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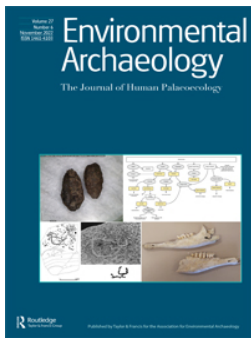
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Life, Death and Teeth of Late Neolithic Sheep and Red Deer Excavated at Ness of Brodgar, Orkney Islands (UK)

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ABSTRACT

The faunal remains from the late Neolithic site of Ness of Brodgar on the Orkney Islands (UK) provide a unique opportunity to investigate past adaptations of animal husbandry strategies to the Northern island environment, as well as the potential management of red deer. In this study, sheep and red deer mandibles and loose teeth (dP₄ & M₃) from the Ness of Brodgar were studied to construct age-at-death profiles, and analysed for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{18}\text{O}$. The mortality profile showed that around half of the analysed sheep were slaughtered when they reached maturity (i.e. after 2–4 years of life), consistent with a husbandry regime targeted at meat production. The stable isotope evidence indicates seaweed consumption in winter by several sheep (domesticates), but not by red deer (wild, possibly managed fauna). This dietary difference may have resulted from anthropogenically mediated influences, e.g. restriction of red deer habitats to upland areas. The varying extent of seaweed consumption between individual sheep and between Neolithic Orkney sites suggests differences in sheep husbandry practices across Orkney, indicating that the adaptation to consume seaweed was not ubiquitous on Orkney in the Neolithic, and did not follow a linear development.

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Introduction

The Ness of Brodgar is a multiphase Neolithic site that spans the whole of the Neolithic period in Orkney (ca. 3500–2300 cal BC), with its main period of site activity in the Later Neolithic (Card et al. 2018, 2020a). It covers over 2.5 hectares at the ‘Heart of Neolithic Orkney’ UNESCO World Heritage Site on the Orkney Islands, Scotland (Figure 1). This site has a density of monumental Neolithic structures unparalleled on Orkney, and is located between two stone circles, the Ring of Brodgar and the Stones of Stenness (both within 1 km of the site). The Ness of Brodgar has been suggested as a key gathering place for communities across Orkney and beyond in the Late Neolithic (Card, Edmonds, and Mitchell 2020b, 2018) based on its sheer size, quality of workmanship, the deliberate placement of large numbers of animal remains (Mainland et al. 2014), and the range of materials from other areas present at the Ness of Brodgar (e.g. pitchstone from Arran in Western Scotland, maceheads from the Scottish Western Isles, and an axe

blank from Langdale in the English Lake District; Card et al. 2018).

Excavations at the Ness of Brodgar are still ongoing, and research on the estimated 175,000 bone fragments recovered to date at the Ness of Brodgar is still in its initial phases (Mainland et al. 2020, 2014). As the largest bone collection in Neolithic Scotland, the study of these animal remains has great potential to further explore the central role the Ness of Brodgar seems to have played in Late Neolithic Orkney, and to investigate animal husbandry practices and adaptations to the environment at this time. However, since the Ness of Brodgar appears to be exceptional not just in its size, but also in the type of deposits, the faunal remains at this site might not reflect domestic Neolithic animal husbandry on Orkney in the way remains at smaller settlement sites would be expected to.

Cattle (*Bos taurus*) dominate the faunal assemblage at the Ness of Brodgar, followed by sheep/goats (ovicaprid), and a small number of pigs (*Sus scrofa domestica*; zooarchaeological analysis ongoing; Mainland

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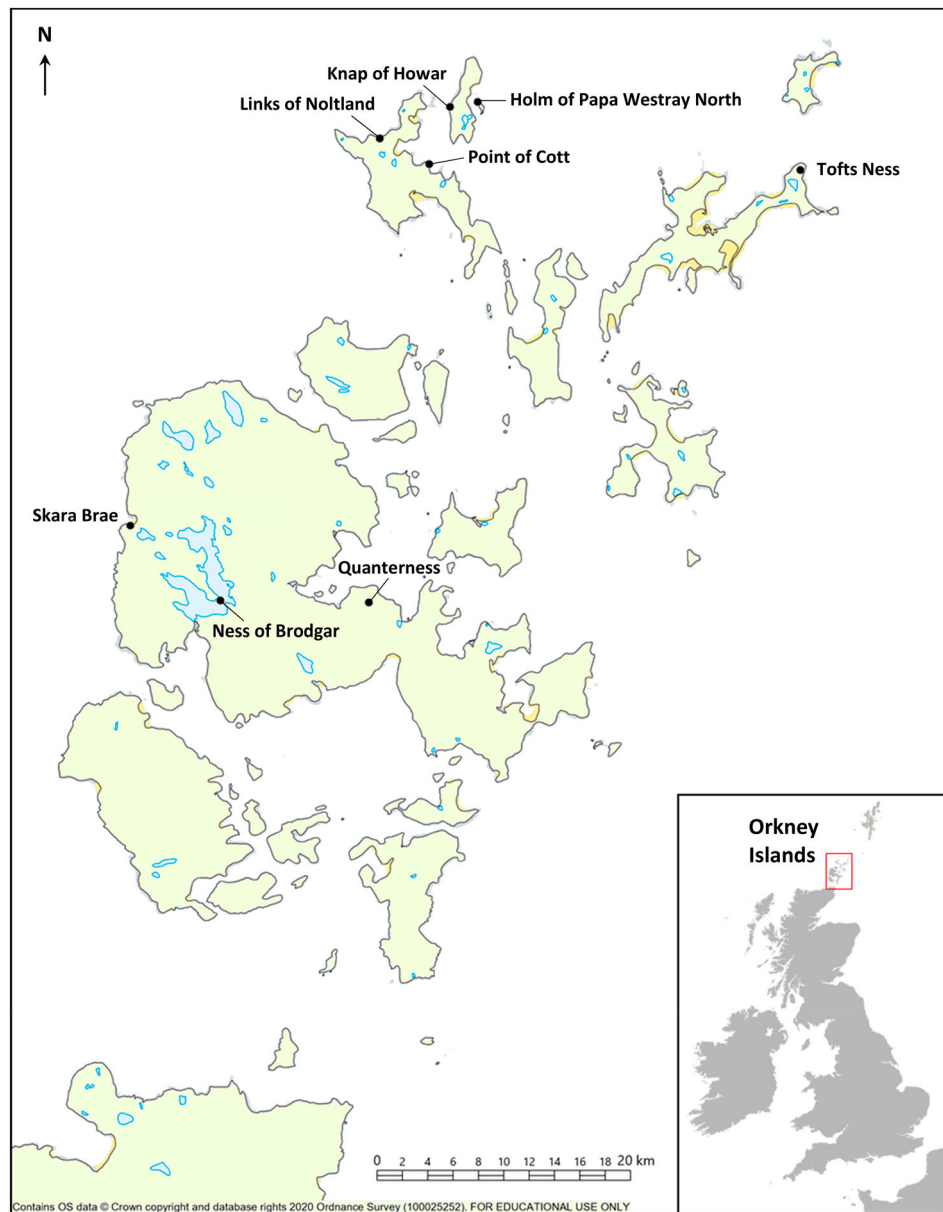


