situations, mainly in pioneer areas where large quantities of wood and other biomass residues are available which could provide energy for its industrialization. On the other hand, cassava grows in poor-quality soil and is also convenient for the employment of nonqualified manpower, that is, people in the lowest income groups. It may also be possible to increase the yield of cassava by undertaking a minimal amount of research. A new field study is being conducted in order to obtain more realistic figures for the cultural energy of a number of crops in Brazil.

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Carbon Isotopic Evidence for Different Feeding Patterns in Two Hyrax Species Occupying the Same Habitat

Abstract. The carbon-13/carbon-12 ratios of the carbonate and collagen fractions of bone of the sympatric hyrax species Procavia johnstoni *and* Heterohyrax brucei *indicate that the former obtains most of its diet by grazing while the latter is primarily a browser. The carbon-13/carbon-12 ratios of these fractions in fossil bone will record information about diet if they have not been altered during diagenesis.*

Closely related animal species living in an environment with restricted resources can coexist if there are differences in their feeding habits. Hoeck (*1*) has shown, from visual observations, that such an ecological separation occurs for sympatric *Procavia johnstoni* and *Heterohyrax brucei*. These herbivorous species of hyrax differ significantly in the amount of feeding time devoted to grazing and browsing on plants in and around the rock outcrops on which they live together in the Serengeti National Park of Tanzania. During the wet season, which extends from November through May, *P. johnstoni* spends 78 percent of its feeding time grazing, whereas grazing accounts for 43 percent of its feeding time during the dry season, when the nutritional quality of the grasses declines. The remainder of the feeding time during both seasons is spent browsing. In contrast, *H. brucei* is predominantly a browser. Grazing accounts for 19 percent of its feeding time during the wet season and 9 percent during the dry season. We have found that the difference in the grazing and browsing habits of these two species is reflected in the $^{13}C/^{12}C$ ratios of the carbonate and collagen fractions of their bones.

Laboratory experiments (*2*) in which animals were raised on diets of known and constant carbon isotopic composition have demonstrated that the isotopic composition of carbon incorporated into an animal is a function of the carbon isotopic composition of its diet. The $^{13}C/^{12}C$ ratio of the diet can be determined from the $^{13}C/^{12}C$ ratio of some component of the animal by taking into account the specific isotopic fractionation which occurs during the assimilation of dietary carbon into that component. The $^{13}C/^{12}C$ ratios of the plants which comprise the diets of herbivores in turn depend on the photosynthetic pathways—C_3, C_4, or crassulacean acid metabolism (CAM) (*3*)—by which they fix carbon dioxide. Plants with C_4 metabolism have characteristically higher $^{13}C/^{12}C$ ratios than C_3 plants; CAM species can, depending on environmental conditions, fix carbon dioxide by either the C_3 or the C_4 pathway, or both, and consequently can have C_3-like, C_4-like, or intermediate $^{13}C/^{12}C$ ratios (*4*). Many tropical grasses are C_4 plants, possessing a collection of biochemical and physiological adaptations for growth in warm environments with high light intensities (*3*). On the other hand, most plants which are classified as browse materials (*1*) are C_3 plants.

Although the photosynthetic types of the plants which are available to *P. johnstoni* and *H. brucei* (*1*) have not been determined directly, most of them can be classified as C_3 or C_4 based on their taxonomic affinities. Of the 27 grass species, 22 either belong to families or genera which have been found to contain only C_4 types or have been identified as C_4 types at the species level; of the 64 species which make up the browse materials, 54 belong to families in which C_4 or CAM photosynthesis have not been found and hence are assumed to contain only C_3 types (*4-6*). Thus it should be possible to measure differences in the relative amounts of grazing and browsing by *P. johnstoni* and *H. brucei* based on differences in the $^{13}C/^{12}C$ ratios of their carbon. The carbon contained in the carbonate and collagen fractions of bone was analyzed for this purpose. These fractions were chosen since applications of this method of dietary analysis to fossil situations would be of considerable interest, and these fractions are generally the only well-preserved animal carbon available in fossil vertebrate material.

