2. DeMenocal P. (1995). Plio-Pleistocene African climate. *Science* **270**, 53–59.
3. Vrba E. (1974). Chronological and ecological implications of the fossil Bovidae at the Sterkfontein Australopithecine site. *Nature* **250**, 19–23.
4. Vrba E (1985). Early hominids in southern Africa: updated observations on chronological and ecological background. In *Hominid Evolution: Past, Present, and Future,* ed. P.V. Tobias, pp. 195–200. Alan R. Liss, New York.
5. Cerling T.E. (1992). Development of grasslands and savannas in East Africa during the Neogene. *Palaeogeog. Palaeoclim. Palaeoecol.* **97**, 241–247.
6. Behrensmeyer A., Todd N., Potts R. and McBrinn G. (1997). Late Pliocene faunal turnover in the Turkana basin, Kenya and Ethiopia. *Science* **278**, 1589–1594.
7. Reed K.E. (1997). Early hominid evolution and ecological change through the African Plio-Pleistocene. *J. hum. Evol.* **32**, 289–322.
8. Partridge T.C., Latham A.G. and Heslop D. (2000). Appendix on magneto-stratigraphy of Makapansgat, Sterkfontein, Taung and Swartkrans. In *The Cenozoic of Africa,* eds T.C. Partridge and R.R. Maud, pp. 126–129. Oxford University Press, New York.
9. Vrba E.S. (1980). The significance of bovid remains as indicators of environment and predation patterns. In *Fossils in the Making,* eds A.K. Behrensmeyer and A.P. Hill, pp. 247–272. University of Chicago Press, Chicago.
10. Bamford M. (1999). Pliocene fossil woods from an early hominid cave deposit, Sterkfontein, South Africa. *S. Afr. J. Sci.* **95**, 231–237.
11. Smith B.N. and Epstein S. (1971). Two categories of $^{13}C/^{12}C$ ratios for higher plants. *Plant Physiol.* **47**, 380–384.
12. Lee-Thorp J. A. and van der Merwe N. J. (1987). Carbon isotope analysis of fossil bone apatite. *S. Afr. J. Sci.* **27**, 361–372.
13. Bocherens H., Koch P., Mariotti A., Geraads D. and Jaeger J. (1996). Isotopic biogeochemistry (^{13}C, ^{18}O) of mammalian enamel from African Pleistocene hominid sites. *Palaios* **11**, 306–318.
14. Sponheimer M. and Lee-Thorp J.A. (2003). Using bovid carbon isotope data to provide palaeoenvironmental information. *S. Afr. J. Sci.* **99**, 273–275.
15. Sponheimer M., Reed K. and Lee-Thorp J.A (1999). Combining isotopic and ecomorphological data to refine bovid paleodietary reconstruction: a case study from the Makapansgat Limeworks hominin locality. *J. hum. Evol.* **36**, 705–718.
16. Lee-Thorp J.A., Manning L. and Sponheimer M. (1997). Exploring problems and opportunities offered by down-scaling sample sizes for carbon isotope analyses of fossils. *Bull. Soc. Geol. Fr.* **168**, 767–773.
17. Luyt C.J. (2001). *Revisiting palaeoenvironments of the hominid-bearing Plio-Pleistocene sites: new isotopic evidence from Sterkfontein.* M.Sc. thesis, University of Cape Town.
18. Kuman K. and Clarke R.J. (2000). Stratigraphy, artefact industries and hominid associations for Sterkfontein, Member 5. *J. hum. Evol.* **38**, 827–847.

Using carbon isotope data of fossil bovid communities for palaeoenvironmental reconstruction

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Reconstructing palaeoenvironments is a major focus of palaeoanthropological research. While many techniques are now available for exploring past environments, fossil bovids remain amongst the most widely utilized sources of environmental information. Most studies of fossil bovids, however, assume implicitly that bovid ecology is the same now as it was in the distant past. Because such uniformitarianist assumptions are not always valid, we have developed a method to provide palaeoenvironmental information from fossil bovids that requires no ecological assumptions. Here, we show that the percentages of C_3 and C_4 vegetation-consuming bovids in modern environments generally vary according to the amount of woody vegetation present. Application of this C_3/C_4 index to the fossil bovid assemblage at Makapansgat shows that, based on carbon isotope data, the percentage of C_3-consuming bovids is high, suggesting a great deal of woody vegetation in this vicinity about 3 million years ago.