Figure 1. Locations of the Neolithic archaeological sites mentioned in this paper on the Orkney Islands (using present-day coast-lines). The inset map shows the location of the Orkney Islands in Britain. Map modified from Digimap.

et al. 2020). A bone deposit around the largest structure at the Ness of Brodgar, Structure 10, has revealed the deliberate placement of tibiae from over 400 cattle, suggesting the importation of non-local cattle (tibiae) due to the sheer number of animals involved (Mainland et al. 2014). This deposit appears to be unique on Neolithic Orkney so far, and gives further evidence of potential ceremonial behaviour, as well as the possibility of conspicuous consumption of beef/marrow (Mainland et al. 2020). Ovicaprid remains are far less common than cattle in the bone deposit at Structure 10, and pigs appear to be absent (minimum numbers of individuals: $MNI_{cattle} = 37$, $MNI_{sheep} = 2$, $MNI_{pigs} = 0$; Mainland et al. 2014). In contrast, in Southern British Late Neolithic feasting contexts, pigs appear to have been the main feasting animal, followed by cattle (reviewed in Serjeantson 2011),

whereas sheep played a minor role (Albarella and Serjeantson 2002; Rowley-Conwy and Owen 2011; Serjeantson 2011). It has been suggested that sheep were more likely to be consumed in more domestic settings due to giving a lower, more manageable amount of meat than e.g. cattle (Serjeantson 2011). It is still unclear whether sheep at the Ness of Brodgar were similarly predominantly locally raised for domestic purposes (possibly for milk rather than meat), or also had a major part in feasting and exchanges during communal gatherings on Orkney.

In addition to domesticated animals, the excavation at the Ness of Brodgar has also yielded remains of red deer (*Cervus elaphus*; Mainland et al. 2020). Red deer were introduced to Orkney and the Outer Hebrides at the beginning of the third millennium BC (Serjeantson 1990; Tresset 2002) from an unknown location;

their genetic diversity is inconsistent with an origin from mainland Scotland, Ireland or Norway (Stanton et al., 2016). Subsequent management by humans has been suggested (Clarke et al. 2017). Red deer seem to have had a special significance for the inhabitants of the Orkney Islands in the Late Neolithic and Early Bronze Age (Morris 2005). This is evidenced most clearly by a deliberately deposited heap of red deer remains at the late Neolithic and Bronze age settlement Links of Noltland on Westray, Orkney. This heap consisted of at least 15 partly articulated individuals, laid out on their left-hand side, and had no evidence of butchery (approximately 2200 cal BC; Clarke et al. 2017; Sharples 2000; Figure 1). Several smaller Late Neolithic deposits of red deer have been found on the Orkney Islands which have been suggested to form a type of 'sealing' (a final deposit overlying other remains), and appear to be associated with an abandonment of houses or places (Clarke et al. 2017; Richards et al. 2015). At the Ness of Brodgar, red deer remains (in some cases articulated) also appear to have been deliberately deposited on top of other remains in several contexts associated with Structure 10 toward the end of the site's activity (Mainland et al. 2020, 2014). In addition to examining the nature of these bone depositions, the study of the lives these animals had prior to death also has great potential to inform current understanding of the significance of red deer. For example, the study of red deer diets enables insights into past habitats, which in turn can reveal information about potential deer management.

Previous studies have shown coastal sheep grazing to have been of particular importance on Orkney in the Neolithic (Jones and Mulville 2016), with dietary studies indicating that sheep consumed moderate amounts of seaweed upon their introduction to Orkney (at Knap of Howar, fourth millennium cal BC; Balasse et al. 2019) and significant amounts later in the Neolithic at Papa Westray North Cairn, Point of Cott, Quanterness, Skara Brae and Tofts Ness (see Figure 1; Balasse et al. 2019, 2009, 2006, 2005; Balasse and Tresset 2009; Dockrill et al. 1994; Schulting et al. 2017). Studies of soil micromorphology at the Ness of Brodgar have shown increased amounts of sand grains in ovicaprid dung, which have been suggested to be due to seaweed consumption (Sawyer, Shillito, and Card n.d.). While still close to the sea (3–4 km walking distance), the Ness of Brodgar was likely further inland than most of these sites and seaweed would not have grown locally, as it is located on an isthmus between two freshwater lakes, with only gradual ingress of ocean water likely from the early Neolithic into the southwestern Loch of Stenness (turning it brackish today; Bates et al. 2016). Fish remains are rare at the Ness of Brodgar (Harland 2020), and apart from remains of a non-determinate whale species (Mainland et al. 2020), there is currently little

evidence of marine animal use at the Ness of Brodgar. It remains to be investigated whether the evidence of seaweed-consumption by sheep follows this trend of marine-food avoidance, or was as wide-spread among sheep excavated from the Ness of Brodgar as it appears to have been at other Late Neolithic sites on Orkney.

Previously published archaeozoological research at the Ness of Brodgar provided reviews of the zooarchaeological remains (Harland 2020; Mainland et al. 2020), and focused on bone deposits, yielding a detailed description and evaluation of a small number of deposits (Mainland et al. 2014). This study takes a large-scale, site-wide approach to gain a further understanding of the lives and deaths of sheep and red deer excavated from the Ness of Brodgar by means of an integrated study of sheep and red deer mandibles and loose teeth excavated at the Ness of Brodgar, comprising the study of dental wear and eruption, and stable carbon, oxygen, and nitrogen isotope ratio analysis ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and $\delta^{15}\text{N}$). These data are analysed to construct mortality profiles, and to investigate diets and the time of birth. The combination of these methods can provide detailed information on past animal management (e.g. by controlling lambing times of sheep to occur when sufficient grazing is available), patterns of human exploitation (e.g. presence or absence of specific age groups in the mortality profile), and land use and land access over time (e.g. coastal grazing or inland grazing). The study and comparison of the diets of Neolithic deer and sheep on the Orkney Islands may also yield more information on the management and significance of deer, whereby similar diets might indicate parallels in sheep and deer management. Additionally, local adaptations to the wider landscape may be studied further by exploring the role of marine resource use at the Ness of Brodgar in the form of seaweed consumption.