Bones were dissected from recently killed hyrax specimens and air-dried (*7*). Jawbones were used exclusively in this study. They were freed of surface contaminants by sonication, then ground in a diamond mortar to pass through a 0.71-mm mesh sieve. The lipid fraction was extracted (*8*) from the bone powder and discarded. The $^{13}C/^{12}C$ ratios of the carbonate and collagen fractions of the defatted bone powder were determined by methods which have been described previously (*2*). The results are reported as $\delta^{13}C$ values (*9*).

The $\delta^{13}C$ values of the bone carbonate and collagen fractions of each of four *P. johnstoni* and *H. brucei* specimens which were analyzed as well as the $\delta^{13}C$ values of the diet of each individual estimated from the $\delta^{13}C$ values of each of the fractions (*10*) are shown in Fig. 1. For each individual, there is good agreement between the $\delta^{13}C$ values of the diet estimated from the two fractions. The differences between the $\delta^{13}C$ values of the diet estimated from the carbonate and collagen fractions range from 0.1 to 1.5 per mil, with the average difference being 0.7 per mil; these are small compared to the differences between the estimated $\delta^{13}C$ values of the diets of the two species. The $\delta^{13}C$ values of the diets of *P. johnstoni* individuals estimated from both fractions range between −12.8 and −16.0 per mil, while the corresponding values for the diets of *H. brucei* individuals range from −22.6 to −23.9 per mil.

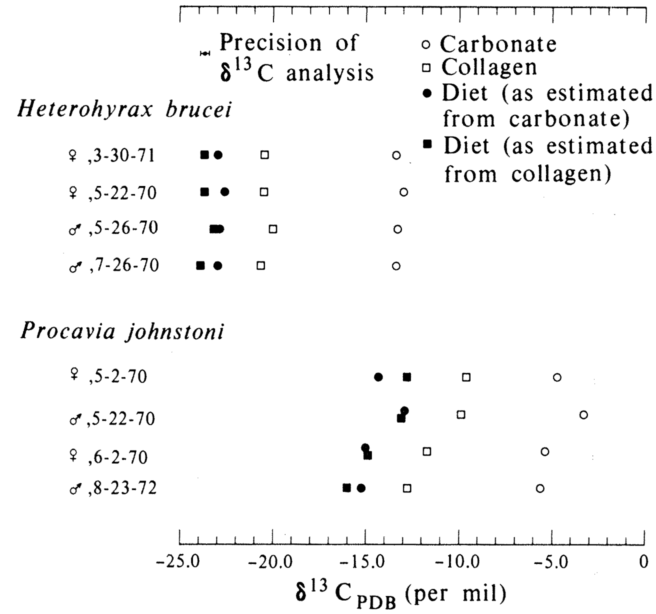

Fig. 1. The $\delta^{13}C$ values of the bone carbonate and collagen fractions of *Heterohyrax brucei* and *Procavia johnstoni* individuals and the $\delta^{13}C$ values of the diets estimated from the $\delta^{13}C$ values of each fraction. The sex and date of collection of each specimen are given.

The $\delta^{13}C$ values of terrestrial C_3 plants lie between −23 and −34 per mil, while the corresponding values for terrestrial C_4 plants range from −10 to −18 per mil (*4*). Thus the $\delta^{13}C$ values of the diets of *P. johnstoni* individuals indicate that their diet is composed largely of C_4 plants. The more negative $\delta^{13}C$ values for the diets of *H. brucei* individuals indicate that most of their diet is derived from C_3 plants. It is not possible at this time to assign relative amounts of browsing and grazing to each species, since there are no data on the actual $\delta^{13}C$ values of the plants available as diet material. However, the results are in qualitative agreement with Hoeck's (*1*) observations on the amount of feeding time devoted to grazing and browsing in the two species. The $\delta^{13}C$ values for the diets of *H. brucei* individuals are at the positive end of the range of $\delta^{13}C$ values of C_3 plants; this distribution would result if the diet were composed primarily of C_3-type browse materials with a small amount of C_4 grasses also being eaten. The $\delta^{13}C$ values of the diets of *P. johnstoni* individuals lie in the middle of the range of $\delta^{13}C$ values of C_4 plants; this distribution is consistent with a diet in which a large fraction of the food was obtained by grazing on C_4 grasses.

