

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

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Received 9 February 2022; Revised 16 May 2022; Accepted 30 May 2022

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 glacials by moving to sheltered, low-lying areas. In this study strontium isotope analysis ($^{87}\text{Sr}/^{86}\text{Sr}$) of sequentially sampled dental enamel is conducted for the first time on giant deer that were previously sampled in the same manner for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, 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.

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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 defined in Europe as an elk, *Alces alces* (Linnaeus, 1758) or in North America, *Cervus canadensis* (Erxleben, 1777). Instead, the fallow deer *Dama dama* (Linnaeus, 1758) is their closest 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; Worman 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*

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(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 retreating 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 Kimbrell, 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), Castleruddery 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; Gignoux *et al.*, 2019), strontium isotope analysis ($^{87}\text{Sr}/^{86}\text{Sr}$) being the most commonly utilised (Hoppe *et al.*, 1999; Hoppe and Koch, 2007; Britton *et al.*, 2009, 2011; Price *et al.*, 2017; Gignoux *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 ^{87}Sr and ^{86}Sr isotopes fractionates negligibly as it moves 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 $^{87}\text{Sr}/^{86}\text{Sr}$ of the vegetation and water in a region (which forms the herbivores' diet) is mainly determined by the underlying geology, with the ^{87}Sr in rocks forming over time due to the radioactive decay of

rubidium (^{87}Rb). This makes the relative content of ^{87}Sr to ^{86}Sr 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 $^{87}\text{Sr}/^{86}\text{Sr}$. Therefore, variations in $^{87}\text{Sr}/^{86}\text{Sr}$ in animal mineral tissue may suggest movement across differing geological areas over a period of the animal's life.

The presence of a bioavailable $^{87}\text{Sr}/^{86}\text{Sr}$ map (BASr map) of Ireland allows us to correlate the $^{87}\text{Sr}/^{86}\text{Sr}$ of the giant deer to $^{87}\text{Sr}/^{86}\text{Sr}$ isoscapes (Fig. 2; Snoeck *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 $^{87}\text{Sr}/^{86}\text{Sr}$ are found (0.7061–0.7070). Carboniferous limestone covers much of the island leading to large areas that are characterised by a $^{87}\text{Sr}/^{86}\text{Sr}$ value between 0.7071 and 0.7080, while the $^{87}\text{Sr}/^{86}\text{Sr}$ at the southern margins of Ireland Devonian 'Old Red' Sandstone ranges between 0.7101 and 0.7110 (Holland and Sanders, 2009; Snoeck *et al.*, 2020).

Oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) 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 $\delta^{18}\text{O}$ of carbonate and phosphate in hydroxyapatite precipitates in equilibrium with body water, and $\delta^{18}\text{O}$ 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 $\delta^{18}\text{O}$ 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 $\delta^{18}\text{O}$ caused by the animal ingesting water in different oxygen isoscapes (Britton *et al.*, 2009; Pellegrini *et al.*, 2016; Pilaar Birch *et al.*, 2016). The $\delta^{18}\text{O}$ 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 $\delta^{13}\text{C}$ of carbonate in the hydroxyapatite of herbivores is related to the vegetation they consumed, as certain types of plants (C_3 or C_4 plants) have distinct $\delta^{13}\text{C}$ ranges due to their differing photosynthetic pathways (Tieszen and Boutton, 1989; Bocherens, 2003). In colder climates, however, almost all plants utilise the C_3 photosynthetic pathway (Bocherens, 2003). Variation in $\delta^{13}\text{C}$ in sequential samples in these conditions is therefore mainly a consequence of feeding on plants that are found in forested (lower $\delta^{13}\text{C}$) and open habitats (higher $\delta^{13}\text{C}$), and/or a diet composed of woody (lower $\delta^{13}\text{C}$) or herbaceous (higher $\delta^{13}\text{C}$) C_3 plant taxa in open environments (Lee-Thorp *et al.*, 1989; Tieszen and Boutton, 1989; Cerling and Harris, 1999; Bonafini *et al.*, 2013). The $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ isotopes can be combined with $^{87}\text{Sr}/^{86}\text{Sr}$ 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; Gignoux *et al.*, 2019).

