Notes and records

Bulk and intra-tooth enamel stable isotopes of waterbuck *Kobus ellipsiprymnus* from Queen Elizabeth National Park, Uganda

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Introduction

Waterbuck *Kobus ellipsiprymnus*, considered to comprise two genetically distinct subspecies *K. e. ellipsiprymnus* and *K. e. defassa*, are predominantly grazers, but they have been observed to include some browse in their diet, especially during the dry season when grasses become higher in structural components and lower in protein (Taylor, Spinage & Lyman, 1969; Tomlinson, 1979, 1980; Spinage, 1982). For example, Spinage (1982:179) observed defassa waterbuck *K. e. defassa* browsing for up to 21% of their feeding time in the dry season. But difficulties of field observations make generalizations about waterbuck diets difficult, and differential habitat use in males and females (Spinage, 1982; Wirtz & Kaiser, 1988) may mean that there are subtle but important differences in the foods they eat.

Here we use stable isotope analysis to investigate defassa waterbuck diets in Queen Elizabeth National Park (QENP), Uganda. Carbon isotopes reflect the proportion of C_4 grass versus C_3 browse consumed by animals (Vogel, 1978), and can be used to track both long-term and seasonal dietary behaviour (Balasse, 2002; Passey & Cerling, 2002). We also present oxygen isotope data, as they are potentially useful for comparing landscape movement patterns between individuals.

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Materials and methods

Defassa waterbuck skulls (eight males and 22 females) were collected by C.A.S. in 1964–1967 from culled animals in the eastern portion of QENP. Overall C_4 grass consumption was estimated with a bulk enamel sample taken along the length of the crown of a mandibular premolar (P_4) tooth from each individual. In addition, intra-tooth samples were taken along the tooth's growth axis for five individuals, representing increments of time throughout enamel mineralization. Cattle and sheep P_4 mineralizes from 10 to 25 months (Brown *et al.*, 1960; Silver, 1969), and we assume the waterbuck P_4 mineralizes over a similar period. Tooth sampling procedures, chemical treatments, and machines used are the same as those described in Copeland *et al.* (in press). To contextualize these data, we compared them to previously published data for African ungulates (Cerling & Harris, 1999; Sponheimer *et al.*, 2003).

Results

The bulk enamel $\delta^{13}C$ values for waterbuck individuals ranged from −1.5 to +2.6‰ with a mean of 0.8 ± 1.2‰ (Fig. 1). The means and variances of bulk $\delta^{13}C$ values were not different between male and female waterbuck (t-test, d.f. = 28, $P = 0.89$; Levene Statistic = 1.313, $P = 0.262$). Mean bulk $\delta^{18}O$ values were also the same for males and females (*t*-test, d.f. = 28, $P = 0.918$), but males had significantly lower variance (Levene Statistic = 6.361, $P = 0.018$), seen by the much narrower range of their $\delta^{18}O$ values (1.3‰) compared with that of females (7.5‰) (Fig. 1).

There are significant differences in the bulk enamel $\delta^{13}C$ of QENP defassa waterbuck and other African grazing and browsing bovids (ANOVA, $F_{[6,112]} = 361.139$, $P < 0.0001$), but the waterbuck are clearly situated amongst the grazers (Fig. 2, Supplementary Table 1). Fisher's PLSD *post-hoc* test confirms that all grazers are different from all browsers ($P < 0.0001$), and the defassa waterbuck are indistinguishable from other grazers except for *Alcelaphus buselaphus* ($P < 0.01$).

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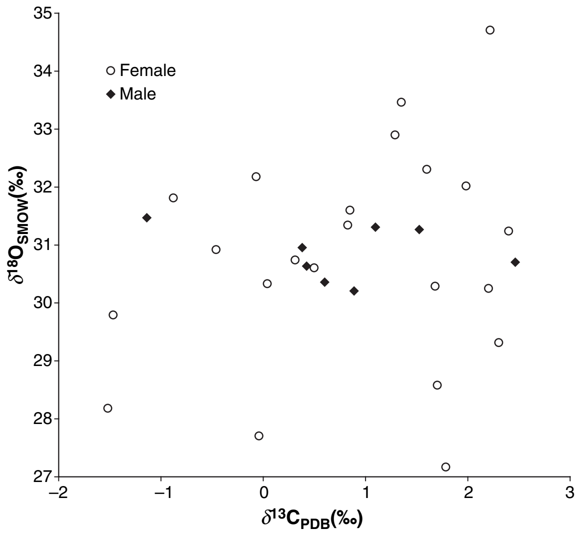

Fig 1 Carbon and oxygen isotope values for bulk enamel samples from the P_4 of 30 adult defassa waterbuck