Introduction

Stable carbon isotope analysis of tooth enamel has been used for palaeoenvironmental reconstruction,[1–3] but it has been more or less limited to establishing the consumption, and thus presence, of C_3 plants (such as trees, bushes and forbs) and C_4 vegetation (for example tropical grasses and sedges). While this information is useful, it does little to elucidate vegetational structure, which is a primary concern of palaeoanthropologists.[4–6] For instance, the presence of C_4 grasses in the ancient Makapansgat Valley was demonstrated,[7] but these grasses may have existed in environments as different as open grassland or closed woodland.

Fossil bovids remain one of the most widely utilized sources of palaeoenvironmental information.[5,8–13] A widely employed method for using bovids in palaeoenvironmental reconstruction was developed by Vrba[8,9] and subsequently adopted and refined by others.[10–12] Vrba's seminal work was based on a literature review of modern bovid population statistics in 16 game parks and reserves.[9] She observed that the percentage of alcelaphini plus antilopini never exceeded 30% of the total bovid population in areas with considerable tree and bush cover (hereafter 'closed' areas). In contrast, these tribes always exceeded 60% of the total bovid population in areas with few trees and bushes (hereafter 'open' areas) (Table 1). She applied this principle to fossil sites in order to reconstruct palaeoenvironments. For example, it was observed that since Makapansgat (at 3 million years ago) had a low percentage of alcelaphini and antilopini (28%), it reflected a relatively closed environment. In contrast, the high percentages of alcelaphini and antilopini (~80%) at the 1.8-Myr sites of Kromdraai and Swartkrans suggested far more open environments.[5]

Vrba's method is based upon the assumption that antilopini and alcelaphini were open landscape- and arid-adapted several million years ago, as they generally are today, using the principle of taxonomic uniformitarianism. While most evidence suggests that fossil alcelaphini shared the same habitat tolerances as their modern counterparts,[6,7,13] the same cannot be said for fossil antilopini. For instance, recent research shows that *G. vanhoepeni* and *Antidorcas recki* were predominantly browsers and not mixed feeders like most modern antilopini, which forces us to question whether they really preferred open, arid environments.[1,7] Such dietary disparities likely indicate differences in habitat preference or tolerance as well. Thus, while variations of Vrba's method have been instructive, it would be helpful to find ways to derive environmental signals from bovids that make no assumptions about the ecology of fossil taxa.

Method

To this end, we modified Vrba's method to test habitat reconstruction based on bovid carbon isotope compositions. The modification is based on a simple ecological principle. In relatively open areas such as grasslands, there will be relatively little C_3 vegetation and thus limited ecospace for C_3 consumers. As the percentage of woody vegetation increases, however, there will be an increasing amount of C_3 vegetation available for consumption, and concomitantly, more C_3-consuming bovids.

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Table 1. Vrba's original alcelaphine plus antilopine criterion for 16 modern reserves and for Makapansgat Member 3.[9] The last three columns show the percentages of C_3 consumers, C_4 consumers, and mixed feeders (MF) as determined by stable carbon isotope analysis.

Area	Habitat	%Alcelaphines + antelopines	$\%C_3$	$\%C_4$	%MF
Kruger	Closed	5	9	19	72
Manyara	Closed	0	1	68	31
Quicama	Closed	0	46	54	0
Bicuar	Closed	18	48	46	0
Luando	Closed	0	29	71	0
Cuelei	Closed	6	52	48	0
Mkuzi	Closed	12	5	13	82
Hluhluwe	Closed	24	21	46	33
Kafue	Closed	28	23	76	1
Wankie	Closed	7	29	50	21
Kalahari	Open	65	12	53	35
Nairobi	Open	73	3	48	49
Lake Turkana	Open	70	0	76	24
Serengeti	Open	82	1	67	32
Ngorongoro	Open	97	2	72	26
Etosha	Open	67	14	38	48
Makapansgat M3	?	28	51	31	18

Thus, in biomes where the grasses are C_4, the percentages of C_3- and C_4-consuming bovids should provide information about the local environment. More specifically, the percentages of C_4 consumers and mixed feeders should provide information similar to the percentage of alcelaphini (which consume C_4 vegetation) and antilopini (which eat C_3 and C_4 vegetation). When applied to the fossil record, however, this isotopic method has the distinct advantage of being derived empirically — we do not need to assume anything about behaviour, it is made manifest from the analytical data.