The primary objectives of this study were therefore: 1) to establish the mortality profiles of sheep and deer at the Ness of Brodgar to assess patterns of exploitation, 2) to study sheep and deer diets using stable isotope ratio analysis to investigate the extent of seaweed consumption and 3) to study sheep birth seasonality.

Materials and Methods

Age-At-Death Assessment

The material studied for age-at-death assessments included all Neolithic unburnt sheep/goat and deer mandible fragments, loose deciduous lower fourth premolars ($\text{dP}_{4\text{s}}$) and lower third molars ($\text{M}_{3\text{s}}$) from the Ness of Brodgar (NOB) excavated prior to 2020 (Supplementary Table S.1). Sheep/goat teeth were categorised as either sheep-like, goat-like, or

indeterminate based on the morphological distinctions described in Payne (1985) and Halstead, Collins, and Isaakidou (2002). The minimum number of individuals (MNI) based on mandible fragments and loose dP₄s and M₃s were assessed taking into account side, size, morphology, tooth wear and state of eruption. Sheep tooth wear was assessed following Payne (1987, 1973) with some alterations necessitated by the predominance of loose teeth (see Supplementary Table S.2). Deer crown heights and tooth development were assessed and converted to estimated ages following Lowe 1967 and Steele and Weaver 2012 (see supplementary material, 1.2 *Deer tooth wear*).

None of the excavated sheep and deer mandibles and loose teeth have yet been dated directly, but the chronology of the surrounding contexts was established based on radiocarbon and magnetic dates as well as stratigraphic analyses (Card et al. 2018). None of the sheep and deer mandibles and loose teeth appear to be associated with pre-Grooved Ware contexts, and the vast majority are associated with contexts postdating 2500 cal BC (see list of contexts in Supplementary Tables S.8 and S.12). A more detailed chronology of these remains cannot yet be given, as excavation, dating, stratigraphic analyses and chronological modelling of the site are still ongoing.

Stable Carbon, Oxygen, and Nitrogen Isotope Ratios

Seaweeds commonly consumed by seaweed-eating sheep have higher $\delta^{13}\text{C}$ values than the terrestrial C₃ plants present on Orkney (Balasse, Mainland, and Richards 2009; Blanz et al. 2020; Hansen, Hector, and Feldmann 2003). Since bone collagen and tooth enamel $\delta^{13}\text{C}$ values reflect dietary $\delta^{13}\text{C}$ values, the consumption of seaweed can be tracked (Balasse, Mainland, and Richards 2009, 2005; Blanz et al. 2020; Guiry and Szpak 2020). Bone collagen $\delta^{13}\text{C}$ values represent dietary averages over the period of tissue formation and remodelling, potentially spanning multiple years, such that smaller seasonal contributions of seaweed to diet may be undetectable (Blanz et al. 2020; Schulting et al. 2017). In contrast, sequential enamel analyses deliver time-resolved datasets and can reveal seasonal changes in the amounts of seaweed consumed (Balasse et al. 2019), as well as allowing the investigation of birth seasonality via the reconstruction of the seasonal cycle record in molars from $\delta^{18}\text{O}$ values (Balasse et al. 2017).

Seven sheep M₃s were selected from the Central Midden Area (CMA), and ten sheep (9 M₃s and 1 M₂) and three deer M₃s from Structure 10, giving preference to M₃s still in mandibles to enable comparisons between bone collagen and tooth enamel isotope ratios from the same individual (see Supplementary Table S.12). The teeth all belonged to

different individuals based on comparisons of side, tooth wear, size and morphology. The CMA, mainly between Structures 1, 8, 11 and 12 (including over a central paved area between these buildings, associated with Structure 25), is composed of widespread, multi-context, deep midden deposits, which postdate the construction of Structure 10 at around circa 2900 cal BC (Card et al. 2018), with some of the upper layers possibly being contemporary with the infills at Structure 10 (i.e. 2500 cal BC). The samples from Structure 10 date to the final abandonment and decommissioning of Structure 10, around 2500 cal BC, with five associated with the bone deposit (NOB_{ovis}59, NOB_{ovis}61, NOB_{ovis}62, NOB_{cervus}10, NOB_{cervus}11), and the remaining 8 being part of the infill at Structure 10.

Sequential tooth enamel samples were taken as described in Balasse et al. (2005) and treated with 0.1M acetic acid for 4 hours (0.1 ml/mg). The pre-treated samples were reacted with 100% phosphoric acid at 70°C in an automated cryogenic distillation system (Kiel IV carbonate device) coupled to an isotope ratio mass spectrometer (DELTA V Advantage, both ThermoFisher Scientific). Laboratory carbonate standard Marbre LM (normalised to the international standard NBS19) was used on a routine basis to monitor the accuracy and precision of the measurements, whereby repeated analyses (N = 6–8) showed standard deviations <0.03‰ for $\delta^{13}\text{C}$ and <0.06‰ for $\delta^{18}\text{O}$. Over the course of the analysis, Marbre LM (N = 80) gave a mean $\delta^{18}\text{O}$ value of −2.08‰ (expected value: −1.83‰) and a mean $\delta^{13}\text{C}$ value of 2.19‰ (expected value: 2.13 ‰), and corrections were made for these offsets.

Seaweed consumption is expected to be higher during winter, at a time when significant amounts of seaweed are driven ashore by the storms. Consuming ^{13}C -enriched seaweed in winter, when rainwater $\delta^{18}\text{O}$ values are the lowest, leads to $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences varying in opposite phase (Balasse et al. 2019). The shift in position between the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ seasonal cyclic variations in enamel (phase shift, expressed in °) was modelled as described in Balasse et al. (2019): in-phase variation of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ is described by a phase shift around 0° or 360°, while phase shifts around 180° express opposed variations in the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences (e.g. as a result of seaweed consumption in the winter).