$\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ 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 cervix (denture-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 <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 $^{87}\text{Sr}/^{86}\text{Sr}$ 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* (Erleben, 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 (Ballantyne 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 these herbivores, as much of the island was dominated by grass plains with birch stands (Watts, 1977; Barnosky, 1986; Van Asch and Hoek, 2012; Monaghan, 2017). After this came the Younger Dryas (GS-1) climatic turn-down, leading to the rapid deterioration of these grasslands and the development of tundra (Watts, 1977, Van Asch and Hoek, 2012). Giant deer remains are often found in lacustrine and occasionally cave deposits across the island (Barnosky, 1986; Monaghan, 2017). During the late Allerød Ireland was probably totally ice free, but with the Younger Dryas came the re-expansion of glaciers in parts of the island (Monaghan, 2017). The faunal composition of Ireland during the Lateglacial does not contain many traditional grazers as opposed to mainland Europe at this time; the only large herbivores found at this time were giant deer, reindeer and red deer (Monaghan, 2017).

At Ballybetagh (Dublin), glacial erratics and solifluction deposits are found in layer 1, the oldest layer detailed by Barnosky (1986). Pollen from this layer indicates sparse vegetation cover mainly comprised of grasses, *Rumex* and *Salix*, indicating cold conditions. Above layer 1 are silt, clay and gyttja deposits, indicating a small lake being present at the time of deposition. Barnosky (1986) denotes these sediments as layer 2. This layer displays an amelioration in climate as

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 *Empetrum* pollen, indicating a dense and diverse vegetation cover and corresponds to the *Juniperus-Empetrum* 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 Bølling-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 north-west 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*, *Koenigia* and *Polygonum viviparum*. This is linked to the climatic turn-down 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 $^{87}\text{Sr}/^{86}\text{Sr}$ analysis; NMING: F7913 (Ballybetagh), F20514 (Castleruddery) 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 were 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 Castleruddery Lower Townsland (Wicklow) or Mountcharles Townsland (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

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 record as cementum begins formation upon tooth eruption (Reimers and Nordby, 1968; Klevezal, 1996; Hillson, 2005; Chritz *et al.*, 2009).

Specimen (NMING:)	County	Locality	Antler cycle	Age at death (months)	Season of first accretion	Season of death
F20514	Wicklow	Castleruddery Lower Townsland	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 Townsland	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 drilled 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 relative change in an isotopic signature in response to environmental change 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 $\delta^{18}\text{O}$ curve, specifically the highest and lowest $\delta^{18}\text{O}$ 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 Kootker *et al.* (2016), but summarised here. The samples were leached in 500 μL 0.1 M $\text{CH}_3\text{CO}_2\text{H}$ to remove labile diagenetic strontium, rinsed with Milli-Q, and dissolved in 500 μL 3 M HNO_3 . Strontium was isolated by ion exchange chromatography using Sr-Resin (EiChrom). Three samples, sample numbers 1.5, 4.5 and 6.6, were spiked with a ^{84}Sr -enriched tracer solution to determine the strontium concentration [Sr] by isotope dilution. The samples were dried down, nitrated overnight with 100 μL 14 M HNO_3 , and dried down again. Next, the samples were dissolved in 2 μL 10% HNO_3 and 50% was loaded on single annealed rhenium filaments with 2 μL TaCl_5 .