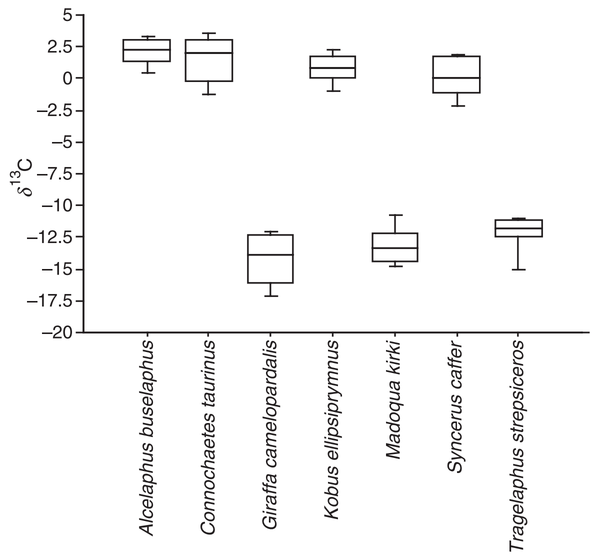

Fig 2 Carbon isotope values of tooth enamel from grazers and browsers of eastern and southern Africa (data from Cerling & Harris, 1999 and Sponheimer *et al.*, 2003) and QENP defassa waterbuck

Intra-tooth samples for five individuals (one male, four females) had $\delta^{13}C$ values that differed by up to 2.4‰ (mean = 1.4‰) within a single tooth, representing a time period of approximately 1 year (Fig. 3, Supplementary Table 2). The difference in $\delta^{18}O$ values within a single tooth varied from 1.8 to 8.4‰ (mean = 3.9‰) (Fig. 3).

Discussion

Carbon isotope ratio data confirm that defassa waterbuck in the QENP consume mainly C_4 grass but include some C_3 browse in their diets (Field, 1972; Tomlinson, 1980; Spinage, 1982; Cerling, Harris & Passey, 2003; Sponheimer *et al.*, 2003; Codron *et al.*, 2005). Assuming a dual source mixing model with −13 and +1 as theoretical pure browser and pure grazer $\delta^{13}C$ values, respectively (see Sponheimer *et al.*, 2003), waterbuck at QENP consume on average a diet of 98% C_4 grass. There is much variation between individuals, as the one with the highest recorded $\delta^{13}C$ (2.5‰) consumed on average 28% more C_4 grass than the individual with the lowest value (−1.5‰). Waterbuck require about four times more protein than other grazers such as African buffalo *Syncerus caffer* and oryx *Oryx beisa* (Taylor *et al.*, 1969), but stable isotopes indicate that the proportion of C_4 grass consumed by defassa waterbuck is indistinguishable from most other grazers including the African buffalo.

Our findings are also consistent with reports that waterbuck consume more browse during dry seasons, as intra-tooth $\delta^{13}C$ values correspond to shifts of at least 4–15% in the proportion of C_4 grass consumed over the course of about a year. Nonetheless, these seasonal shifts are small, and individuals such as W13 (Fig. 3) consumed almost entirely C_4 grass throughout the sequence. Seasonal changes in carbon and oxygen isotopes are not sinusoidal as they are in some intra-tooth studies of temperate taxa (e.g. Balasse *et al.*, 2002, 2005; Balasse, Tresset & Ambrose, 2006) (Fig. 3).

An intriguing result from this study is the difference in variability of oxygen isotope ratios between male and female waterbuck (Fig. 1). The oxygen isotope compositions of drinking water and plant foods can vary greatly over the landscape because of differences in water sources (e.g. rainwater versus groundwater) and evaporation rates (Fricke, Clyde & O'neil, 1998). For this reason, oxygen isotope compositions are used to look at the movements of individuals or populations across a landscape (e.g. White *et al.*, 2004). Isotope ratios in P_4 reflect behaviour between ages 10 and 25 months, at which time males live in bachelor groups and females range with other adult does (Spinage, 1982). Females have on average larger home ranges than bachelor males, for example in the 'Ogsa' study area of QENP, females' home range averaged 730 ha, whereas bachelor groups' home range averaged 340 ha (Spinage, 1982). As waterbuck