We determined the percentages of C_3 and C_4 consumers in modern habitats using stable carbon isotope analyses of 312 individual bovids,[14] and gleaning isotope data for another 408 individuals from the literature[15] (Table 2). Based on these results, we then determined the percentages of bovids that eat more than 80% C_3 vegetation (hereafter C_3 consumers), eat more than 80% C_4 vegetation (hereafter C_4 consumers), and all others (hereafter mixed feeders) from each park in Vrba's original study (Table 1). The carbon isotope data show that the vast majority of all African bovids are C_3 or C_4 specialists that change their diets very little anywhere within their range.[14,15] A few taxa, however, such as impala (*Aepyceros melampus*), are mixed feeders whose diets can vary markedly from place to place.[14,16] In order to test our isotope-based classifications we divided the bovids from these parks into the same three groups using a literature review

Table 2. Stable isotope compositions, standard deviations, sample sizes, percentage C_4 grass consumed, and dietary classifications [C_3, C_4, or MF (mixed feeder)] for 720 individual bovid specimens divided into nine tribes, as tribes form the basis of most palaeoenvironmental reconstructions.

Tribe	$\delta^{13}C$	s.d.	*n*	$\%C_4$	Diet
Aepycerotini	–5.9	2.9	63	52	MF
Alcelaphini	1.2	1.1	119	97	C_4
Antilopini	–9.2	1.5	78	29	MF
Bovini	–1.9	0.6	120	80	C_4
Cephalophini	–14.6	1.7	46	1	C_3
Hippotragini	0.8	1.1	62	92	C_4
Neotragini	–13.1	1.6	37	19	C_3
Reduncini	0.6	1.7	82	93	C_4
Tragelaphini	–12.5	2.2	113	9	C_3

The percentages of C_4 consumption ($\%C_4$) represent an average calculated directly from southern and East Africa datasets.[15,16] References 15 and 16 also contain carbon isotope data for individual species.

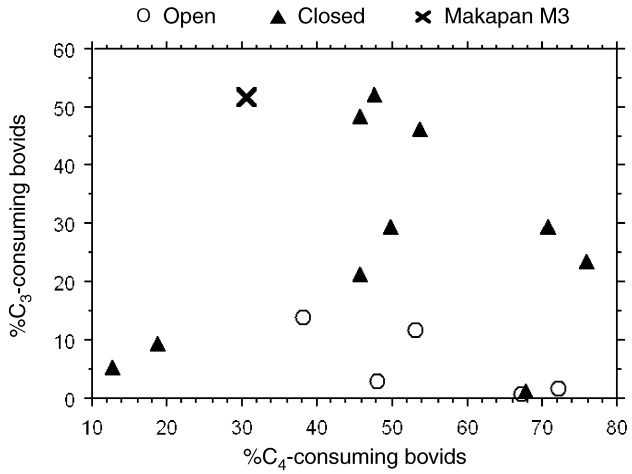

Fig. 1. Plot of the percentage of bovids that consume more than 80% C_3 vegetation against those that eat more than 80% C_4 vegetation from modern 'closed' and 'open' environments.

of their diets.[17] The two methods provided identical results, demonstrating remarkable agreement between the stable isotope and traditional ecological data. Thus, we are confident that our isotopically derived results are robust.

