Investigating seasonal mobility in Irish giant deer *Megaloceros giganteus* (Blumenbach, 1799) through strontium isotope ($^{87}$Sr/$^{86}$Sr) analysis

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ABSTRACT: Giant deer *Megaloceros giganteus* (Blumenbach, 1799) fossils are commonly found in Lateglacial deposits throughout Ireland. While their migrational behaviour has been suggested, it has never been researched. We hypothesise that giant deer underwent seasonal migrations, specifically during Late Pleistocene cold periods as a behavioural adaptation. Giant deer required a high nutrient uptake and were maladapted to the cold-dry steppe of the Pleistocene glacials. Migration allowed for optimal nutrient uptake during summer, while avoiding the harsh winter conditions of the glacial by moving to sheltered, low-lying areas. In this study strontium isotope analysis ($^{87}$Sr/$^{86}$Sr) of sequentially sampled dental enamel is conducted for the first time on giant deer that were previously sampled in the same manner for $\delta^{13}$C and $\delta^{18}$O, allowing correlations between the isotope data sets. One specimen from Ballybetagh, Dublin generated results indicating seasonal mobility behaviour. This individual was perhaps pushed to migrate at the Younger Dryas stadial onset as the vegetation giant deer depended on disappeared in Ireland. Adaptive mobility behaviour in response to climate was perhaps imperative to their survival through previous glacial periods, but other Eurasian populations would need to be analysed to make such a general conclusion.

KEYWORDS: *Megaloceros giganteus*; mobility; Sr isotope analysis; Ireland; Lateglacial

Introduction

The giant deer *Megaloceros giganteus* (Blumenbach, 1799) have become synonymous with Ireland, as their remains have been found commonly throughout the island (Monaghan, 2017). While sometimes referred to as the ‘Irish elk’, it is strictly neither Irish nor an elk. They are unrelated to what is now living relative (Lister et al., 2005). While their abundance in the Late Pleistocene fossil record in Ireland is unmatched in any other location, they have been found across Eurasia in deposits dating from between 400 and 7.6 ka BP (Lister and Stuart, 2019).

The main episode of Irish giant deer presence in Ireland was during the late Allerød to the Younger Dryas onset (Monaghan, 2017; Lister and Stuart, 2019), broadly referred to as the Lateglacial; a relatively warm period after the Last Glacial Maximum (LGM) when vegetation productivity was high and dominated by grasses with birch stands (Watts, 1977; Barnosky, 1986; Monaghan, 2017). While giant deer have been found in cave deposits from 40 ka BP, the LGM likely caused substantial ice cover over the island, although some small refugia may have been present but unsuitable for giant deer (Ballantyne and Ó Cofaigh, 2017; Carden et al., 2020). Therefore, the Lateglacial population is most likely a Bølling/Allerød reintroduction (Woodman et al., 1997; Monaghan, 2017; Lister and Stuart, 2019). The island lacked large grazing herbivores at this time, and giant deer subsequently began to spread throughout (Monaghan, 2017). This came to an end, however, with the onset of the Younger Dryas climatic turndown, where arctic-alpine conditions began to spread and caused the deterioration of grasslands on the island, and the development of tundra conditions (Watts, 1977; Barnosky, 1986; Monaghan, 2017). It is thought that this climatic event led to their extinction, while hunting has generally been ruled out as it is thought that humans did not colonise Ireland until 10 290–9790 cal a BP, some 2000 years after the disappearance of the giant deer (Barnosky, 1986; Monaghan, 2017; Lister and Stuart, 2019; but see Dowd and Carden, 2016). The absence of palatable vegetation, coupled by competition with other cervids, and wolf (*Canis lupus* Linnaeus, 1758) and brown bear (*Ursus arctos* Linnaeus, 1758) predation are believed to have driven the Irish population to extinction (Barnosky, 1986; Woman and Kimbrell, 2008; Monaghan, 2017; Lister and Stuart, 2019). The species as a whole survived up until the Holocene, 7600 cal a BP, in the Urals, Russia (Stuart et al., 2004; van der Plicht et al., 2015; Rey-Iglesia et al., 2021).

Based on migrational behaviour observed in other cervids, most famously in caribou/reindeer *Rangifer tarandus*...
(Linnaeus, 1799), similar mobility behaviour has also been suggested in giant deer (Geist, 1986; Gunn et al., 2009; Vislobokova, 2012). During the Late Pleistocene glacial, giant deer were associated with the boreal parkland habitat. This consisted of scattered pine and spruce forests in a herb-shrub matrix sandwiched between steppe-tundra conditions to the north and to the south desert to semi-desert conditions (Allen et al., 2010; Lister and Stuart, 2019). Vislobokova (2012) suggested that during summer periods, giant deer ventured out to the open steppe to benefit from the productive grasses and sedges, while in the winter treating to boreal/steppe forests to the south for shelter and for browse. This migrational behaviour would have allowed giant deer to collect enough nutrients for survival, reproduction and gestation, as well as to fuel antler growth, which could reach a span of 3.6 m (Barnosky, 1986; Moen et al., 1999; Worman and Kimberl, 2008; Monaghan, 2017; van Geel et al., 2018). Like the migrating reindeer, the relatively short limbs (compared with other modern cervids) in giant deer may have been an adaptation to a more cursorial lifestyle which would have aided in long migration journeys (Geist, 1986; Gunn et al., 2009; Vislobokova, 2012).

