Introduction

Of all cervids, the European fallow deer (*Dama dama dama*) is of particular interest from a zooarchaeological perspective because it owes its present-day distribution mainly to human influence. Prior to the Last Glacial Maximum (Devensian, Weichselian) fallow deer were widespread across northern Europe but evidence indicates that their range became restricted to refugia in southern and south-eastern Europe (Stuart 1977; Provan and Bennett 2008; Stewart et al. 2010; Stewart and Lister 2001). Their northward rediffusion appears to have been a slow process. Fallow deer, including the Persian sub-species (*Dama dama mesopotamica*), were introduced to some large Mediterranean islands during the early Neolithic, c. 8000–7000 BC (Masseti et al. 2006; Vigne 1999; Daujat 2013; Vigne 2014; Vigne et al. 2014). Remains from mainland Greece, Sicily, Sardinia and Italy point to their introduction by the time of the Bronze Age (Yannouli and Trantalidou 1999; MacKinnon...
2004; Vigne 1999) and to the Balearic Islands and Iberia by the Roman period (Davis and MacKinnon 2009). There are few pre-medieval sites with fallow deer remains in mainland Western Europe: isolated finds are known from France, the Netherlands and Switzerland, mainly of metapodia which may indicate trade in body parts (Sykes et al. 2011).

Research by Sykes et al. (2006) has shown that the earliest known occurrence of fallow deer in Britain is found at Fishbourne Roman Palace in Sussex. Two jaw bones from the site were analysed in detail through a combination of AMS radiocarbon dating and strontium isotope analysis. From this it was possible to identify a first generation import (dated to 60 ± 40 cal AD: Beta-201535) while the slightly later-dated mandible (90 ± 40 cal AD: Beta-201534) provided strontium isotope ratios indicative of having been born and raised at Fishbourne: evidence that a breeding population had been established in the Fishbourne area by this time (Sykes 2004; Sykes et al. 2006). Other Roman sites in the Thanet area of Kent – Monkton (Bendrey 2003), Minster (Morris no date) and the East Kent Access Road (Madgwick et al. 2013) – have also yielded a number of postcranial bones and antlers which have been dated to the 1st and 2nd centuries AD and later. It seems likely that breeding populations were also established here, on the Roman island of Thanet. However, beyond these two sites, the extent to which fallow deer were managed in Roman Britain has been obscured by the potential trade in body parts, especially since many Roman (also some Iron Age) sites have purported the presence of shed antlers, elements that could have been traded in their own right (see Osborne 2013 and Miller et al. 2016).

On the basis of seemingly anomalous stable isotope results from Roman specimens (in particular antler specimens) recovered from across Britain, Madgwick et al. (2013) proposed that some shed antlers may indeed have been imported. Furthermore, they suggested that stable isotope analysis may even offer an opportunity to identify long-distance trade of fallow deer body parts. These claims were made, however, without any clear understanding of the isotopic relationship between bone and antler, or how isotope ratios vary across the entirety of the fallow deer’s large and fast-growing antlers. To redress this knowledge gap, a carbon and nitrogen (Δ13C, Δ15N) isotope study was undertaken on modern fallow deer antler of known provenance to generate some baseline data. The results of this study are summarised in Miller et al. (2016), where the archaeological applicability of the dataset is also presented, concluding that the initial hypothesis of antler trading was most probably an artefact of variations in different skeletal tissues. However, this paper provides an more in-depth analysis of the results, highlighting further intra-element and age-related variation of both carbon and nitrogen isotope ratios in fallow deer antler.

Materials and methods

In the opinion of developmental biologist Richard Goss, ‘The antlers of deer are so improbable that if they had not evolved in the first place they would never have been conceived even in the wildest fantasies of the most imaginative biologists’ (Goss 1983: 1). Antlers are indeed astonishing structures, renewed annually over a relatively short period, with their growth making huge demands on the buck’s physiology, in preparation for the autumn rut, when males use their antlers for display and in combat for the right to mate with a group of females. They represent one of the fastest-growing mammalian tissues, developing as much as 14 kg in a 6 month period, with a peak growth rate of 2–4 cm per day (Chen, Stokes and McKittrick 2009), although one estimate states that the antlers of a 200 kg red deer (Cervus elaphus) stag can reach a weight of 30 kg and grow in only three months (Price et al. 2005). Unlike horn, which consists of keratinized tissue over a bony core, antlers comprise skin, nerves, blood vessels, fibrous tissue, cartilage and bone (Price et al. 2005). They are remarkable in many respects: in their rate of growth,
in their ability to regenerate, and for their role in the social life of deer.

