

## Original Papers

# Stable isotope analysis of termite food habits in East African grasslands

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**Summary.** Stable carbon isotope techniques were employed to study the food habits of the termite *Macrotermes michaelseni* (Isoptera: Termitidae) in a semiarid savanna habitat in Kenya. At Kajiado this species utilized approximately 70% herbaceous vegetation (mostly grass) and 30% woody vegetation, while at Ruiru approximately 64% of the vegetation utilized was woody and 36% herbaceous. Stable carbon isotope ratios varied between castes within sites, but were consistent with the manner in which carbon flows through termite colonies.  $\delta^{13}\text{C}$  values increased in the sequence: diet → fungus comb → nonreproductive castes → reproductive castes. These results are in agreement with the idea that organic carbon becomes enriched in  $^{13}\text{C}$  as it passes through a food chain.

### Introduction

Termites are major components of many subtropical and tropical ecosystems. The results of their activities frequently include the decomposition of cellulose and lignin-containing material (LaFage and Nutting, 1978), alteration of soil properties (Arshad, 1981), and changes in the species composition (Glover et al., 1964) and productivity (Arshad, 1982) of plant communities.

The Macrotermitinae (Isoptera: Termitidae) represent the apex of termite evolution and are the most important group of termites in the Old World tropics, where they frequently damage timber and agricultural crops (Wood, 1978). Macrotermitinae are largely subterranean and construct conspicuous mound-like nests. Workers forage for dead plant material, and a basidiomycete fungus is cultivated on their feces in the nest. The fungi decompose cellulose and lignin present in the feces and concentrate N, P, and K into fungal tissue, much of which is ultimately consumed by members of the colony (Rohrmann and Rossmann, 1980; Martin, 1979; Wood, 1978). Thus, the symbiosis with the fungus provides the Macrotermitinae with an "external digestive system" which decomposes their feces

and produces a high quality food that is assimilated easily (Collins, 1981).

*Macrotermes subhyalinus* (Rambur) and *Macrotermes michaelseni* (Sjost) are the most common of the mound building termites in the semiarid savanna lands of Kenya. Both species can coexist in a given area, but generally one species tends to dominate at a particular site. Available evidence indicates that these species prefer to feed on grass litter, but they also will consume live plant material or roots if litter is in short supply (Lepage, 1978; Ruyooka, 1980). Nests of *Macrotermes michaelseni* (mistakenly named *Macrotermes subhyalinus* in previous papers published from Kenya) usually contain two to three million individuals (Darlington, 1977). This species alone may consume 1 to 1.5 tonnes/ha/yr of plant material, an amount comparable to the quantity of plant material consumed by domestic and wild mammalian herbivores living in the same habitat (Lepage, 1978, 1979). In spite of this potentially competitive situation between termites and range-land herbivores, little is known about the food habits of these *Macrotermes* species.

Previous attempts to study termite food habits have not always been successful. Gut contents and fecal material of termites are too finely comminuted to be recognizable by microscopic examination, a standard method of dietary analysis (R.M. Hansen, personal communication; Adamson, 1943). Stable carbon isotope analysis of body tissue has been successful in many studies of insect food habits (Boutton et al., 1978, 1980; Fry et al. 1978; Rau, 1980), but has not yet been applied to termites. The method is based on the fact that plants with the  $\text{C}_3$  pathway of photosynthesis have stable carbon isotope ratios ranging from  $-21$  to  $-33\text{‰}$  vs PDB, while plants with the  $\text{C}_4$  photosynthetic pathway have stable carbon isotope ratios ranging from  $-9$  to  $-17\text{‰}$  vs PDB (Smith and Epstein, 1971). Consequently, there are two isotopically distinct groups of plants. Because animals do not significantly fractionate the stable carbon isotope composition of their food (DeNiro and Epstein, 1978), the isotope ratio of an animal is approximately the same as its food source. Stable isotope ratios of animal tissues thus indicate whether an animal consumes only  $\text{C}_3$  plants, only  $\text{C}_4$  plants, or a mixture of both.

In the savanna ecosystems of East Africa, the herb layer is composed of  $\text{C}_4$  plants only; all of the trees and shrubs, however, are  $\text{C}_3$  plants (Tieszen et al., 1979). Therefore, stable isotope analysis of animals from the savanna habitat would indicate relative dependence of the animal on herb

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layer vegetation (nearly all grass) or on woody vegetation (trees and shrubs).