One of the most famous sites for Lateglacial Irish giant deer remains is Ballybetagh, Dublin (Fig. 2, Location 1). Here, more than 100 skulls have been exhumed (Monaghan, 2017). This location was noted by Barnosky (1986) to be an area of low-lying topography, perhaps sought after by overwintering stags to take shelter from the elements and have access to water. They may have subsequently made their way to more open areas at the turn of spring. To date, no specific research has been conducted on seasonal mobility in giant deer. The hypothesis to be tested is that giant deer, specifically giant Irish deer of the Lateglacial period, were seasonally mobile mainly as a response to plant phenology. To test this, strontium isotope analysis was conducted on the enamel of three Irish giant deer from the Lateglacial period from Ballybetagh (Dublin), Casteruaddery Lower Townland (Wicklow), and Mountcharles Townland (Donegal). The strontium isotope data were used in conjunction with previously published oxygen and carbon isotope data (Chritz et al., 2009) to gain the first insight into mobility behaviour in Irish giant deer.

Seasonal mobility and isotope analysis

The application of stable and radiogenic isotope systems for the investigation of palaeomobility has become widely used on both extant and extinct species; examples include mammoths (Hoppe et al., 1999; Wooller et al., 2021), mastodons, tapirs, deer, equids (Hoppe and Koch, 2007), red deer (Pilaar Birch et al., 2016) and reindeer (Britton et al., 2011; Price et al., 2017; Gigleux et al., 2019), strontium isotope analysis (87Sr/86Sr) being the most commonly utilised (Hoppe et al., 1999; Hoppe and Koch, 2007; Britton et al., 2009, 2011; Price et al., 2017; Gigleux et al., 2019; Wooller et al., 2021).

The Sr that can be assimilated into the mineral tissue of animals living in a specific geological area (bioavailable Sr) is taken up into a herbivore’s body through ingested vegetation and water, and the ratio between the 87Sr and 86Sr isotopes fractions negligibly as it travels through the food chain (Hurst and Davis, 1981; Slovak and Paytan, 2012; Lahtinen et al., 2021). Once ingested, the Sr readily substitutes for calcium and is incorporated into the structure of hydroxyapatite crystal in animal dental enamel and bones (Comar et al., 1957; Slovak and Paytan, 2012). The bioavailable 87Sr/86Sr of the vegetation and water in a region (which forms the herbivores’ diet) is mainly determined by the underlying geology, with the 86Sr in rocks forming over time due to the radioactive decay of rubidium (87Rb). This makes the relative content of 87Sr to 86Sr determined by both the age of the rock and how much Rb was originally present in the underlying bedrock (Faure, 1977). Thus, generally older geological structures will have a higher 87Sr/86Sr. Therefore, variations in 87Sr/86Sr in animal mineral tissue may suggest movement across differing geological areas over a period of the animal’s life.

The presence of a bioavailable 87Sr/86Sr map (BASr map) of Ireland allows us to correlate the 87Sr/86Sr of the giant deer to 87Sr/86Sr isoscapes (Fig. 2; Sneock et al., 2020). The bedrock of the island is mainly composed of Palaeozoic rock with some rare Mesozoic outcrops and large lava flow basalt outcrops from the Tertiary to the north (Holland and Sanders, 2009), where very low 86Sr68Sr are found (0.7061–0.7070). Carboniferous limestone covers much of the island leading to large areas that are characterised by a 87Sr/86Sr value between 0.7071 and 0.7080, while the 87Sr/86Sr at the southern margins of Ireland Devonian ‘Old Red’ Sandstone ranges between 0.7101 and 0.7110 (Holland and Sanders, 2009; Sneock et al., 2020).

Oxygen (δ18O) and carbon (δ13C) isotope analysis focusing specifically on Irish giant deer has been previously conducted by Chritz et al. (2009) investigating diet and general palaeobiology of the animal. The δ13C of carbonate and phosphate in hydroxyapatite precipitates in equilibrium with body water, and δ18O is known to be directly correlated to the meteoric water temperature that an animal ingests. Therefore, when sequentially sampled it can display changes in temperature due to seasonality at mid to high latitudes (Dansgaard, 1964; Britton, 2010). However, due to Rayleigh fractionation, different areas within a region can have varying isotopic composition in their precipitation, the current δ18O isoscapes in Ireland become more depleted in a north-easterly direction with a range of -4 to -7‰ (Darling et al., 2003; Diefendorf and Patterson, 2005; Pellegrini et al., 2016). This can generate variations in δ18O caused by the animal ingesting water in different oxygen isoscapes (Britton et al., 2009; Pellegrini et al., 2016; Pilaar Birch et al., 2016). The δ18O composition of surface water in an area is affected by a combination of meteoric water temperature and how the precipitation that contributes to it was affected by Rayleigh fractionation (Darling et al., 2003; Pellegrini et al., 2016).

