

# Inter- and Intra-habitat Dietary Variability of Chacma Baboons (*Papio ursinus*) in South African Savannas Based on Fecal $\delta^{13}\text{C}$ , $\delta^{15}\text{N}$ , and %N

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**ABSTRACT** Baboons are dietary generalists, consuming a wide range of food items in varying proportions. It is thus difficult to quantify and explain the dietary behavior of these primates. We present stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotopic data, and percentage nitrogen (%N), of feces from chacma baboons (*Papio ursinus*) living in two savanna environments of South Africa: the mountainous Waterberg region and the low-lying Kruger National Park. Baboons living in the more homogeneous landscapes of the Waterberg consume a more isotopically heterogeneous diet than their counterparts living in Kruger Park. Grasses and other  $\text{C}_4$ -based foods comprise between ~10–20% (on average) of the bulk diet of Kruger Park baboons. Carbon isotopic data from the Waterberg suggest diets of ~30–50% grass, which is higher than generally reported for baboons across the

African savanna. Based on observations of succulent-feeding, we propose that baboons in the Waterberg consume a mix of  $\text{C}_4$  grasses and CAM-photosynthesizing succulents in combined proportions varying between ~5–75% (average, ~35%). Fecal  $\delta^{15}\text{N}$  of baboons is lower than that of sympatric ungulates, which may be due to a combination of low levels of faunivory, foraging on subterranean plant parts, or the use of human foods in the case of Kruger Park populations. Fecal N levels in baboons are consistently higher than those of sympatric ungulate herbivores, indicating that baboons consume a greater proportion of protein-rich foods than do other savanna mammals. These data suggest that chacma baboons adapt their dietary behavior so as to maximize protein intake, regardless of their environment. *Am J Phys Anthropol* 129:204–214, 2006. © 2005 Wiley-Liss, Inc.

Baboons are widely regarded as ecological generalists, being among the most opportunistic feeders in African savanna mammal communities (DeVore and Hall, 1965; Whiten et al., 1991; Jolly, 2001). Their diets comprise an extremely variable mix of leaves, fruits, underground storage organs, grasses, and animal matter (DeVore and Hall, 1965; Dunbar and Dunbar, 1974; Moolman and Breytenbach, 1976; Whiten et al., 1991; Byrne et al., 1993; Barton et al., 1993). Difficulties associated with quantifying and qualifying the feeding habits of such a highly flexible species often lead to problems in understanding the degree of dietary variability and selection baboons may display. The problem was highlighted several decades ago by DeVore and Hall (1965), who stated that it is easier to list the non-dietary items than the items utilized by baboons in a given area.

The feeding ecology of baboons (*Papio* spp.) was extensively researched in East Africa (e.g., Dunbar and Dunbar, 1974; Norton et al., 1987; Barton et al., 1993) and in the desert environments of Namibia (e.g., Hamilton, 1985; Brain, 1988). In South Africa, chacma baboons (*P. ursinus*) are abundant throughout, but studies have been restricted mostly to the Western Cape (DeVore and Hall, 1965; Davidge, 1978) and the Drakensberg mountains of Kwazulu-Natal (e.g., Byrne et al., 1993). Thus, very little is known about baboon ecology in South African savanna ecosystems.

One method for examining the diets of savanna mammals is through stable carbon isotopic analysis (Lee-Thorp and Van der Merwe, 1987; Cerling and Harris, 1999). Stable carbon isotope ecology in African savanna environ-

ments is based on biochemical and anatomical differences in plants at the base of the food chain. Plants that follow the  $\text{C}_3$ -photosynthetic pathway (dicotyledonous trees, shrubs, and forbs) have distinctly lower  $^{13}\text{C}/^{12}\text{C}$  ratios compared to  $\text{C}_4$ -photosynthesizing plants (grasses), and the ranges do not overlap (Smith and Epstein, 1971; Vogel, 1978; Vogel et al., 1978). Plants that use the Crassulacean acid metabolism (CAM) pathway (mainly succulents) have a carbon isotopic signature intermediate between  $\text{C}_3$  and  $\text{C}_4$  plants, or are commonly indistinguishable from  $\text{C}_4$  plants (O'Leary, 1988). Animal tissues and feces faithfully record the carbon isotopic composition of the basic plant diet, and thus reflect proportions of  $\text{C}_3/\text{C}_4$  (or CAM) plants consumed (Vogel, 1978; Lee-Thorp and Van der Merwe, 1987; Tieszen et al., 1989; Cerling and Harris, 1999). Thus, stable carbon isotope analysis has been used to

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assess the dietary habits of numerous modern and fossil taxa (e.g., Ambrose and DeNiro, 1986; Koch et al., 1991; Quade et al., 1995; Bocherens et al., 1996; Schoeninger et al., 1999; Cerling et al., 2003).

Stable nitrogen isotope ratios ( $^{15}\text{N}/^{14}\text{N}$ ) in mammalian body tissues and excreta appear to be related to a combination of environmental variables. The complexity of the nitrogen cycle leads to inconsistent patterns in soil and plant  $\delta^{15}\text{N}$  values at the base of the food chain (e.g., Muzuka 1999; Schmidt and Stewart, 2003). In animals, nitrogen isotopes are further fractionated.  $^{15}\text{N}$ -enrichment in mammals was ascribed to feeding at higher trophic levels, higher protein intake, and aridity (Sealy et al., 1987; Ambrose, 1991; Schoeninger et al., 1997; Sponheimer et al., 2003a).