Information about diet can be obtained from the $\delta^{13}C$ values of the carbonate and collagen fractions of fossil bone if it can be shown that their original $\delta^{13}C$ values have not been altered during diagenesis. The carbonate fraction of bone is usually susceptible to diagenetic alteration of its carbon isotopic composition. This follows from observations that bones which are dated from the ^{14}C content of their carbonate fractions generally give erroneous ages, presumably because of exchange, after the death of the animal, with atmospheric CO_2 (*11*) or CO_2 dissolved in groundwater (*12*). Such exchange would also alter the $\delta^{13}C$ value of the carbonate fraction. The collagen fraction of bone is not subject to exchange with carbon in the postmortem environment and thus may preserve its original $\delta^{13}C$ value, in which case information about diet can be obtained. For example, the $\delta^{13}C$ values of the collagen fraction of fossil human bones from the Viru Valley in Peru increase with decreasing age over the period from roughly 5000 to 2000 years ago. This trend can be correlated with archeological evidence for increasing consumption of maize, a C_4 plant, over the same period (*13*). The $\delta^{13}C$ values of the carbonate fraction of these bones do not follow such a trend.

In summary, we have shown that the $\delta^{13}C$ values of both the carbonate and collagen fractions of bone of extant animals record information about diet, in this case the relative amounts of grazing and browsing in sympatric hyrax species. It may be possible to apply this type of analysis to fossil animals. However, it is expected that in many fossil bones the $\delta^{13}C$ value of the carbonate fraction will be influenced by carbon sources in the postmortem environment. Consequently, an important internal check on the method, namely, a comparison of the dietary $\delta^{13}C$ values estimated from the $\delta^{13}C$ values of the carbonate and collagen fractions, cannot be performed. Even in cases in which the $\delta^{13}C$ values of the collagen fraction of fossil bone appear to record information about the diets of the animals, it must be rigorously demonstrated that changes in the concentration of collagen and in its amino acid composition, which may occur during diagenesis (*14*), did not significantly alter its original $\delta^{13}C$ value.

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For the work reported here, the standard is the Pee Dee belemnite (PDB) carbonate.
10. Studies (*2*) in which bones from mice raised on diets of known and constant $\delta^{13}C$ values were analyzed have shown that the $\delta^{13}C$ value of the diet is on average -3.2 per mil relative to the $\delta^{13}C$ value of the collagen fraction. Similarly, the diet has a $\delta^{13}C$ value which is on average -9.6 per mil relative to the $\delta^{13}C$ value of the carbonate fraction. The accuracy of the $\delta^{13}C$ value of a diet estimated from the $\delta^{13}C$ value of either fraction is on the order of ± 0.5 per mil.
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Microwear of Mammalian Teeth as an Indicator of Diet

Abstract. *Microwear details on teeth of two sympatric species of hyrax are correlated with major dietary differences observed in the wild. Grazing (*Procavia johnstoni*) and browsing (*Heterohyrax brucei*) species can be distinguished. The results show that diets of extinct species may be deduced from tooth microwear.*

Hypotheses concerning the diets of extinct hominoid species have played an important part in discussions of human origins (*1–4*). Direct testing of these hypotheses has proved difficult; most research has involved ambiguous comparisons of early hominoid teeth with those of living mammals and conclusions drawn from either associated archeological finds or inferred local paleoecology. Two of us (A.W. and L.P.) are attempting to test dietary hypotheses directly by finding correlations between known diet and tooth microwear in a variety of living mammals. If the correlations prove to be strong, it will be possible to test dietary hypotheses by examining the microwear on extinct hominoid teeth.

To establish stringent controls, we sought to examine teeth of pairs of extant species that meet the following criteria: (i) the feeding behaviors of the two species are known from careful field observations; (ii) the specimens used are from wild populations; (iii) the two species are of similar size, with similar teeth and masticatory systems; and (iv) the specimens are from the same local area, to avoid variations produced by local soils and climate. Several pairs of such species have been examined, although it has proved difficult to meet the fourth criterion, that of sympatry. Collecting samples of larger, and sometimes rare, mammals is impossible today, which made it necessary to use museum collections, the composition of which has been influenced by many historical factors. Even when two appropriate species are known to be sympatric, museum collections often do not include sympatric samples. However, one pair of closely related species does meet all the criteria for this study and can be used to determine the relative influence of browsing and grazing on tooth microwear.