The δ13C of carbonate in the hydroxyapatite of herbivores is related to the vegetation they consumed, as certain types of plants (C3 or C4 plants) have distinct δ13C ranges due to their differing photosynthetic pathways (Tieszen and Bontout, 1989; Bocherens, 2003). In colder climates, however, almost all plants utilise the C3 photosynthetic pathway (Bocherens, 2003). Variation in δ13C in sequential samples in these conditions is therefore mainly a consequence of feeding on plants that are found in forested (lower δ13C) and open habitats (higher δ13C), and/or a diet composed of woody (lower δ13C) or herbaceous (higher δ13C) C3 plant taxa in open environments (Lee-Thorp et al., 1989; Tieszen and Bontout, 1989; Cerling and Harris, 1999; Bonanini et al., 2013). The δ18O and δ13C isotopes can be combined with 87Sr/86Sr in order to link movement across geological areas to seasonal changes, movement to different oxygen zones, and changes in diet and habitat (Britton et al., 2009, 2011; Gigleux et al., 2019).

δ18O and δ13C isotope analysis was conducted by Chritz et al. (2009) through sequentially sampled dental enamel of the right second (M2) and third (M3) maxillary molars. Tooth enamel forms in approximately horizontal bands from the apex (occlusal surface) to the cervices (dentine-root junction) and these layers of enamel can be analysed to assemble a sclerochronology of isotopic variation (Gadbury et al., 2000; Balasse et al., 2003; Britton et al., 2009; Chritz et al., 2009).
Depending on which dental element is being analysed, its enamel records the isotopic composition of dietary intake during that specific tooth’s growth and mineralisation period. For fallow deer and red deer (Cervus elaphus Linnaeus, 1758) mineralisation of the M2 commences at 3.5 months of age and is complete by the age of 9 months; this is approximately when the M3 begins mineralisation, and finishes at c.18 months (Brown and Chapman, 1991a,b; Britton et al., 2009). Once the enamel has been completely mineralised it is highly resistant to alteration by diagenesis due to its highly crystalline nature, low organic matter, and lack of porosity (Hillson, 1996; Koch et al., 1997; Slovak and Paytan, 2012). In contrast, dentine and bone are highly susceptible to diagenesis, making it unsuitable for $^{87}$Sr/$^{86}$Sr analysis in most circumstances (Copeland et al., 2010; Britton et al., 2011; Slovak and Paytan, 2012).

**Regional setting**

Based on the remains of mammoth steppe fauna such as woolly mammoth *Mammuthus primigenius* (Blumenbach 1799), spotted hyena *Crocuta crocuta* (Erxleben, 1777) and muskox *Ovibos moschatus* (Zimmermann, 1780) being found in Ireland, it has been suggested that Ireland was connected to mainland Europe during the Late Pleistocene (Monaghan, 2017). During the LGM, however, Ireland was probably almost totally covered by ice sheets and only became habitable again around 16 ka BP (Bálintynte and Ó Cofaigh, 2017; Monaghan, 2017; Carden et al., 2020). After this came the Lateglacial giant deer population (Lister and Stuart, 2019; Fig. 1). This population lived in Ireland during the Bølling-Allerød (GI-1), or the Woodgrange interstadial, where conditions were suitable for most giant deer fossils found in Ireland dated to this period (Barnosky, 1986). Layer 2 is linked to Belling-Allerød interstadial (Watts, 1977; Barnosky, 1986), and the herb-rich grassland dominance seen in Ireland is in contrast to the birch forests that developed in northwest continental Europe and Britain at this time (Watts, 1977; Van Asch and Hoek, 2012). Reasons why vegetation developed in Ireland the way it did is discussed by Van Asch and Hoek (2012) and include exposure to strong cold winds from the Atlantic, limited soil development, precipitation, wildfires and intensive browsing/grazing by giant deer. The overlying layer 3 mainly comprises gravels, dark grey silts and sand, with pollen records consisting mainly of *Artemisia*, Caryophyllaceae, *Thalictrum*, *Sedum rosea*, *Armeria*, *Koennigia* and *Polygonum viviparum*. This is linked to the climatic turndown and deterioration of grasslands caused by the Younger Dryas (Watts, 1977; Barnosky, 1986). This generalised stratigraphy is typical for most Lateglacial lake deposit sites where giant deer remains are found (Barnosky, 1986).

**Material and methods**

The right maxillary M2 and M3 of three *Megaloceros giganteus* specimens from the National Museum of Ireland, Natural History Division, Geology collections (NMING) were selected for $^{87}$Sr/$^{86}$Sr analysis; NMING: F7913 (Ballybetagh), F20514 (Castleudder) and F21647 (Mountcharles), i.e. the same molars from the same giant deer stags analysed by Chritz et al. (2009). The details of the specimens are listed in Table 1. The specimens come from various parts of Ireland, as they were selected for analysis by Chritz et al. (2009) for the minimal wear on their molars. These specimens date to the late Allerød and beginning of the Younger Dryas. This is inferred as they are exhumed from marl deposits overlain by peat, as are most giant deer fossils found in Ireland dated to this period (Chritz et al., 2009; Monaghan, 2017; Lister and Stuart, 2019). However, no radiocarbon dates are available for giant deer from the Castleudder Lower Townland (Wicklow) or Mountcharles Townland (Donegal) at the time of writing.