Another useful dietary indicator is percentage nitrogen (%N) of feces. Fecal N is generally representative of the N (and thus crude protein) content of an animal's plant foods, and is thus considered a useful measure of diet quality (e.g., Holecheck et al., 1982; Leslie and Starkey, 1985). Interpretation of fecal %N may be complicated, however, by the protein-precipitating effects of plant secondary compounds, such as condensed tannins, and other digestion-inhibiting substances such as lignin and non-natural proteins (Robbins et al., 1987; Meissner et al., 1999). Nevertheless, numerous studies have shown that %N is a good indicator of diet quality for mammalian herbivores (e.g., Wrench et al., 1997; Grant et al., 2000).

In this study, we measured  $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$  ratios, and %N, in plants and feces of browsers (*Giraffa camelopardalis*), grazers (*Equus burchellii*), mixed feeders (*Aepyceros melampus*), and chacma baboons (*Papio ursinus*) to interpret baboon dietary behavior in the context of savanna community ecology. Traditionally, stable isotopic studies of animal diets involve the use of body tissues, such as bones, teeth, and hair, which archive ecological information during the growth period (e.g., Lee-Thorp and Van der Merwe, 1987; Schoeninger et al., 1997, 1999; Cerling and Harris, 1999). We specifically sought feces, as they provide insight into dietary ecology over a short time scale (several days), allowing for detailed spatial and seasonal comparisons (Jones et al., 1981; Tieszen et al., 1989; Sponheimer et al., 2003b). Fecal samples are also relatively easy to collect without causing animal stress or necessitating slaughter.

With these fecal data, we document spatial and temporal feeding patterns in chacma baboons (*Papio ursinus*) living in two South African savanna habitats, the Waterberg region and the Kruger National Park. We compare our findings with results of previous studies based on observational techniques (Dunbar and Dunbar, 1974; Barton et al., 1993; Byrne et al., 1993), analyses of stomach contents (Moolman and Breytenbach, 1976), and carbon isotopic analysis of bone collagen (Ambrose and DeNiro, 1986; Thackeray et al., 1996) to determine dietary contributions of  $\text{C}_3$ ,  $\text{C}_4$ , and CAM-based foods for baboons living in different environmental conditions. We further test whether chacma baboons could be opportunist feeders, utilizing resources as these occur, or whether they select preferred foods regardless of habitat. Finally, we discuss the implications of  $^{15}\text{N}$  abundances in baboon feces compared to those of sympatric herbivores.

## MATERIALS AND METHODS

### Study areas

The Waterberg is an area of mountainous savanna "bushveld," lying in the warm, temperate, summer rain-

fall area situated in the southwestern parts of South Africa's Limpopo Province. Annual rainfall often exceeds 600 mm, with the wet season occurring between October–March, while April–September are characteristically dry months (Kilian, personal communication). Acocks (1988) classified the Waterberg as "sour bushveld," comprised of tall straight trees (predominantly *Faurea saligna*) with tufted sour grassveld in the less rocky areas. In the Waterberg, fieldwork was carried out on two reserves: Zoetfontein Private Game Farm (ca. 7 km<sup>2</sup>) and Welgevonden Private Game Reserve (330 km<sup>2</sup>, situated approximately 60 km south of Zoetfontein).

The Kruger National Park covers almost 20,000 km<sup>2</sup> of deciduous "lowveld" savanna in the northeast of South Africa, situated along the border between South Africa and Mozambique. Average annual rainfall is about 500 mm, but this varies throughout the reserve, generally decreasing from south to north, and to a lesser extent from west to east (Venter and Gertenbach, 1986). The decrease in rainfall from west to east corresponds to an altitudinal cline, from about 900 m at Pretoriuskop in the southwest to about 200 m in the east. December, January, and February are the wettest months, while July and August are the driest (Gertenbach, 1980). The current study was carried out only in the southern parts of Kruger Park, an area characterized as "mixed bushveld" (Tainton, 1999). The geology in this region can be crudely divided into the western granites associated with sandy soils, and the basaltic, clay-rich soils of the eastern regions. Crests and midslopes on the sandy, granitic soils are characterized by *Combretum* spp. and *Terminalia sericea* woodland savanna, while *Acacia nigrescens*, *Dichrostachys cinerea*, and *Euclea divinorum* dominate the clayey duplex soils on the footslopes (Venter and Gertenbach, 1986). Grasses are sparse on the crests, but on the footslopes they occur in denser stands of palatable species. In the east, basaltic soils support a more open grassland savanna, with lush grasses, such as *Themeda triandra*, *Panicum coloratum*, and *Bothriochloa radicans*, interspersed with *Acacia nigrescens* and *Sclerocarya birrea* subspecies *caffra* trees (Venter and Gertenbach, 1986).

### Sample collections and analytical methods

Plants and feces were obtained from Zoetfontein and Welgevonden during September 2003, and samples were again collected from Welgevonden during January 2003, and from Kruger Park during June 2002 and January 2003. Thus, samples represent one dry season (September/June) and one wet season (January) in each region. Only the most recently deposited feces were sampled, ensuring that these did not represent mammal diets during previous seasons.