The purpose of this study was to use stable carbon isotope methods to investigate the food habits of one of the dominant termite species of the semiarid savanna of Kenya, *Macrotermes michaelseni*. The study was designed to 1) determine the relative dependence of *Macrotermes michaelseni* on herb layer plants vs woody plants; 2) determine differences in food habits between castes; and 3) compare the food habits of this termite in two communities of differing plant species composition.

### Study Areas

Termites and plant samples were collected from Kajiado and Ruiru study areas. Kajiado is located approximately 80 km south of Nairobi, Kenya (02°04' S, 36°47' E) at an elevation of 1620 m. Annual precipitation is normally 400 to 600 mm and the temperature ranges from 12 to 28° C, with an annual mean of 22° C. The most common grasses include *Themeda triandra*, *Pennisetum mezianum* and *Cynodon dactylon*. The most common woody species is *Acacia tortilis* with a density of approximately 1 tree/100 m<sup>2</sup>.

Ruiru site is situated approximately 15 km north of Nairobi (01°08' S, 36°54' E) at an elevation of 1610 m. The average annual precipitation is 1065 mm. Mean annual temperature is 19.0° C and ranges between 13 to 25° C. *Aristida adoensis*, *Cynodon dactylon*, *Setaria sphacelata* and *Themeda triandra* are among the most common grasses; the tree stratum consists almost exclusively of *Eucalyptus* sp. with a density of approximately 4 trees/100 m<sup>2</sup>.

### Methods

An active nest of *M. michaelseni* from each study area was exposed by digging, and the bulk soil, containing various castes of termites, was sampled. Fresh insect specimens were collected manually with forceps and dropped into a killing jar containing ethyl acetate. Approximately 20 specimens from each caste were collected, except for the king and queen for which only one sample of each was available; each nest usually contains only one king and one queen. To minimize isotopic variation that might arise from sampling different body parts, only head tissue was analyzed for  $\delta^{13}\text{C}$ .

In order to determine the stable carbon isotope ratios of potential food sources, dominant plant species from both the Ruiru and Kajiado study areas also were collected, washed thoroughly, dried, and ground to a powder.

Termite and plant samples were combusted to CO<sub>2</sub> for mass spectrometric analysis of <sup>13</sup>C/<sup>12</sup>C according to the method of Buchanan and Corcoran (1959). Five to ten mg of dried sample were placed in a baked-out length (~16 cm) of 6 mm O.D. quartz or Vycor tubing previously sealed at one end. Samples were mixed with 0.5 g of oxidant (CuO:MnO<sub>2</sub>:CuCl<sub>3</sub> in a 5:1:1 ratio) and a 1 cm length of silver wire. Sample tubes then were attached to a vacuum manifold, evacuated to <10<sup>-2</sup> mbar, and sealed. Sealed tubes were combusted in a muffle furnace at 850° C for one hour.

Carbon dioxide from the combustion then was released from the sample tube and admitted to the evacuated inlet system of the mass spectrometer. Water vapor was removed by passing the sample through a dry ice trap prior to the

collection of CO<sub>2</sub> in a liquid nitrogen trap. Gases that were not frozen in the liquid nitrogen trap were pumped away, and purified CO<sub>2</sub> was admitted to the mass spectrometer for <sup>13</sup>C/<sup>12</sup>C determinations.

All isotope analyses were performed on a Micromass 602E isotope ratio mass spectrometer. Results are expressed as:

$$\delta^{13}\text{C} \text{ ‰} = \left[ \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \right] \times 1000$$

where  $R_{\text{standard}}$  is the mass 45 to mass 44 ratio of CO<sub>2</sub> of carbonate from the fossil *Belemnitella americana* from the Peedee formation of South Carolina (Craig, 1953, 1957). Values were corrected for errors from <sup>17</sup>O contribution to mass 45 abundance, switching valve leakage, and background. The standard error of the combustion procedure was determined to be 0.14‰, while the standard error due to instrument effects was 0.05‰, for an overall precision of 0.2‰ on each determination.

### Results

Stable carbon isotope ratios indicated that the major woody plant species at both study areas had the C<sub>3</sub> photosynthetic pathway with  $\delta^{13}\text{C}$  values of approximately -27.0‰ vs PDB (Table 1). By contrast, the major herbaceous plant species at both study areas, all of which were grasses, had the C<sub>4</sub> photosynthetic pathway with  $\delta^{13}\text{C}$  values that averaged approximately -12.5‰ vs PDB. These  $\delta^{13}\text{C}$  values agreed well with those previously reported for C<sub>3</sub> and C<sub>4</sub> plants (Smith and Epstein, 1971). Variation in the  $\delta^{13}\text{C}$  values within photosynthetic categories in Table 1 is relatively small and attributable to differences in growth conditions (Smith et al., 1976; Farquhar, 1980). No major or consistent differences between the  $\delta^{13}\text{C}$  values of the vegetation at Kajiado site and Ruiru site were evident. In addition, there were no differences in  $\delta^{13}\text{C}$  between live and dead plant material (unpublished data).

