

DIETS OF SOUTHERN AFRICAN BOVIDAE: STABLE ISOTOPE EVIDENCE

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Although bovids have been studied for decades, debate still exists about their diets. To address this problem, we examined bovid dietary ecology through analysis of stable carbon isotopes. We analyzed tooth enamel, bone collagen, and hair from 312 individual bovids, representing 27 species from southern Africa. Although dietary information from the literature is usually supported by this technique, our results and the literature are sometimes highly divergent. For instance, our results indicate that *Taurotragus oryx* and *Raphicerus campestris* eat less grass than is widely believed. Furthermore, contrary to most theoretical expectations, our data indicate no relationship between body size and percentage of monocots consumed by southern African Bovidae. Although many researchers have abandoned the idea that bovid soft-tissue anatomy is strongly indicative of diet, we demonstrate a strong relationship between the percentage of grass in a bovid's diet and several hard-tissue craniodental indices.

Key words: Africa, bovid, Bovidae, carbon isotopes, diet, morphology

Bovids are among the most conspicuous mammals of modern African savannas. Although this family has representatives in Eurasia and North America, most modern species of bovids are African endemics (Spinage 1986). Bovids are not only an integral part of modern African savanna ecosystems but also represent the largest component of the African Pliocene fossil record (Gentry 1978; Harris 1991; Vrba 1974). Hence, bovids are crucial to our under-

standing of both African neocology and paleoecology. But despite decades of investigation into the nutritional ecology of African bovids, there still exists considerable debate about the diets of many taxa (Gagnon and Chew 2000; Watson and Owen-Smith 2000). Some of this confusion likely results from the relevant literature on bovid ecology, which is vast and sometimes contradictory.

To address this problem, Gagnon and Chew (2000) undertook a critical literature

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review in an attempt to synthesize what is known about diets of African bovids. Their study represents an important step in understanding bovid trophic ecology but is nonetheless limited by the lack of an objective way to judge reliability and universality of data they reviewed. They could only assume that the more specific the data, the more accurate they were. Furthermore, they assumed that behavior of populations in these studies was representative of the species in toto. Here, we test the dietary information Gagnon and Chew (2000) provided about southern African bovids through analysis of stable carbon isotopes. We also compare these data with stable carbon isotope results from East African bovids (Cerling et al. 2003). Finally, we use these data to explore relationships among bovid diets, body size, and morphology.

Stable carbon isotope analysis has proven a useful tool for investigating ecology of modern and fossil taxa (Ambrose and DeNiro 1986; Koch et al. 1995; Lee-Thorp and van der Merwe 1987; Schoeninger et al. 1999; Sponheimer and Lee-Thorp 1999a; Tieszen and Imbamba 1980; Vogel 1978). The foundation of this technique is our knowledge of photosynthesis in plants. In African savannas, grasses and sedges use the C_4 photosynthetic pathway, whereas almost all trees, bushes, shrubs, and forbs use the C_3 photosynthetic pathway (Sage et al. 1999; Vogel et al. 1978). C_3 plants discriminate more strongly against the heavy ^{13}C isotope than do C_4 plants, resulting in C_3 plants having lower ratios of $^{13}C:^{12}C$ than C_4 plants (Bender, 1968; Deines 1980; Smith and Epstein 1971; Vogel et al. 1978). This carbon is then passed down to animals that consume the vegetation, with some further fractionation (Ambrose and Norr 1993; Cerling and Harris 1999; Lee-Thorp et al. 1989; Tieszen and Fagre 1993; Vogel 1978). Thus, animals that eat grasses, such as zebras (*Equus burchelli*), have much higher tissue $^{13}C:^{12}C$ ratios than do browsers, such as giraffes (*Giraffa camelopardalis*). This makes carbon isotope analysis

uniquely suited for testing hypotheses about diets of grazing and browsing herbivores in tropical environments. This is not to say, however, that carbon isotope data alone can resolve all our questions about the diets of African bovids. Indeed, carbon isotope analysis has a number of weaknesses, one of which is that many substantially different foods, such as leaves and fruits of dicots, cannot be distinguished using carbon isotopes. Thus, carbon isotope analysis is more or less limited to telling us the relative proportions of C_4 grass and C_3 foliage and fruit in bovid diets.