Plant specimens (which comprised leaves, roots, bark, fruits, and seeds) were collected from small, circular transects (~10 m diameter) established in different microhabitats within each reserve, and included representative samples of trees, forbs, grasses, and succulents (Table 1). From each site, 3–5 specimens of each tree, forb, and grass species present were collected. Fecal samples, collected randomly throughout the study areas, included those from grazing Burchell's zebra, browsing giraffe, and mixed-feeding impala so as to provide an appropriate ecological context. Each individual fecal specimen encountered was taken to represent one individual of the relevant species.

The majority of baboon fecal samples from Welgevonden were obtained from three commonly used sleep sites

TABLE 1. List and details of plant and feces collection sites in Waterberg and in Kruger National Park

| Collection site    | Samples                 | Visual description               | Latitude      | Longitude     |
|--------------------|-------------------------|----------------------------------|---------------|---------------|
| Waterberg          |                         |                                  |               |               |
| Zoetfontein        | Plants and feces        | Open woodland                    | 23°54'08, 5'S | 27°49'05, 5'E |
| Welgevonden        |                         |                                  |               |               |
| Keg and fig        | Plants                  | Open grassland                   | 24°17'42, 8'S | 27°49'37, 8'E |
| Acacia loop        | Plants                  | Open woodland                    | 24°13'54, 2'S | 27°44'02, 4'E |
| Bushman's Painting | Plants and baboon feces | Dense woodland                   | 24°13'53, 3'S | 27°50'53, 6'E |
| Mziki              | Plants and baboon feces | Riparian zone                    | 24°14'44, 8'S | 27°50'41, 7'E |
| Motswedi           | Plants and baboon feces | Plateau woodland                 | 24°14'47, 3'S | 27°58'00, 1'E |
| Nalana             | Baboon feces            | Solitary <i>Euphorbia ingens</i> | 24°15'13, 5'S | 27°50'24, 4'E |
| Tshetshepi         | Baboon feces            | Riparian zone                    |               | Not available |
| Kruger Park        |                         |                                  |               |               |
| Site 1             | Plants and feces        | Open grassland on basalt         | 25°14'12, 0'S | 31°59'08, 4'E |
| Site 2             | Plants and feces        | Riparian zone on basalt          | 25°20'30, 4'S | 31°56'25, 7'E |
| Site 3             | Plants and feces        | Open shrubland on granite        | 25°04'19, 1'S | 31°36'37, 9'E |
| Site 4             | Plants and feces        | Riparian zone on granite         | 25°01'02, 3'S | 31°46'55, 8'E |
| Sabie-Skukuza      | Baboon feces            | Riparian zone on granite         | 24°56'05, 8'S | 31°42'6, 0'E  |
| Lower Sabie Bridge | Baboon feces            | Open grassland on basalt         | 25°05'37, 8'S | 31°54'46, 1'E |
| Salitje River      | Baboon feces            | Dry riverbed on basalt           | 24°57'04, 5'S | 31°43'18, 4'E |
| Stolsnek           | Baboon feces            | Mountain bushveld on granite     |               | Not available |
| Stevenson Hamilton | Baboon feces            | Woodland on granite              |               | Not available |

situated in riparian zones at the lower reaches of cliff faces ("Bushman's Painting," "Mziki," and "Tshetshepi") (Table 1). During September, five samples were found along the roadsides (designated as "Motswedi"), and six samples were collected beneath a solitary *Euphorbia ingens* tree on which baboons had reportedly been feeding (Burger, personal communication in 2002), and on which bite marks were visible ("Nalana"). Feces from Zoetfontein were collected at random throughout the reserve. Baboon feces from Kruger Park were collected along the roadsides (near the "Skukuza" and "Lower Sabie" rest camps) and at a tourist lookout point ("Stevenson Hamilton"). An attempt was also made to collect feces from areas where baboons were less likely to come into contact with humans and human food items ("Stolsnek" and "Salitje River").

Plants and feces were oven-dried at 60°C for 24 hr, and mill-ground into a homogeneous powder. Samples were combusted individually in an automated Carlo-Erba device, and the resultant CO<sub>2</sub> gas was analyzed for stable carbon isotope ratios, using a continuous flow-through inlet system attached to a Finnigan MAT 252 Mass Spectrometer. <sup>13</sup>C/<sup>12</sup>C and <sup>15</sup>N/<sup>14</sup>N ratios are presented in conventional delta (δ) notation in parts per thousand, or permil (‰), relative to the PeeDee Belemnite (PDB) and atmospheric N<sub>2</sub> standards, respectively, derived from the expression:

$$R(‰) = (R_{\text{sample}}/R_{\text{PDB}} - 1) * 1000,$$

where R denotes the isotopic ratios <sup>13</sup>C/<sup>12</sup>C or <sup>15</sup>N/<sup>14</sup>N.

Standard deviations for repeated measurements of laboratory protein, plant, and chocolate standards were less than 0.1‰ for δ<sup>13</sup>C and 0.3‰ for δ<sup>15</sup>N. Mass spectrometry also provided the %C and %N for each sample, of which %N values are reported here.