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 $^{86}\text{Sr}/^{88}\text{Sr}$ of 0.1194. The intra-run NIST SRM 987 gave a mean $^{87}\text{Sr}/^{86}\text{Sr}$ value of 0.710259 ± 0.000008 (2 s, $n=33$) during the course of this study (2020). All measurements were normalised using a standard bracketing method to an accepted $^{87}\text{Sr}/^{86}\text{Sr}$ 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 $^{87}\text{Sr}/^{86}\text{Sr}$ are reported plus or 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 $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values obtained by Chritz *et al.* (2009) (Fig. 3) and are displayed against the distance from the cervix (mm). The $^{87}\text{Sr}/^{86}\text{Sr}$ in the *Megaloceros giganteus* samples range from 0.708594 to 0.709926 (this study), $\delta^{13}\text{C}$ values

range from -7.8 to -10.5‰ , and $\delta^{18}\text{O}$ values range from -6.5 to -1.5‰ (Chritz *et al.*, 2009). The individual isotope ranges are 0.709330 to 0.709510 ($^{87}\text{Sr}/^{86}\text{Sr}$), -9.9 to -8.0‰ ($\delta^{13}\text{C}$) and -6.5 to -3.9‰ ($\delta^{18}\text{O}$) for the Castleruddery stag; 0.709493 to 0.709926 ($^{87}\text{Sr}/^{86}\text{Sr}$), -10.5 to -8.4‰ ($\delta^{13}\text{C}$) and -5.5 to -3.8‰ ($\delta^{18}\text{O}$) for the Ballybetagh stag; and 0.708594 to 0.708724 ($^{87}\text{Sr}/^{86}\text{Sr}$), -10.4 to -7.8‰ ($\delta^{13}\text{C}$) and -5.4 to -1.5‰ ($\delta^{18}\text{O}$) for the Mountcharles stag.

The concentration of Sr in samples 1.5 (Castleruddery), 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 $^{87}\text{Sr}/^{86}\text{Sr}$ from all samples of the Mountcharles stag are consistent with the local bioavailable $^{87}\text{Sr}/^{86}\text{Sr}$ may be indicative for diagenetic alteration (Britton *et al.*, 2011).

Discussion

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

Variation in the $\delta^{18}\text{O}$ 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 $^{87}\text{Sr}/^{86}\text{Sr}$ and $\delta^{18}\text{O}$ variations can help to determine whether any mobility occurred (Britton *et al.*, 2009, 2011; Gignoux *et al.*, 2019). In only observing $^{87}\text{Sr}/^{86}\text{Sr}$ variation, especially on an island like Ireland with limited regional $^{87}\text{Sr}/^{86}\text{Sr}$ variation, the issue arises that if an animal had travelled large distances, but not crossed different geological areas, the variation in $^{87}\text{Sr}/^{86}\text{Sr}$ 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 $\delta^{18}\text{O}$ isotope may be dampened by mobility behaviour. This occurs as the animal's rapid migration into different oxygen isoscapes overprints the local seasonal $\delta^{18}\text{O}$ signal which is probably trending in the opposite direction, creating a smaller $\delta^{18}\text{O}$ range (Britton *et al.*, 2009, 2011; Pilaar Birch *et al.*, 2016). For example, red deer and caprids from Late Pleistocene deposits in Croatia demonstrate that migrational red deer display a $\delta^{18}\text{O}$ variation as low as 1–2‰, compared with non-migrational caprids 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 $\delta^{18}\text{O}$ ranges of $<2\text{‰}$ for the Ballybetagh stag, it suggests that this animal migrated far enough to be in northern or southern $\delta^{18}\text{O}$ isoscapes in Ireland during warmer or colder seasons, respectively (Britton *et al.*, 2009). Ireland's current $\delta^{18}\text{O}$ isoscapes are more depleted in a north-easterly direction (Darling *et al.*, 2003; Pellegrini *et al.*, 2016).

Table 2. Sample information and results from $^{87}\text{Sr}/^{86}\text{Sr}$ data (this study) of three *Megaloceros giganteus* specimens with corresponding $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ data from Chritz *et al.* (2009).