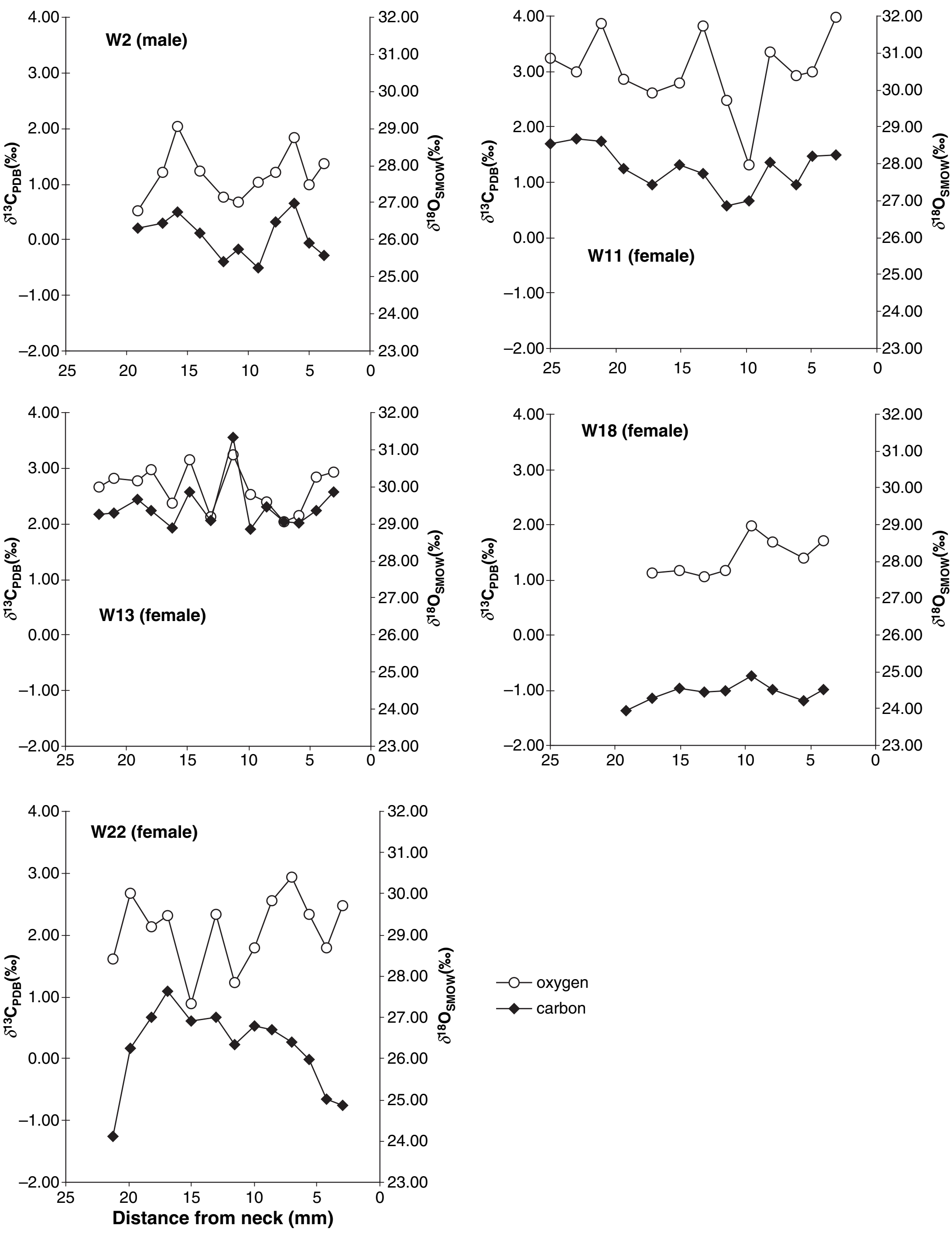

Fig 3 Intra-tooth carbon and oxygen isotopes of the P_4 enamel of five adult defassa waterbuck

have an unusually high water requirement and must drink every day (Taylor *et al.*, 1969), it is possible that the greater variability in female $\delta^{18}O$ values reflects a greater variety of drinking water sources in their larger home ranges. Further investigation is clearly warranted on how oxygen isotopes reflect ecological and behavioral aspects of animals and their environment (Sponheimer & Lee-Thorp, 2001).

In conclusion, the carbon isotope data from QENP waterbuck indicate that they are mainly grazers, with individuals ranging from eating pure grass to those that consume a small but significant amount of browse. In some cases, at least, this results from seasonal variation in browse consumption as evidenced by intra-tooth variability (Fig. 3). Intra-tooth oxygen isotope values track carbon to some degree (Fig. 3), and the significantly larger variation in bulk oxygen isotope values in females versus males may reflect differences in ranging patterns, although further evidence is needed to confirm this hypothesis.

Acknowledgements

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Supplementary material

The following supplementary material is available for this article:

All carbon and oxygen isotope data from the defassa waterbuck tooth enamel bulk samples and intra-tooth samples are presented in two supplementary tables.

Table S1 Bulk enamel samples of the mandibular P_4 enamel for 30 adult defassa waterbuck from Queen Elizabeth National Park, Uganda

Table S2 Intra-tooth samples of mandibular tooth enamel of adult defassa waterbuck from Queen Elizabeth National Park, Uganda

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