Results and discussion

Using the percentages of C_3 specialists (rather like an inverse of the alcelaphini plus antilopini criterion), the areas Vrba termed 'closed' and 'open' were successfully separated in 13 of 16 cases (ANOVA; $P < 0.02$). In every case, the 'open' areas contained less than 15% C_3-consuming bovids. In 7 of the 10 'closed' areas, C_3 consumers accounted for more than 20% of the bovids present. In the three cases in which 'closed' areas had less than 15% C_3 eaters, the bovids were dominated by grass-eating yet woodland-loving buffalo (*Syncerus caffer*) or impala. When the percentages of C_3 consumers are plotted against the percentages of C_4 consumers, however, the distinction between 'open' and 'closed' environments is improved, as 'open' areas are isolated in the bottom right corner of Fig. 1. The only 'closed' area that clusters with 'open' habitats is Lake Manyara in Tanzania, for which buffaloes comprise 66% of the total bovid population. It is highly unlikely, however, that bovines would be so preponderant had the local ecosystem suffered less from human incursion.

These data indicate that the presence of more than 20% C_3-consuming bovids indicates a relatively 'closed' environment. Equally important, however, this C_3/C_4 index eliminates a host of assumptions and supplants them with an ecological imperative: an animal can only eat food that is available. When applied to the fossil site of Makapansgat, the carbon isotope data show that 51% of its bovids were C_3 consumers (Table 1; Fig. 1), which is a higher percentage of C_3 consumers than all but one of Vrba's modern 'closed' areas (Culei, Angola, at 52% contains woodland, thicket, and riverine forest). Hence, these results strengthen previous environmental reconstructions that suggest that significant amounts of woody vegetation were present in the 3-Myr Makapansgat Valley.

Several caveats should be considered. For one, further such analyses should be undertaken in more modern environments to determine the universality of these patterns. Ideally, one should analyse the entire macrofauna, as bovids alone may not be peerless environmental indicators. For instance, a relatively high percentage of C_3 consumers within the larger faunal community might leave limited ecospace for C_3-consuming bovids, leading to a disproportionately high percentage of C_4

consumers among the bovid fauna. If this were the case, the percentage of C_3 vegetation would be under-represented in the bovid sample. Analyses of entire modern and fossil communities will go a long way towards eliminating such potential biases. Another problem is the unknown length of time in which a fossil assemblage accumulated. The Makapansgat Member 3 fauna, for instance, may have accumulated in a few thousand or even 100 000 years.[20,21] Thus, the fauna do not represent a 'snapshot' in time, but rather a series of snapshots lain atop each other. Therefore, the composite assemblage may or may not fairly represent the fauna found in the vicinity of the cave at any given time. This is further exacerbated by the fact that the percentages of animals found at Makapan may not accurately reflect the living community during Member 3 times due to collection biases.[22–24] However, these last two difficulties plague *all* faunal and palynological analyses.

Notwithstanding these constraints, in the case of Makapansgat it seems unlikely that the very large percentage of C_3 consumers could be due to predator selection alone, since the most abundant bovid species is the fresh-grass grazing *R. darti* (16% of all bovids)[17] — hence C_4 consumers were also abundant and preyed upon. Moreover, even if we were to halve the number of C_3 consumers at Makapan, it would still cluster with the modern 'closed' environments. The great excess of C_3-consuming bovids from Makapan is consistent with earlier studies that suggested 'closed' environments with riparian forest and edaphic grasslands.[7,18,21] Importantly, the carbon isotope-based C_3/C_4 index requires no assumptions about the behaviour of fossil taxa, as the only data used are those established empirically by carbon isotope analysis. Further research on the percentages of C_3 and C_4 consumers in modern habitats among all taxa will greatly improve the utility of this tool.