For the stable isotope analysis of modern fallow antlers, specimens obtained from Phoenix Park, Dublin, Ireland were used. Phoenix Park is a large managed park covering some 707 ha and antlers from the fallow herd came mostly from identified individuals with known dates of birth and death. The animals have access to typical parkland grazing, predominantly of grass with some 25 per cent under mixed woodland (Carden 2006). Stable isotopes of carbon and nitrogen were chosen for analysis because of their relationship to diet (DeNiro 1985; DeNiro and Epstein 1978, 1981; Heaton et al. 1986; Heaton 1999). Diet is an important factor when considering antlers, as their annual regeneration may place additional stress on the animal’s system and it is reasonable to assume that the dietary proteins involved in antler development are reflected in carbon and nitrogen.

Nine antlers were sampled. Four sample locations along the length of each antler were chosen to record isotope values at different stages of growth. These were the proximal end (P), the beam near the brow tine (B), the trez tine (T) and the distal tip of the palm (D) (Figure 1). From each of these locations, a small sample was cut using a diamond-tipped circular saw attached to a hand-held drill. Each sample was then treated to extract bone collagen for analysis using a modified Longin method as described by Brown et al. (1988) and modified by Richards and Hedges (1999). $\delta^{13}C$ and $\delta^{15}N$ isotope values were obtained via continuous flow–elemental analysis–isotope ratio mass spectrometry (CF-EA-IRMS) from two sub-samples taken from each sample at the NERC Isotope Geoscience Laboratory (NIGL), Keyworth, using a Thermo Finnigan Flash 1112 series elemental analyser, coupled via a ConFlo III interface to a Delta Plus XL mass spectrometer. Mean values for $\delta^{13}C$ and $\delta^{15}N$ were calculated from each pair of duplicate sub-samples, the mean difference between each pair being 0.042‰ (standard deviation 0.038) for $\delta^{13}C$, and 0.1‰ (standard deviation

**Figure 1:** Sample locations on antlers.
0.072) for $\delta^{15}$N. All sample atomic C:N ratios were within the acceptable range 2.9–3.6 for bone collagen (DeNiro 1985), indicating that the antler collagen had not degraded and therefore that the isotopic values were valid. To allow comparison with results from archaeological specimens, the carbon values were corrected using a formula from Long et al. (2005: 150) to compensate for the emission of CO$_2$ from fossil fuels following the Industrial Revolution, which makes modern $\delta^{13}$C values lower (more negative) (Heaton et al. 1986).

<table>
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<tr>
<th>Antler</th>
<th>Location</th>
<th>$\delta^{13}$C‰</th>
<th>$\delta^{15}$N‰</th>
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<th>$\delta^{13}$C corr‰</th>
<th>Age</th>
<th>Dist</th>
<th>AgeCB</th>
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**Table 1:** Modern antler samples: isotope and measurement data.
Location: P = Pedicle, B = Brow tine, T = Trez tine, D = Distal palm; $\delta^{13}$C corr‰: CO$_2$-corrected $\delta^{13}$C using model from Long et al. (2005); Age: months; Dist: mm from base of burr; AgeCB, AgeWB: age in years predicted from circumference, width of beam (from Billson 2008).
Results
Values for $\delta^{13}$C ranged from $-24.9$ to $-22.8\%$, with a mean of $-24.0\%$ and standard deviation 0.5. After correction using the formula from Long et al. (2005), values for $\delta^{13}$C$_{\text{corr}}$ ranged from $-23.2\%$ to $-21.6\%$, with a mean of $-22.7\%$ and standard deviation 0.43. Values for $\delta^{15}$N ranged from 5.4 to 6.4\%, with a mean of 5.9\% and standard deviation 0.23. See Table 1 for data.