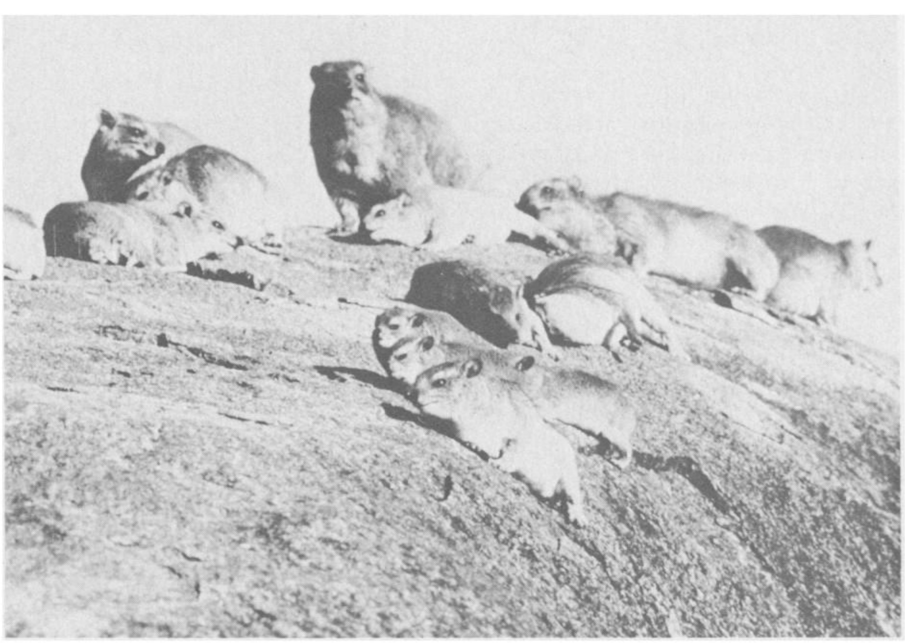

Fig. 1. Basking hyraxes. A group of *H. brucei* is in the foreground and several larger *P. johnstoni* are in the background.

Hoeck (*5*) has made a detailed study of the feeding behavior of two sympatric species of hyrax, *Procavia johnstoni matschiei* Neuman 1900 and *Heterohyrax brucei dieseneri* Brauer 1917, which live together in the Serengeti National Park, Tanzania. Feeding and reproductive behaviors separate individuals of these two species, which otherwise share living holes, urinate and defecate in the same places, have similar feeding periods, and bask together (Fig. 1). *Procavia johnstoni* is almost exclusively a grazer and *H. brucei* is almost exclusively a browser (*5, 6*). In addition, *P. johnstoni* is larger than *H. brucei*. The mean adult body weight of *P. johnstoni* is 3.14 kg (standard deviation, 0.60 kg; $N = 60$) while that of *H. brucei* is 1.79 kg (standard deviation, 0.26 kg; $N = 121$).

In the field study, the feeding characteristics of three allopatric family groups (two *H. brucei* and one *P. johnstoni*) and four sympatric family groups (two of each species) living on five kopjes (rocky outcrops) were studied. The vegetation of the kopjes was divided into four classes (grass, forb, bush, and tree), the plant species were identified, and indices of diversity and similarity were calculated. Plant biomass was approximated by a foliage density factor and the seasonal variation was recorded. Counts of plant species ranged from 65 to 95. Bushes and trees account for only about a quarter of the species, but they gave the highest foliage density. Seasonal leaf, flower, and fruit cycles were found in the grasses, forbs, and small bushes, but larger bushes and trees never lost leaves completely. There are marked dry and wet seasons. The latter is November to May, with a rainfall peak in March and April.

The feeding behavior of the hyrax groups was recorded regularly during both wet and dry seasons. *Heterohyrax brucei* fed on 64 plant species, but between 2 and 11 species made up 90 percent of the diet. There was a high correlation (correlation coefficient $\bar{r} = .90$, $P < .01$) between the comparative abundance of vegetation and the proportion of the vegetation classes eaten by *H. brucei*. While showing preference for certain plants, all four groups fed roughly in proportion to foliage density. *Heterohyrax brucei* browsed on bushes and trees in both wet (81 percent) and dry (92 percent) seasons, but ate some grass in the wet season. *Procavia johnstoni* was seen feeding on 79 plant species. This species showed great seasonal