MATERIALS AND METHODS

We analyzed 312 bovids collected during the last 30 years from Botswana, Malawi, Namibia, South Africa, and Zimbabwe. Most of these specimens originated in the South African provinces of Mpumalanga, Free State, Northern Province, Northwest Province, and Gauteng. Because specimens were collected sporadically from several countries during a 30-year period, they do not represent particular populations or even a particular time period. Most stable carbon isotope data were collected from tooth enamel, which is the preferred material for such analyses because it is resistant to fossilization processes (Lee-Thorp and van der Merwe 1991; Rink and Schwarcz 1995; Sponheimer and Lee-Thorp 1999b; Wang and Cerling 1994), making it usable in both modern and paleontological contexts. Specimens analyzed before 1996 were prepared as described by Lee-Thorp (1989), but subsequent analyses followed microsampling procedures that decreased damage to specimens by >100 times (Lee-Thorp et al. 1997). Carbon isotope ratios produced using the 2 methods are indistinguishable (Lee-Thorp et al. 1997). We also included data from bone collagen and hair because they have also been shown to provide accurate information about an animal's diet (Jones et al. 1981; Katzenberg and Krouse 1989; Nakamura et al. 1982; O'Connell and Hedges 1999; Schoeninger et al. 1999). All 3 tissues produce highly comparable results (Cerling and Harris 1999; Lee-Thorp et al. 1989). Collagen and hair were analyzed as described by Sealy (1986) and Jones et al. (1981). To facilitate analysis, these values were then converted to equivalent enamel-apatite values as described by Cer-

ling and Harris (1999) and Lee-Thorp et al. (1989). Analysis of variance (ANOVA) of these converted values for enamel, collagen, and hair (of the one taxon for which all 3 are available) reveals no significant differences (ANOVA, $F = 1.24$, $d.f. = 31$, $P = 0.30$). All $^{13}\text{C}:^{12}\text{C}$ ratios are expressed as $\delta^{13}\text{C}$ values in parts per thousand (‰) relative to the Pee Dee Belemnite standard (Table 1). The standard deviation of repeated measurements for all materials and methods was less than 0.2‰.

Gagnon and Chew (2000) expressed bovid diets in terms of percentages of fruits, dicots, and monocots consumed. Because fruits and dicots have similar carbon isotope ratios, we have converted their data into percentages of C_3 (fruits and dicots) and C_4 (monocots) foods. Thus, if Gagnon and Chew (2000) reported that an animal eats 10% fruits, 20% dicots, and 70% monocots, we converted these to 30% C_3 and 70% C_4 foods (Table 1). Furthermore, to make our data more comparable with those of Gagnon and Chew (2000), we used a dual-source mixing model so we could express the isotope data in percentages of C_3 and C_4 foods consumed (Table 1). It should be understood, however, that there are several potential sources of error. Percentages of C_4 foods we present are sensitive to the $\delta^{13}\text{C}$ values of idealized C_3 (-13.5‰) and C_4 (+1.5‰) consumers chosen. C_3 plants, in particular, can have significant variation, especially in hyperarid areas or in closed-canopy forests (Cerling et al. 2003; Ehleringer and Cooper 1988; van der Merwe 1989). To limit this potential bias, we have excluded data from forests and hyperarid areas. Moreover, samples we analyzed were collected during 3 decades, during which time the burning of fossil fuels has led to a small depletion in atmospheric $\delta^{13}\text{C}$ of <1‰ (Friedli et al. 1986; Keeling et al. 1995). We do not attempt to correct for this depletion because we do not have the exact dates of collection for all specimens. Despite the variation introduced by temporal and environmental factors, variation within species is generally small, and clear distinctions are evident between groups eating primarily C_3 and C_4 vegetation (Table 1). Nonetheless, because of the fossil-fuel effect, environmental differences, and conversions of hair and collagen to enamel apatite, a potential error of up to 14% (2‰) has been introduced. Thus, we only reject information of Gagnon and Chew (2000) about diets of individual species, if the

difference between measured and predicted (Gagnon and Chew 2000) percentage of C_4 grass in the diet is 15% or greater.