Birth seasonality (i.e. the length and timing of the lambing period) was investigated by studying inter-individual variability in the position of the highest value of the $\delta^{18}\text{O}$ annual cycle in the tooth crown (x_0 ; distance from the enamel-root-junction in mm). Since sequential sampling is undertaken at discrete intervals, this x_0 position is not measured directly, and was therefore modelled (following Balasse et al. 2012; see also supplementary material, 1.3 *Stable isotope ratio modelling*). The distance x_0 was normalised

to the $\delta^{18}\text{O}$ cycle period (X; length of crown formed over one year in mm) for each tooth to eliminate inter-individual variability in tooth size (Balasse *et al.* 2012). The season of birth was then established by comparison to modern reference teeth (Balasse *et al.* 2020). Seasonal consumption of seaweed in winter has been shown to elevate $\delta^{18}\text{O}$ values due to the ingestion of oceanic water, whose large reservoir size dampens seasonal variations (Balasse, Mainland, and Richards 2009, 2005). Therefore, large extents of seaweed consumption in the middle and end of winter may shift the x-axis position of the minimum $\delta^{18}\text{O}$ value to a small extent. This would affect the modelled period length. For this reason, the determination of the time of birth of sheep that consumed large amounts of seaweed may be slightly less accurate than for solely terrestrially feeding sheep.

All excavated sheep and deer mandibles with M_{3s} (and in the case of NOB_{ovis}107, an M_2) *in situ* were analysed for bone collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($n_{\text{Str.10}} = 3$ and $n_{\text{CMA}} = 2$ for sheep; $n_{\text{Str.10}} = 1$ for deer). Collagen was extracted following a modified Longin (1971) procedure described in Dunbar *et al.* (2017). Extracted collagen was analysed by isotope ratio mass spectrometry (IRMS) on a Delta V Advantage instrument following combustion in an EA IsoLink that was coupled to the Delta V via a ConFlo IV (all ThermoFisher Scientific). Typical analytical precisions were $\pm 0.15\text{‰}$ for $\delta^{15}\text{N}$ and $\pm 0.1\text{‰}$ for $\delta^{13}\text{C}$ (see Sayle *et al.* 2019).

Results and Discussion

Sheep Ages-At-Death

None of the sheep/goat teeth from the Ness of Brodgar showed a majority of goat-like features and are therefore all referred to as sheep. Only one matching, and one possibly matching pair of sheep teeth were identified among the 116 sheep mandible fragments and loose teeth, indicating almost all mandible fragments/loose M_3/dP_4 likely represent different individuals. For this reason, the mortality profiles were plotted including all sample material. However, considering that several of the severely broken teeth could technically match others, and that dP_4s and M_3s may co-exist in the mandible during Payne wear stage D, a total MNI of 78 was calculated (Supplementary Tables S.3, S.4, S.5, S.6).

Around half of the sheep mandible fragments and loose teeth indicate death after 2–4 years (Figure 2; ages following Payne 1973). The primitive seaweed-eating sheep populating North Ronaldsay (Orkney) today reach maturity after three to four years (Ryder 1983) and are slaughtered after three years (K. Woodbridge, personal communication 2019). This suggests sheep husbandry at the Ness of Brodgar was aimed primarily at meat production (although hides, sinews,

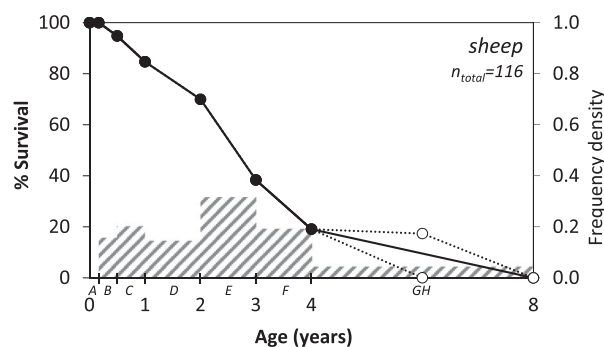


Figure 2. Ness of Brodgar sheep mortality profile. The line graph indicates the estimated survival percentage until the specified age (dotted lines: all Payne wear stage 'GH' teeth considered as either G (lower), or H (upper)). The histogram shows the frequency density of sheep mortalities using a 12-month time unit (after Brochier 2013 and Payne 1973).

etc., would likely also have been valued). Only a fifth of the sheep were estimated to be aged 4–8 years, and none were older than 8 years old. This low amount of longer-lived sheep at the Ness of Brodgar indicates that hair production was not of importance (cf. Payne 1973; Serjeantson 2011), consistent with the earliest evidence of wool-producing sheep in Europe not appearing until the Bronze Age (Sabatini *et al.* 2019).

The lack of remains of 0–2-month-olds suggests that young sheep were not routinely slaughtered for dairying purposes (Payne 1973), and, as lambs would regularly have died naturally at birth, may also indicate that sheep were not generally lambing close to the site - or at least that dead lambs were disposed of elsewhere. However, bone preservation at the Ness of Brodgar is comparatively poor considering the large amount of loose teeth compared to intact mandibles, and younger mandibles appear to be more susceptible to postdepositional loss of material (Munson and Garniewicz 2003). But while dog bones were recovered from the Ness of Brodgar, gnawing appears to have been minimal at the Ness of Brodgar, with only 1% of bone fragments recovered from structure 10 having been gnawed, 0.09% in Trench T, and none in Structure 8 (I. Mainland, unpublished data). Of the 218 ageable cattle hemimandible fragments and loose dP_4s and M_3s , 3–5 were from cattle that were foetal or up to a few days old at birth (Ayres *et al.* in prep.), suggesting that the lack of recovered sheep teeth aged less than 0–2 months may indeed be due to a low frequency/absence of such young sheep.

There was no evidence of systematic differences in the sheep age distributions between Structure 10, the CMA and the remaining material at the Ness of Brodgar (see Supplementary Fig. S.1 and Table S.7).

Red Deer Ages-At-Death

Wear comparison between left and right loose dP_4s and M_3s indicates an MNI of 12 deer, with three

well-matching pairs and several possible pairs of teeth. Around a third of the red deer were younger than 26 months (likely mostly around 10 months old), and around two thirds were older than five years (Figure 3 and Supplementary Table S.8). It was impossible to age the M₃s precisely enough to distinguish between prime-aged and older deer. In contrast, the deposit of at least fifteen partly articulated red deer at the Links of Noltland comprises generally younger deer, with eleven deer aged approximately 9 months, two 2-year-olds, and two 5-year-olds (Clarke et al. 2017).