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1. Lee-Thorp J.A. and van der Merwe N.J. (1993). Carbon isotope studies of Swartkrans fauna and hominids. In *Swartkrans: A Cave's Chronicle of Early Man,* ed. C.K. Brain. Transvaal Museum Monograph No. 8, Pretoria.
2. Lee-Thorp J.A. and Beaumont P.B. (1995). Vegetation and seasonality shifts during the Late Quaternary deduced from $^{13}C/^{12}C$ ratios of grazers at Equus Cave, South Africa. *Quat Res.* **43**, 426–432.
3. Cerling T.E., Harris J.M., Ambrose S.H., Leakey M.G. and Solounias N. (1997). Dietary and environmental reconstruction with stable isotope analyses of herbivore tooth enamel from the Miocene locality of Fort Ternan, Kenya. *J. hum. Evol.* **33**, 635–650.
4. Coppens Y. (1975). Evolution des hominides et de leur environement au cours du Plio-Pleistocene dans la basse vallée de l'Omo en Ethiopie. *C.R. Acad. Sci.* **281**, 1693–1696.
5. Vrba E.S. (1985). Ecological and adaptive changes associated with early hominid evolution. In *Ancestors: The Hard Evidence,* ed. E. Delson, pp. 63–71. Alan R. Liss, New York.
6. Reed K. (1997). Early hominid evolution and ecological change through the African Plio-Pleistocene. *J. hum. Evol.* **32**, 289–322.
7. Sponheimer M., Reed K. and Lee-Thorp J.A. (1999). Combining isotopic and ecomorphological data to refine bovid paleodietary reconstruction: a case study from the Makapansgat Limeworks hominin locality. *J. hum. Evol.* **36**, 705–718.
8. Vrba E. (1974). Chronological and ecological implications of the fossil Bovidae at the Sterkfontein Australopithecine site. *Nature* **250**, 19–23.
9. Vrba E.S. (1980). The significance of bovid remains as indicators of environment and predation patterns. In *Fossils in the Making,* eds A.K. Behrensmeyer and A.P. Hill, pp. 247–272. University of Chicago Press, Chicago.
10. Shipman P. and Harris J.M. (1988). Habitat preference and paleoecology of *Australopithecus boisei* in Eastern Africa. In *The Evolutionary History of the 'Robust' Australopithecines,* ed. F.E. Grine, pp. 343–381. Aldine de Gruyter, New York.
11. Harris J.M. (1991). *Koobi Fora Research Project, Vol. 3. The Fossil Ungulates: Geology, Fossil Artiodactyls, and Paleoenvironments.* Clarendon Press, Oxford.
12. Plummer T.W. and Bishop L.C. (1994). Hominid paleoecology at Olduvai Gorge, Tanzania as indicated by antelope remains. *J. hum. Evol.* **27**, 47–75.
13. Kappelman J., Plummer T., Bishop L., Duncan A. and Appleton S. (1997). Bovids as indicators of Plio-Pleistocene paleoenvironments in East Africa. *J. hum. Evol.* **32**, 229–256.
14. Sponheimer M., Lee-Thorp J., de Ruiter D., Smith J., van der Merwe N., Reed K., Ayliffe L., Heidelberger C. and Marcus W. (2003). Dietary preferences of southern African Bovidae: the stable isotope evidence. *J. Mammal.* **84**, 471–479.
15. Cerling T.E., Harris J.M. and Passey B.H. (2003). Diets of East African Bovidae based upon stable isotope analysis. *J. Mammal.* **84**, 456–470.
16. Sponheimer M., Grant C.C., de Ruiter D., Lee-Thorp J., Codron D. and Codron J. (2003). Diets of impala from Kruger National Park: evidence from stable carbon isotopes. *Koedoe* **46**, 1–6.
17. Gagnon M. and Chew A.E. (2000). Dietary preferences in extant African Bovidae. *J. Mammal.* **81**, 490–511.
18. Vrba E.S. (1987). A revision of the Bovini (Bovidae) and a preliminary revised checklist of Bovidae from Makapansgat. *Palaeontol. afr.* **26**, 33–46.
19. Sponheimer M., Lee-Thorp J., Reed K. and De Ruiter, D. (submitted). Isotopic ecology of the Makapansgat Limeworks vertebrate fauna. *J. Vert.Paleontol.*
20. McFadden P.L., Brock A. and Partridge T.C. (1979). Paleomagnetism and the age of the Makapansgat hominid site. *Earth Planet. Sci. Lett.* **44**, 411–415.
21. Reed K. (1996). *The Paleoecology of Makapansgat and other African Plio-Pleistocene hominid localities.* Ph.D. dissertation, State University of New York at Stony Brook, New York.
22. Brain C.K. (1981). *The Hunters or the Hunted?* University of Chicago Press, Chicago.
23. Behrensmeyer A.K. (1991). Terrestrial vertebrate accumulations. In *Taphonomy: Releasing the Data Locked in the Fossil Record,* eds P.A. Allison and D.E.G. Briggs. Plenum, New York.
24. Lyman R.L. (1994). *Vertebrate Taphonomy.* Cambridge University Press, Cambridge.

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