Specimen (NMING:)	Locality	Molar No.	Sample No.	Distance from cervix (mm)	$^{87}\text{Sr}/^{86}\text{Sr}$	2 SE error	$\delta^{13}\text{C}$ (‰) V-PDB	$\delta^{18}\text{O}$ (‰) V-PDB	
F20514	Castleruddery Lower Townland (Wicklow)	2	1.1	3.5	0.709412	0.000008	-9.1	-4.6	
			1.2	5.6	0.709412	0.000008	-8.4	-4.9	
		3	1.4	7.1				-9.0	-5.1
			1.5	8.5	0.709390	0.000006	-8.5	-5.1	
			2.1	10.5	0.709330	0.000007	-8.0	-5.4	
			2.2	1.1	0.709435	0.000008	-9.8	-5.7	
				2.4	0.709477	0.000008	-9.9	-6.5	
				4.3			-9.5	-6.1	
				5.8			-8.3	-5.5	
			2.5	8.0	0.709505	0.000008	-9.2	-5.9	
			2.6	11.4	0.709510	0.000010	-8.5	-4.6	
				14.6			-9.2	-4.4	
			16.8			-9.4	-3.9		
		F7913	Ballybetagh (Dublin)	2	3.1	3.1	0.709493	0.000007	-10.5
3.2	4.7				0.709512	0.000008	-9.0	-3.9	
3				5.7				-9.3	-4.0
				6.7				-10.3	-4.2
	3.5			7.6	0.709680	0.000006	-9.8	-4.7	
	3.6			9.8	0.709634	0.000008	-9.9	-4.9	
				1.9			-10.4	-3.9	
	4.1			4.5	0.709926	0.000008	-9.1	-4.6	
				6.2			-10.3	-5.3	
	4.3			7.5	0.709898	0.000008	-9.1	-5.0	
				9.7			-9.1	-5.4	
	12.2	0.709556	0.000007	-8.5	-5.5				
F21647	Mountcharles Townsland (Donegal)	2	4.7	16.6	0.709798	0.000007	-8.4	-4.9	
			5.1	3.5	0.708594	0.000008	-9.3	-1.8	
		3	5.3	4.9				-9.4	-2.3
				6.8	0.708647	0.000010	-9.5	-3.4	
				9.06			-9.8	-3.5	
				11.6			-9.5	-3.4	
			5.6	12.6	0.708670	0.000008	-10.4	-5.3	
			5.7	15.3	0.708684	0.000007	-7.8	-4.7	
			6.1	2.8	0.708724	0.000008	-10.0	-5.4	
				4.5			-9.7	-5.0	
			6.3	6.5	0.708666	0.000008	-9.6	-4.6	
				8.5			-10.2	-4.0	
			10.2			-9.5	-4.1		
		6.6	13.1	0.708661	0.000009	-9.5	-4.5		
	14.8			-9.5	-3.0				
	16.9			-9.4	-1.8				
	18.4			-9.9	-2.2				
	6.10	19.7	0.708702	0.000009	-9.2	-1.5			

The $\delta^{13}\text{C}$ values from dental enamel are converted to $\delta^{13}\text{C}_{\text{diet}}$ with the diet-to-apatite fractionation factor of 14.1‰ (Cerling and Harris, 1999). The $\delta^{13}\text{C}_{\text{diet}}$ 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 $\delta^{13}\text{C}_{\text{diet}}$ 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 $\delta^{13}\text{C}_{\text{diet}}$ in conjunction with higher $\delta^{18}\text{O}$, 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; Trepel and Eskina, 2017). The Castleruddery stag, however, displays the opposite; lower $\delta^{13}\text{C}_{\text{diet}}$ while $\delta^{18}\text{O}$ is high, except at the $\delta^{18}\text{O}$ low of the M3. This relationship may be due to increased water stress on the vegetation that the animal fed on during colder months (Bocherens, 2003).

The pattern of $\delta^{13}\text{C}$ variation in the M2 but also the tail-end of the M3 of the Ballybetagh stag displays an unusual pattern, shooting from very negative to positive within the trend. This is strange as it would be expected to follow a general trend as seen in the other specimen, although some values in the M3 of the Castleruddery specimen are similarly unusual. No explanation for this pattern was detailed in the research by Chritz *et al.* (2009), but the contamination of the enamel sampled by Chritz *et al.* (2009) with underlying dentine is unlikely given the expected trend of $\delta^{18}\text{O}$ observed from the same enamel samples. Perhaps sharp and significant changes