RESULTS

The most conspicuous result of this study is the general concordance between bovid diets as gleaned from the literature by Gagnon and Chew (2000) and the carbon isotope data (Table 1). Out of the 27 southern African species that we analyzed, our results were consistent with expectations from the literature in 22 cases (82%). We were unable to test dietary information for 3 species (7%), all of which are reputed to eat C_3 reeds, bulrushes, or sedges. In these instances, we were only able to determine amounts of C_4 monocots consumed and not relative percentages of browse and graze. In a few cases, however, our results clearly conflicted with predicted diets (11%).

DISCUSSION

Despite the broad concordance between the bovid dietary ecology literature and our results, there are a few important discrepancies that need to be addressed. Carbon isotope data show, for instance, that although eland (*Taurotragus oryx*) might eat some grass, the populations that we sampled ate very little, probably about 10% of their diets (Table 1). Gagnon and Chew (2000), in contrast, report that 50% of the eland's diet is grass. There are a number of possible explanations for this divergence. Many studies of eland populations were carried out in East Africa (Hofmann and Stewart 1972; Lamprey 1963). It may be that eland populations in East Africa consume more graze than their southern African counterparts. Indeed, Watson and Owen-Smith (2000) report that an eland population in South Africa consumes 94% browse, much less than has been argued for their East African conspecifics (Hofmann and Stewart 1972; Lamprey 1963). Stable carbon isotope analysis of East African eland also suggests that they eat slightly more grass than South African populations

TABLE 1.—Diets of 27 bovid species as determined by stable carbon isotope analysis. The measured percentages of C₄ grass consumed in southern Africa and East Africa are also shown, as well the predicted percentage of C₄ grass consumed based on data from Gagnon and Chew (2000). Blanks in percent C₄ (eastern Africa column) indicates that there are no species in common between this study and Cerling et al. (2003). Hypsodonty index (HI) data are from Janis (1988) and Reed (1996). Female body mass data are from Smithers (1983) and Estes (1991).

Species	Mean $\delta^{13}\text{C}$ (‰)	SD	n	Percent C ₄			HI	Body mass of female (kg)
				Southern Africa	Eastern Africa	Predicted		
Aepycerotinae								
<i>Aepyceros melampus</i>	-5.8	2.9	25	51	54	45	4.9	40
Alcelaphini								
<i>Alcelaphus buselaphus</i>	1.2	0.7	6	98	100	75	5.2	120
<i>Connochaetes gnou</i>	0.6	0.6	2	94		81	4.8	170
<i>Connochaetes taurinus</i>	0.0	1.8	13	90	100	88	4.9	180
<i>Damaliscus lunatus</i>	2.4	0.7	7	100	100	95	5.1	126
<i>Damaliscus pygargus</i>	0.5	1.5	3	94		90	4.8	61
<i>Sigmocerus lichtensteinii</i>	1.4	1.5	5	99		95	5.2	166
Antilopini								
<i>Antidorcas marsupialis</i>	-10.1	1.5	21	23		33	4.9	37
Bovini								
<i>Syncerus caffer</i>	-0.3	0.6	33	88	100	78	3.0	576
Cephalophini								
<i>Cephalophus monticola</i>	-13.3	1.4	8	2	0	1	1.9	5
<i>Cephalophus natalensis</i>	-13.0	1.5	8	3	0	1	2.2	14
<i>Sylvicapra grimmia</i>	-13.3	2.2	16	2	0	12	3.0	19
Hippotragini								
<i>Hippotragus equinus</i>	0.1	1.2	22	91	100	85	4.3	260
<i>Hippotragus niger</i>	2.0	1.1	6	100	94	85	3.8	220
<i>Oryx gazella</i>	-1.4	1.0	12	81	88	75	3.4	210
Neotragini								
<i>Ourebia ourebi</i>	-1.2	2.1	2	82	84	90	3.8	14
<i>Raphicerus campestris</i>	-12.3	1.1	9	10	18	34	3.4	11
Reduncini								
<i>Kobus ellipsiprymnus</i>	1.8	0.5	7	100	97	84	3.5	186
<i>Kobus leche</i>	-4.1	3.2	6	62		95	3.6	79
<i>Kobus vardonii</i>	0.9	1.8	3	96		93		61
<i>Redunca arundinum</i>	0.9	1.6	10	96		95	3.6	48
<i>Redunca fulvorufula</i>	1.4	1.2	6	99	94	95	3.8	29
Tragelaphini								
<i>Taurotragus oryx</i>	-12.3	1.4	13	8	18	50	2.9	393
<i>Tragelaphus angasii</i>	-8.6	2.6	13	33		20	2.5	62
<i>Tragelaphus scriptus</i>	-15.1	2.1	18	0	0	10	2.5	30
<i>Tragelaphus spekii</i>	-8.4	3.5	5	34	0	68	2.9	54
<i>Tragelaphus strepsiceros</i>	-13.0	1.2	33	4	4	15	2.3	170

