaf-dominated browsers and browse-dominated mixed-feeders.
- From the Early and Middle Devensian fossil specimens, the lower number of pits were similar to the diets of modern *R. t. tarandus* occupying forest habitats in northern Scandinavia. Although lichen was an important component of the summer and winter diets of the modern herds, the amount of lichen in the winter diet of the forest specimens was reduced compared to other modern populations. This was probably due to a higher snow cover in the boreal forests.
- Where season of death was known in the modern and fossil specimens, DMA demonstrated clear differences between the summer/autumn and winter/spring signals. An increase in the number of pits during winter/spring, was primarily associated with a rise in the percentage of ground lichen in the winter diet of *R. tarandus* and a reduction of graminoids and general diversity of species consumed. Migrational distance and the diversity of plant species consumed also affected the number of pits.
- There was a latitudinal difference in the seasonal microwear signals measured from Late Pleistocene sites. The lower latitude Kents Cavern revealed a higher scratch count during the summer/autumn than the higher latitude Pin Hole Cave and Windy Knoll. This further demonstrated the similarities in diet between the Early and Middle Devensian sites at this higher latitude.
- Seasonal differences in the microwear signal at Pin Hole Cave and Kents Cavern could represent either sedentary herds exploiting surrounding forage with seasonal variability, or migratory herds using the site as part of their route between summer and winter ranges. It is also possible that non-contemporary individuals were measured, with the changing microwear signal representing palaeoenvironmental changes at the site over time.
- Patterns of dental microwear at Kents Cavern and Pin Hole Cave have confirmed the findings of previous studies that *R. tarandus* from northern European fossil sites were leaf-dominated browsers during the Middle Devensian/Weichselian. Similarities between the palaeodiet and therefore palaeoenvironment of *R. tarandus* were also observed between northern European sites from the Middle Devensian/Weichselian, Early Devensian (Windy Knoll) and the Younger Dryas (GS-1).

The following chapter presents the results of a pilot study that uses the strontium isotopic analysis of fossil *R. tarandus* teeth in order to test the reconstructed seasonal migration patterns presented in earlier chapters. The chapter will therefore begin by outlining the techniques of strontium isotopic analysis applied to fossil assemblages, with the aim of understanding palaeo-mobility. The current understanding of the bioavailability of strontium across the British Isles will also be described. Strontium analysis from the sites of Kents Cavern and Pin Hole Cave will then be presented and used as a pilot study to investigate the potential of this technique for supporting and complementing traditional palaeontological studies.

8.1. Introduction to Isotopic Studies of Rangifer tarandus Mobility

The reconstruction of multiple seasons of occupation from the ageing and sexing of specimens has previously entailed limited awareness of whether R. tarandus were sedentary or migratory in the past, especially when sites may cover a broad chronological interval (see Chapter 6). This is further complicated by evidence for seasonal variability in the diets of individuals at these sites (see Chapter 7). The ability to determine which niche was occupied by R. tarandus would therefore improve our understanding of the impacts of the varying climatic and environmental conditions during the Late Pleistocene, as well as the influence of more herd-specific factors on R. tarandus mobility. R. tarandus mobility was therefore investigated further by comparing the seasonality of site occupations with the strontium isotopic signature from Late Pleistocene sites. Strontium isotope analysis has been an effective method for establishing seasonal mobility in a number of species (Hoppe et al., 1999; Balasse et al., 2002; Hoppe et al., 2004; Pellegrini et al., 2008; Widga et al., 2010; Britton et al., 2011; Julien et al., 2012; Copeland et al., 2016; Lugli et al., 2017) which include modern and fossil R. tarandus (Price et al., 2008; Britton 2010; Britton et al., 2011; Pryor et al., 2016; Price et al., 2017; Gigleux et al., 2019). The technique operates on the principle that the isotopic composition of skeletal tissues is representative of the food and water ingested, which, in turn, is strongly controlled by the bedrock (Bentley, 2006). As the isotopic composition of bedrock varies spatially (Bentley, 2006), the technique works to geochemically "fingerprint" the region where an individual spent their early years. Strontium isotope analysis was therefore selected for a discrete case study within this

research project. By comparing key sites of the same age, it should be possible to discern the presence of migratory and sedentary individuals, as well as constrain the centres and directions of *R. tarandus* movements within the Late Pleistocene.

Two fossil sites from the Middle Devensian were selected for the application of strontium isotope analysis. Fossil analysis from the site of Kents Cavern in Devon represented seasonality indicative of spring, summer, autumn and winter occupations. This is characteristic of the signals seen in more sedentary herds of *R. tarandus*, which require only a small degree of mobility in order to sustain the productivity of forage. On the other hand, at Pin Hole Cave in Derbyshire, R. tarandus were present during two separate seasons, autumn and spring, which could potentially reflect part of a larger bi-annual migration route. As such, both sites might provide potential insights into the mobility of R. tarandus. Furthermore, if herds are migratory, the potential exists for movements along an east-west axis due to the fluctuating terrestrial connection between Britain and continental Europe during the last cold stage, in addition to movements within Britain from north-south. To achieve this analysis, the three mandibles selected for dental microwear analysis from Kents Cavern were also analysed for strontium isotopes. However, due to the constraints of sequential sampling, only one mandible from Pin Hole Cave met with the sampling criteria and this individual had not been included in the previous dental microwear analyses.

8.2. Methods for Strontium Isotope Analysis

8.2.1. Geologically and Biologically Available Strontium

Four isotopes of strontium occur naturally in the environment and can be divided into the non-radiogenic ⁸⁴Sr (0.56%), ⁸⁶Sr (9.8%) and ⁸⁸Sr (82.53%) and the radiogenic ⁸⁷Sr (7.04%) (Bentley, 2006). Because radiogenic ⁸⁷Sr is formed from the β -decay of ⁸⁷Rb (half-life 4.88x10¹⁰ years), the ratio of ⁸⁷Sr/⁸⁶Sr in geological material represents the relative abundance of rubidium and strontium present in the rock (Bentley, 2006). This varies between lithologies of different ages and mineral content, with rocks which are older and more abundant in rubidium exhibiting higher proportions of ⁸⁷Sr/⁸⁶Sr (Montgomery *et al.*, 2010), as demonstrated by the younger basalts and older granites of oceanic and continental crusts (**Table 8.1**) (Bentley, 2006). The isotopic signal of bedrock also has a direct impact on the environment, as strontium is eroded into the surrounding groundwater, rivers and soils, where it is incorporated into the food chain through the ingestion of plants and water (Montgomery *et al.*, 2005a). Skeletal tissues will only reflect the strontium isotopic signal of food consumed during the mineralisation phase, when strontium ions (Sr²⁺) will substitute for calcium ions (Ca²⁺) in hydroxyapatite,

the mineral component of bones and teeth (McConnell, 1973; Bentley, 2006). However, the influence of strontium decreases by around 20% with each trophic level as mammals only absorb between 10-40% of the strontium they ingest (Bentley, 2006; Knudson *et al.*, 2010).

| Source | Average ⁸⁷ Sr/ ⁸⁶ Sr |
|-------------------------------|--|
| Oceanic Crust (Basalts) | 0.702-0.704 |
| Continental Crusts (Granites) | 0.710-0.740 |
| Continental Crusts (Basalts) | 0.703-0.704 |

Table 8.1. Average ⁸⁷Sr/⁸⁶Sr Value of Different Source Rocks. (Source: Bentley, 2006).

Therefore, where the isotopic signal of an area is known, it is possible to differentiate between local and non-local individuals by analysing the ⁸⁷Sr/⁸⁶Sr values of bones and teeth. However, there is not a simple one to one relationship between the ratio of strontium isotopes that go into and out of the biosphere (Bentley, 2006). Although the overriding ⁸⁷Sr/⁸⁶Sr values are dominated by the underlying bedrock geology, mixing of aeolian, alluvial and glacial deposits in the soil will dampen the geological signal that is taken up by the biosphere (Bentley, 2006; Evans *et al.*, 2010; Price *et al.*, 2017). Non-geological inputs can also be influential, particularly in areas where rain or coastal spray might saturate the soil (Capo *et al.*, 1998; Whipkey *et al.*, 2000; Raiber *et al.*, 2009; Evans *et al.*, 2010). For rainwater which is derived from oceans, the bioavailable strontium will always be influenced to some degree by the ⁸⁷Sr/⁸⁶Sr value of seawater which is currently 0.7092 (Montgomery *et al.*, 2005b; Bentley, 2006). It is therefore unreliable to define the geographic origin of an individual purely from the bedrock geology. Instead, the local biologically available range of strontium must be established.

For this purpose, datasets of bioavailable strontium are continuously being compiled through the analysis of contemporary plants, soil and water (Evans *et al.*, 2010). Although modern pollutant levels may affect the reliability of such samples (Evans *et al.*, 2010), local archaeological remains of non-migratory species can help to provide a more accurate estimate of Late Pleistocene values (Bentley, 2006). In Britain, ⁸⁷Sr/⁸⁶Sr values ranging from 0.707-0.720 have been derived from >900 samples (Evans *et al.*, 2018), enabling subdivisions of bioavailable strontium to be mapped (**Figure 8.1**) (Evans *et al.*, 2010; 2018). Unfortunately, skeletal tissues will typically preserve a weighted mean of all of the areas that an individual occupied during their early years, which may not allow the precise identification of a specific area or region (Montgomery *et al.*, 2005a; Britton *et al.*, 2009; Montgomery *et al.*, 2010; Britton *et al.*, 2011). Nevertheless, the presence of migratory or sedentary *R. tarandus* can still be inferred from where the isotopic signature within an individual is characteristic of the bedrock close to the site or is non-



Figure 8.1. Map of Biosphere Strontium Isotope Variation across Britain. The bioavailability of strontium in Britain was determined from plant and water samples from distinct lithological and geographical areas. (Source: Evans *et al.*, 2010, p.2.).

local in origin. This is made easier where a wide range of isotopically-distinct bedrock types occur in close proximity (Julian *et al.*, 2012). In contrast, areas of wide-ranging isotopic homogeny and natural barriers such as rivers limit interpretations of the scale of movement (Price *et al.*, 2017). Any inferences regarding species migration based on isotopic analysis can be further supported by evidence of intra-group homogeny, which can suggest similar migratory behaviours and routes between individuals (Britton *et al.*, 2011; Price *et al.*, 2017).