Inter- and intragroup comparisons were carried out using one-way ANOVAs and Tukey's post hoc HSD. An estimate of the percentage of C<sub>3</sub>-based foods incorporated into baboon (and the other mammal species') diets, as reflected by fecal δ<sup>13</sup>C values, was calculated. To do this, we established regionally and seasonally specific values for pure C<sub>3</sub> and pure C<sub>4</sub> feeders, respectively. These isotopic "end-member" values were obtained using regional and seasonal mean δ<sup>13</sup>C values of C<sub>3</sub> trees and forbs and

TABLE 2. Mean δ<sup>13</sup>C and δ<sup>15</sup>N values (in per mil, relative to the PDB and air standards, respectively), and %N, of plants from Waterberg and Kruger National Park<sup>1</sup>

| Region      | Growth form | n   | δ <sup>13</sup> C (‰) |     | δ <sup>15</sup> N (‰) |     | %N   |     |
|-------------|-------------|-----|-----------------------|-----|-----------------------|-----|------|-----|
|             |             |     | Mean                  | SD  | Mean                  | SD  | Mean | SD  |
| Waterberg   | Trees       | 125 | -25.5                 | 1.8 | 3.7                   | 2.9 | 1.3  | 0.7 |
|             | Forbs       | 14  | -25.8                 | 1.6 | 3.2                   | 2.4 | 1.5  | 0.8 |
|             | Grasses     | 50  | -11.7                 | 1.6 | 3.2                   | 1.9 | 0.9  | 0.3 |
|             | Succulents  | 4   | -12.1                 | 2.4 | 7.7                   | 3.8 | 1.1  | 0.5 |
|             | Geophytes   | 2   | -27.2                 | 0.1 | -2.8                  | 1.5 | 1.0  | 0.6 |
| Kruger Park | Trees       | 109 | -26.4                 | 1.7 | 3.0                   | 2.5 | 1.6  | 0.7 |
|             | Forbs       | 76  | -26.0                 | 2.8 | 3.9                   | 2.5 | 1.7  | 0.9 |
|             | Grasses     | 110 | -12.1                 | 1.2 | 3.0                   | 2.0 | 0.8  | 0.4 |
|             | Geophytes   | 5   | -16.5                 | 8.9 | 4.7                   | 0.9 | 1.5  | 1.5 |

<sup>1</sup> n, total number of samples from all species combined; SD, standard deviation.

C<sub>4</sub> grasses, and we assumed a diet-tissue fractionation factor of -0.9‰ for feces (Sponheimer et al., 2003b). For example, the combined mean δ<sup>13</sup>C value for C<sub>3</sub> trees and forbs collected in the Waterberg during September was -25.2‰, while that for grasses was -11.0‰. Hence, feces collected from the Waterberg during September were considered to reflect a pure C<sub>3</sub>-based diet if they had a δ<sup>13</sup>C value of -26.1‰. Conversely, a fecal value of -11.9‰ for the Waterberg in September represented a 100% grass diet.

## RESULTS

### Intra- and interhabitat variations

Trees, forbs, and grasses displayed δ<sup>13</sup>C values consistent with those expected (e.g., Smith and Epstein, 1971; Vogel, 1978; Cerling and Harris, 1999) for C<sub>3</sub> and C<sub>4</sub> photosynthesizing plants, respectively (Table 2). Waterberg trees (mean = -25.5 ± 1.8‰, n = 125) had higher mean δ<sup>13</sup>C values than those from Kruger Park (mean = -26.4 ± 1.7‰, n = 109), and the difference is significant (P < 0.0001). All forbs were C<sub>3</sub>, and the mean δ<sup>13</sup>C values of this plant group did not differ between the two regions (mean = -25.8 ± 1.6‰, n = 14 for the Waterberg; mean = -26.0 ± 2.8‰, n = 76 for Kruger Park).

TABLE 3. Summary of mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (in per mil, relative to the PDB and air standards, respectively), and %N, of mammal feces from Waterberg and Kruger National Park<sup>1</sup>

| Region      | Species | n   | $\delta^{13}\text{C}$ (‰) |     | Estimated %C <sub>3</sub> -intake |        | $\delta^{15}\text{N}$ (‰) |     | %N   |     |
|-------------|---------|-----|---------------------------|-----|-----------------------------------|--------|---------------------------|-----|------|-----|
|             |         |     | Mean                      | SD  | Mean                              | Range  | Mean                      | SD  | Mean | SD  |
| Waterberg   | Giraffe | 9   | -26.0                     | 0.5 | 95                                | 85–100 | 4.9                       | 0.8 | 2.0  | 0.3 |
|             | Zebra   | 21  | -13.9                     | 0.7 | 15                                | 0–25   | 4.1                       | 0.8 | 0.8  | 0.1 |
|             | Impala  | 14  | -19.4                     | 4.0 | 50                                | 0–90   | 5.3                       | 0.8 | 1.4  | 0.3 |
|             | Baboon  | 185 | -21.5                     | 1.9 | 65                                | 25–95  | 3.9                       | 1.1 | 2.6  | 0.7 |
| Kruger Park | Giraffe | 19  | -27.1                     | 0.8 | 95                                | 85–100 | 4.3                       | 1.4 | 2.7  | 0.9 |
|             | Zebra   | 19  | -14.5                     | 0.8 | 10                                | 5–20   | 4.2                       | 2.2 | 1.3  | 0.8 |
|             | Impala  | 44  | -19.5                     | 2.6 | 45                                | 5–95   | 5.8                       | 2.1 | 2.1  | 0.5 |
|             | Baboon  | 86  | -25.6                     | 1.2 | 90                                | 60–100 | 4.7                       | 1.3 | 3.0  | 1.1 |

<sup>1</sup> Estimates of %C<sub>3</sub>-intake for each species are presented, rounded to nearest 5. n, number of fecal samples for each species; SD, standard deviation.