Sampling was conducted at the Vrije Universiteit Amsterdam by the first two authors. The exact sample locations from the previous study (Chritz et al., 2009) were targeted to correlate the old and new isotope data sets. When drilling the sample lines from the previous study, care was taken to make sure that the molars were not drilled too extensively to avoid contamination of the enamel with there is a high organic content (up to 60%) present along with an abundance of plant fossil remains. The lower (older) half of this layer contains *Juniperus* and *Emetrum* pollen, indicating a dense and diverse vegetation cover and corresponds to the *Juniperus-Emetrum* phase detailed by Watts (1977). The upper half contains Gramineae with some *Helianthemum* and stands of *Betula pubescens* and is described as the Grass phase (Watts, 1977; Fig. 1). It is in the Grass phase that almost all giant deer fossils are found (Barnosky, 1986). Layer 2 is linked to Belling-Allerød interstadial (Watts, 1977; Barnosky, 1986), and the herb-rich grassland dominance seen in Ireland is in contrast to the birch forests that developed in northwest continental Europe and Britain at this time (Watts, 1977; Van Asch and Hoek, 2012). Reasons why vegetation developed in Ireland the way it did is discussed by Van Asch and Hoek (2012) and include exposure to strong cold winds from the Atlantic, limited soil development, precipitation, wildfires and intensive browsing/grazing by giant deer. The overlying layer 3 mainly comprises gravels, dark grey silts and sand, with pollen records consisting mainly of *Artemisia*, Caryophyllaceae, *Thalictrum*, *Sedum rosea*, *Armeria*, *Koennigia* and *Polygonum viviparum*. This is linked to the climatic turndown and deterioration of grasslands caused by the Younger Dryas (Watts, 1977; Barnosky, 1986). This generalised stratigraphy is typical for most Lateglacial lake deposit sites where giant deer remains are found (Barnosky, 1986).

**Table 1.** Information on the *Megaloceros giganteus* specimens previously analysed by Chritz et al. (2009). Age, season of first accretion and season of death are interpreted from the M2. The M2 is considered more reliable than the M3 as it erupts before the latter and thus has a longer cementum layer. The M2 is measured for $^{87}$Sr/$^{86}$Sr analysis in most circumstances (Copeland et al., 2010; Britton et al., 2011; Slovak and Paytan, 2012).

| Specimen (NMING) | County | Locality | Antler cycle | Age at death (months) | Season of first accretion | Season of death |
|------------------|--------|----------|--------------|-----------------------|---------------------------|-----------------|
| F20514           | Wicklow| Castleudder Lower Townland | Both antlers intact | 126 | Partial summer | Late summer/autumn |
| F7913            | Dublin | Ballybetagh | Shed one antler, one partially shed | 96–100 | Summer | Early summer |
| F21647           | Donegal| Mountcharles Townland | Both antlers intact | 84 | Summer | Late winter |
dentine. Enamel surfaces were first abraded using a dental drill with a diamond-tipped drill bit to clean the enamel surface, even though the enamel surfaces had already been abraded during analysis by Chritz et al. (2009). Bands perpendicular to the growth axis were drillled sequentially from apex to cervix (occlusal surface to root) by Chritz et al. (2009), following the direction of mineralisation. When sampling molars in this way, it is almost impossible to sample individual enamel growth bands perfectly, but rather several are likely being sampled (Balasse, 2003; Blumenthal et al., 2014; Bower, 2017). However, although this sampling strategy may not be perfectly representative of single (daily) growth lines, they are still chronological and are sufficient to obtain a reliable change in an isotopic signature in response to environmental changes at the scale we are interested in (Balasse, 2003; Chritz et al., 2009; Britton, 2017). Some 5–7 mg of enamel powder was collected using a handheld drill onto weighing paper, then transferred into acid-cleaned polyethylene Eppendorf centrifuge tubes and weighed. The diamond drill bit was cleaned between each sample using Milli-Q ultrapure water, hydrochloric acid (HCl), Milli-Q ultrapure water again and then ethanol and left to dry. A total of 24 samples were analysed in this study. The samples were chosen based on their associated point in the δ¹⁸O curve, specifically the highest and lowest δ¹⁸O values. Sr purification of the samples was carried out at the US Federal Standard Class 1000 clean laboratory facility at the Vrije Universiteit Amsterdam.

A detailed description of the strontium column extraction and sample loading procedures is provided in Kooker et al. (2016), but summarised here. The samples were leached in 500 μL 0.1 M CH₃CO₂H to remove labile diagenetic strontium, rinsed with Milli-Q, and dissolved in 500 μL 3 M HNO₃. Strontium was isolated by ion exchange chromatography using Sr-Resin (EChrom). Three samples, sample numbers 1.5, 4.5 and 6.6, were spiked with a ⁸⁴Sr-enriched tracer solution to determine the strontium concentration [Sr] by isotope dilution. The samples were dried down, nitrated overnight with 100 μL 14 M HNO₃, and dried down again. Next, the samples were dissolved in 2 μL 10 % HNO₃ and 50 % was loaded on single annealed rhenium filaments with 2 μL TaCl₅. The isotope compositions were measured using a Thermo Scientific Triton Plus instrument at the Vrije Universiteit Amsterdam, the Netherlands. The strontium ratios were determined using a static routine and were corrected for mass fractionation to ⁸⁶Sr/⁸⁸Sr of 0.1194. The intra-run NIST SRM 987 gave a mean ⁸⁶Sr/⁸⁸Sr value of 0.710259 ± 0.000008 (2σ, n = 33) during the course of this study (2020). All measurements were normalised using a standard bracketing method to an accepted ⁸⁷Sr/⁸⁶Sr of 0.710240 (certified ratio SRM 987: 0.71034 ± 0.00026). The procedural blanks were considered negligible: 11.1 and 31.5 pg strontium. For each sample the ⁸⁷Sr/⁸⁶Sr are reported plus minus two standard error (±2 SE), representing the typical measurement precision obtained from 240 cycles of 8.1 s integration time (12 blocks of 20 cycles) within each run.