$\delta^{13}\text{C}$  values of the termites from the two sites were intermediate between  $\delta^{13}\text{C}$  values of herbaceous plants and woody plants, indicating that woody and herbaceous plant material was utilized at both sites (Table 2). Isotope ratios of termites at Kajiado ranged from -14.8‰ to -15.9‰, and from -16.8‰ to -19.5‰ at Ruiru.  $\delta^{13}\text{C}$  values of *M. michaelseni* individuals were clearly more negative at the Ruiru site, indicating a greater consumption of woody plant material compared with that at the Kajiado site. Paired comparisons analysis of variance (Sokal and Rohlf, 1969) revealed that the  $\delta^{13}\text{C}$  values of individual castes and the fungus comb were significantly more negative at the Ruiru site than at Kajiado ( $F_{1,7} = 64.6$ ,  $P < 0.001$ ).

When animals consume isotopically different food items (such as C<sub>3</sub> and C<sub>4</sub> plants), it becomes possible to construct simple mixing models to determine the relative importance of the two food items in the diet. In this case, *M. michaelseni* was consuming both C<sub>3</sub> (woody plants) and C<sub>4</sub> (herbaceous plants) species. Because little is known about the relative abundance of woody vs herbaceous plant material in the diet of *M. michaelseni*, it was important to try to estimate the significance of these different food sources.

Other investigators (DeNiro and Epstein, 1978) have determined that animals have  $\delta^{13}\text{C}$  values that are up to 2.7‰ more positive than their diets, the average being approximately 1.0‰. In other words, animals are slightly

**Table 1.** Stable carbon isotope ratios of plants from both study areas. All analyses were performed on leaves only. Results are expressed as ‰ vs PDB standard

Kajiado site		Ruiru site	
Woody Species:		Woody Species:	
<i>Acacia tortilis</i>	−27.0	<i>Eucalyptus sp.</i>	−26.9
Herbaceous species:		Herbaceous species:	
<i>Cynodon dactylon</i>	−12.2	<i>Aristida adoensis</i>	−13.1
<i>Pennisetum mezianum</i>	−12.0	<i>Cenchrus ciliaris</i>	−12.4
<i>Themeda triandra</i>	−12.8	<i>Cynodon dactylon</i>	−13.6
		<i>Dichanthium insculpta</i>	−12.5
$\bar{X} \pm SD$	−12.3 ± 0.4	<i>Eragrostis braunii</i>	−13.1
		<i>Eragrostis heteromera</i>	−13.2
		<i>Panicum coloratum</i>	−12.4
		<i>Rhynchelytrum repens</i>	−13.2
		<i>Setaria sphacelata</i>	−10.9
		<i>Themeda triandra</i>	−11.9
		$\bar{X} \pm SD$	−12.6 ± 0.8

**Table 2.**  $\delta^{13}\text{C}$  values of termites and their potential food sources expressed as ‰ vs PDB standard. Values shown are  $\bar{X} \pm SD$ . Numbers in parentheses indicate number of replicates. Termite values were determined on head tissue only

	Kajiado	Ruiru
Major workers	−15.4 ± 0.1 (3)	−19.5 ± 0.1 (3)
Minor workers	−15.2 ± 0.1 (3)	−18.8 ± 0.6 (3)
Major soldiers	−15.0 ± 0.5 (3)	−19.4 ± 1.3 (3)
Minor soldiers	−14.9 ± 0.3 (3)	−18.9 ± 0.4 (2)
Queen	−14.8 (1)	−17.4 (1)
King	−15.9 (1)	−16.8 (1)
Fungus comb	−15.8 ± 0.1 (4)	−20.8 ± 0.3 (4)
Herbaceous vegetation	−12.3 ± 0.4 (3)	−12.6 ± 0.8 (10)
Woody vegetation	−27.0 (1)	−26.9 (1)

more enriched in  $^{13}\text{C}$  than their diets. This probably is due to the fact that respired  $\text{CO}_2$  is relatively depleted in  $^{13}\text{C}$  compared to the diet (Mosora et al., 1971; DeNiro and Epstein, 1978). In addition, these investigators have found that the feces of invertebrates are approximately 1.0‰ more positive than the diet. Because consumers are approximately 1.0‰ more positive than their food source,  $^{13}\text{C}$  undergoes a modest biomagnification as carbon progresses through a food chain (McConnaughey and McRoy, 1979).