8.2.2. Sequential Sampling of Tooth Enamel

Isotopic studies of *R. tarandus* mobility primarily concentrate on the analysis of teeth (Britton 2010; Britton *et al.*, 2011; Pryor *et al.*, 2016; Price *et al.*, 2017; Gigleux *et al.*, 2019). Both the enamel and dentine components of a tooth preserve the strontium isotopic signal of an individual; however, the porous structure of dentine makes the tissue much more susceptible to diagenetic contamination (Bentley, 2006). Diagenesis is the process whereby strontium is incorporated from the burial environment into pores and microcracks in the sample, ultimately altering the isotopic signature (Bentley, 2006). Enamel, on the other hand, has a much harder and denser non-porous structure (Bentley, 2006), stability that makes its analysis preferable to that of dentine, bones or antlers (Hoppe *et al.*, 2004).

Because the ⁸⁷Sr/⁸⁶Sr value of enamel only represents the mineralisation phase of skeletal tissues, it is important to understand the direction and duration of this process in *R. tarandus*. Enamel mineralisation is a two-stage process, whereby thin and lightly mineralised enamel crystallites are laid down during matrix production as an outline for the mature enamel crystallites that replace them during the final enamel maturation phase (Hillson, 2005). This process occurs in incremental lines (Retzius striae) which develop along both a vertical (cusp to cervix) and horizontal (enamel-dentine junction outwards) mineralisation gradient (Zazzo *et al.*, 2005). Although daily variations in the orientation and spacing of the formation of enamel striae demonstrate how potentially complex mineralisation is, the process is broadly sequential (Robinson *et al.*, 1979; Smith, 1998). Therefore, by comparing the intra-tooth variability in ⁸⁷Sr/⁸⁶Sr ratios from the cusp to cervix, it is possible to create a temporal view of an individual's movement during tooth formation (Humphrey *et al.*, 2008).

One significant limitation in the application of this technique to *R. tarandus* is the lack of published studies regarding the timing and nature of enamel mineralization in the species. Previous analyses of strontium in modern and fossil *R. tarandus* have used the similarities observed between the timings of tooth eruption in cervids (**Table 8.2**), to infer

that patterns of tooth formation established from these species are a reliable reference for *R. tarandus* (Britton *et al.*, 2009; 2011; Price *et al.*, 2017, Pryor *et al*, 2016; Gigleux *et al.*, 2019). Timings for the onset and completion of mineralisation in fallow deer (*Dama dama*, Linnaeus, 1758) and red deer (*Cervus elaphus*, Linnaeus, 1758) were measured by Brown and Chapman (1991a; 1991b) using radiographs of known age individuals, to identify patterns and rate of striae formation (**Table 8.3**). From both species, the growth intervals of premolars are less well constrained (Brown and Chapman, 1991a; 1991b) however, mineralisation in mandibular molars occurs over six months in the M₁ (*in utero*-3 months) and M₂ (2-8 months) and nine months in the M₃ (9-18 months) (**Table 8.3**). In the first molar, this corresponds to a time during which the isotopic signature reflected is mainly that of the mother, either *in utero*, or before calves are weaned at 3-4 months (Holand *et al.*, 2012). Although fractionation between trophic levels, and so from mother to milk, are negligible and should not affect interpretations of mobility (Montgomery *et al.*, 2005a; Bentley, 2006; Knudson *et al.*, 2010), significantly less is known about the relationship between mothers and neonates (Pryor *et al.*, 2016).

Table 8.2. Timing of Tooth Eruption in Cervids. *Rangifer tarandus* (Bromée-Skuncke, 1952; Miller, 1972) eruption ages (in months) for the first, second and third molars are compared to the timings in *Dama dama* (Brown and Chapman, 1990; Moore *et al.*, 1995; Bowen *et al.*, 2016) and *Cervus elaphus* (Azorit *et al.*, 2002).

| Dentition | Rangifer tarandus (reindeer) Eruption | | Dam a (fallo | a dama w deer) | Cervus elaphus (Red deer) | |
|----------------|---|----------|------------------------|--------------------------|------------------------------|----------|
| | | | Eruption | | Eruption | |
| | Begins | Complete | Begins | Complete | Begins | Complete |
| M ₁ | 3 | 5 | | 5-7 | 2 | 6 |
| M ₂ | 10 | 15 | | 15-20 | 12 | 16 |
| M ₃ | 15 | 29 | 18-20 | 24-28 | 18 | 32 |

Table 8.3. Timing of Tooth Mineralisation in Cervids. Ages (in months) indicatingmineralisation onset, when mineralisation was first present, and completion, when thecomplete crown was first present, were derived from radiographs of the first, secondand third mandibular molars of Dama dama (Brown and Chapman, 1991a) and Cervuselaphus (Brown and Chapman, 1991b).

| | Dama dama | a (fallow deer) | Cervus elaphus (red deer) | | |
|----------------|-----------|-----------------|---------------------------|----------|--|
| Dentition | Minera | alisation | Mineralisation | | |
| | Begins | Complete | Begins | Complete | |
| M ₁ | in utero | <4 | in utero | <4 | |
| M ₂ | <3-5 | 8 | <3 | <9 | |
| Mз | 9 | <18 | 9 | 18 | |

For this reason, strontium isotope analysis was only carried out on the second and third molars (M_2 and M_3) of Late Pleistocene *R. tarandus* samples. Based on modern *R. tarandus*, the timing of mineralisation in the two teeth would represent July to January in

the second molar and February to October in the third molar. The sequential sampling of mandibles containing both teeth therefore enables movements from an entire year, and potentially multiple migrations, to be included in the isotopic signal. As such, three horizontal slices of enamel (each 20-30 mg) were taken from the top, middle and bottom of the buccal face of the second and third molars from each mandible sampled (**Figure 8.2**). Ideally, these should be focussed on the anterior loph where the enamel is thicker (Britton *et al.*, 2009; 2011) however, the level of preservation in fossil specimens did not always permit this. The mandibles selected for strontium isotope analysis were either 29 months or 3-5 years old, ensuring that the crown height of each tooth was sufficiently high for the three enamel slices to be recovered.



Figure 8.2. Tooth Enamel Sampling Location for Strontium Isotope Analysis. Three horizontal slices of enamel were taken from the top, middle and bottom of the buccal face of the second (a, b, c) and third (d, e, f) molars.

8.2.3. Strontium Isotope Analysis

Strontium isotope analysis was conducted in collaboration with Dr Jane Evans of the British Geological Survey (BGS) and used the NERC Isotope Geosciences Facilities for the sampling and analysis of dental enamel. The approach followed standard methods for solution analysis (Balasse, 2002; Copeland *et al.*, 2008). The buccal face of the sampled loph was first cleaned using a flexible diamond-edged rotary dental saw, before a small burr attachment was used to remove three horizontal enamel slices from each tooth. After being mixed with SrOD13 tracer, samples were dissolved in nitric acid (8M HNO₃) and the strontium chemically isolated using Eichrom AG50 X8 resin columns. Strontium isotopic compositions and concentrations were then determined by thermal ionisation mass spectroscopy (TIMS) using a Thermo Triton multi-collector mass spectrometer. The precision of this method was maintained by continually analysing the international standard for ⁸⁷Sr/⁸⁶Sr NBS987 and correcting for this value.

Traditional solution methods, such as TIMS or multicollector inductively coupled plasma mass spectrometry (MC-ICP-MS), are precise and accurate (Copeland et al., 2008) and have been used in multiple studies analysing the strontium isotopic signal of *R. tarandus* (Britton et al., 2009; 2011; Price et al., 2017; Gigleux et al., 2019). However, both approaches are relatively destructive, requiring between 5-30 mg of enamel per sample. Recent developments in the analysis of strontium have focused on the micro-destructive laser ablation MC-ICP-MS, a technique that has also been applied successfully to fossil *R. tarandus* (Pryor *et al.*, 2016). Measuring samples $250x750 \mu m$ *in situ* and without the need for chemical preparation, laser ablation multicollector inductively coupled plasma mass spectrometry (LA-MC-ICP-MS) is not only much less destructive, but can be conducted more quickly and cheaply than solution methods (Copeland et al., 2008; Copeland et al., 2010). Although it is not yet possible to fully understand the heterogeneity of strontium through the measurement of individual enamel crystals (Montgomery et al., 2010), small sample sizes have resulted in a higher spatial resolution of analysis (Copeland et al., 2008; Lugli et al., 2017). One of the major limitations of LA-MC-ICP-MS is the isobaric molecular interference of ⁴⁰C³¹P¹⁶O⁺, which with a mass of 87, inaccurately increases the ⁸⁷Sr/⁸⁶Sr ratio measurement of a sample (Copeland et al., 2008). Similarly, potential interferences from rare earth elements and ⁸⁷Rb and ⁸⁷Sr, must also be corrected for (Copeland et al., 2008; Krabbenhoft, 2009). This may ultimately explain the reduced precision of laser ablation MC-ICP-MS. Compared to solution MC-ICP-MS which accurately reports ⁸⁷Sr/⁸⁶Sr values to five decimal places and TIMS which achieves six decimal places, LA-MC-ICP-MS is only accurate to three or four decimal places (Copeland et al., 2010). While it is important to understand the limitations of the technique being applied, the level of precision required by an analysis technique is highly dependent on the local and non-local strontium ranges present at a study range (Copeland et al., 2010). Nevertheless, TIMS is the most precise approach and was implemented in this research.