Results

The results are presented in Table 2. For comparison, the data have been plotted together with a previously published dataset of δ¹³C and δ¹⁸O values obtained by Chritz et al. (2009) (Fig. 3) and are displayed against the distance from the cervix (mm). The ⁸⁷Sr/⁸⁶Sr in the Megaloceros giganteus samples range from 0.708594 to 0.709926 (this study), ⁸⁷Sr/⁸⁶Sr range from -7.8 to -10.5‰, and δ¹⁸O values range from -6.5 to -1.5‰ (Chritz et al., 2009). The individual isotope ranges are 0.709330 to 0.709510 (⁸⁷Sr/⁸⁶Sr), -9.9 to -8.0‰ (δ¹³C) and -6.5 to -3.9‰ (δ¹⁸O) for the Castleruddery stag; 0.709493 to 0.709926 (⁸⁷Sr/⁸⁶Sr), -10.5 to -8.4‰ (δ¹³C) and -5.5 to -3.8‰ (δ¹⁸O) for the Ballybetagh stag; and 0.708594 to 0.708724 (⁸⁷Sr/⁸⁶Sr), -10.4 to -7.8‰ (δ¹³C) and -5.4 to -1.5‰ (δ¹⁸O) for the Mountcharles stag.

The concentration of Sr in samples 1.5 (Castleruddery) and 4.5 (Ballybetagh) and 6.6 (Mountcharles) were 227, 157 and 323 ppm (ng/mg), respectively. The Sr concentrations of samples 1.5 (Castleruddery) and 4.5 (Ballybetagh) fall within the range of domestic cattle, suggesting minimal diagenetic alteration (Evans, 2007; Britton et al., 2009, 2011). The relatively high Sr concentration in sample 6.6 (Mountcharles) and the fact that the ⁸⁷Sr/⁸⁶Sr from all samples of the Mountcharles stag are consistent with the local bioavailable ⁸⁷Sr/⁸⁶Sr may be indicative for diagenetic alteration (Britton et al., 2011).

Discussion

The absence of variation in ⁸⁷Sr/⁸⁶Sr (Δ⁸⁷Sr/⁸⁶Sr_MAX-MIN = 0.000180) in the Castleruddery specimen (F20514) suggests a limited amount of mobility or mobility within or between geological substrates that exhibit similar ⁸⁷Sr/⁸⁶Sr. The more pronounced, but still limited ⁸⁷Sr/⁸⁶Sr variation (Δ⁸⁷Sr/⁸⁶Sr_MAX-MIN = 0.000433) in the Ballybetagh stag (F7913) does not initially point to extensive mobility, or at least mobility across distinct geological areas. The ⁸⁷Sr/⁸⁶Sr of both the Castleruddery and Ballybetagh stags are comparable with the local bioavailable Sr ranges (Fig. 2).

Variation in the δ¹³C between the Castleruddery, Ballybetagh and Mountcharles (F21647) stags were noticeably different, with ranges of 2.6‰, 1.7‰ and 3.9‰, respectively (Chritz et al., 2009). As found in migrating reindeer both from modern and early Holocene populations, the relationship between ⁸⁷Sr/⁸⁶Sr and δ¹⁸O variations can help to determine whether any mobility occurred (Britton et al., 2009, 2011; Gigleux et al., 2019). In only observing ⁸⁷Sr/⁸⁶Sr variation, especially on an island like Ireland with limited regional ⁸⁷Sr/⁸⁶Sr variation, the issue arises that if an animal had travelled large distances, but not crossed different geological areas, the variation in ⁸⁷Sr/⁸⁶Sr would suggest no or limited mobility (Britton, 2010; Slovak and Paytan, 2012; Rogers et al., 2018; Snoeck et al., 2020). However, as pointed out by Britton et al. (2009), the variation in the δ¹⁸O isotope may be dampened by mobility behaviour. This occurs as the animal’s rapid migration into different oxygen isoscapes overprints the local seasonal δ¹⁸O signal which is probably trending in the opposite direction, creating a smaller δ¹⁸O range (Britton et al., 2009, 2011; Pilaar Birch et al., 2016). For example, red deer and caprins from Late Pleistocene deposits in Croatia demonstrate that migrational red deer display a δ¹⁸O variation as low as 1–2‰, compared with non-migrational caprins with variation in the range of 3–4‰ (Pilaar Birch et al., 2016). Studies on non-migratory red deer from Scotland display a variation of around 3–4‰ (Stevens et al., 2011), while migrational caribou display variation as low as 1‰ (Britton et al., 2009). Given the δ¹⁸O ranges of <2‰ for the Ballybetagh stag, it suggests that this animal migrated far enough to be in northern or southern δ¹⁸O isoscapes in Ireland during warmer or colder seasons, respectively (Britton et al., 2009). Ireland’s current δ¹⁸O isoscapes are more depleted in a north-easterly direction (Darling et al., 2003; Pellegrini et al., 2016).
Table 2. Sample information and results from $^{87}$Sr/$^{86}$Sr data (this study) of three *Megaloceros giganteus* specimens with corresponding $^{13}$C and $^{18}$O data from Chritz et al. (2009).