Due to complex feeding patterns (e.g., stomodeal feeding) in termite colonies, care must be exercised to determine how to use  $\delta^{13}\text{C}$  values to estimate plant resources utilized by the colony. Major workers forage for food outside the nest and actually consume plant material. Consequently, much of their carbon probably is obtained in this way, although some of their carbon may be derived from feeding on the more nutritious fungus comb or from stomodeal feeding. Inside the nest, feces from the major workers are used to construct the fungus comb, which is the major food source for the nonreproductive castes (Wood, 1978). Reproductive castes, in turn, are dependent largely on the minor workers for stomodeal meals. Thus, the termite colony might be envisioned as a food chain: plant material → major workers → fungus comb → nonreproductive castes → reproductive castes. Because stomodeal meals potentially could be exchanged between any of the castes, carbon flow through this “food chain” is not entirely one-way.

Because of these complications, it seemed best to use  $\delta^{13}\text{C}$  values of fungus combs to estimate plant resources used by these termite colonies. The fungus comb should have been approximately 1.0‰ more positive than the food consumed by the major workers as they foraged outside the colony. The fungus should have had the same isotope ratio as the feces, because it acquired carbon directly and only from the feces. The fungus comb  $\delta^{13}\text{C}$  values probably slightly underestimated utilization of plant material derived from woody species because: 1) fungi, like other heterotrophs, may respire  $\text{CO}_2$  that is more depleted in  $^{13}\text{C}$  than the food source, which would cause a slight enrichment in  $^{13}\text{C}$  in the fungus comb; 2) saliva and feces from castes other than the major workers may go into the construction of the fungus comb, also causing the  $^{13}\text{C}$  enrichment of the fungus comb since these castes are further down the “food chain;” 3) major workers may feed on the fungus comb which would have a  $\delta^{13}\text{C}$  value more positive than the food they consume while foraging, slightly enriching with  $^{13}\text{C}$  feces that may be added to the comb. However, even if all the above events occurred with regularity, it seems unlikely that they could have changed the  $\delta^{13}\text{C}$  value of the fungus comb by more than +1‰.

Based on the data in Table 1, it is reasonable to assume that the average  $\text{C}_3$  (woody) plant had a  $\delta^{13}\text{C}$  value of  $-27.0$ ‰, and the average  $\text{C}_4$  (herbaceous) plant had a  $\delta^{13}\text{C}$  value of  $-12.5$ ‰ at both study areas. Because fungus combs are constructed from the feces of the major workers, and because insect feces are +1.0‰ relative to ingested food, the fungus comb of a termite colony feeding only on herbaceous vegetation should be  $-11.5$ ‰. By the same reasoning, a colony feeding only on woody plant material should have a fungus comb with a  $\delta^{13}\text{C}$  value of  $-26.0$ ‰. Using this information, it then becomes possible to construct a mass balance equation that will estimate the relative proportions of woody vs herbaceous plant material in the diet of *M. michaelsoni*:

$$(p_w)(\delta_{fw}) + (1 - p_w)(\delta_{fg}) = \delta_{fc}$$

where  $p_w$  is the proportion of woody plant material in the diet,  $\delta_{fw}$  is the  $\delta^{13}\text{C}$  value of a fungus comb in a colony consuming only woody plants ( $-26.0$ ),  $1 - p_w$  is the proportion of grass in the diet,  $\delta_{fg}$  is the  $\delta^{13}\text{C}$  value of a fungus comb in a colony consuming only grass ( $-11.5$ ), and  $\delta_{fc}$  is the observed  $\delta^{13}\text{C}$  value of a fungus comb.