Sheep and Red Deer Diets, and the Marine Reservoir Effect

For 14 of 17 sheep and all three deer, enamel $\delta^{13}\text{C}$ values ranged between -14.2‰ and -11.0‰ (Figure 4 and Supplementary Tables S.9, S.10 and Fig. S.2), with $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values varying nearly in-phase (phase shift range $271\text{--}349^\circ$), reflecting terrestrial diets throughout the year (Figure 5). However, three sheep M₃s (NOB_{ovis}39, NOB_{ovis}61, NOB_{ovis}111), all from Structure 10, had elevated enamel $\delta^{13}\text{C}_{\text{max}}$ values and showed opposite variations in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values (phase shifts close to 180°). This reflects mixed diets with an increased contribution of seaweed in winter for these sheep (Figure 5). A fourth sheep M₃ (NOB33) from the central midden area may also have consumed small amounts of seaweed in the cold season (Figure 4). In contrast to the enamel $\delta^{13}\text{C}$ data, none of the sheep and deer mandible $\delta^{13}\text{C}_{\text{collagen}}$ values (Figure 6) were indicative of seaweed consumption. This is likely in part due to different individuals being sampled (only 6 individuals could be sampled both for enamel and bone due to poor mandible preservation; unfortunately, NOB_{ovis}39, NOB_{ovis}61 and NOB_{ovis}111, showing evidence for winter

consumption of seaweed from tooth enamel $\delta^{13}\text{C}$ values, are loose teeth and therefore could not provide bone collagen values), but possibly also because $\delta^{13}\text{C}_{\text{collagen}}$ is less sensitive to seasonal seaweed-consumption (Blanz et al. 2020). Therefore, at the Ness of Brodgar none of the $\delta^{13}\text{C}$ values measured in sheep bone collagen ($n=8$, this study; Budd and Schulting 2011; Jones and Mulville 2016) clearly indicate seaweed consumption, while in 3–4 cases (out of 17) the $\delta^{13}\text{C}$ values measured in enamel reflect winter consumption of seaweed. Consequently, seaweed consumption is attested, but was not a dominant pattern among sheep or at least did not regularly contribute to an extent that could be measured in bone collagen.

Despite evidence from present-day that red deer may eat seaweed (Conradt 2000), it did not contribute substantially to any of the analysed deer's diets during the time reflected in the M₃ enamel (likely mid-late winter to early summer, as reflected in the $\delta^{18}\text{O}$ values). This is consistent with deer $\delta^{13}\text{C}_{\text{collagen}}$ values from the Ness of Brodgar (Figure 6), and with data from other M₂s and M₃s of deer from Neolithic Orkney (from Skara Brae, $n=3$, Links of Noltland, $n=3$, Balasse *et al.* unpublished results; Holm of Papa Westray, $n=1$; Balasse and Tresset 2009).

These results also have implications for radiocarbon dating at the Ness of Brodgar and across Neolithic Orkney due to the marine reservoir effect (i.e. the proportion of radiocarbon in the ocean being depleted compared to that in the contemporaneous atmosphere; Alves et al. 2018; Stuiver, Pearson, and Braziunas 1986). In unburnt bones, corrections for the marine reservoir effect may be made based on $\delta^{13}\text{C}$ results (giving the amount of marine food consumption). However, in calcined bones, the unknown extent of carbon isotope replacement and fractionation during the burning process prevents the accurate quantification of marine carbon in burnt bones (Zazzo et al. 2012), and thereby also the correction of radiocarbon dates for the marine reservoir effect. Therefore, radiocarbon dates from calcined sheep bones (and unidentified bones) may be unreliable at the Ness of Brodgar and across Neolithic Orkney due to the possibility of seaweed consumption. This may affect three radiocarbon dates of unidentified calcined bone from Structure 5 at the Ness of Brodgar (OxA-X-2633-41, UBA-29753, UBA-29754; Card et al. 2018), which may be younger if these bones were from seaweed-eaters. However, the extent of the potential marine reservoir effect for seaweed-eaters from Late Neolithic Orkney has not yet been determined and may well be low. Photosynthesis by some intertidal seaweeds during periods of exposure to air appears to incorporate carbon from atmospheric CO_2 (Ni Longphuirt et al. 2013; instead of the use of dissolved inorganic carbon from the ocean when submerged). Additionally, even when submerged, seaweeds

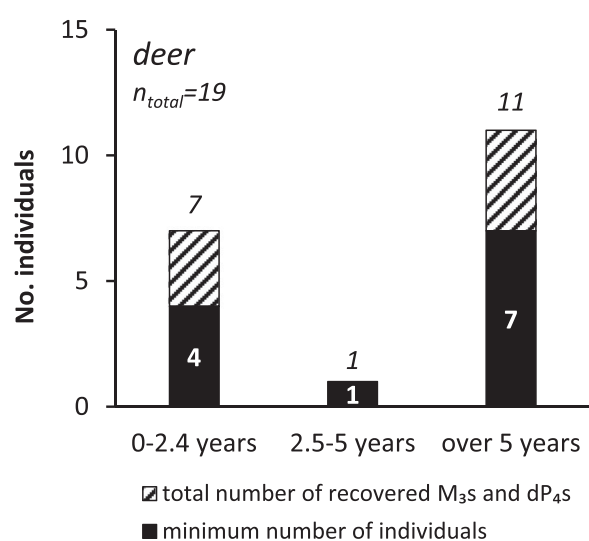


Figure 3. Age-at-death of Ness of Brodgar red deer, showing the MNI in the columns and the total number of recovered dP₄s and M₃s above the columns.