| Specimen (NMING) | Locality       | Molar No. | Sample No. | Distance from cervix (mm) | $^{87}$Sr/$^{86}$Sr | 2 SE error | $^{13}$C (%) V-PDB | $^{18}$O (%) V-PDB |
|------------------|----------------|-----------|------------|---------------------------|--------------------|------------|----------------|-----------------|
| F20514           | Castleruddery Lower (Wicklow) | 2         | 1.1        | 3.5                       | 0.709412           | 0.000008   | -9.1           | -6.4            |
|                  |                |           | 1.2        | 5.6                       | 0.709412           | 0.000008   | -8.4           | -4.9            |
|                  |                |           | 1.4        | 8.5                       | 0.709390           | 0.000006   | -8.5           | -5.1            |
|                  |                |           | 1.5        | 10.5                      | 0.709330           | 0.000007   | -8.0           | -5.4            |
|                  |                |           | 3.1        | 1.1                       | 0.709435           | 0.000008   | -9.8           | -5.7            |
|                  |                |           | 3.2        | 2.4                       | 0.709477           | 0.000008   | -9.9           | -6.5            |
|                  |                |           | 3.6        | 9.8                       | 0.709634           | 0.000008   | -9.9           | -4.9            |
|                  |                |           | 3.8        | 16.8                      | 0.709449           | 0.000008   | -9.4           | -3.9            |
| F7913            | Ballybetagh (Dublin) | 2         | 3.1        | 3.1                       | 0.709493           | 0.000007   | -10.5          | -3.8            |
|                  |                |           | 3.2        | 4.7                       | 0.709512           | 0.000008   | -9.0           | -3.9            |
|                  |                |           | 3.5        | 6.7                       | 0.709680           | 0.000006   | -9.8           | -4.2            |
|                  |                |           | 3.6        | 9.8                       | 0.709634           | 0.000008   | -9.9           | -4.9            |
|                  |                |           | 3.8        | 16.7                      | 0.709449           | 0.000008   | -9.4           | -3.9            |
| F21647           | Mountcharles Townland (Donegal) | 2         | 5.1        | 3.5                       | 0.708594           | 0.000008   | -9.3           | -1.8            |
|                  |                |           | 5.3        | 4.9                       | 0.708647           | 0.000010   | -9.5           | -3.4            |
|                  |                |           | 5.6        | 6.8                       | 0.708670           | 0.000006   | -10.4          | -5.3            |
|                  |                |           | 5.7        | 11.6                      | 0.708684           | 0.000007   | -7.8           | -4.7            |
|                  |                |           | 6.1        | 16.6                      | 0.707998           | 0.000007   | -8.4           | -4.9            |
|                  |                |           | 6.3        | 18.4                      | 0.708666           | 0.000008   | -9.6           | -4.6            |
|                  |                |           | 6.6        | 20.2                      | 0.708724           | 0.000008   | -10.0          | -5.4            |
|                  |                |           | 6.8        | 22.6                      | 0.708712           | 0.000008   | -9.5           | -4.5            |
|                  |                |           | 7.1        | 24.6                      | 0.708702           | 0.000009   | -9.2           | -1.5            |

The $^{13}$C values from dental enamel are converted to $^{13}$C$_{diet}$ with the diet-to-apatite fractionation factor of 14.1‰ (Cerling and Harris, 1999). The $^{13}$C$_{diet}$ data for all three specimens is between -21.9 and -24.6‰ and thus within the C$_3$ plant range (Bocherens, 2003). As mentioned by Chritz et al. (2009), this indicates that these animals occupied open habitats and fed mainly on grasses and sedges, as values lower than -27‰ indicate browsing in densely forested environments (Bocherens, 2003). This is in agreement with vegetation reconstructions of Ireland for the late Allerød and Younger Dryas onset, where open landscapes and grasslands dominated with sparse birch stands (Watts, 1977; Van Asch and Hoek, 2012). The range of $^{13}$C$_{diet}$ within specimens may indicate changes between woody or herbaceous C$_3$ plant taxa in open environments, perhaps in conjunction with seasonality (Tieszen and Boutton, 1989). The Ballybetagh and Mountcharles stags generally have higher $^{13}$C$_{diet}$ in conjunction with higher $^{18}$O, although variation to this pattern is observed. This could suggest that these specimens occupied open grasslands in the warmer months, and for the colder months moved to lightly forested areas for browse, a tactic observed in modern cervids (Bützler, 2001; Vislobokova, 2012; Trepet and Eskina, 2017). The Castleruddery stag, however, displays the opposite; lower $^{13}$C$_{diet}$ while $^{18}$O is high, except at the tail end ($^{13}$Cdiet) within specimens may indicate browsing in densely forested areas for browse, a tactic observed in modern cervids (Bützler, 2001; Vislobokova, 2012; Trepet and Eskina, 2017).
in diet could be responsible for this pattern, but this is also unlikely given the averaging effect of the δ¹³C over the course of molar mineralisation (Passey and Cerling, 2002; Zazzo et al., 2010). There was no significant difference observed in the range of δ¹³Cdiet between the giant deer, which would indicate how varied the diet was between different specimens. The more negative values from the Ballybetagh stag may be an indication of a diet consisting more of woody taxa, decreasing temperatures or depletion of nutrients in ingested plants, while the other giant deer may have had more herbaceous taxa in their diet or may have been subject to water stress (Bocherens, 2003).