8.3. Results of Strontium Isotope Analysis

The results of the strontium isotope analysis are presented in **Table 8.4**. In studies of sequentially sampled strontium, many methods of statistical analysis are inappropriate due to the small number of samples and non-normal distribution of ⁸⁷Sr/⁸⁶Sr values, therefore statistical analysis was not completed in this study (Montgomery *et al.*, 2007; Britton *et al.*, 2009; 2011).

| Table 8.4. Summary of Late Pleistocene Rangifer tarandus Isotopic Data. 87Sr/86Sr |
|--|
| values and concentration are presented for R. tarandus tooth enamel samples from the |
| sites of Pin Hole Cave and Kents Cavern. The batch number was P905. |
| |

| Site | Sample | Tooth | Sample | ⁸⁷ Sr/ ⁸⁶ Sr | Sr Conc. (ppm) |
|---------------|---------------|----------------|--------|------------------------------------|-------------------|
| Pin Hole Cave | LL.15954.2796 | M_2 | EW-01a | 0.7094 | 150 |
| | | | EW-01b | 0.7099 | 301 |
| | | | EW-01c | 0.7104 | 222 |
| | | M ₃ | EW-01d | 0.7115 | 100 |
| | | | EW-01e | 0.7119 | 120 |
| | | | EW-01f | 0.7121 | 115 |
| Kents Cavern | NHMUK PV | M_2 | EW-02a | 0.7091 | 74 |
| | M706 | | EW-02b | 0.7088 | 124 |
| | | | EW-02c | 0.7089 | 128 |
| | | M3 | EW-02d | 0.7087 | 132 |
| | | | EW-02e | 0.7088 | 151 |
| | | | EW-02f | 0.7087 | 163 |
| | NHMUK PV | M_2 | EW-03a | 0.7100 | 205 |
| | OR16741 | | EW-03b | No data | 206 |
| | | | EW-03c | 0.7103 | 199 |
| | | M ₃ | EW-03d | 0.7104 | 196 |
| | | | EW-03e | 0.7104 | 126 |
| | | | EW-03f | 0.7108 | 153 |
| | NHMUK PV | M_2 | EW-04a | 0.7110 | 139 |
| | M104644 | | EW-04b | 0.7110 | 159 |
| | | | EW-04c | 0.7112 | 155 |
| | | M ₃ | EW-04d | 0.7122 | 106 |
| | | | EW-04e | 0.7125 | 84 |
| | | | EW-04f | 0.7111 | 108 |

Although the exact causes of variability in the concentrations of strontium are rarely identifiable (Viner *et al.*, 2010), a larger range of strontium concentrations was observed at Pin Hole Cave, from 100-301 ppm, compared to the three individuals from Kents Cavern that measured 74-163 ppm, 84-159 ppm and 126-206 ppm respectively. Values for the ⁸⁷Sr/⁸⁶Sr ratio were measured from all enamel samples with the exception of the M₂ sample (EW-03b) from Kents Cavern, for which no data was returned. This was likely due to an instrumentational error. At Pin Hole Cave (**Figure 8.3**), the single mandible (EW-01) demonstrated a large range of ⁸⁷Sr/⁸⁶Sr values across the M₂ and M₃ from 0.7094 to 0.7121. However, when compared to the local bioavailable strontium signal



Figure 8.3. ⁸⁷Sr/⁸⁶Sr Values for *Rangifer tarandus* from Pin Hole Cave. Three enamel slices were sampled from the top, middle and bottom of the buccal face of both the second (a, b, c) and third (d, e, f) molar of one mandible from Pin Hole Cave. The area of grey shading indicates the local bioavailable strontium signal (Evans *et al.*, 2018).



Figure 8.4. ⁸⁷Sr/⁸⁶Sr Values for *Rangifer tarandus* from Kents Cavern. Three enamel slices were sampled from the top, middle and bottom of the buccal face of both the second (a, b, c) and third (d, e, f) of three mandibles from Kents Cavern. No data was returned from the M₂ sample EW-03b. The area of grey shading indicates the local bioavailable strontium signal (Evans *et al.*, 2018).

(0.7087-0.7096), only EW-01a plotted within this range. At Kents Cavern (**Figure 8.4**), there was no overlap between the absolute values of the three mandibles measured. The two individuals, EW-02 and EW-03, showed relatively little deviation in their range of ⁸⁷Sr/⁸⁶Sr values from the M₂ to the M₃, although there was a distinct difference between the higher values from EW-03, which ranged from 0.7100-0.7108, and the lower values from EW-02, which ranged from 0.7091-0.7086. EW-03 was also the only mandible from Kents Cavern to plot within the local bioavailable strontium signal (0.7096-0.7106),

although the EW-03f sample exceeded this range. The 87 Sr/ 86 Sr values from EW-04 were not only higher than those of EW-02 and EW-03, but showed significantly more variation than either of the other two mandibles at Kents Cavern. In measurements from the M₂, 87 Sr/ 86 Sr values remained relatively stable between 0.7110-0.7112 however, in the M₃, values increased to a peak of 0.125 in the M₃ sample EW-04e, before returning to the lower value of 0.7111 in the M₃ sample EW-04f.

8.4. Strontium Inferred Mobility of Rangifer tarandus

8.4.1. Pin Hole Cave

The Pin Hole Cave sample, EW-01, demonstrated a 0.0028 range in ⁸⁷Sr/⁸⁶Sr values with a clear continuation between the two teeth of this single individual (**Table 8.4, Figure 8.3**). For one animal to exhibit variability on this scale is unusual in Britain. At the later prehistoric henge site of Durrington Walls, Wiltshire, where cattle (*Bos taurus*, Linnaeus, 1758) was brought from grazing areas across Britain, the largest range recorded for a single individual was 0.0017 (Viner *et al.*, 2010). Therefore, the strontium signal from the Pin Hole Cave *R. tarandus* clearly indicates movement across different geological boundaries. Only the uppermost, and therefore the youngest, enamel slice taken from the EW-01 M₂ sample (**Figure 8.3**) overlapped with the local bioavailable strontium range of 0.7087-0.7096 (Evans *et al.*, 2018) from the carboniferous limestone gorge of Creswell Crags, where Pin Hole Cave is located. Higher ⁸⁷Sr/⁸⁶Sr values from EW-01 are therefore representative of a non-local signal.

Areas with more radiogenic ⁸⁷Sr/⁸⁶Sr values of 0.7121 that could have contributed to the signal are found primarily to the west of Pin Hole Cave in Wales or the Lake District, as well as Scotland, Devon and Cornwall (Evans *et al.*, 2018). Movement either across or specifically to any of these areas would suggest that Middle Devensian *R. tarandus* travelled distances of at least 200 km, but could potentially have exceeded 500 km once natural barriers (hills, water bodies) were accounted for. However, within 100 km, the nearest area that could supply the peak value of 0.7121 are the Millstone Grits which intersperse the Carboniferous Limestone of the Peak District and Pennines to the west of Pin Hole Cave. The combination of these two lithologies has created bimodality in the strontium bioavailability of the area (Johnson *et al.*, 2019). While studies of Carboniferous Gritstones have recorded bioavailable strontium values of 0.7115 (Johnson *et al.*, 2019) and 0.7119, 0.0014 SD (Evans *et al.*, 2018), ratios between 0.7096-0.7112 have been recorded from Early Medieval cemeteries at Masham, North Yorkshire, on areas of Millstone Grit (Buckberry *et al.*, 2014). Nevertheless, the Peak District has also generated unusually high ⁸⁷Sr/⁸⁶Sr values greater than 0.7145 (Parker

Pearson *et al.*, 2016) and up to 0.721 (Jane Evans, pers. comm.) from human enamel. Although these could represent incomers, in regions where the bedrock geology is heterogeneous, such as the Peak District, the bioavailable signal will be dominated by the strontium-rich feldspar component which is easily weathered (Evans and Tetham, 2004) and high in Millstone Grits (Johnson *et al.*, 2019). Another important influence on the strontium isotopic signal in *R. tarandus* could be the whole rock value. As terrestrial lichens are an important component of the diet of present-day *R. tarandus* (Bergerud, 1972; Gaare and Skogland, 1975), rock grit could easily be ingested. The whole rock ⁸⁷Sr/⁸⁶Sr value which is relatively high in Millstone Grits at 0.7208, could therefore be directly incorporated into the individual's strontium signal (Johnson *et al.*, 2019). The dental microwear signal measured from *R. tarandus* at Pin Hole Cave suggested that while lichen was perhaps not consumed abundantly; it may still have been part of the yearly diet (see Chapter 7). The Pin Hole Cave sample therefore provides an important insight into the variable strontium in this area.

A Peak District signal would also imply that *R. tarandus* used upland areas as part of their seasonal ranges. This differs somewhat from the patterns observed in fossil R. tarandus from Europe. Strontium isotope analysis from the Middle Weichselian site of Jonzac in France (Britton et al., 2011), as well as the Late Weichselian sites of Stellmoor and Meiendorf in Germany (Price et al., 2017) and Dolní Věstonice in the Czech Republic (Pryor et al., 2016), suggest that migratory R. tarandus avoided highland areas and instead moved within large grazing plains. This could provide evidence for differences in the environments of Britain and continental Europe, whereby Middle Devensian R. tarandus had to exploit resources in both lowland plains and upland outcrops in order to survive. Even if it is not possible to confirm the precise direction or endmembers of R. tarandus migrations, the variability in the seasonal microwear signal during both autumn and spring (Figure 8.5, see Chapter 7) when site occupations were reconstructed (see Chapter 6), further imply that Pin Hole Cave was part of a larger migratory route. In modern *R. tarandus*, the period over which a herd migrates can be several months, but the movements of individual animals are relatively quick (Birtton et al., 2009). Therefore, if Pin Hole Cave was part of a migration route, the increased daily mobility of individuals would reduce the exposure to the local strontium signal (Price et al., 2017). This would explain the minimal influence of the local bioavailable signature of strontium at Pin Hole Cave (Figure 8.3). Nevertheless, the analysis represents only one individual. Therefore, in light of the intra-herd behavioural variability expressed in modern herds (Britton et al., 2011), the isotopic values of additional R. tarandus specimens from this fossil site should be compared in order to establish patterns of mobility more confidently.



Figure 8.5. Number of Scratches versus Number of Pits from Middle Devensian *Rangifer tarandus*. Separate specimens from Pin Hole Cave were submitted to strontium isotope analysis (EW-01) and dental microwear analysis (PHC). The same three specimens from Kents Cavern (EW-02, EW-03, EW-04) were submitted to both analyses.