(18%; Table 1; Cerling et al. 2003) but still <50%. Thus, it is likely that few eland populations consume up to 50% grass.

Similarly, our data show that steenbok (*Raphicerus campestris*) in South Africa eat

only about 10% C₄ grass (Table 1), not 34% grass as predicted by Gagnon and Chew (2000). Other studies of steenbok in South Africa also suggest that they are nearly pure browsers that specialize on forbs amidst the

grass (Cohen 1976; du Toit 1993). Furthermore, Cerling et al. (2003) found that steenbok in East Africa eat only 18% grass. Thus, it is likely that steenbok throughout Africa eat fewer monocots than predicted by Gagnon and Chew (2000).

The only other taxon over which stable isotope data and the interpretations of Gagnon and Chew (2000) are discordant is the red hartebeest (*Alcelaphus buselaphus*). Gagnon and Chew (2000) report that the hartebeest is a 75% grazer, 25% browser. Our results, however, show very little evidence of C₃ browse in the red hartebeest's diet (Table 1). Isotopic data from East Africa also indicate that *A. buselaphus* is an exclusive grazer (Table 1).

In some cases, stable isotope data are revealing even when they agree with the literature. For instance, Gagnon and Chew (2000) report that impala (*Aepyceros melampus*) eat 45% grass on average, which fits well with carbon isotope data from southern and East Africa (Table 1). Despite this congruence, $\delta^{13}\text{C}$ values for impala are more variable than those for any other bovid we have sampled. Indeed, some individuals consumed >90% graze, whereas others ate up to 80% browse. This probably results from sex differences and differing availabilities of C₃ browse and C₄ graze throughout southern Africa. Although such extreme variability was unusual, it nonetheless underscores the need to appreciate the potential dietary variability of some taxa.

We analyzed 18 bovid taxa that were also analyzed by Cerling et al. (2003; Table 1) for their stable isotope study of East African bovids. Of these 18 taxa, southern African and East African data differed only for the sitatunga (*Tragelaphus spekii*). However, this discrepancy does not necessarily indicate regional differences in consumption of browse and graze because sitatunga are among the few species that have regular access to both C₃ and C₄ monocots (Estes 1991; Kingdon 1997; Owen 1970). Thus, there were no unequivocal intraspecific differences in the percentages of

browse and graze consumed in southern and East Africa.

Diet, body mass, and morphology.—Numerous studies suggest that body size plays a key role in determining ruminant diets (Bell 1971; Case 1979; Demment and Van Soest 1985; Foose 1982; Hofmann 1973; Jarman 1974; Owen-Smith 1988). This is because gut size is directly proportional to body size, whereas metabolic requirements scale to body weight^{0.75}, suggesting that small-bodied ruminants must maintain higher-quality diets than do large ruminants (Demment and Van Soest 1985). This pattern was observed among modern bovids: small-bodied taxa such as duiker and dik dik were largely browsers (concentrate selectors *sensu* Hofmann 1989), whereas larger species such as buffalo and wildebeest were grazers (Case 1979). Most recently, Gagnon and Chew (2000) noted that the percentage of monocots in bovid diets was positively correlated with body size.