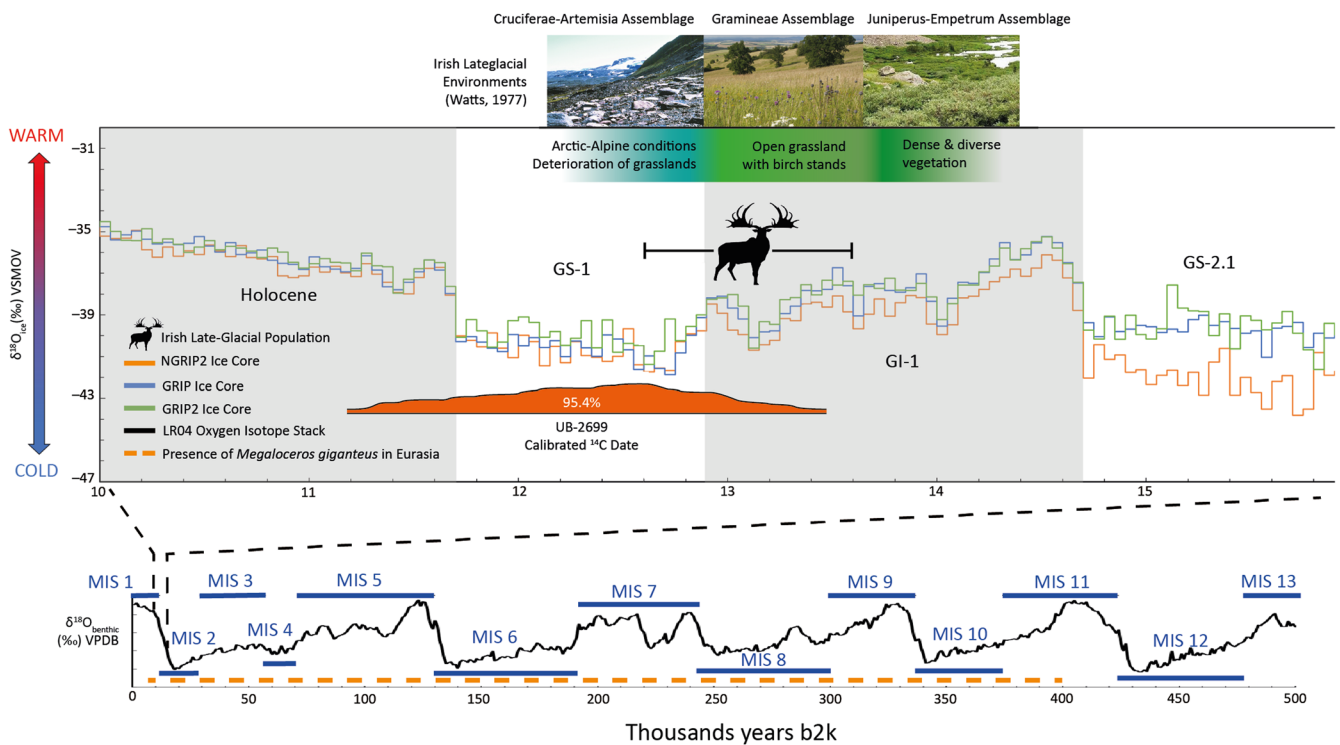


Figure 1. Marine Isotope Stages (MIS), benthic carbonate oxygen isotope data (Lisiecki and Raymo, 2005) and Greenland ice core chronology (Rasmussen *et al.*, 2014) of the Pleistocene Lateglacial with vegetation assemblages and environments described by Watts (1977) and Barnosky (1986). Shaded areas 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 ^{14}C 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]

in diet could be responsible for this pattern, but this is also unlikely given the averaging effect of the $\delta^{13}\text{C}$ over the course of molar mineralisation (Passey and Cerling, 2002; Zazzo *et al.*, 2010).