TABLE 4. Mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (in per mil, relative to PDB and air standards, respectively), and %N, of baboon feces from different localities in Waterberg and Kruger National Park<sup>1</sup>

| Region      | Collection site     | n   | $\delta^{13}\text{C}$ (‰) |     | $\delta^{15}\text{N}$ (‰) |     | %N   |     |
|-------------|---------------------|-----|---------------------------|-----|---------------------------|-----|------|-----|
|             |                     |     | Mean                      | SD  | Mean                      | SD  | Mean | SD  |
| Waterberg   | Zoetfontein         | 50  | -23.3                     | 1.2 | 4.4                       | 0.9 | 2.9  | 0.7 |
| Welgevonden | Motswedi            | 5   | -21.4                     | 1.3 | 4.2                       | 2.2 | 2.8  | 1.0 |
|             | Bushman's Painting  | 45  | -20.3                     | 1.5 | 3.6                       | 0.6 | 2.8  | 0.7 |
|             | Mziki               | 40  | -21.4                     | 1.4 | 3.7                       | 1.2 | 2.4  | 0.6 |
|             | Nalana              | 6   | -18.4                     | 2.0 | 4.8                       | 1.6 | 2.4  | 0.4 |
|             | Tshetshepi          | 39  | -21.1                     | 1.5 | 3.9                       | 1.0 | 2.1  | 0.5 |
|             | Welgevonden average | 135 | -20.8                     | 1.6 | 3.8                       | 1.0 | 2.5  | 0.7 |
| Kruger Park | Skukuza             | 42  | -25.7                     | 0.8 | 2.4                       | 0.6 | 2.7  | 0.8 |
|             | Lower Sable         | 15  | -25.0                     | 0.9 | 3.1                       | 0.7 | 3.6  | 1.2 |
|             | Salitje River       | 6   | -25.0                     | 0.7 | 5.3                       | 1.1 | 3.0  | 0.7 |
|             | Stolsnek            | 9   | -24.6                     | 0.5 | 4.9                       | 0.9 | 2.6  | 0.9 |
|             | Stevenson Hamilton  | 14  | -27.0                     | 1.6 | 5.3                       | 1.2 | 3.3  | 1.8 |
|             | KNP average         | 86  | -25.6                     | 1.2 | 4.7                       | 1.3 | 3.0  | 1.1 |

<sup>1</sup> n, number of individual baboon fecal samples; SD, standard deviation.

Mean  $\delta^{13}\text{C}$  values of grasses were not significantly different between the two regions, although those from the Waterberg were slightly  $^{13}\text{C}$ -enriched (Waterberg mean =  $-11.7 \pm 1.6\text{‰}$ , n = 50; Kruger Park mean =  $-12.1 \pm 1.2\text{‰}$ , n = 110). Succulent plants had  $\delta^{13}\text{C}$  values (mean =  $-12.1 \pm 2.4\text{‰}$ , n = 4) indistinct from those of grasses, and are thus considered obligate CAM photosynthesizing plants.

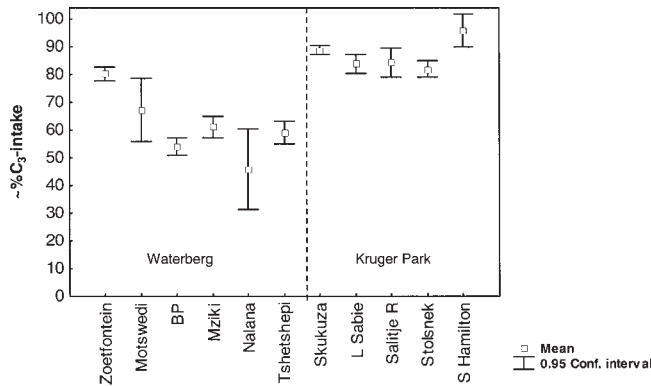
$\delta^{15}\text{N}$  values of plants ranged between  $\sim 0$ –8‰, although most samples (25% and 75% of the range) had values between 1.8–4.7‰. Mean  $\delta^{15}\text{N}$  values for plants did not differ significantly between the two regions (see Table 2). Leguminous trees (superfamily Fabaceae) were generally  $^{15}\text{N}$ -depleted (mean  $\delta^{15}\text{N} = 2.4 \pm 3.3\text{‰}$ , n = 23 for the Waterberg;  $2.0 \pm 2.2\text{‰}$ , n = 44 for Kruger Park) compared to nonleguminous trees (mean  $\delta^{15}\text{N} = 4.0 \pm 2.8\text{‰}$ , n = 102 for the Waterberg;  $3.7 \pm 2.5\text{‰}$ , n = 65 for Kruger Park). This difference is significant for Kruger Park ( $P < 0.01$ ), but not for the Waterberg.