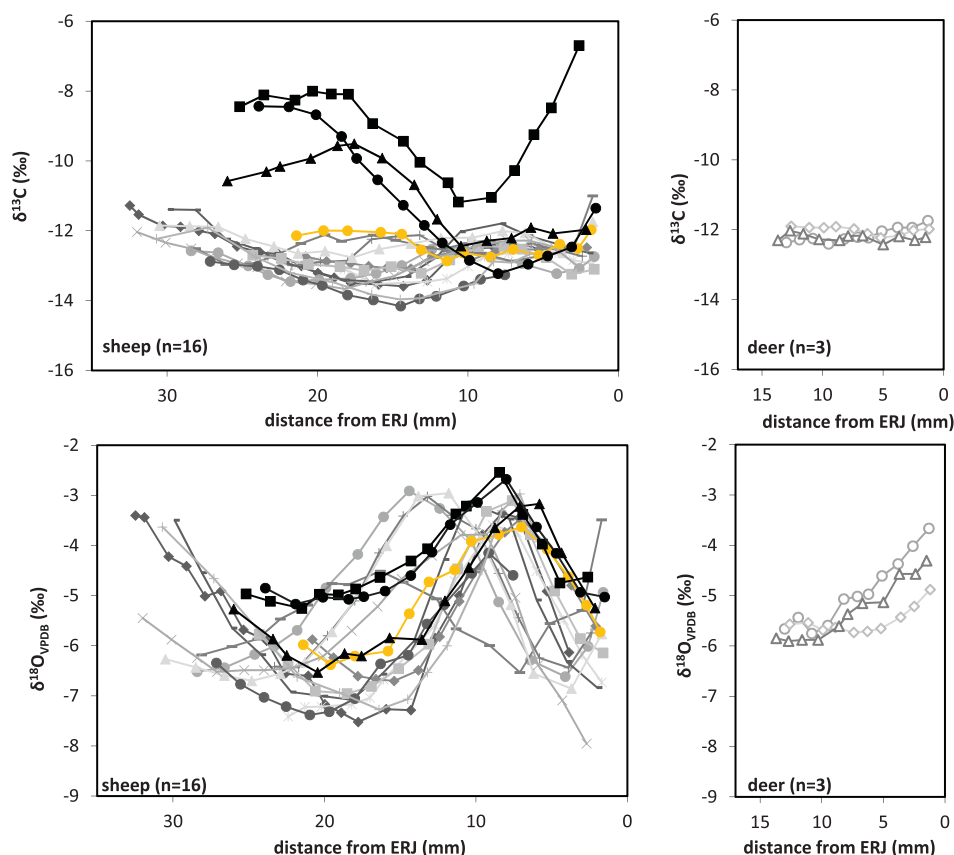


Figure 4. Intra-tooth sequential $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of sheep and deer M_3 s. Sample positions on the tooth crown are expressed as distances from the enamel-root junction. The three teeth with the highest $\delta^{13}\text{C}_{\text{max}}$ are shown in black (with high $\delta^{13}\text{C}$ values attributed to seaweed consumption in the cold season), and NOB_{ovis}33 (possible seaweed consumption in the cold season) in yellow. M_2 NOB_{ovis}107 was excluded here.

growing close to the surface will also incorporate newly dissolved atmospheric CO_2 . This means that the marine reservoir effect of these seaweeds will be less than that of deep-sea organisms obtaining 100% of their carbon from the marine environment.

Sheep Birth Seasonality

Close grouping of x_0/X values (range: 0.38–0.45) was observed for 8 of 14 modellable M_3 $\delta^{18}\text{O}$ sequences (Figure 7), indicating that over half of the sheep

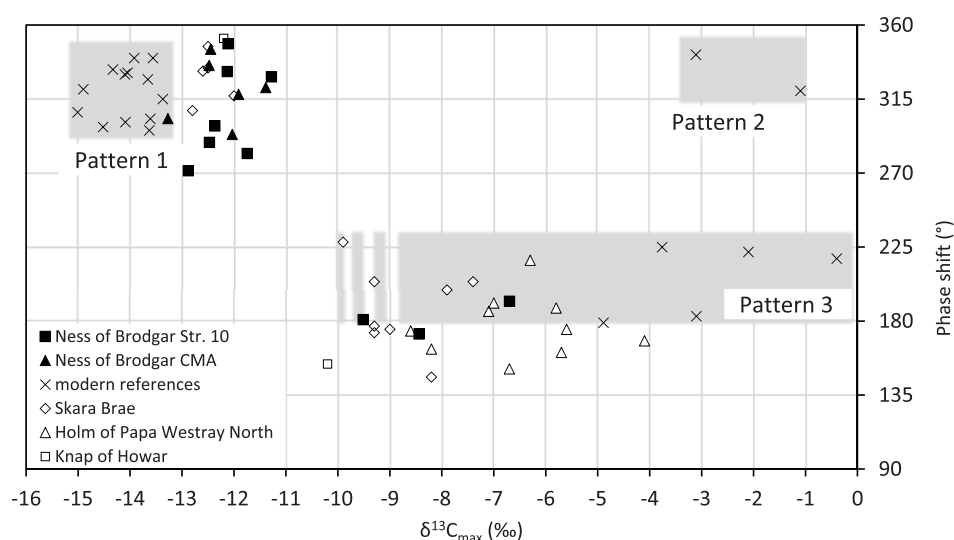


Figure 5. Phase shift between the intra-tooth seasonal variations in sheep enamel $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values, plotted against the highest $\delta^{13}\text{C}$ value of the intra-tooth sequence ($\delta^{13}\text{C}_{\text{max}}$). The patterns refer to the diets of modern reference sheep, with Pattern 1: terrestrial grazing, Pattern 2: almost only seaweed, Pattern 3: mixed diet with increased contribution of seaweed in winter. NOB_{ovis}33 and the deer were excluded as they had too low $\delta^{13}\text{C}$ amplitudes to be modelable. Data: this study (NOB); Balasse, Tresset, and Ambrose 2006, 2009, 2019.