There was no significant difference observed in the range of $\delta^{13}\text{C}_{\text{diet}}$ 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 of 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 $^{87}\text{Sr}/^{86}\text{Sr}$ and low $\delta^{18}\text{O}$ 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 $\delta^{18}\text{O}$ range (1.7‰) between all specimens studied, while also demonstrating the largest range for $^{87}\text{Sr}/^{86}\text{Sr}$ (0.000433). However, it should be noted that the variation in $^{87}\text{Sr}/^{86}\text{Sr}$ in the Ballybetagh stag still falls within the range of the bioavailable $^{87}\text{Sr}/^{86}\text{Sr}$ 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 turnaround.

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-adapted species in Europe such as the straight-tusked elephant *Palaeoloxodon/Elephas antiquus* (Falconer and Cautley, 1847) and wild boar *Sus scrofa* Linnaeus, 1758 (Vislobokova, 2012). They are also completely absent from the Siberian and northern Asian mammoth steppe deposits. Giant deer were not well-adapted for grazing, instead having mesodont molars more suited to less abrasive vegetation (Rivals and Lister, 2016; Saarinen *et al.*, 2016; Lister and Stuart, 2019). However, later populations became increasingly more adapted to grazing by the increase in their tooth size relative to body

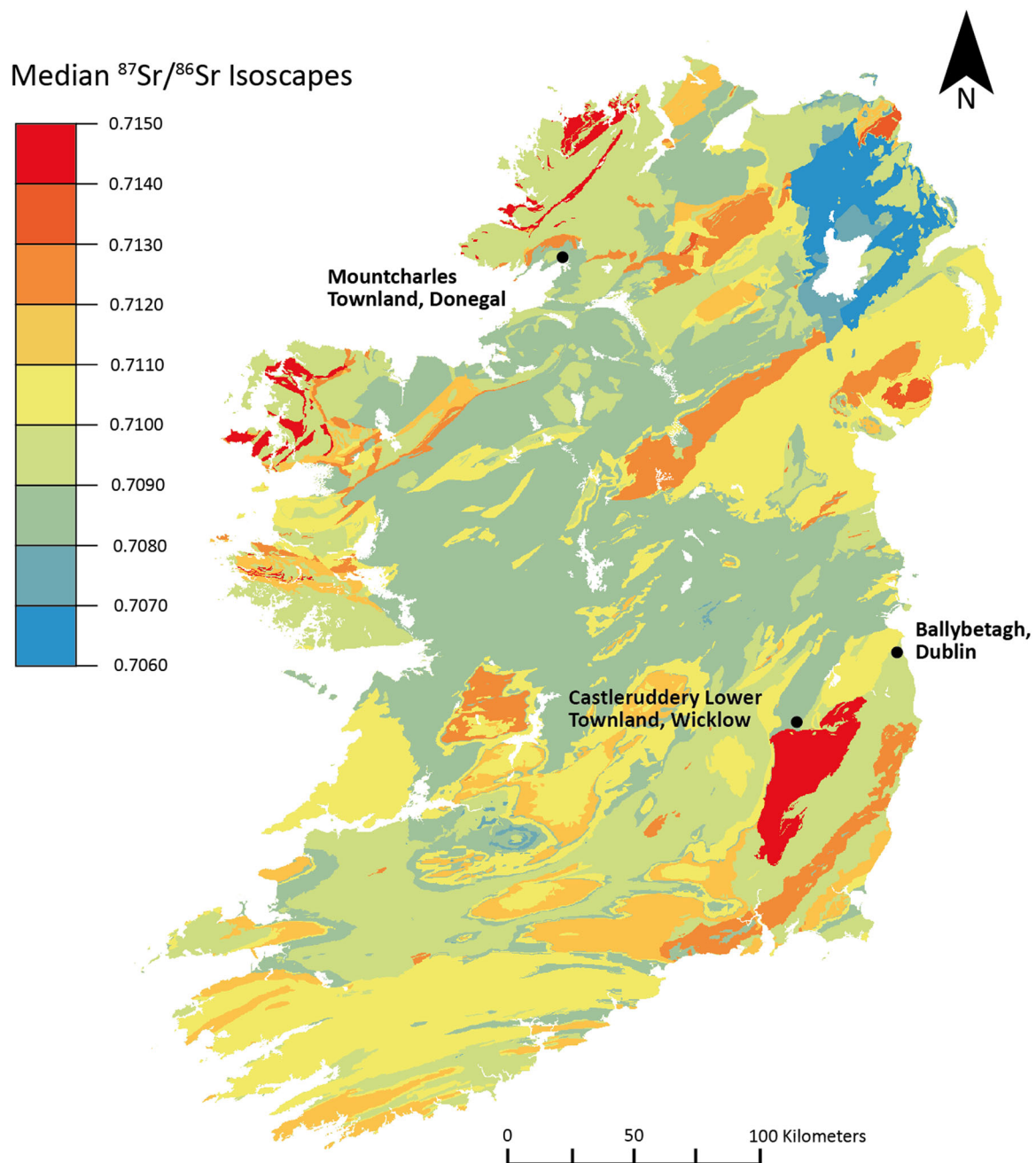


Figure 2. Median Bioavailable Strontium isotope ratio map (BASR map) of Ireland created with ArcMap 10.8 based on data published by Snoeck *et al.* (2020) with sample locations displayed as black dots. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

size (Vislobokova, 2012). 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 $\delta^{18}\text{O}$ curve may also be a response to altitudinal 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 $\delta^{18}\text{O}$ 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 $\delta^{18}\text{O}$ and largest variation in $^{87}\text{Sr}/^{86}\text{Sr}$ in this study, the $^{87}\text{Sr}/^{86}\text{Sr}$ from this specimen is comparable to the bioavailable $^{87}\text{Sr}/^{86}\text{Sr}$ 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 $^{87}\text{Sr}/^{86}\text{Sr}$) and moving in elevation seasonally, causing a dampening of the $\delta^{18}\text{O}$. 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 (Carrauntoohil), Ballybetagh itself is located at about 250 m above sea level. Given an altitudinal trend of 1 – 3‰ per km in