8.4.2. Kents Cavern

There was no overlap between the absolute values of ⁸⁷Sr/⁸⁶Sr in EW-02, EW-03, and EW-04, the three individuals sampled from Kents Cavern (Table 8.4, Figure 8.4). The only sample to plot within the local bioavailable strontium range of 0.7096-0.7106 (Evans et al., 2018) for the underlying Devonian Limestone found at Kents Cavern, was EW-03 (Figure 8.4). This individual showed a relatively flat curve with little deviation in the range of ⁸⁷Sr/⁸⁶Sr values from 0.7100-0.7108, suggesting that unlike the Pin Hole Cave animal, this R. tarandus was more sedentary in its movements or at least remained in more geologically homogeneous areas. Even the ⁸⁷Sr/⁸⁶Sr value of 0.7108 that exceeded the local bioavailable strontium range was consistent with that of many parts of Devon and Cornwall (Evans et al., 2018), further supporting the restricted mobility of this individual within southwest Britain. Although the sample EW-02 also showed a relatively flat curve of ⁸⁷Sr/⁸⁶Sr values from 0.7091-0.7086 (Figure 8.4), these lower values are only present sparsely in Devon and Cornwall and are much more extensive throughout the rest of Britain (Evans et al., 2018). Therefore, despite the behavioural similarity between the two *R. tarandus*, with both individuals remaining more sedentary, the animals were clearly using separate areas. This use of distinct grazing areas would also correspond to the differences in diet observed from the dental microwear signals of these two individuals (Figure 8.5, see Chapter 7).

The lower ⁸⁷Sr/⁸⁶Sr values recorded from the sample EW-02, could also have been influenced by the location of Kents Cavern on the southwest coast of Britain. In coastal

areas, the bioavailability of strontium is often dampened by higher levels of rainfall and sea-spray which incorporate the 0.7092 ⁸⁷Sr/⁸⁶Sr value of seawater into soils (Capo et al., 1998; Whipkey et al., 2000; Montgomery et al., 2005b; Bentley, 2006; Raiber et al., 2009; Evans et al., 2010). However, during the Middle Devensian, the exact position of the coast in relation to Kents Cavern is unknown, as sea level was an estimated 70 m lower than the present day (Cutler et al., 2003). Therefore, while it is unlikely that the local bioavailable strontium signal at Kents Cavern was directly influenced by sea-spray, R. tarandus could have moved onto the exposed coastal areas. Price et al. (2017) predicted that strontium values for Doggerland would be close to the 0.7092 ⁸⁷Sr/⁸⁶Sr value recorded for seawater today. This was confirmed by the sampling of dredged R. tarandus teeth off the coast of the Netherlands (Price et al., 2017), which recorded ⁸⁷Sr/⁸⁶Sr values of 0.7091 and 0.7096 (Price *et al.*, 2017). This overlaps the upper range of the ⁸⁷Sr/⁸⁶Sr values measured from EW-02 (0.7091-0.7086) at Kents Cavern, suggesting that the coastal environment may have been more significant in the mobility of this individual than in EW-03 where strontium was higher. Nevertheless, it would be interesting to compare the apparently more sedentary EW-02 and EW-03 to strontium isotopes in other species from Kents Cavern that are known to be non-migratory, in order to provide further insight into the variability in ⁸⁷Sr/⁸⁶Sr values of individuals using only the local area (Britton, 2010; Britton et al., 2011).

Another important influence that lowers the strontium isotopic signal of animals in coastal environments are salty marine plants such as seaweeds (Montgomery *et al.*, 2007). Although *R. tarandus* are typically terrestrial foragers, focussing predominately on lichens and graminoids (grasses, sedges) (Bergerud, 1972; Gaare and Skogland, 1975), this is a generalist species (Skogland, 1984). On Svalbard, *R. tarandus* forage terrestrially during the majority of the year but have also been observed to exploit marine biomasses such as kelp during the winter (Hansen *et al.*, 2019b). However, a diet high in kelp will result in diarrhoea, so the Svalbard *R. tarandus* will only select kelp when thick ice or snow cover limit access to more preferable forage (Hansen *et al.*, 2019b). As such, it is possible that shoreline plants could have been part of the diet of *R. tarandus* at Kents Cavern, particularly if terrestrial forage was locked under ice or snow. In fossil *R. tarandus*, unless a specific dental microwear signal can be identified for marine forage, the only way to determine whether marine biomasses were part of the diet would be to measure the δ^{13} C, which was higher in the Svalbard individuals consuming kelp (Hansen *et al.*, 2019b).

In contrast to both EW-02 and EW-03, the 87 Sr/ 86 Sr values of the final individual measured from Kents Cavern, EW-04, showed considerably more variation (**Figure 8.4**). The lower 87 Sr/ 86 Sr values in both the M₂ and M₃ of EW-04 ranged from 0.7110-0.7112.

This was consistent with the more sedentary signal observed in EW-03, which despite exceeding the local bioavailable strontium range, supported the presence of *R. tarandus* within Devon or Cornwall (Evans et al., 2018). However, the increase throughout the samples EW-04d and EW-04e to a peak ⁸⁷Sr/⁸⁶Sr value of 0.7125, suggests that the individual also moved across a geological boundary. As previously outlined, ⁸⁷Sr/⁸⁶Sr values in excess of 0.7120 are found in Wales, the Lake District, Scotland and areas of the Peak District (Evans et al., 2018), although it is probable that the signals from Devon and Cornwall had significantly more influence on the Kents Cavern individual. Within 50 km of Kents Cavern, the bioavailable strontium signal of Igneous Granite Batholiths in Dartmoor is 0.7125, 0.0016 SD (Evans et al., 2018) and could therefore infer the seasonal movement of this individual. Unlike the pattern observed at Pin Hole Cave, the sample EW-04f, which was taken from the base of the third molar, represents a return to a lower ⁸⁷Sr/⁸⁶Sr value of 0.7111 (Figure 8.4). Cyclicity in the strontium isotopic signal of R. tarandus has been observed from modern migratory herds in Alaska (Britton et al., 2009; Britton, 2010), highlighting the fidelity of *R. tarandus* which will return to the same sites year after year (Schaefer et al., 2000). It has been suggested that mineralisation of the third molar in *R. tarandus* occurred over nine months from February to October (Brown and Chapman, 1991a; 1991b). As modern R. tarandus typically move to upland areas for the spring calving and summer grazing pastures to reduce the risk of predators (Bergerud and Luttich, 2003), this behaviour could also have been exhibited by this Kents Cavern R. tarandus. Again, this movement to high, open topography differs from the patterns observed from European fossil R. tarandus, but is potentially consistent with the individual at Pin Hole Cave.

The lack of any clear evidence for the spatial proximity of *R. tarandus* individuals at Kents Cavern also differed somewhat from fossil studies where similarities in the absolute values and patterns of ⁸⁷Sr/⁸⁶Sr indicated that animals belonged to the same herd (Britton *et al.*, 2011; Price *et al.*, 2017; Gigleux *et al.*, 2019). If individuals at Kents Cavern were contemporaries, this would represent a level of natural dispersion that although not common, has been observed from modern herds (Britton *et al.*, 2011). In the Western Arctic Herd in Alaska, a cyclical migration signal was recognisable from all but one individual, which showed little variation in the ⁸⁷Sr/⁸⁶Sr values suggesting that it was more sedentary (Britton *et al.*, 2011). All of these animals lived within ten years of each other, so it is likely that differences in the specific geological boundaries crossed by individuals represented intra-herd behavioural differences (Britton *et al.*, 2011). It would therefore be useful to have more studies of modern individuals in order to better characterises trends of intra-herd mobility from European as well as North American *R. tarandus* herds. However, if the Kents Cavern individuals were not contemporaries, this may represent a change in the migratory behaviour of herds through time. Both hypotheses are possible

due to the extended period of accumulation of *R. tarandus* remains at the site of Kents Cavern. Similarly, the overlap in the dental microwear signals of EW-02 and EW-04 (**Figure 8.5**, see Chapter 7), shows individuals occupying different sedentary or migratory niches generating the same dietary signal in the area surrounding Kents Cavern. Without knowing the season of death for either specimen, it is difficult to make further interpretations relating to diet and mobility at Kents Cavern; nevertheless, this would have different implications depending on the size of temporal separation between the two individuals.

8.4.3. Oxygen Isotope Analysis

The migrational patterns recognised at Kents Cavern and Pin Hole Cave could be further improved by analysing the oxygen isotopic signal, which places the strontium observed from sequentially sampled enamel into a seasonal context (Britton et al., 2009; Britton, 2010; Pryor et al., 2016; Price et al., 2017; Gigleux et al., 2019). In skeletal tissues, the oxygen isotopic signal is derived from drinking water and is therefore a product of precipitation. The ratio of δ^{18} O in precipitation varies seasonally with temperature and humidity (Dansgaard, 1964; Gat, 1980; 1996gig), so that values are higher in the summer and lower in the winter. By combining the two independent isotopes, this could therefore be useful in constraining the timing of seasonal movements to and from upland areas by Middle Devensian *R. tarandus* in Britain. However, the application of oxygen isotopic analysis specifically in *R. tarandus*, is limited by the reduced intake of water by this species during periods of high lichen consumption (Soppela et al., 1988). Due to the lack of studies on the timing and nature of enamel mineralization in *R. tarandus*, there is also uncertainty over whether the strontium and oxygen isotopes ingested together will be mineralised at the same time (Gigleux et al., 2019). Nevertheless, the studies of modern and fossil R. tarandus (Britton et al., 2009; Britton, 2010; Pryor et al., 2016; Price et al., 2017; Gigleux et al., 2019) have demonstrated the applicability of this approach to R. tarandus mobility, which would provide an interesting extension to this work.