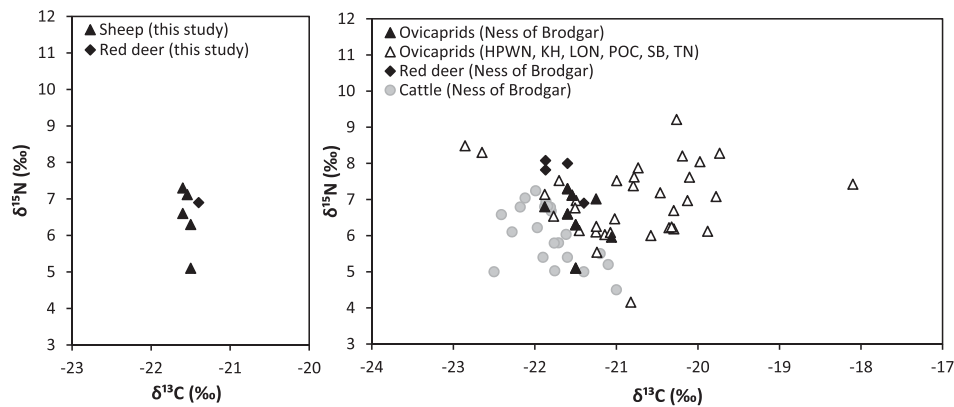


Figure 6. Bone collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from the Ness of Brodgar (left; this study), and comparison to other Neolithic Orkney sites (right; includes literature data): Holm of Papa Westray North Cairn (HPWN), Knap of Howar (KH), Links of Noltland (LON), Point of Cott (POC), Skara Brae (SB) and Tofts Ness (TN). Excludes animals reported as <6 months to avoid the inclusion of elevated $\delta^{15}\text{N}$ values that are due to milk consumption, and effects of seaweed-consumption by the mother ewe on lamb $\delta^{13}\text{C}$ values (see Schulting et al. 2017). Data: this study; Schulting and Richards 2009; Budd and Schulting 2011; Jones and Mulville 2016; Card et al. 2018; Blanz et al. 2020.

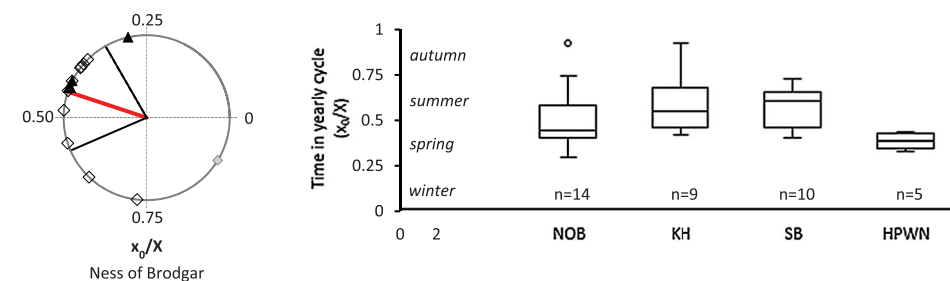


Figure 7. Timing of births of sheep in Neolithic Orkney, shown as x_0/X values for M_3 s and corrected x_0/X values for M^3 s (see Balasse et al. 2020). The circular graph shows the individual datapoints, the mean (red line) and 66% confidence interval (black lines), with outliers outside of the 95% confidence interval in grey. Sheep showing evidence of seaweed consumption are indicated as black triangles without adjustments to x_0/X for potential dietary effects. NOB_{ovis}83 and NOB_{ovis}50 were not modelable and excluded. Data: this study (NOB), Knap of Howar (KH), Skara Brae (SB) and Holm of Papa Westray North (HPWN) from Balasse et al. 2017, 2020.

teeth analysed from the Ness of Brodgar were of sheep born within the same 1–2 months in mid to late spring/early summer, two thirds were born over approximately 3 months, and only a few individuals in late summer and autumn. This restricted lambing period is expected in temperate Europe, where sheep have a photoperiodic-controlled seasonal reproductive behaviour, alternating between a period of sexual activity and a period of sexual rest (Hafez 1952; Karsch et al. 1984). Previous studies at other Neolithic sites in Orkney have shown similarly restricted lambing periods occurring at the same time of the year (Figure 7), *i.e.* slightly later than the late winter/spring lambing observed at lower latitudes sites (Balasse et al. 2020). The occurrence of a few late births (in late summer and autumn) also suggests that sheep reproduction was not generally strictly controlled by humans in Neolithic Orkney, or at least not with the objective of concentrating births to a minimally short lambing period.

To study whether differences in the time of birth correlate with differences in diet, comparisons between dietary groups were made encompassing all

analysed sheep from Neolithic Orkney sites, *i.e.* Ness of Brodgar, Knap of Howar, Holm of Papa Westray North and Skara Brae (data: this study and Balasse et al. 2020, 2019). Sheep that consumed seaweed in their first winter had largely similar x_0/X values ($\text{mean}(x_0/X) = 0.46$, $\sigma = 0.12$, $n = 18$) compared to those which did not display evidence of seaweed consumption ($\text{mean}(x_0/X) = 0.56$, $\sigma = 0.16$, $n = 20$; $t(36) = 2.03$, $p = 0.501$; see Supplementary Fig. S.3).

Seaweed-Consumption and Adaptations to the Environment

Previous evidence from Neolithic Orkney has shown a gradual introduction of seaweed into the Neolithic sheep diet on Orkney. Stable isotope analyses of tooth enamel have shown only minor consumption of seaweed by sheep excavated from Knap of Howar (mid-late 4th millennium cal BC; Balasse et al. 2019; Bayliss et al. 2017) and no evidence of seaweed consumption in Phase 0 at Skara Brae (ca. 3400–3200 cal BC; Balasse et al. 2019; Bayliss et al. 2017), followed by an increased uptake of seaweed at Skara Brae in

phase 1 (ca. 2900 cal BC; Balasse et al. 2019; Bayliss et al. 2017), in turn followed by seaweed consumption becoming predominant among sheep from Holm of Papa Westray North Cairn (third quarter of the third millennium cal BC; Balasse and Tresset 2009; Bayliss et al. 2017), and Phase 2 of Skara Brae (ca. 2750–2500 cal BC; Balasse et al. 2019; Bayliss et al. 2017). Additional evidence from Point of Cott (mid-4th to mid-3rd millennia BC, Balasse, Mainland, and Richards 2009) and Quanterness (third millennium cal BC; Schulting et al. 2017) also indicates seaweed consumption. This chronological development suggests an ongoing adaptation to the coastal environment; but with only 3–4 out of 17 analysed sheep excavated from the Ness of Brodgar consuming significant amounts of seaweed (sheep postdating 2500 cal BC), this study shows that by the Late Neolithic, seaweed-consumption was not a ubiquitous adaptation on Orkney as a result of a simple linear development, but was pluridirectional, and subject to considerable local and chronological variability. By the Middle Iron Age at Mine Howe, one of three analysed sheep teeth showed evidence of seaweed consumption (Balasse, Mainland, and Richards 2009). This variability is likely the result of many different factors, including access and distance to terrestrial and shore grazing, the amount of stock to overwinter and the severity of the current and previous winters, and potentially even the herders' previous experiences with seaweed (as excessive seaweed-consumption may be harmful; see seaweed-stagger description in Blanz et al. 2020; and Ingimundarson 1995).