Carbon isotope data reveal no correlation between body size and percentage of C₄ foods (grass) in bovid diets (Fig. 1; $r^2 = 0.076$; $P = 0.164$). The most important reason that this relationship does not hold is that browsers and concentrate selectors (which eat C₃ vegetation) are found at all body sizes. Tragelaphini, in particular, are problematic because they have what are generally considered to be higher-quality diets than are expected for their body sizes. However, this problem is based on the assumption that browse is of higher quality (high-protein, low-fiber) than graze. Much available browse is highly lignified, however, which greatly reduces digestibility, and browse has high levels of defensive secondary compounds such as phenolics and terpenes (Hanley et al. 1992). Studies of digestibility of tree and shrub leaves have shown that they are generally no more digestible than grasses (Hanley et al. 1992; Robbins et al. 1995). Some authors have even argued that browse is, on average, less digestible than graze (Gordon and Illius 1996; Illius 1997). Furthermore, dietary

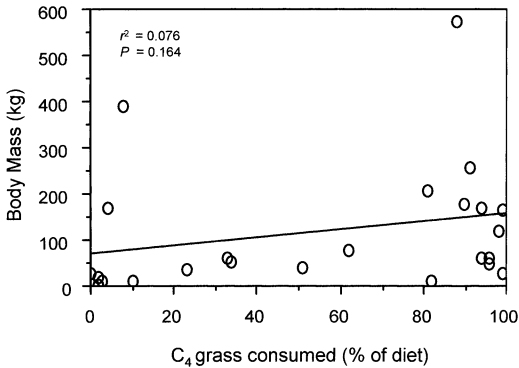


FIG. 1.—Percentage of C_4 grass consumed relative to body mass of female bovids from southern Africa. The relationship was not statistically significant ($r^2 = 0.076$, $P = 0.165$). Symbols indicate means for each species. Body weight data are from Smithers (1983) and Estes (1991).

quality of many fruits has probably been overestimated. Mueller et al. (1998) showed that wild figs, a favorite food of duiker in the Congo, are about 63% neutral detergent fiber, which is similar to that found in many grasses. Additionally, lignin comprises 33% of the neutral detergent fiber component, a much higher value than found in most grasses. It is not surprising, therefore, that duiker digested only 54% of wild fig dry matter—a digestibility similar to that of grasses for most ruminants (Foose 1982). In addition, Hart (1985) discovered that many fruits eaten by forest antelopes are very high in fiber, high in digestion-reducing phenolic compounds, and low in protein. Hence, it appears that at present it is very difficult to determine relative dietary values of foods eaten by bovids. It may be that some grazing diets are of a higher quality than is generally supposed. This makes it less surprising that there is no relationship (in southern Africa at least) between percentage of monocots in bovid diets and body size. Further study of bovid diets with emphasis on deleterious or quality-reducing compounds such as lignin and phenolics are needed.

Hofmann (1973, 1989) indicated that soft-tissue anatomy is highly correlated

with diet. He argued that anatomy of browsers leads to relatively brief retention of digesta and, consequently, reduced fiber digestibility compared with grazers. More recent studies have shown, however, that there is little, if any, difference in digestive efficiency between browsers and grazers (Gordon and Illius 1996; Illius 1997; Robbins et al. 1995). Thus, the relationship between soft-tissue anatomy and diet has proven equivocal. Numerous researchers have also argued that bovid hard-tissue anatomy (especially craniodental) is strongly correlated with diet (Janis 1988; Reed 1996; Spencer 1995; Sponheimer et al. 1999). Most notably, it has been observed that percentage of grass in bovid diets is positively correlated with degree of molar hypsodonty (Janis 1988; Reed 1996). Carbon isotope data support this contention (Table 1, Fig. 2; $r^2 = 0.461$, $P < 0.0001$). Moreover, other craniodental indices from Reed (1996) are even more highly correlated with percentage of C_4 food eaten. For example, relative length of the premolar row is negatively correlated ($r^2 = 0.605$, $P < 0.0001$) and depth of the mandible is positively correlated ($r^2 = 0.623$, $P < 0.0001$) with consumption of C_4 grass. The high correlation between diet and craniodental morphology is of significance for mammalian paleontologists because morphology is one of the few clues available as to the ecology of extinct taxa (Kappelman et al. 1997; Reed 1996; Solounias and Dawson-Saunders 1988; Spencer 1995). Nevertheless, the morphological signal bears a strong phylogenetic component that can complicate paleodietary reconstruction (Sponheimer et al. 1999).