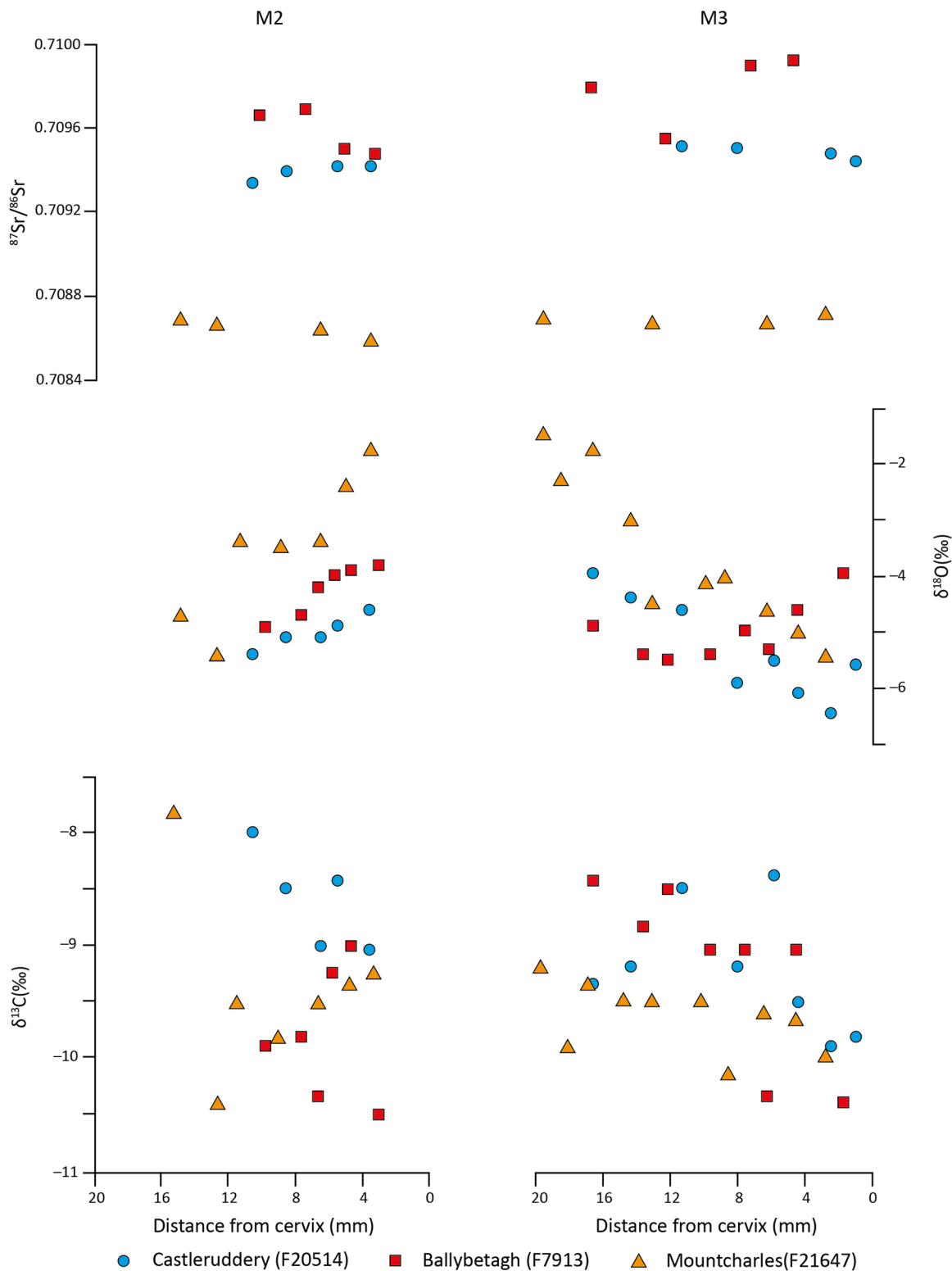


Figure 3. $^{87}\text{Sr}/^{86}\text{Sr}$ (current study), $\delta^{13}\text{C}$ (Chritz *et al.*, 2009) and $\delta^{18}\text{O}$ (Chritz *et al.*, 2009) plotted against the distance from cervix for the M2 (left) and M3 (right) from specimens F20514 (blue circles), F7913 (red squares) and F21647 (orange triangles). Error bars are smaller than the symbols. [Color figure can be viewed at wileyonlinelibrary.com]

temperate climates (Gonfiantini *et al.*, 2001; Ferrio and Voltas, 2005; Tornero *et al.*, 2018) for $\delta^{18}\text{O}$, 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

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; Myserud *et al.*, 2011; Martin *et al.*, 2018). Thus, it could be suggested that the difference in an individual's migration 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 $^{87}\text{Sr}/^{86}\text{Sr}$ and $\delta^{18}\text{O}$ over the span of a year have been documented in modern caribou that are known to have migrated large distances (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; Gignoux *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 $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ 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 $\delta^{18}\text{O}$ coupled with the largest variation in $^{87}\text{Sr}/^{86}\text{Sr}$ found in the three specimens studied. This contrasts with the Castleruddery (F20514) and Mountcharles (F21647) stags that exhibit little variation in $^{87}\text{Sr}/^{86}\text{Sr}$, and significant (seasonal) fluctuations in $\delta^{18}\text{O}$ ranges.

The fact that seasonal mobility was found in the Ballybetagh specimen sparks particular interest, as ^{14}C 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 turndown 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 interglacial 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 Ballybetagh specimens and other Irish specimens are recommended so as to strengthen the claim that stags at Ballybetagh were indeed more mobile as a response to the climatic deterioration of the Younger Dryas.

Acknowledgements. D. Douw and T. Giltaij thank Gert-Jan Reichart and Bas van der Wagt (Royal Netherlands Institute for Sea Research) for assisting in methodology understanding and facilitating our research project. Further thanks to Adrian Lister (Natural History Museum, London) who gave guidance during the early stages of the project. We also wish to thank the two anonymous reviewers for their pertinent comments and feedback. Funding was provided by the Olaf Schuiling and the Hans de Bruijn funds.

Conflict of interest—The authors of this paper declare no conflicts of interest.

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