**Table 3.** Results of t-tests for differences between castes at Ruiru and Kajiado study areas. Values presented are t-values, and numbers in parentheses are degrees of freedom

	Fungus comb	Major workers	Minor workers	Major soldiers
Ruiru:				
Major workers	8.7** (5)	–	–	–
Minor workers	6.1* (5)	2.0 (4)	–	–
Major soldiers	2.1 (5)	0.1 (4)	0.7 (4)	–
Minor soldiers	7.1* (4)	2.5 (3)	0.3 (3)	0.5 (3)
Kajiado:				
Major workers	6.6* (5)	–	–	–
Minor workers	15.0** (5)	3.5* (4)	–	–
Major soldiers	3.1* (5)	1.3 (4)	0.5 (4)	–
Minor soldiers	6.0* (5)	2.9 (4)	1.7 (4)	0.5 (4)

\*  $P < 0.05$

\*\*  $P < 0.001$

By plugging the  $\delta^{13}\text{C}$  values of the fungus combs into the above equation and solving for  $p_w$ , the importance of woody vs herbaceous vegetation to colonies of *M. michaelseni* can be estimated. At Kajiado, the fungus comb had a  $\delta^{13}\text{C}$  value of  $-15.8\text{‰}$ , which yields an estimate of 30% woody vegetation and 70% herbaceous vegetation used by *M. michaelseni* at this site. At Ruiru site, the fungus comb had a  $\delta^{13}\text{C}$  value of  $-20.8\text{‰}$ , indicating that 64% of the plant material utilized was derived from woody plants, and 36% from herbaceous plants. As reasoned above, if there are errors in these estimates, they are likely to underestimate the importance of plant material derived from woody species to the colonies.

Table 2 shows that isotope ratios varied between castes at each site. At Kajiado site,  $\delta^{13}\text{C}$  values of termites ranged from  $-15.9\text{‰}$  in the king to  $-14.8\text{‰}$  in the queen. At Ruiru site, values ranged from  $-19.5\text{‰}$  in the major workers to  $-16.8\text{‰}$  in the king.  $\delta^{13}\text{C}$  values of the fungus combs at both sites also differed slightly from the termites that fed on them.

In order to determine whether these differences were significant, t-tests (Sokal and Rohlf, 1969) were conducted. The king and queen were omitted from these analyses because each colony has only one king and one queen, and replicate analyses were not possible. Table 3 shows that  $\delta^{13}\text{C}$  values of the fungus comb at Ruiru were significantly more negative than the  $\delta^{13}\text{C}$  values of all of the nonreproductive castes, except the major soldiers. All of the castes had more positive  $\delta^{13}\text{C}$  values than the fungus comb, an expected relationship between consumers and their food source. There were no significant differences between the termite castes at Ruiru.

As at Ruiru, the fungus comb at the Kajiado site was significantly more negative than all of the termite castes (Table 3). Major workers were significantly more negative than both the minor workers and minor soldiers. There were no other significant differences between castes at Kajiado.

Because  $^{13}\text{C}$  undergoes slight biomagnification as it passes through a food chain (McConnaughey and McRoy, 1979), these small differences within colonies probably were due to complex trophic relations in the termites (Wilson, 1971; Wood, 1978). If  $\delta^{13}\text{C}$  values are considered with respect to carbon flow through the colony, differences between castes become understandable.

Major workers forage for and consume plant material outside of the nest (Wilson, 1971; Rohrmann and Rossman, 1980); some of this plant material is digested and assimilated, and their feces are used to construct a fungus comb. Assuming that the  $\delta^{13}\text{C}$  values of the fungus combs are the same as the feces, the  $\delta^{13}\text{C}$  values of the diets would then be  $-21.8\text{‰}$  at Ruiru and  $-16.8\text{‰}$  at Kajiado. Major workers at Ruiru were  $+2.3\text{‰}$  relative to the diet; major workers at Kajiado were  $+1.4\text{‰}$  relative to the diet. Although differences of this magnitude between  $\delta^{13}\text{C}$  values of the diet and consumer are not unusual (DeNiro and Epstein, 1978), it seems likely that some of this difference resulted from additional feeding on the fungus comb, which was more positive than the food consumed while foraging. Other nonreproductive castes remained within the nests and fed on the fungus comb. Values of minor workers, major soldiers, and minor soldiers at both sites ranged from  $+0.6$  to  $+2.0\text{‰}$  relative to the fungus comb, a difference to be expected between consumers and their food source.