Seaweed-consumption by Neolithic sheep on Orkney appears to have been largely restricted to the cold season (this work; Balasse et al. 2019, 2009, 2006, 2005; Balasse and Tresset 2009), and accordingly, it seems that seasonal seaweed consumption by sheep was the result of shortages of winter grazing (Balasse et al. 2005) or fodder. For Late Neolithic farmers on Orkney, these shortages of winter grazing would have been a regular (annual) occurrence that effectively controlled the size of the flock that could be kept, and accordingly calculations would have been made every autumn as to how many animals to cull with reference to the amount of likely available winter grazing, and already collected winter fodder (Amorosi et al. 1998). Without availability of seaweed or winter fodder, nutritional stress is particularly high in early spring, when resources from the previous year have been exhausted but new vegetation has yet to grow (Upex and Dobney 2012). However, the sequential tooth enamel $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ results of Neolithic seaweed-eating sheep on Orkney show that the peak of seaweed-consumption generally occurred earlier, i.e. already in winter, rather than in early spring (e.g. on Holm of Papa Westray; Balasse, Tresset, and Ambrose 2006; Balasse and Tresset 2009; at Skara

Brae; Balasse et al. 2019; and at the Ness of Brodgar). This corresponds with stranded seaweed being readily available from late autumn to early spring, when it is cast onto the shores following storms (Fenton 1986, 65–66). Accordingly, for the sampled sheep (i.e. those that survived into adulthood and developed sampleable molars) seaweed-consumption was likely not a last-ditch effort to ensure survival in the beginning of spring, but was more likely part of a planned decision by the herders before winter, or the result of animals with a taste for seaweed being left to roam freely.

Only 3–4 of the analysed sheep excavated from the Ness of Brodgar consumed significant amounts of seaweed, whereas seaweed-consumption appears to have been more common during Phase 2 of the smaller, domestic site of Skara Brae (Balasse et al. 2019). The observed difference in sheep diet may be due to the Ness of Brodgar having been a particularly affluent and prestigious site with access to a larger extent of terrestrial grazing areas compared to Skara Brae, but could also be due to the Ness of Brodgar being situated at a further distance to the sea (Figure 1). However, the origin of the sheep excavated from the Ness of Brodgar is also still unclear, apart from the seaweed diets of 3–4 sheep indicating likely proximity to the coast during winter.

So far, there is no evidence of cattle consuming significant amounts of seaweed in Neolithic Orkney (Figure 6; Balasse et al. 2019; Schulting et al. 2017), despite numerous reports of cattle consuming seaweed elsewhere (Hall and Moore 1986; Hallsson 1964; Landsborough 1857; Martin 1716; Sauvageau 1920). The lack of seaweed consumption by Neolithic Orkney cattle could simply be an indication of a lack of adaptation and suitability to the foreshore. However, this difference in diet to sheep could also be the result of cattle being pastured on differing grazing areas. Coupled with the apparent greater importance of cattle to sheep in Late Neolithic Orkney, this could possibly indicate that terrestrial resources were held to be of higher value than seaweed.

Red deer appear to have had a special significance in Neolithic Orkney, as several deposits of articulated and disarticulated deer carcasses without evidence of butchery or consumption have been reported at the Ness of Brodgar (Mainland et al. 2020, 2014), adjacent to Skara Brae (Richards et al. 2015) and at the Links of Noltland (Clarke et al. 2017). At the Ness of Brodgar, all deer hemimandible fragments and loose dP_4s and M_3s ($n = 19$, $\text{MNI} = 12$) were from Structure 10, in contrast to only 34% of sheep so far excavated ($n = 116$). This may also indicate a special significance of red deer. Historically and in present-day, red deer have been reported to consume significant amounts of seaweed in the Scottish Western Isles and on Rùm (Inner Hebrides, Scotland) when access to seaweed-

rich shores is available (Conradt 2000; Martin 1716). The lack of evidence of seaweed consumption even on a seasonal basis by deer in Neolithic Orkney is therefore noteworthy and may be related to a possible lack of shore access, which could be due to anthropogenic influences. The prevalence of human activity near the coast in Neolithic Orkney may have restricted the range of red deer, perhaps confining populations to the interior of the islands.

However, on the isle of Rùm, not all deer that have access to seaweed make use of it in present-day. Mother's preferences for seaweed were shown to be passed on to the offspring, implying that seaweed consumption is learnt early in life (Conradt 2000). Therefore, it is also possible that the Neolithic deer on Orkney had access to seaweed but chose not to consume it to a measurable extent – potentially because they had not 'developed a taste' for seaweed.

Conclusion

Age-at-death analyses revealed most sheep at the Ness of Brodgar died after 2–4 years of life, with a lack of very young and old animals. This deviation of the assemblage from a viable herd structure suggests that prime-aged sheep were preferentially brought to the site, likely for exploitation of their meat. Further work on the characteristics of the faunal assemblage (selection of parts of the carcass, intensity of butchery practices, joints in articulation) will be undertaken to study the importance of sheep for feasting at the Ness of Brodgar.

Only 3–4 of 17 analysed sheep teeth excavated from Late Neolithic Ness of Brodgar showed evidence of seaweed consumption based on stable isotope ratio analyses. This, in combination with the scarcity of marine animal remains (Harland 2020), supports previous suggestions that marine resources likely did not play a major role at the Ness of Brodgar. The scarcity of seaweed-eating sheep at the Ness of Brodgar also indicates that seaweed consumption was not a ubiquitous adaptation to the coastal environment on Orkney in the Late Neolithic. Combined with the breadth of evidence of seaweed consumption by sheep from other sites in Neolithic, Chalcolithic and Iron Age Orkney (Balasse et al. 2019, 2009, 2006, 2005; Dockrill et al. 1994; Jones and Mulville 2016; Schulting et al. 2017), the results show that the extent of prehistoric seaweed consumption by sheep varied both geographically and chronologically throughout the archipelago, possibly reflecting changes to animal ranges, stocking density, terrestrial resource abundance and landscapes.

Red deer appear to have had a special status at the Ness of Brodgar, with red deer mandibles and loose dP₄s and M₃s only being found associated with the largest structure at the Ness of Brodgar, Structure 10. In

contrast to sheep, none of the analysed Neolithic red deer on Orkney were found to have consumed measurable amounts of seaweed, potentially indicating differing grazing ranges due to anthropogenic influences, which bears further investigation.

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