The combination of significant intra-dental variation in ⁸⁷Sr/⁸⁶Sr and low δ¹⁸O variation is indicative of seasonal mobility, which has been observed in modern caribou populations, the migratory behaviour of which has been well studied (Britton et al., 2009). The Ballybetagh stag demonstrates the smallest δ¹⁸O range (1.7‰) between all specimens studied, while also demonstrating the largest range for ⁸⁷Sr/⁸⁶Sr (0.000433). However, it should be noted that the variation in ⁸⁷Sr/⁸⁶Sr in the Ballybetagh stag still falls within the range of the bioavailable ⁸⁷Sr/⁸⁶Sr in the Ballybetagh region (Snoeck et al., 2020). This suggests that while this individual partook in seasonally mobile behaviour, the two other specimens did not. Possible explanations as to why the Ballybetagh stag displayed seasonal mobility behaviour and not the others are discussed below.

While Ballybetagh has been well studied, some aspects of its depositional history are unclear. Barnosky (1985, 1986) suggested that the stags found at the site were a segregated overwintering bachelor herd that was present at the onset of the Younger Dryas stadial. Barnosky (1985, 1986) points to features of malnutrition and stunted growth in specimens studied here as evidence for a dwindling population due to the deterioration of grasslands caused by the climatic turmoil. An uncalibrated radiocarbon date of a specimen from the site (UB–2699, lab number Queen’s University Belfast) was published by Barnosky (1985), but when this date was calibrated by Lister and Stuart (2019) it produced a very wide 95.4% range (13 551 – 11 101 cal a BP; Fig. 1), causing Lister and Stuart (2019) to question the usefulness of this specimen’s radiocarbon age. The stunted growth of these deer was small while being statistically significant at 2% (Barnosky 1985; Lister and Stuart, 2019). Nonetheless, these uncalibrated dates from Ballybetagh are the youngest found on the island and suggest that the animals were attempting to behaviourally respond to the climate deterioration of the Younger Dryas before becoming extinct. It could be inferred that the increased mobility of the Ballybetagh stag in this study highlights a behavioural response in giant deer to climatic deterioration in order to obtain enough nutrients for growth. Perhaps the other specimens were deposited earlier than the Ballybetagh stag in the late Allerød when conditions were more favourable for giant deer and seasonal mobility was unnecessary.

As noted by Lister and Stuart (2019), giant deer cannot be ascribed as typical members of the mammoth steppe fauna such as woolly mammoths. Ignoring the Irish Lateglacial population, giant deer remains are seldom found in the fossil record of Late Pleistocene glacial, in fact they are more commonly found in interglacial deposits with warm environments described by Watts (1977) and Barnosky (1986). Shaded areas reflect interstadials and the Holocene defined by Rasmussen et al. (2014): 95.4% confidence interval of Ballybetagh specimen UB–2699 (lab number Queen’s University Belfast) calibrated ¹⁴C date analysed by Barnosky (1986), suggested to be one of the youngest giant deer in Ireland (Lister and Stuart, 2019). [Color figure can be viewed at wileyonlinelibrary.com]
Giant deer were seemingly more adapted to the warmer climatic intervals of the Late Pleistocene as suggested by Vislobokova (2012) but were still found in the mammoth steppe faunal assemblages. While not as well adapted to the mammoth steppe, they may have survived by seasonally moving between boreal parklands and the steppe/tundra (Vislobokova, 2012; Lister and Stuart, 2019). Therefore, we suggest that enhanced seasonal mobility behaviour during the colder periods of the Late Pleistocene was an adaptation to find enough palatable vegetation for growth, and this is reflected in the Ballybetagh specimen which is possibly from the Younger Dryas onset in Ireland. However, this conclusion is tentative as this study focuses only on the Irish Lateglacial population, which is unique compared with the ecosystem it occupied over the rest of the Late Pleistocene.

The dampening of the δ¹⁸O curve may also be a response to attitudinal migration as opposed to latitudinal migration. This behaviour has been observed in many ungulates, moving up in elevation in warmer months and moving to lower elevations in the colder months, which would cause a similar dampening effect to be observed in the δ¹⁸O of tooth enamel (Carvalho et al., 2008; Hsiung et al., 2018; Smolko et al., 2018). While the Ballybetagh stag does show the lowest variation in δ¹⁸O and largest variation in ⁸⁷Sr/⁸⁶Sr in this study, the ⁸⁷Sr/⁸⁶Sr from this specimen is comparable to the bioavailable ⁸⁷Sr/⁸⁶Sr in the Ballybetagh region. This may be explained by the animal not moving over distinct geological regions over the course of enamel mineralisation, but rather over a small area (causing less significant variation in ⁸⁷Sr/⁸⁶Sr) and moving in elevation seasonally, causing a dampening of the δ¹⁸O. The Wicklow mountains would be a good candidate, but are not very high, only 925 m above sea level at the highest peak (Lugnaquilla). In fact, the tallest mountain in Ireland is only 1038 m high (Carranutoohill), Ballybetagh itself is located at about 250 m above sea level. Given an altitudinal trend of 1 – 3‰ per km in

Figure 2. Median Bioavailable Strontium isotope ratio map (BASR map) of Ireland created with ArcMap 10.8 based on data published by Snoeck et al. (2020) with sample locations displayed as black dots. [Color figure can be viewed at wileyonlinelibrary.com]
temperate climates (Gonfiantini et al., 2001; Ferrio and Voltas, 2005; Tornero et al., 2018) for $\delta^{18}O$, it is unclear whether altitudinal movement would be as effective as latitudinal movement in Ireland. Nevertheless, this type of movement should not be excluded.