Crude protein content (as denoted by %N) of trees and forbs was greater than that of grasses in both the Waterberg and Kruger Park (Table 2;  $P < 0.001$  and  $0.0001$ , for the Waterberg and Kruger Park, respectively). Trees from the Waterberg (mean =  $1.3 \pm 0.7\%$ , n = 125) had lower %N than trees from Kruger Park (mean =  $1.6 \pm 0.7\%$ , n = 109), and the difference is significant ( $P < 0.001$ ). Forbs displayed a similar trend (mean =  $1.5 \pm 0.8\%$ , n = 14 for the Waterberg; mean =  $1.7 \pm 0.9\%$ , n = 76 for Kruger

Park), though the difference between the Waterberg and Kruger Park is not significant. Grasses did not differ significantly in N content between regions (mean =  $0.9 \pm 0.3\%$ , n = 50 for the Waterberg; mean =  $0.8 \pm 0.4\%$ , n = 110 for Kruger Park). Overall, available browse from Kruger Park seems to be of greater nutritional value than that in the Waterberg, but available grasses appear to have been equally proteinaceous in both areas.

$\delta^{13}\text{C}$  values of zebra feces reflected a C<sub>4</sub> grass-dominated diet ( $\sim -14\text{‰}$ ), giraffe feces depicted a C<sub>3</sub> browse diet ( $\sim -26\text{‰}$ ), and feces of impala had  $\delta^{13}\text{C}$  values indicating a mixed diet ( $\sim 0$ –95% C<sub>3</sub>-intake in both regions) (Table 3). Zebra and giraffe feces did not differ significantly between the Waterberg and Kruger Park. Baboon feces exhibited  $\delta^{13}\text{C}$  values reflecting a mixed diet, lying between the means for zebra and giraffe, respectively. Baboons from the Waterberg had feces with significantly higher  $\delta^{13}\text{C}$  values (mean =  $-21.5 \pm 1.9\text{‰}$ , n = 185) than those from Kruger Park (mean =  $-25.6 \pm 1.2\text{‰}$ , n = 86) ( $P < 0.0001$ ). Based on results for local vegetation,  $\delta^{13}\text{C}$  data from baboon feces correspond to diets comprising an average  $\sim 65\%$  C<sub>3</sub>-based foods in the Waterberg, compared to a predominantly C<sub>3</sub>-based diet ( $\sim 90\%$ ) in Kruger Park.

A wider range of  $\delta^{13}\text{C}$  values was observed in baboon feces from the Waterberg, as compared to Kruger Park (Table 4). Within the Waterberg, baboon feces from Zoetfontein had lower  $\delta^{13}\text{C}$  values (mean =  $-23.3 \pm 1.2$ , n = 50) than those from Welgevonden (mean =  $-20.8 \pm 1.6$ ,



**Fig. 1.** Estimated %C<sub>3</sub>-intake of baboons within Waterberg and Kruger Park, calculated from  $\delta^{13}\text{C}$  values of feces. For calculation, regional and seasonal mean  $\delta^{13}\text{C}$  values of C<sub>3</sub> and C<sub>4</sub> plants were used as isotopic “end-members,” and a diet-feces fractionation of  $-0.9\text{‰}$  was assumed (Sponheimer et al., 2003a). Collection sites BP, L Sabie, Salitje R, and S Hamilton refer to Bushman’s Painting, Lower Sabie, Salitje River, and Stevenson Hamilton, respectively.

$n = 135$ ) ( $P < 0.0001$ ). This indicates that in Zoetfontein, baboon diets comprised an average  $\sim 80\%$  C<sub>3</sub>-foods, whereas in Welgevonden, they consumed  $\sim 60\%$  C<sub>3</sub>-foods on average (ranging from  $\sim 30\text{--}80\%$  at 95% confidence intervals) (Fig. 1). On Welgevonden, the most  $^{13}\text{C}$ -enriched baboon feces were from Nalana (mean =  $-18.4 \pm 2.0\text{‰}$ ,  $n = 6$ ), indicating a diet of only  $\sim 45\%$  C<sub>3</sub>-foods. Feces from Nalana have a significantly higher mean  $\delta^{13}\text{C}$  value than feces from all other sites on Welgevonden ( $P < 0.01$ ).

Mean  $\delta^{13}\text{C}$  values of baboon feces from Kruger Park did not differ significantly between collection sites. The data portray a consistent diet of between  $\sim 80\text{--}90\%$  C<sub>3</sub> across all Kruger microhabitats, including the riverine thickets of Skukuza and Salitje River, the grassland savanna of Lower Sabie, and the mountain bushveld habitats of Stolsnek and Stevenson Hamilton (Table 4; Fig. 1).

Overall, baboon feces from the Waterberg are significantly depleted in  $^{15}\text{N}$  compared to those from Kruger Park ( $P < 0.001$ ). More importantly, baboon fecal  $\delta^{15}\text{N}$  values were lower in the Waterberg (mean =  $3.9 \pm 1.1\text{‰}$ ,  $n = 185$ ) than for all other species. In Kruger Park, baboon feces showed  $\delta^{15}\text{N}$  values (mean =  $4.7 \pm 1.3\text{‰}$ ,  $n = 86$ ) intermediate between those of impala and the relatively  $^{15}\text{N}$ -depleted zebra and giraffe.