8.5. Summary

- Strontium isotope analysis from the Middle Devensian sites of Kents Cavern and Pin Hole Cave demonstrated behavioural differences in the mobility of individual *R. tarandus* both within, and between, fossil sites.
- At Pin Hole Cave, the large range of ⁸⁷Sr/⁸⁶Sr values implied that *R. tarandus* were non-local individuals moving over various geological boundaries, perhaps

in the nearby Peak District. As such, the time spent in the area surrounding Pin Hole Cave was minimal.

- Two separate patterns of mobility were recognised from the Kents Cavern *R. tarandus*. While two individuals appear to have remained relatively sedentary, only one animal overlapped with the local bioavailable strontium signal. This suggested that individuals were using separate, but geologically homogenous areas within southwest Britain. The values of the third individual at Kents Cavern represented a more cyclical pattern of ⁸⁷Sr/⁸⁶Sr values, implying seasonal migration and the regular use of defined areas over a distinct geological boundary, perhaps in nearby Dartmoor.
- These differences at Kents Cavern suggest that *R. tarandus* were either contemporaries and represent the natural dispersion within herds that use geologically different areas, or that the individuals were not contemporaries and there may have been a change in the migratory behaviour of herds through time. Both hypotheses are possible due to the extended accumulation of *R. tarandus* remains at the site.
- While the few studies that have been done on their European counterparts highlighted that *R. tarandus* apparently only exploited large grazing plains, the additional use of the high, open topography of upland areas, which potentially included Dartmoor and the Peak District, was typical of British *R. tarandus*. This could provide evidence for differences in the environments of Britain and continental Europe.

As one of the last northern hemisphere ungulates to undergo large-scale bi-annual migrations, *Rangifer tarandus* represent an important component of Arctic and Subarctic environments but are currently listed vulnerable in terms of their conservation status. This study therefore investigated the richer and more widespread record of Late Pleistocene *R. tarandus*, in order to improve our understanding of the impacts of climatic, environmental and anthropogenic changes on *R. tarandus* ecology and its future resilience.

Both modern and fossil *R. tarandus* were studied in order to achieve the three primary aims of this study, namely: (1) to reconstruct the palaeobiogeography, including patterns of seasonal movement, of Late Pleistocene *R. tarandus* in Britain and western Europe, (2) to establish patterns of palaeodiet in the Late Pleistocene *R. tarandus* and (3) to assess morphological variations of modern and historical specimens of *R. tarandus* in western Europe in response to environmental and climatic change. The fossil specimens represented 38 Late Pleistocene sites, spatially distributed along a north-south transect from northern Scotland to southern France and along an east-west transect from east Germany to southwest Britain. In addition to well-known assemblages, the inclusion of lesser studied sites provided a wide scope for the analysis of seasonal movements across Britain and western Europe. The study of modern and historical specimens not only enabled the development of a training set from which to reconstruct *R. tarandus* palaeodiet from dental microwear analysis, but also provided an important comparison for the body masses of Late Pleistocene specimens. The key findings of this research will now be summarised.

9.1. Patterns of Seasonality and Migration

The seasonality of site occupations was used to identify the migrational behaviour of Late Pleistocene *R. tarandus*, by establishing the age at death and season of death from the dental, postcranial, cranial and antler remains of fossil specimens. This research highlighted the renewed importance of non-invasive techniques for establishing age at death and season of death, which compared to their destructive counterparts, have previously been criticised as less precise when identifying seasonality. As such, an important aspect of the approach of this study has been the development and ground-

truthing of a new mandibular tooth wear profile for fossil *R. tarandus*. The profile replaces indicative stages of tooth wear with chronological ages, due in part to the high synchronicity of *R. tarandus* calving in May. This provided an efficient way to directly determine age at death from both mandibles and isolated cheek teeth, which are often abundant in fossil assemblages and might otherwise be excluded from palaeontological studies. For individuals 0-29 months in age, the monthly precision of the profile also enabled season of death to be inferred, something otherwise only achieved by the use of destructive thin-sectioning techniques.

By studying sites from the Early Devensian, Middle Devensian/Weichselian and Late Devensian/Weichselian, it was concluded that there was a difference both spatially and temporally in the seasonality of R. tarandus site occupations, a rejection of null hypothesis 1. Across all three stages, R. tarandus seasonality primarily represented migrational herds moving along a north-south trajectory. In Britain, seasonal movements potentially occurred from autumn/winter ranges in Devon, Somerset and Middlesex in the south of Britain, towards spring/summer ranges further north in Derbyshire, North Yorkshire and north west Scotland. Between these ranges, the seasonality reconstructed from the Early Devensian site of Windy Knoll, the Middle Devensian Creswell Crags sites of Pin Hole Cave, Church Hole Cave and Robin Hood Cave and the Late Devensian site of Ossom's Cave, also demonstrated the continued use of valleys in Derbyshire and Staffordshire as lower topography migration routes through the Peak District, during the major autumn and spring migrations. However, multiple signals of seasonality representative of occupation throughout the whole year have also been recognised from Middle Devensian/Weichselian *R. tarandus*, particularly in the south of Britain at Kents Cavern and Goyet in the Belgian Ardennes. This could support the presence of more sedentary herds, displaying only a small degree of mobility in order to sustain the productivity of grazing pastures. Alternatively, terrestrial connections between Britain and continental Europe could have provided the potential for additional movements along an east-west axis, visible as continuous site occupation in the fossil record. Such a migration pathway could further be supported by the spring/summer occupation observed from the Middle Devensian unit at Picken's Hole, which differed from the autumn/winter occupation reconstructed from the Early Devensian unit at the same site. Otherwise, R. tarandus from southern France, Belgium, Germany and Denmark appeared to occupy migrational niches, although without further evidence it is difficult to identify the centres and directions of migrations. As such, null hypothesis 2, which stated that the fluctuating presence of a landbridge connecting Britain to the European mainland during the last glaciation would not dictate migration routes undertaken by Late Pleistocene *R. tarandus* could neither be accepted nor rejected.

In Britain, *R. tarandus* seasonality from two Middle Devensian sites was investigated further in a pilot study of strontium isotope analysis. At Pin Hole Cave, the 0.0028 range of ⁸⁷Sr/⁸⁶Sr values was relatively large for a single individual and implied that the R. tarandus was non-local, moving instead over various geological boundaries perhaps in the nearby Peak District. This corresponded with the two separate seasons of occupation at Pin Hole Cave during the autumn and spring. As periods of annual migration, the time R. tarandus spent in the area surrounding Pin Hole Cave was probably minimal. However, at Kents Cavern, where *R. tarandus* potentially occupied the site throughout the whole year, two separate patterns of mobility were recognised in the strontium isotope analysis. While two individuals appeared to remain relatively sedentary, only one animal overlapped with the local bioavailable strontium signal. This suggested that individuals were using separate, but geologically homogenous areas within southwest Britain. The third individual at Kents Cavern represented a more cyclical pattern of ⁸⁷Sr/⁸⁶Sr values, implying seasonal migration and the regular use of defined areas over a distinct geological boundary, perhaps in nearby Dartmoor. This use of high, open topography was similar to the movement towards the Peak District suggested for the Pin Hole Cave *R. tarandus*, something which although might be typical of British *R. tarandus* has not been observed in their European counterparts occupying large grazing plains. This could provide evidence for differences in the environments of Britain and continental Europe. Due to the slow accumulation of *R. tarandus* remains at Kents Cavern, it is difficult to know whether or not the distinct behavioural differences in mobility represent the natural dispersion of contemporary animals, or a shift in the migratory behaviour of herds through time.

The differences observed could be explained by the geographical location of Kents Cavern, since the location of fossil sites in relation to geological boundaries can have significant implications for the interpretation of strontium isotope analysis. For example, at Kents Cavern, unless *R. tarandus* were moving over the more radiogenic granites of Dartmoor, where ⁸⁶Sr/⁸⁷Sr values rose above 0.7120, the local bioavailable strontium signal is relatively homogenous within the south of Britain. Therefore, it can be difficult to separate individuals with truly sedentary or migratory behaviours. Furthermore, the precise sampling requirements of strontium isotope analysis for mandibles containing both the M₂ and M₃ teeth, further limits the specimens and therefore fossil sites that are suitable for this analysis. In fact, one of the most significant limitations when using fossil assemblages to study patterns of mobility is the spatial distribution of fossil bearing study sites. Some of the richest assemblages are found in caves and fiesures, particularly in limestone regions. This accounts for the large number of sites studied from certain geographical localities, including Creswell Crags in Derbyshire (Church Hole Cave, Pin Hole Cave, Robin Hood Cave), the Mendip Hills in Somerset (Banwell Bone Cave,

Chelm's Combe, Gully Cave, Picken's Hole, Sandford Hill, Soldier's Hole, Wookey Hole), as well as the cave sites along the River Meuse in the Belgian Ardennes region (Goyet, Caverne Marie-Jeanne, Trou Al'Wesse, Trou de Chaleux, Trou Magrite, Trou du Moulin, Trou des Nutons, Trou du Sureau). Nevertheless, while this may limit the spatial scope of a study, the continued preservation of fossils within certain regions, particularly in the Mendip Hills, enables patterns of seasonality to be directly compared across the Early, Middle and Late Devensian.

9.2. Dietary Variability in Late Pleistocene Rangifer tarandus

In the strongly seasonal environments of the Arctic and Subarctic, forage availability is an important influence on *R. tarandus* migrations. Therefore, where multiple seasons of occupation were reconstructed for British sites from the Early (Windy Knoll) and Middle (Kents Cavern and Pin Hole Cave) Devensian, dental microwear analysis was also conducted to provide insight into the palaeodiet of *R. tarandus*. However, similar to the strict sampling criteria of strontium isotope analysis, the fossil sites and specimens selected for this analysis were limited by the preservation of the M₂. The modern training set developed for this analysis was significant as it represented the first time that examples of both the North American and European R. tarandus subspecies had been included in studies of diet. R. tarandus from the Derbyshire sites of Windy Knoll and Pin Hole Cave reconstructed microwear features consistent with leaf-dominated browsers, while at the lower latitude Kents Cavern, a browse-dominated to mixed-feeding niche was also represented. Therefore, although null hypothesis 3, that the changing climatic and environmental conditions during the Late Pleistocene in north west Europe will not lead to the formation of distinct ecotypes in *R. tarandus*, must be accepted, latitudinal differences within the browsing niche were evident from fossil R. tarandus. Furthermore, compared to modern subspecies where lichen is an important component of the diet, the lower number of pits in the fossil specimens was more consistent with the forest R. t. tarandus of Scandinavia where lichen consumption is closer to 25%, rather than 50%, of the winter diet.