The Lateglacial Irish population appeared to have had a differing diet compared with many of the Late Pleistocene populations. While adapted for processing softer vegetation with their mesodont dentition, Irish giant deer subsisted almost exclusively on grasses and sedges based on isotope and microwear patterns on their molars, unlike other giant deer populations which subsisted on a mix of browsing and grazing (Hayden, 2000; Aaris-Sørensen and Liljegren, 2004; Chritz et al., 2009; Rivals and Lister, 2016; Saarinen et al., 2016). This shift from their preferred diet can be explained by two arguments; one being that the underlying geology over much of Ireland consists of calcium-rich limestone, which meant that lime-rich grasses here were packed with enough nutrients for

Figure 3. $^{87}$Sr/$^{86}$Sr (current study), $^{13}$C (Chritz et al., 2009) and $^{18}$O (Chritz et al., 2009) plotted against the distance from cervix for the M2 (left) and M3 (right) from specimens F20514 (blue circles), F7913 (red squares) and F21647 (orange triangles). Error bars are smaller than the symbols. [Color figure can be viewed at wileyonlinelibrary.com]
antler development but also general growth for these deer (Monaghan, 2017). However, the presence of lime-rich soils would suggest a low phosphorus concentration in plants, due to the lower mobility of phosphorus bound to calcium phosphates in lime-rich soils (Wilson et al., 1995; Zohlen and Tyler, 2004; Niinemets and Kull, 2005; Reumer and Robert, 2005). Given that phosphorus is another key mineral for antler growth, the presence of lime-rich soils may have been a limiting factor for Irish giant deer. Secondly, the lack of any other major grazers on the island (Monaghan, 2017) could suggest that while Irish giant deer were not well adapted to grazing, the ecological niche was open for them to occupy. These factors may also have consequences enhancing or discouraging seasonal mobility in Irish Lateglacial giant deer compared with other populations over the Late Pleistocene in Eurasia. For example, Abraham et al. (2021) suggests that, generally, herbivores with a wider dietary niche may be less inclined to migrate than grazers and instead shift their diet seasonally according to food availability.

Another reason why some but not all giant deer demonstrate migrational behaviour includes spatial variation in the population. This can be seen with extant cervids such as caribou and red deer, where populations can have co-occurring migrational and residence strategies (Chapman et al., 2011; Martin et al., 2018). This could be for several reasons, being differences in topography in a region, predation, or intraspecific competition (Chapman et al., 2011; Mysterud et al., 2011; Martin et al., 2018). Thus, it could be suggested that the difference in an individual’s migrational behaviour could be within a population itself and suggests that, similar to many extant cervids (Ball et al., 2001; Cagnacci et al., 2011; Martin et al., 2018), seasonal migrational behaviour was expressed in some but not all individuals of the Irish giant deer population.

It should be noted that the scope of this study limits the conclusions one can make regarding mobility in Irish giant deer, as only three specimens were analysed from various locations in Ireland, and only a span of one year is represented in their dental enamel (Chritz et al., 2009). Therefore, it is imperative that more specimens should be studied in order to make more conclusive statements regarding their mobility behaviour. However, similar patterns in δ87Sr/86Sr and δ18O over the span of a year have been documented in modern caribou (Britton et al., 2009), and this baseline has been successfully applied to the study of cervids from the Late Pleistocene (Britton et al., 2011; Pilaar Birch et al., 2016; Price et al., 2017; Gigleux et al., 2019). Therefore, this study should be seen as an initial step in the study of seasonal mobility in giant deer, with more individuals from specific localities to be studied in the future.

**Conclusion**

Strontium isotope data obtained in this study were interpreted with previously published δ18O and δ13C data from three Lateglacial Irish giant deer *Megaloceros giganteus*. The results suggest that the Ballybetagh stag (F7913) was seasonally mobile, indicated by the limited range in δ18O coupled with the largest variation in δ87Sr/86Sr found in the three specimens studied. This contrasts with the Castleruddery (F20514) and Mountcharles (F21647) stags that exhibit little variation in δ87Sr/86Sr, and significant (seasonal) fluctuations in δ18O ranges.

The fact that seasonal mobility was found in the Ballybetagh specimen sparks particular interest, as 14C dates from this site are the youngest in Ireland, but do not yield fully reliable calibrated radiocarbon dates. Regardless, reasoning as to why this specimen exhibited such mobility includes a behavioural response to the climatic turnover of the Younger Dryas and the subsequent deterioration of productive grasslands across the island. This may have been employed in older European populations as well, as evidenced by their presence in, but maladaptation to, the mammoth steppe biome and their more abundant presence during the potential climatic periods. However, the applicability of such conclusions is tentative given the unique qualities of the Lateglacial Irish giant deer population.

Further research into this topic is recommended, in order to make more concrete conclusions on the mobility of giant deer in Eurasia in response to changes in climate. For the Irish Lateglacial giant deer, comparative studies between Ballybetalgh specimens and other Irish specimens are recommended so as to strengthen the claim that stags at Ballybetalgh were indeed more mobile as a response to the climatic deterioration of the Younger Dryas.

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