No significant differences were observed between mean  $\delta^{15}\text{N}$  values of baboon feces from any of the localities in Welgevonden (Table 3). However, fecal  $\delta^{15}\text{N}$  values at Nalana (mean =  $4.8 \pm 1.6\text{‰}$ ,  $n = 6$ ,  $P < 0.01$ ) were higher than those of feces from the rest of the reserve, further indicating the input of succulents to these baboons’ diets (succulents were  $^{15}\text{N}$ -enriched compared to other plants; Table 2). Feces from Zoetfontein displayed significantly higher  $\delta^{15}\text{N}$  values (mean =  $4.4 \pm 0.9\text{‰}$ ,  $n = 50$ ) than those from Welgevonden ( $P < 0.01$ ). In Kruger Park, feces from sites where baboons more regularly come into contact with humans and human food items (Skukuza, Lower Sabie, and Stevenson Hamilton) had higher  $\delta^{15}\text{N}$  values (mean =  $4.9 \pm 0.9\text{‰}$ ,  $n = 42$ ;  $5.3 \pm 1.1\text{‰}$ ,  $n = 15$ ; and  $5.3 \pm 1.2\text{‰}$ ,  $n = 14$ , for Skukuza, Lower Sabie, and Stevenson Hamilton, respectively) than feces from sites located further from rest camps and other visitor areas (mean =  $3.1 \pm 0.7\text{‰}$ ,  $n = 6$ ; and  $2.4 \pm 0.6\text{‰}$ ,  $n = 9$ , for Salitje River

and Stolsnek, respectively). Differences in fecal  $\delta^{15}\text{N}$  values between specimens from the former three localities and the latter two are significant ( $P < 0.01$  for Salitje River;  $P < 0.0001$  for Stolsnek).

Fecal N content of giraffe, impala, and zebra from both regions mirrored the trend observed in plants, i.e., browse was more proteinaceous than grass (Table 2). Browsing giraffe had higher fecal %N than grazing zebra, while mixed-feeding impala had intermediate fecal %N (Table 3). Baboon feces in both regions had significantly higher N content than all other herbivores examined ( $P < 0.01$ ). The three ungulate species displayed lower fecal N concentrations in the Waterberg than in Kruger Park, and this trend was also observed for baboons (mean =  $2.6 \pm 0.7\%$ ,  $n = 185$  in the Waterberg; mean =  $3.0 \pm 1.1\%$ ,  $n = 86$  in Kruger Park,  $P < 0.01$ ).

Intrahabitat variations in baboon fecal N content were observed, although within each region, these differences were generally small (Table 4). Zoetfontein feces (mean =  $2.9 \pm 0.7\%$ ,  $n = 50$ ) are significantly higher in N than feces from the Welgevonden site Tshetshepi (mean =  $2.1 \pm 0.5\%$ ,  $n = 35$ ) ( $P < 0.001$ ). Tshetshepi feces also differed from those at Bushman’s Painting (mean =  $2.8 \pm 0.7\%$ ,  $n = 45$ ) ( $P < 0.01$ ). In Kruger Park, the only significant difference in baboon fecal %N was observed between Skukuza (mean =  $2.7 \pm 0.8\%$ ,  $n = 42$ ) and Lower Sabie (mean =  $3.6 \pm 1.2\%$ ,  $n = 15$ ) ( $P < 0.01$ ).

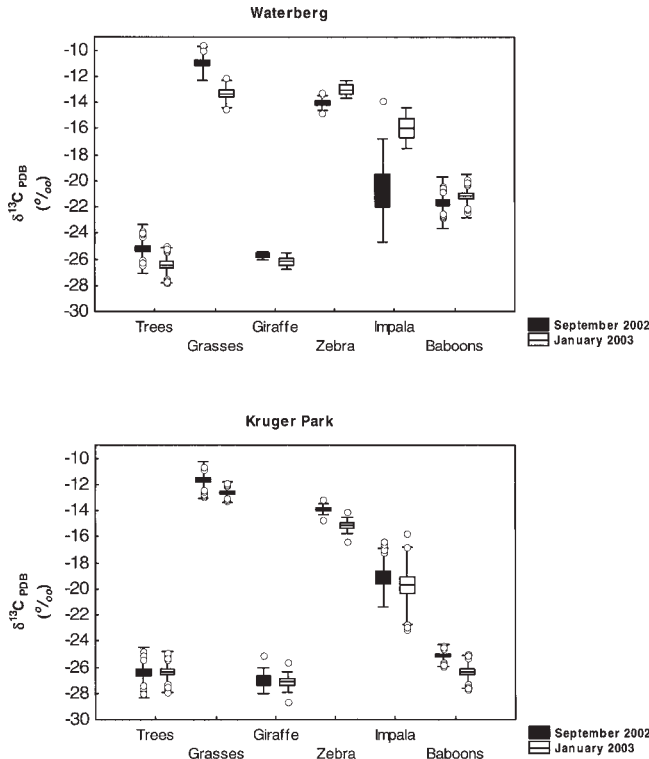
Kruger baboons exposed to human food (Skukuza, Lower Sabie, and Stevenson Hamilton) did not display different fecal nitrogen levels from feces in other areas (Stolsnek and Salitje River); nor did  $\delta^{13}\text{C}$  values differ between these localities. Thus, we are confident that consumption of human foods did not affect our analysis or interpretation.