Figure 2: Modern antlers: scatter plots of $\delta^{15}$N against $\delta^{13}$C$_{\text{corr}}$.

Figure 3: Modern antlers: mean values of $\delta^{15}$N against $\delta^{13}$C$_{\text{corr}}$ for each sample location.
Scatter plots of $\delta^{13}$N against $\delta^{15}$N$_{\text{corr}}$, with sample points on each antler indicated by a connecting path showed that several of the first seven antlers have $\delta^{15}$N values which are higher or highest at the distal end (shown as a triangle symbol). To investigate this trend, a second batch of two antlers, 8 and 9, was analysed along with three more samples from batch 1, which seemed to confirm that the distal and proximal samples (shown in Figure 2 by triangle and square symbols, respectively) usually have higher $\delta^{13}$N values and also that the distal sample usually has the highest $\delta^{13}$C value.

Figure 3 shows a scatter plot of $\delta^{15}$N against $\delta^{13}$C$_{\text{corr}}$, with symbols indicating the sample location on the antler. Mean values of $\delta^{13}$C$_{\text{corr}}$ and $\delta^{15}$N for each sample location are indicated with larger symbols and error bars showing the mean plus or minus its standard error, suggesting that in this small set of samples ($n = 9$), the distal samples (triangle) had the highest mean values in both $\delta^{13}$C$_{\text{corr}}$ and $\delta^{15}$N, while the proximal, pedicle samples (square) ($n = 6$) had the lowest mean $\delta^{13}$C$_{\text{corr}}$ value.

From measurements of the sample positions along those antlers which are complete, it is possible to examine trends of variation along the antler length for both isotopes (Figure 4). Antlers 4, 6 and 7 were incomplete, lacking the proximal end including the coronet, and so are not

Figure 4: Variation of $\delta^{13}$C and $\delta^{15}$N along length of antler. Path representing antler between sample points shown as grey line; linear regression line of best fit shown as dashed line. Key: P = pedicle, B = brow tine, T = trez tine, D = distal palm.
Figure 5: Variation of $\delta^{13}$C and $\delta^{15}$N with age of deer. NA = no age data available.
**Figure 6a:** Variation of $\delta^{13}C$ and N with predicted age from Billson (2008).
Figure 6b: Variation of δ¹⁵N with predicted age from Billson (2008).
included in the figure. Values for both $\delta^{13}C$ and $\delta^{15}N$ usually increase slightly with distance from the coronet, towards the distal sample (triangle).

To investigate whether $\delta^{13}C$ and $\delta^{15}N$ vary with antler development and the ages of the animals which produced them, boxplots for the antlers shed by animals of known age suggest a slight positive relationship of $\delta^{13}C$ with age, and a corresponding negative relationship of $\delta^{15}N$ (Figure 5). Fallow deer antlers become larger and more elaborate with animal maturity, as with red deer (Chapman 1975). To investigate this, Billson (2008) used various antler metrics such as circumference and width of beam to estimate the age of the buck which produced them. Applying these metrics to the present set of samples, it is possible to examine changes in $\delta^{13}C$ and $\delta^{15}N$ with predicted age and to compare them with those of antlers from animals of known ages. The plots for both $\delta^{13}C$ and $\delta^{15}N$ (Figures 6a and 6b) using ages estimated from the beam circumference and width show that both metrics agree with the trend from the known ages (Figure 5) as well as with each other, suggesting they are both reasonable estimators of age of the animal.