Given the observable seasonality in modern *R. tarandus* diets, another unique aspect of this research was the ability to reconstruct seasonal variability in the dietary signals of microwear from both modern and fossil specimens where the season of death was known. This enabled clear differences to be identified between the increased number of pits during the winter/spring, associated with a rise in the percentage low lying lichen in the winter diet compared to the graminoid dominated summer diets. The seasonal differences in the microwear signal at Pin Hole Cave and Kents Cavern could represent

either sedentary herds exploiting surrounding forage with seasonal variability, or migratory herds using the site as part of their route between summer and winter ranges. It is also possible that non-contemporary individuals were measured, with the changing microwear signal representing palaeoenvironmental changes at the site over time.

9.3. Modern Versus Late Pleistocene Body Masses

The application of the average mass estimating equation to the postcrania of *R. tarandus* not only enabled the body masses of males and females to be reconstructed separately, but allowed direct comparisons to be made between the sizes of modern and fossil specimens. The body sizes of wild R. tarandus occupying alpine tundra dominated mountain regions are generally smaller than semi-domestic populations from either similar regions or the taiga forest. Between 1861-2006, fluctuations in body masses of modern R. tarandus from localities throughout Scandinavia have occurred in response to changes in group size or population density, snow or ice cover and migrational range. However, in both the R. t. platyrhynchus from Svalbard and R. t. tarandus from northern Sweden, the most significant decreases in body mass have been observed in response to a reduced access to forage, either as a result of changing climatic regimes or increased human activity. As such, it was possible to reject null hypothesis 4 and conclude that differences in the body sizes of historical through to modern populations have occurred as a result of changing Holocene climatic and anthropogenic influences. In Svalbard in particular, the average body mass of 56.23±2.18 kg reconstructed from females in 1975 was above 50 kg, a critical threshold for survival which populations today have surpassed in response to increased rain-on-snow events. Nevertheless, with average estimates of female body mass in excess of 75 kg, the fact that no Late Pleistocene populations appear to have reached the critical threshold also highlights the true extent of both the current and future vulnerability of *R. tarandus*.

This distinction between Late Pleistocene and Holocene body masses further implies that perhaps Late Pleistocene winters were neither as warm nor as wet as the present day, with forage unrestricted by rain-on-snow events. Otherwise, the Late Pleistocene specimens showed good consistency with the range of sizes observed from modern *R. t. tarandus*. From the Early Devensian, the male average body mass of 128.80 ± 8.67 kg was most consistent with the body masses of modern semi-domesticated forest *R. tarandus* herds from Finnmark and Norrbotten. As well as occupying areas of softer taiga snow cover which can be up to 65 cm deep, these herds are characterised by smaller group sizes of around 184 individuals, conditions which could therefore have been evident during the Early Devensian. However, the female average body mass of

 95.90 ± 5.19 kg was more like the mountain herds of Jämtland, where herds are larger and snow more hard-packed.

From the Middle and Late Devensian/Weichselian, the 119 kg average body mass of males from both stages was more consistent with the size of mountain herds from Jämtland, Härjedalen, Lappland and Oppland. In these modern herds, groups of around 419 animals occupy regions of hard-packed tundra snow <50 cm deep. Despite the variability between females weighing an average of 89.25 ± 3.11 kg from the Middle Devensian/Weichselian and 95.09 ± 4.03 kg from the Late Devensian/Weichselian, both body masses still overlapped with the range of modern mountain herds. It could therefore be inferred that these represent similar herd densities and snow conditions to both Late Pleistocene stages.

9.4. Future Work

Although reconstructions of the seasonality and migrations of Late Pleistocene *R. tarandus* were improved by the addition of dental microwear analysis, as well as the more destructive strontium isotope analysis, both of these techniques represented a relatively small component of this study. As such, future work should focus on increasing the sample sizes of these analyses in order to improve the robustness of the findings. For dental microwear analysis, the ability to reconstruct diet with seasonal resolution provides great potential for better understanding the palaeodiet of *R. tarandus*. Therefore, in addition to sampling more specimens from the three fossil sites already investigated, which represented assemblages where multiple seasons of occupation had been identified, sites where *R. tarandus* were clearly migrating should also be studied. From Early, Middle and Late Devensian Britain, this could include specimens with a season of death in autumn/winter from Devon, Somerset and Middlesex in southern Britain, as well as specimen's representative of spring/summer from North Yorkshire and north west Scotland.

Furthermore, it would also be interesting to directly compare the palaeodiet of *R. tarandus* from layers/units where different patterns of seasonality were observed from the same site, to assess the variability in diets under different palaeoenvironmental and palaeoclimatic conditions. These would include Picken's Hole, which represented both the Early and Middle Devensian, and Gully Cave, where Middle and Late Devensian *R. tarandus* were studied. Strontium isotope analysis at the two sites would also test whether the differences in the seasonality corresponded to a change in movement direction. However, as observed at Kents Cavern, it can be difficult to determine the scale of movement when the local bioavailable strontium is relatively homogenous.
Therefore, further work at this site should concentrate on species which are known to be non-migratory in the present day and likely expressed this trait during the Late Pleistocene. This should enable the migratory or sedentary nature of Kents Cavern *R. tarandus* to be more tightly constrained.

Nevertheless, one of the most significant findings from this research, in regards to the current state of *R. tarandus*, has been the relatively stable body masses of the Late Pleistocene compared to the critical and rapidly decreasing weights in modern populations. It is therefore essential to continue to improve our understanding of the mechanisms affecting body size and *R. tarandus* resilience, particularly pertaining to climatic and anthropogenic changes, to ensure the success of future conservation programmes.

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Appendix 1 Attritional Tooth Wear Profile

Appendix 1.1. Total Number of Specimens. The table outlines the total number of specimens, both modern and fossil, included in the development of the attritional tooth wear profile.

| Age | Number of Specimens | | Total |
|--------------|---------------------|--------|-------|
| - | Modern | Fossil | _ |
| 0-3 months | | 3 | 3 |
| 3 months | 1 | 3 | 4 |
| 4 months | 2 | 1 | 3 |
| 5-10 months | 1 | 7 | 8 |
| 10-12 months | | 7 | 7 |
| 15 months | 2 | | 2 |
| 16 months | 2 | | 2 |
| 17 months | | 4 | 4 |
| 18 months | 6 | | 6 |
| 21 months | 1 | | 1 |
| 21-22 months | | 1 | 1 |
| 22 months | | 2 | 2 |
| 15-22 months | | 1 | 1 |
| 22-24 months | | 2 | 2 |
| 27 months | 1 | 2 | 3 |
| 27-29 months | | 1 | 1 |
| 29 months | | 5 | 5 |
| 30 months | 3 | | 3 |
| 3-5 years | 23 | 9 | 32 |
| 6-9 years | 10 | 6 | 16 |
| >10 years | 4 | 2 | 6 |
| Total | 56 | 56 | 112 |

| ٨٩٥ | Pern | nanen | t | | | | Deci | duous | |
|--------------|----------------|----------------|----|-----------------------|----------------|-------|------|-------|-----------------|
| Age | M ₁ | M ₂ | Mз | P ₄ | P ₃ | P_2 | dp₄ | dp₃ | dp ₂ |
| 0-3 months | | | | | | | | | |
| 3 months | 1 | | | | | | 1 | 1 | 1 |
| 4 months | 2 | | | | | | 2 | 2 | 2 |
| 5-10 months | 1 | | | | | | 1 | 1 | 1 |
| 10-12 months | | | | | | | | | |
| 15 months | 2 | 2 | 2 | | | | | | |
| 16 months | 2 | 2 | 1 | | | | 2 | 2 | 2 |
| 17 months | | | | | | | | | |
| 18 months | 4 | 6 | 2 | 1 | 1 | 1 | 2 | 2 | 2 |
| 21 months | 1 | 1 | 1 | | | | | | |
| 21-22 months | | | | | | | | | |
| 22 months | | | | | | | | | |
| 15-22 months | | | | | | | | | |
| 22-24 months | | | | | | | | | |
| 27 months | 1 | 1 | 1 | | | | | | |
| 27-29 months | | | | | | | | | |
| 29 months | | | | | | | | | |
| 30 months | 3 | 3 | 3 | 3 | 3 | 2 | | | |
| 3-5 years | 23 | 23 | 23 | 23 | 23 | 23 | | | |
| 6-9 years | 9 | 10 | 10 | 10 | 10 | 10 | | | |
| >10 years | 2 | 3 | 4 | 1 | 3 | 4 | | | |

Appendix 1.2. Total Number of Teeth (Modern). The table outines the total number of teeth from modern specimens included in the development of the attritional tooth wear profile.

Appendix 1.3. Total Number of Teeth (Fossil). The table outlines the total number of teeth from fossil specimens included in the development of the attritional tooth wear profile.

| Ago | Perm | nanent | | | | | Decic | luous | |
|--------------|----------------|----------------|----|-------|----------------|-------|-------|-------|-----------------|
| Age | M ₁ | M ₂ | Mз | P_4 | P ₃ | P_2 | dp₄ | dp₃ | dp ₂ |
| 0-3 months | 2 | | | | | | 2 | 1 | 1 |
| 3 months | 3 | | | | | | 3 | 2 | 2 |
| 4 months | 1 | | | | | | 1 | 1 | 1 |
| 5-10 months | 7 | | | | | | 3 | 3 | 3 |
| 10-12 months | 7 | 4 | | | | | 5 | 2 | 2 |
| 15 months | | | | | | | | | |
| 16 months | | | | | | | | | |
| 17 months | 3 | 3 | 1 | | | | 2 | 2 | 1 |
| 18 months | | | | | | | | | |
| 21 months | | | | | | | | | |
| 21-22 months | 1 | 1 | | | | | 1 | | |
| 22 months | 2 | 2 | | 1 | 1 | 1 | | | |
| 15-22 months | 1 | | | | | | 1 | | |
| 22-24 months | 2 | 1 | 1 | | | | | | |
| 27 months | | 1 | 2 | | | | | | |
| 27-29 months | 1 | 1 | 1 | | | | | | |
| 29 months | 1 | 3 | 4 | 1 | 1 | 1 | | | |
| 30 months | | | | | | | | | |
| 3-5 years | 5 | 5 | 6 | 6 | 6 | 6 | | | |
| 6-9 years | 5 | 6 | 4 | 5 | 4 | 2 | | | |
| >10 years | 1 | 1 | | | 1 | 1 | | | |



Appendix 1.4. Tooth Wear in the M₁ of Calves and Subadults (0-30 months).