Suggestions for future research.—In this study, we have tried to provide very broad information about diets of southern African bovids. However, by simply giving the average percentage of C_4 grass consumed by each species, we actually belie the complexity of bovid diets. Within a given species, we often had individuals that lived in different countries at different times. This

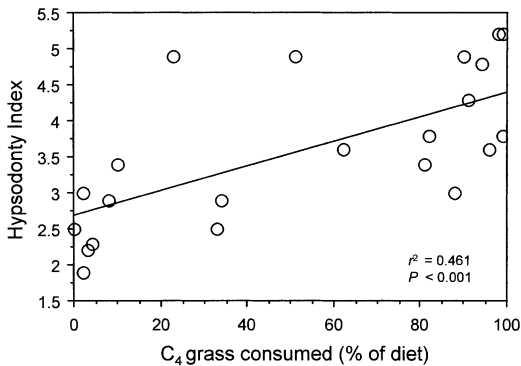


FIG. 2.—Molar hypsodonty relative to consumption of C_4 grass by bovids from southern Africa. The relationship was highly significant ($r^2 = 0.526$, $P < 0.0001$). Molar hypsodonty is, as shown by hypsodonty index, from Janis (1988) and Reed (1996). Symbols indicate means for each species.

may be ideal for making broad generalizations about a species' diet but does little to aid in understanding dietary variability within populations. For instance, do males and females have different diets and, if so, are these differences linked to social structure and breeding behavior? Furthermore, our sampling strategy limited our ability to study interpopulational differences because we rarely had more than 3 individuals from any given population. Thus, we were unable to ask questions like "Do impalas in different areas have different diets that reflect the composition of local vegetation?" To begin addressing these kinds of questions, we must begin to collect adequate samples of known age and sex from multiple populations. Because stable isotope analysis can be performed on feces or hair, acquiring such samples should prove fairly easy.

Recent advances in incremental sampling procedures might also allow us to address completely new kinds of questions. For instance, samples taken from every few millimeters along the growth trajectory of a tooth crown can reveal distinct carbon isotope patterns, probably reflecting seasonal changes in diet (Balasse et al. 1999). It

might also be possible to sample along a bovid tail hair to trace changes in an individual's diet over time. If coupled with observational data, it may be possible to tie diet to social dynamics. For instance, if a male is known to leave a bachelor herd and establish a harem, one could conceivably obtain a sample of its tail hair to determine whether this change in social status affected its diet. This same technique might also prove useful for improving our understanding of seasonal dietary changes and dietary responses to drought.

In conclusion, stable carbon isotope analysis is an underutilized technique for studying mammalian nutritional ecology. Feces, hair, and hard tissues can all be analyzed for stable carbon isotopes, making it an easy and widely applicable technique. Although carbon isotopes cannot provide us with the rich detail often found in observational studies, they are extremely effective at quantifying relative proportions of graze and browse in an animal's diet. Furthermore, isotopic analysis can be used to investigate diets of animals that have been dead for hundreds, or even millions, of years so long as hair or tooth enamel is preserved (Macko et al. 1999; Sponheimer et al. 1999). Thus, analysis of carbon isotopes can not only improve our understanding of the ecology of modern bovid taxa, but might also be used to trace the development of dietary ecology within these lineages through time.

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