Discussion
The relationship of both $\delta^{13}C$ and $\delta^{15}N$ values to diet, (DeNiro and Epstein 1978, 1981; Kohn 1999), as well as the reflection of food isotope values in consumer tissues are well understood (Codron et al. 2011, 2012). There is also a known relationship between both stable isotopes and climate, as well as the environment (Heaton et al. 1986; Heaton 1999). However, there are many causes of variation which can result in consumer isotope levels differing from those in their diet. In carbon, for example, the “canopy effect” results in a reduction in $\delta^{13}C$ values by 2–5‰ in plants growing on a shaded woodland floor, compared to those in more open settings (Heaton 1999) and this reduction is thought to be passed on to consumers (Drucker et al. 2008), although Stevens, Lister and Hedges (2006) did not find evidence of it in a study of five red deer populations in Scotland, Exmoor, and Poland. In nitrogen, $\delta^{15}N$ values reflect an organism’s trophic level and unweaned mammals exhibit elevated nitrogen values due to their higher trophic level from feeding on their mother’s milk, the so-called “nursing signal”, which can raise $\delta^{15}N$ values by 2–3‰, although this varies with species, environment and diet (Jenkins et al. 2001). For the modern antler samples, both of these effects should be negligible. With less than 25 per cent woodland cover in Phoenix Park, any canopy effect on $\delta^{13}C$ values should be minimal. Weaning of fallow fawns occurs during the rut in the year of birth at an approximate age of four months (Mammal Society 2014) and as the minimum age of the sampled animals in this study is 24 months, the antler $\delta^{15}N$ values will not reflect a nursing signal. Diet must, of course, be related to the browse available in the environment and may also be influenced by the choice of individual animals. For example, a study by Focardi, Poli and Tinelli (1995) of Mediterranean fallow deer habitats to estimate the carrying capacity of each habitat assumes that the animals will selectively browse higher quality forage. However, Alm, Birgerson and Leimar (2002) found in a long-term study that while fallow deer observed for diet choice tended to choose a diet higher in nutrients and lower in toxins, they did not always choose high-quality, nutrient-rich foods exclusively but adopted an intermediate level of selectivity which they then maintained.

Bone remodelling is most active during the peak of antler development and may be the source of much of the mineral making up the antlers. In a study of mule deer (Odocoileus hemionus), Hillman, Davis and Abdelbaki (1973) examined ribs, metacarpals, metatarsals, and tibiae during antler development and found that the greatest amount of osteoporosis due to remodelling occurred in the ribs. More recent research has confirmed that bone remodelling takes
place during antler development but also shows that it declines at an earlier stage in the cycle, with bone repletion beginning before final hardening of the antler (Baxter et al. 1999; Landete-Castillejos et al. 2007, 2012), indicating that both bones and antler undergo accretion simultaneously. In a study of red deer, Landete-Castillejos et al. (2007, 2012) examined variation in zinc and potassium along the length of the antler in conjunction with measurement of osteoporosis, finding both Zn and K levels to be good statistical explanatory variables for the porosity in the bone, all of which increased towards the distal end, and hence they related both elements to the amount of physiological stress of antler growth. Although not statistically significant in the present small set of modern samples (Miller et al. 2016), the increase in $\delta^{15}N$ towards the distal end of the antler is in accordance with results from a herd of red deer on the Hebridean island of Rum, off the west coast of Scotland (Stevens, pers. comm.).

While the biochemical process resulting in raised distal $\delta^{15}N$ is not fully understood, it seems plausible that, similarly to the raised Zn and K observed by Landete-Castillejos et al. (2012), it is related to the physiological effort required for antler growth.

**Summary**

The analysis of modern antlers described in this paper has provided some interesting information and comparisons. Although slight, the tendency for $^{15}N$ to increase towards the distal end of the antlers is in accordance with measurements of zinc and potassium in other work on red deer antlers, and seems to be related to physiological stress during antler growth (Landete-Castillejos et al. 2007, 2012). Also, the slight increase in $^{13}C$ and decrease in $^{15}N$ with age of the animals which produced the antlers agrees with the same comparison when using ages estimated from antler metrics (Billson 2008), which suggests that the metric-based ageing scheme has validity. However, due to the small sample size ($n = 9$) in this study, it would be prudent to assume that variation of isotope values between antlers as well as in consumer diet would prevent the use of the isotope values to estimate the age of the animal which produced an antler. Given these observed intra-element and age-related variations in $\delta^{13}C$ and $\delta^{15}N$ values of modern antlers, archaeological scientists should give due consideration to the sample location and, if known, the age of the animals which produced the antlers being analysed.

**Acknowledgements**

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**Competing Interests**

The author has no competing interests to declare.
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