Appendix 1.5. Tooth Wear in the M₁ of Adults (3-13 years).



Appendix 1.6. Tooth Wear in the M₂ of Calves and Subadults (0-30 months).



Appendix 1.7. Tooth Wear in the M₂ of Adults (3-13 years).



Appendix 1.8. Tooth Wear in the M₃ of Calves and Subadults (0-30 months).



Appendix 1.9. Tooth Wear in the M₃ of Adults (3-13 years).



Appendix 1.10. Tooth Wear in the dp₄/P₄ of Calves and Subadults (0-30 months).



Appendix 1.11. Tooth Wear in the P₄ of Adults (3-13 years).



Appendix 1.12. Tooth Wear in the dp₃/ P₃ of Calves and Subadults (0-30 months).



Appendix 1.13. Tooth Wear in the P₃ of Adults (3-13 years).



Appendix 1.14. Tooth Wear in the dp₂/P₂ of Calves and Subadults (0-30 months).

| P2 | Fossil Specimens (MSc, PhD) | Modern Specimens (Norway, <mark>Sweden</mark> , Greenland) |
|--------------|---|---|
| 3-5 years | 970 RN 1877 In 180 R 804 843 805 383 825 167 | 41 |
| 3 years | | でのです。 BM1640 4505 4072 |
| 4 years | | 4352 4352 |
| | | 4343 4343 |
| 5 years | | 4227 4227 4094 4094 |
| 6-9 | | 4208 4208 4432 4432 |
| years | 802 839 | |
| 6 years | | 200 E20 4494 4494 |
| 7 years | | 4489 <u>4489</u> |
| 8 years | | |
| 9 years | | |
| >10 years | 852 | |
| 10 years | | |
| 11 years | | |
| 12 years | | |
| 13 years | | |

Appendix 1.15. Tooth Wear in the P_2 of Adults (3-13 years).

Appendix 2. Postcranial Measurements

Dimensions for postcranial measurements were taken from Von den Driesch (1976), Weinstock (2000a) and Collinge (2001).



Appendix 2.1. Humerus Measurements





Appendix 2.3. Ulna Measurements



Ulna

- Lo length of olecranon
- Dpa depth across Processus anconaeus
- Sdo smallest depth of olecranon
- Bpc greatest breadth of proximal articular surface

Appendix 2.4. Metacarpal Measurements









| I I - Gic | greatest length norn caput |
|-----------|--------------------------------|
| F2 | breadth from the greater to |
| | the lesser trochanter |
| F3 | breadth from the fovea capitis |
| | to the lesser trochanter |
| F4 - Bt | smallest breadth of trochlea |
| F5 - Bd | greastest distal breadth |
| | |









Tibia

| T1 - GI | greatest length |
|---------|---------------------------|
| T2 - Bp | greatest proximal breadth |
| T3 - Dp | proximal depth |
| T4 - Bd | greatest distal breadth |
| T5 - Dd | distal depth |

Appendix 2.7. Calcaneum Measurements



Appendix 2.8. Metatarsal Measurements



Appendix 3. Mass Estimating Equations for Cervidae

Predictive equations for estimating the body mass of Cervidae were developed by Collinge (2001) following modifications of work by Scott (1990). Measure dimensions for postcranial elements use Von den Driesch (1976), Weinstock (2000a) and Collinge (2001). Statistical analysis of the accuracy of body mass estimates included R² (coefficient of determination), %PE (percentage predictive error) and %SEE (percentage standard error of the estimate). After Collinge (2001), modified from Scott (1990).

| | Measure | Slope | Intercept | R ² | %SEE | %PE |
|-------------|----------|--------|-----------|----------------|------|-----|
| | | (m) | (c) | | | |
| Humerus | H1 (Glc) | 3.4337 | -2.4141 | 0.9183 | 40 | 27 |
| | H2 (GI) | 3.3580 | -2.4788 | 0.9260 | 37 | 24 |
| | H3 (Bp) | 2.7080 | 0.2432 | 0.9463 | 27 | 17 |
| | H4 (Bt) | 2.5568 | 0.4084 | 0.9590 | 27 | 20 |
| | H5 (Bd) | 2.6389 | 0.2582 | 0.9596 | 27 | 19 |
| | H6 | 2.7230 | 1.3730 | 0.9241 | 29 | 31 |
| Radius | R1 (GI) | 3.0795 | -2.1515 | 0.8549 | 45 | 36 |
| | R2 (Bfp) | 2.5150 | 0.4304 | 0.9630 | 35 | 18 |
| | R3 (Dp) | 2.5588 | 1.0498 | 0.9606 | 33 | 24 |
| | R4 (Bp) | 2.4301 | 0.3842 | 0.9560 | 23 | 19 |
| | R5 (Bd) | 2.4956 | 0.4581 | 0.9600 | 26 | 20 |
| Metacarpals | Mc1 (GI) | 2.5036 | -1.2742 | 0.5404 | 57 | 37 |
| | Mc2 (Bp) | 2.6568 | 0.6070 | 0.9500 | 32 | 26 |
| | Mc3 (Dp) | 2.8040 | 1.0687 | 0.9393 | 35 | 24 |
| | Mc4 (Bd) | 2.3300 | 0.7466 | 0.8664 | 98 | 28 |
| | Mc5 (Dd) | 2.6352 | 1.2473 | 0.9184 | 34 | 23 |
| Femur | F1 (Glc) | 3.5335 | -2.9926 | 0.9299 | 34 | 24 |
| | F2 | 2.6928 | -0.2670 | 0.9526 | 27 | 17 |
| | F3 | 2.9500 | -0.1030 | 0.9348 | 33 | 23 |
| | F4 (Bt) | 2.9714 | 0.7268 | 0.9433 | 30 | 21 |
| | F5 (Bd) | 2.9100 | -0.0883 | 0.9509 | 32 | 22 |
| Tibia | T1 (GI) | 3.8551 | -3.6352 | 0.8513 | 46 | 21 |
| | T2 (Bp) | 2.8861 | -0.2841 | 0.9548 | 30 | 29 |
| | Т3 | 3.1432 | 0.1174 | 0.9193 | 42 | 23 |
| | T4 (Bd) | 2.8486 | 0.3000 | 0.9494 | 31 | 23 |
| | T5 (Dd) | 2.9628 | 0.6159 | 0.9429 | 36 | 18 |
| Metatarsals | Mt1 (GI) | 3.0039 | -2.0105 | 0.5936 | 55 | 24 |
| | Mt2 (Bp) | 2.9334 | 0.6132 | 0.9398 | 36 | 24 |
| | Mt3 (Dp) | 2.8848 | 0.6369 | 0.8879 | 82 | 27 |
| | Mt4 (Bd) | 2.7521 | 0.5397 | 0.9356 | 38 | 25 |
| | Mt5 (Dd) | 2.9391 | 1.1375 | 0.9232 | 36 | 24 |

Appendix 4. Body Mass

Appendix 4.1. Skeletal Elements and Dimensions Excluded (modern). The table details the skeletal elements and dimensions that were excluded from the reconstructions of average body mass for modern and historical *R. tarandus*. Generally, these were estimates that either generated inconsistent results, or overestimated or underestimated body mass or when compared to other elements or dimensions from the same individual.

| Country | Locality and Date of Collection | Sample ID | Sex | Skeletal Element/ Dimension Excluded | Reason for Exclusion |
|---------|---------------------------------------|-----------------------|------------------|---|----------------------------------|
| Canada | Alberta 1930s | 122668 | Male | H1-Glc H2-Gl | Overestimated |
| | British Columbia 1936 | 70566 | Male | H1-Glc Femur | Overestimated |
| | Northwest Territories 1911 | 34439 | Male | Femur | Underestimated |
| Norway | Buskerud 1970 | B.1857 | Female | Metacarpal Metatarsal | Inconsistent |
| | | B.1862 B.1865 | Female Female | Femur Femur | Inconsistent Inconsistent |
| | Hordaland 1970s | B.2084 | Female | F2 | Underestimated |
| | Oppland 2006 Svalbard 1975 | B.8486 B.2592 | Female Female | Metatarsal F2 | Underestimated Underestimated |
| Sweden | Lappland 1950s (forest) | AJN:4142 (A649889) | Male | Metatarsal | Overestimated |
| | Norrbotten 1950s | (A601348) | Male | Femur | Overestimated |
| USA | Maine 1888 | 5141 | Female | R1-GI | Overestimated |

Appendix 4.2. Specimens with Mislabelled Sex. The table details the Swedish *Rangifer tarandus* specimens from the Ájtte Museum collection.

| Locality and Date of Collection | Sample ID | Sex (Original Incorrect Label) |
|---------------------------------------|--------------------|--------------------------------------|
| Norrbotten | AJN:4236 (A649112) | Male |
| 1950s | AJN:4216 (A649102) | Male |
| | AJN:4731 (A649149) | Male |
| | AJN:4188 (A649161) | Male |
| | AJN:4741 (A649160) | Male |
| | AJN:4208 (A649101) | Female |
| | AJN:4211 (A649103) | Female |
| | AJN:4186 (A649162) | Female |
| Lappland | AJN:4578 (A649297) | Female |
| 1950s | AJN:4579 (A649299) | Female |
| (mountain) | AJN:4580 (A649301) | Female |
| - | AJN:4581 (A649302) | Female |