Values of reproductive castes generally were more positive than nonreproductive castes at both study areas. Due to a greatly enlarged abdomen, a termite queen is relatively immobile and remains within the royal chamber, being fed stomodeal meals by minor workers. These stomodeal meals are liquid and produced by the salivary glands of the minor workers, and are primarily secretory in origin (Wilson, 1971). Because stomodeal meals are derived from carbon already assimilated by the minor workers, values of the queen were expected to approximate  $+1.0\text{‰}$  relative to the minor workers. At Ruiru, the queen was  $+1.4\text{‰}$  relative to the minor workers, although at Kajiado the difference was  $+0.4\text{‰}$ . The abdomens of the kings are not as enlarged as those of queens. The king therefore may feed directly on the fungus comb, and also may receive stomodeal meals from the minor workers. At Ruiru, the king was  $+2.0\text{‰}$  relative to the minor workers, suggesting total reliance on stomodeal meals. However, at Kajiado the king was  $-1.1\text{‰}$  relative to the minor workers and  $-0.1\text{‰}$  relative to the fungus comb, suggesting that this king derived his carbon from the fungus comb and not from stomodeal feeding. Analytical error cannot be ruled out in this case because only one king was analyzed at each site.

## Discussion

The results of this study demonstrate the utility of the stable carbon isotope method to study carbon flow in termites. This method should be most useful in habitats where isotopically distinct food items, such as  $\text{C}_3$  and  $\text{C}_4$  plants, are present. In both east and west tropical Africa, where termites are important components of ecosystems, all grasses below approximately 2000 m elevation have the  $\text{C}_4$  pathway of photosynthesis (Tieszen et al., 1979; Livingstone and Clayton, 1980). All trees and shrubs examined in this area to date have the  $\text{C}_3$  photosynthetic pathway. Not only are the grasses isotopically different from trees and shrubs, but these two groups also have different functional roles in the ecosystem, with differences in growth strategies and nutrient content among the most obvious. Consequently, stable isotope methods permit the study of tropical termite food habits with respect to ecologically meaningful plant categories (i.e., grasses vs trees and shrubs).

In this study  $\delta^{13}\text{C}$  values of *Macrotermes michaelseni* indicated that the diet of this species was composed of both woody and herbaceous plant material at the two study areas. Previous reports have suggested that grass is the basic source of energy for *M. michaelseni* (Ruyooka, 1980), but the results of this study indicated that plant material derived from woody species was a significant component of this termite's diet. Unfortunately, the stable carbon isotope technique cannot reveal specifically which plant species were being utilized, nor can it determine whether the termites were utilizing wood or leaves derived from woody plants. However, inspection of the litter at Ruiru site clearly indicated that termites were consuming both decaying and relatively fresh *Eucalyptus* leaves which had fallen to the ground recently.

The relative importance of woody vs herbaceous vegetation in the diet of *M. michaelseni* differed between the Ruiru and Kajiado study areas. At Kajiado, *M. michaelseni* colonies utilized approximately 30% woody vegetation and 70% herbaceous vegetation; at Ruiru this species utilized about 64% woody plant material and 36% herbaceous plant material. At Kajiado, the dominant woody plant is *Acacia tortilis*, and at Ruiru *Eucalyptus* sp. is the dominant woody plant. It is possible that physical, nutritional, or chemical differences between these two trees was the cause of the variation in this termite species' diet between the two study areas. The dietary flexibility of *M. michaelseni* demonstrated in this study may be one reason why the species is so abundant in the semiarid savanna lands of Kenya.

These results also suggest that the stable isotope technique is useful for studying carbon flow within termite colonies. McConnaughey and McRoy (1979) have shown that the greater the number of links or energy transfers separating an organism from the ultimate food source, the more enriched in  $^{13}\text{C}$  that organism will be relative to the food source. In other words,  $^{13}\text{C}$  undergoes biomagnification as carbon passes through a food chain. Results of this study also show that carbon isotope ratios became more positive (more  $^{13}\text{C}$ -enriched) as carbon passed through the termite "food chain." In general,  $\delta^{13}\text{C}$  values increased in the sequence: diet  $\rightarrow$  fungus comb  $\rightarrow$  nonreproductive castes  $\rightarrow$  reproductive castes. This progression of carbon through a colony was consistent with what is generally known about trophic dynamics in termite colonies.

**Acknowledgements.** This work was supported by research grants from the U.S. National Science Foundation (DEB-78-19552), the United Nations Environmental Program (UNEP), and the William and Flora Hewlett Foundation of Research Corporation. We thank the Government of Kenya for research clearance. Support for manuscript preparation was provided by the USDA/ARS Children's Nutrition Research Center, Department of Pediatrics, Baylor College of Medicine and Texas Children's Hospital, Houston, TX. We also thank Natalie Tieszen and Janet Boutton who assisted with laboratory analyses; W.W. Wong and B. Fry for useful comments on the manuscript; Jaye Weaver and Mary Boyd who prepared, and Roseland Klein who edited, the manuscript.

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Received January 10, 1983