Appendix 4.3. Results of Shapiro-Wilks Test for Normality.

| Locality and | | Shapiro-Wilks Analysis | | | | |
|------------------|--------|------------------------|-----|---------|--|--|
| Collection Date | Sex | w | df | P value | | |
| | | Statistic | | | | |
| Alberta 1930s | Male | 0.944 | 26 | 0.164 | | |
| | Female | 0.902 | 19 | 0.053 | | |
| Nunavut 1905 | Female | 0.927 | 27 | 0.060 | | |
| NWT 1911 | Male | 0.952 | 21 | 0.371 | | |
| Finnmark 1869 | Male | 0.962 | 25 | 0.460 | | |
| Oppland 1947 | Male | 0.888 | 6 | 0.308 | | |
| Buskerud 1948 | Male | 0.992 | 85 | 0.866 | | |
| | Female | 0.954 | 50 | 0.050 | | |
| Buskerud 1970 | Male | 0.974 | 37 | 0.512 | | |
| | Female | 0.992 | 169 | 0.514 | | |
| Hordaland 1970 | Male | 0.987 | 213 | 0.051 | | |
| | Female | 0.983 | 128 | 0.111 | | |
| Oppland 2006 | Male | 0.891 | 14 | 0.083 | | |
| | Female | 0.976 | 103 | 0.055 | | |
| Norrbotten 1909 | Male | 0.962 | 53 | 0.088 | | |
| Jamtland 1950s | Male | 0.978 | 45 | 0.557 | | |
| | Female | 0.979 | 41 | 0.641 | | |
| Harjedalen 1950s | Male | 0.963 | 49 | 0.131 | | |
| | Female | 0.973 | 28 | 0.663 | | |
| Lappland f | Male | 0.825 | 7 | 0.072 | | |
| Lappland m | Male | 0.991 | 75 | 0.897 | | |
| | Female | 0.957 | 20 | 0.482 | | |
| Norrbotten 1950s | Male | 0.934 | 28 | 0.080 | | |
| | Female | 0.964 | 12 | 0.842 | | |
| Spitsbergen 1861 | Male | 0.956 | 34 | 0.190 | | |
| Spitsbergen 1960 | Male | 0.952 | 32 | 0.163 | | |
| Spitsbergen 1975 | Male | 0.942 | 21 | 0.239 | | |
| | Female | 0.966 | 25 | 0.552 | | |

Appendix 4.3.1. Shapiro-Wilks Test for Normality for Modern and Historical Specimens.

| | | Shapiro-Wilks Analysis | | | |
|---------------------------------|--------|------------------------|----------------|---------|--|
| Subspecies | Sex | W | df | P value | |
| | | Statistic | | | |
| Canada <i>R.t.caribou</i> | Male | | Sample omitted | t l | |
| | Female | | Sample omitted | t | |
| Canada <i>R.t.groenlandicus</i> | Male | | Sample omitted | t d | |
| Norway R.t.tarandus | Male | 0.830 | 6 | 0.106 | |
| | Female | 0.889 | 4 | 0.379 | |
| Sweden R.t.tarandus | Male | 0.937 | 6 | 0.636 | |
| | Female | 0.926 | 4 | 0.571 | |
| Svalbard R.t.platyrhynchus | Male | 0.998 | 3 | 0.917 | |
| | Female | | Sample omitted | t d | |
| R.t.caribou | Male | | Sample omitted | t d | |
| | Female | | Sample omitted | t d | |
| R.t.groenlandicus | Male | | Sample omitted | t d | |
| R.t.tarandus | Male | 0.937 | 12 | 0.465 | |
| | Female | 0.949 | 8 | 0.705 | |
| R.t.platyrhynchus | Male | 0.998 | 3 | 0.917 | |
| | Female | | Sample omitted | t | |

Appendix 4.3.2. Shapiro-Wilks Test for Normality for Rangifer tarandus Subspecies.

Appendix 4.3.3. Shapiro-Wilks Test for Normality for Early Devensian Specimens.

| | | Shapiro-Wilks Analysis | | | |
|------------------------|--------|------------------------|-------------|---------|--|
| Site | Sex | W | df | P value | |
| | | Statistic | | | |
| Banwell Bone Cave | Male | 0.972 | 42 | 0.396 | |
| | Female | 0.983 | 65 | 0.521 | |
| Isleworth | Male | 0.956 | 18 | 0.526 | |
| | Female | 0.915 | 14 | 0.184 | |
| Picken's Hole (Unit 5) | Male | 0.864 | 10 | 0.086 | |
| | Female | 0.808 | 4 | 0.117 | |
| Stump Cross Cavern | Male | Sa | ample omitt | ed | |
| | Female | 0.905 | 12 | 0.184 | |
| Windy Knoll | Male | 0.912 | 4 | 0.491 | |
| | Female | 0.928 | 6 | 0.567 | |
| | | | | | |
| Early Devensian | Male | 0.897 | 5 | 0.395 | |
| | Female | 0.853 | 5 | 0.203 | |

| | | Shapiro-Wilks Analysis | | | |
|-------------------------|--------|------------------------|----------------|---------|--|
| Site | Sex | W | df | P value | |
| | | Statistic | | | |
| Brixham Cave | Male | 0.973 | 16 | 0.888 | |
| | Female | 0.913 | 6 | 0.458 | |
| Gully Cave | Male | 0.860 | 7 | 0.151 | |
| | Female | 0.961 | 10 | 0.792 | |
| Inchnadamph Bone Cave | Male | Sa | Sample omitted | | |
| | Female | 0.814 | 3 | 0.149 | |
| Kents Cavern | Male | 0.9499 | 21 | 0.332 | |
| | Female | 0.965 | 18 | 0.709 | |
| Mammoth Cave | Male | Sa | Sample omitted | | |
| | Female | 0.950 | 6 | 0.739 | |
| Picken's Hole (Unit 3) | Male | Sa | Sample omitted | | |
| Pin Hole Cave | Male | 0.934 | 13 | 0.380 | |
| | Female | 0.987 | 15 | 0.997 | |
| Robin Hood Cave | Female | 0.912 | 3 | 0.425 | |
| Sandford Hill | Male | 0.955 | 15 | 0.604 | |
| | Female | 0.979 | 52 | 0.474 | |
| Goyet Troisième Caverne | Male | 0.924 | 15 | 0.225 | |
| | Female | 0.987 | 36 | 0.941 | |
| Caverne Marie-Jeanne | Male | 0.921 | 6 | 0.515 | |
| | Female | 0.987 | 22 | 0.987 | |
| Trou Al'Wesse | Male | Sa | Sample omitted | | |
| | Female | 0.915 | 7 | 0.429 | |
| Trou Magrite | Male | 0.931 | 16 | 0.254 | |
| | Female | 0.943 | 28 | 0.135 | |
| Trou du Moulin | Male | Sa | Sample omitted | | |
| | Female | 0.944 | 6 | 0.690 | |
| Trou du Sureau | Male | 0.926 | 20 | 0.128 | |
| | Female | 0.982 | 28 | 0.895 | |
| Salzgitter-Lebenstedt | Male | 0.989 | 251 | 0.057 | |
| | Female | 0.987 | 127 | 0.202 | |
| Westeregeln | Male | 0.970 | 10 | 0.888 | |
| Ellewoutsdijk | Male | Sa | Sample omitted | | |
| | Female | Sa | Sample omitted | | |
| Raalte | Male | 0.946 | 16 | 0.430 | |
| | Female | 0.901 | 19 | 0.051 | |
| Middle | Male | 0.955 | 18 | 0.603 | |
| Devensian/Weichselian | Female | 0.960 | 17 | 0.630 | |

Appendix 4.3.4. Shapiro-Wilks Test for Normality for Middle Devensian/Weichselian Specimens.
| | | Shapiro-Wilks Analysis | | |
|------------------------|--------|------------------------|----|----------------|
| Site | Sex | W | df | P value |
| | | Statistic | | |
| Chelm's Combe | Male | 0.934 | 8 | 0.553 |
| | Female | 0.945 | 6 | 0.969 |
| Gully Cave | Male | 0.942 | 3 | 0.536 |
| | Female | Sample omitted | | |
| Ossom's Cave | Male | 0.972 | 5 | 0.886 |
| | Female | 0.952 | 5 | 0.748 |
| Soldier's Hole | Male | 0.975 | 55 | 0.306 |
| | Female | 0.950 | 25 | 0.256 |
| Trou de Chaleux | Male | Sample omitted | | |
| | Female | 0.898 | 8 | 0.276 |
| Trou des Nutons | Female | 0.908 | 8 | 0.338 |
| Køge Bugt | Male | 0.986 | 21 | 0.982 |
| | Female | 0.973 | 19 | 0.843 |
| Nørre Lyngby | Male | Sample omitted | | |
| | Female | 0.999 | 3 | 0.938 |
| Abri de Laugerie Haute | Male | 0.950 | 12 | 0.630 |
| - | Female | 0.924 | 18 | 0.153 |
| Abri de la Madeleine | Male | 0.976 | 34 | 0.654 |
| | Female | 0.982 | 87 | 0.266 |
| Late | Male | 0.858 | 9 | 0.091 |
| Devensian/Weichselian | Female | 0.954 | 10 | 0.722 |

Appendix 4.3.5. Shapiro-Wilks Test for Normality for Late Devensian/Weichselian Specimens.

Supplementary Data

- SD 1 Late Pleistocene Material Britain
- SD 2 Late Pleistocene Material Belgium
- SD 3 Late Pleistocene Material Denmark
- **SD 4 Late Pleistocene Material France**
- SD 5 Late Pleistocene Material Germany
- SD 6 Late Pleistocene Material Switzerland
- SD 7 Late Pleistocene Material The Netherlands
- SD 8 Late Pleistocene Material Poland
- **SD 9 Modern and Historical Material**
- SD 10 Average Estimated Body Mass
- **SD 11 Dental Microwear Analysis**