### Seasonal trends

$\delta^{13}\text{C}$  values of trees from the Waterberg decreased by  $\sim 1.5\text{‰}$  from the dry to the wet season ( $P < 0.01$ ). Kruger Park trees showed no seasonal changes in mean  $\delta^{13}\text{C}$  values (Fig. 2). No significant seasonal differences were found for mean forb  $\delta^{13}\text{C}$  values from either area. Mean  $\delta^{13}\text{C}$  values for grasses changed seasonally in both regions. In Kruger Park, grasses had  $\delta^{13}\text{C}$  values  $\sim 1\text{‰}$  lower during the wet season than the dry ( $P < 0.01$ ), while the seasonal difference was  $\sim 2.5\text{‰}$  in the Waterberg ( $P < 0.0001$ ).

Feces from zebra and giraffe did not change significantly in mean  $\delta^{13}\text{C}$  values from one season to the next. In Kruger Park, impala feces also showed no seasonal changes in  $\delta^{13}\text{C}$  values, but those from the Waterberg displayed an increase of  $\sim 4\text{‰}$  in mean  $\delta^{13}\text{C}$  from September–January; thus they switched from eating  $\sim 60\%$  C<sub>3</sub>-based foods during the dry season to only  $\sim 15\%$  C<sub>3</sub>-foods during the wet season. No seasonal differences were observed for mean  $\delta^{13}\text{C}$  values of baboon feces from the Waterberg. In Kruger Park, baboon fecal  $\delta^{13}\text{C}$  values were  $\sim 1\text{‰}$  lower in the wet season compared to the dry, but the difference is not significant. Thus, during both seasons, Waterberg baboons consumed an average  $\sim 50\text{--}70\%$  C<sub>3</sub>-based foods, and in Kruger Park they utilized between  $\sim 80\text{--}90\%$  C<sub>3</sub>-foods.

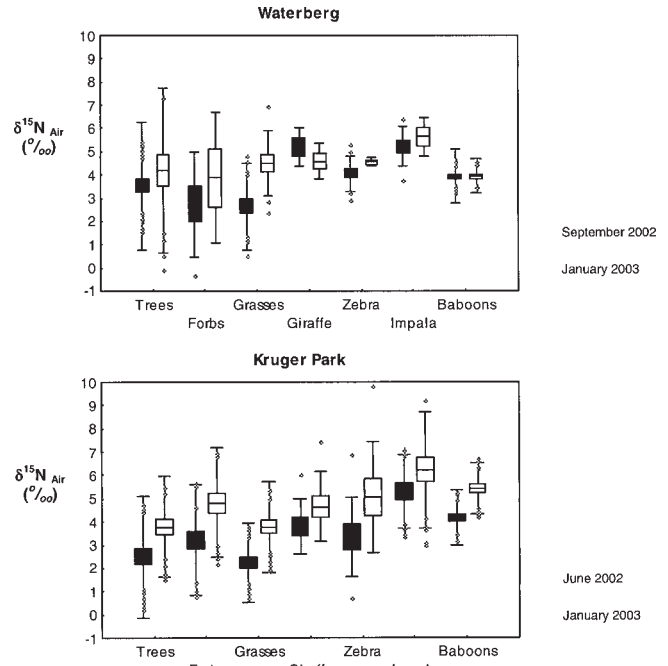
The  $\delta^{15}\text{N}$  values of trees, forbs, and grasses showed an increase of between  $1\text{--}2\text{‰}$  from the dry to the wet season in both reserves (Fig. 3), but the difference is significant only for grasses from Kruger Park ( $P < 0.01$ ). All mammal feces from Kruger Park, including baboons, displayed an



**Fig. 2.** Seasonal comparison of  $\delta^{13}\text{C}$  values of plants and mammal feces in the Waterberg and Kruger National Park. The dry season is represented by September in the Waterberg, and June in Kruger Park, while January represents the wet season. On the graph, the horizontal lines denote the mean values, the box widths indicate standard error from the mean, whiskers the standard deviation, and circles represent outliers.

increase of  $\sim 1\%$  ( $\sim 1.5\%$  for zebras) in mean  $\delta^{15}\text{N}$  values from the dry to wet season, as observed in plants (Fig. 3). In the case of baboon feces from Kruger Park, the difference in mean  $\delta^{15}\text{N}$  values between June (mean =  $4.2 \pm 1.2\%$ ,  $n = 50$ ) and January (mean =  $5.4 \pm 1.1\%$ ,  $n = 36$ ) is significant ( $P < 0.01$ ). Zebra and impala feces from the Waterberg had  $\delta^{15}\text{N}$  values  $\sim 0.5\%$  higher in January compared to September, but giraffe feces from January were  $\sim 0.5\%$  lower in January than September. Baboon feces collected from the Waterberg during different months did not differ in  $\delta^{15}\text{N}$  values (mean =  $3.9 \pm 1.2\%$ ,  $n = 126$  for September; mean =  $3.9 \pm 0.7\%$ ,  $n = 59$  for January).

Percentage N of all plants showed an increase from the dry to the wet season in both regions (Fig. 4). This change was significant for all plant groups, except for grasses from the Waterberg ( $P < 0.001$  for Waterberg trees;  $P < 0.001$  for Kruger Park trees;  $P < 0.01$  for Waterberg forbs;  $P < 0.0001$  for Kruger Park forbs;  $P < 0.001$  for Kruger Park grasses). Mammal feces also displayed a general increase in N content from dry to wet season (significant only for Kruger Park baboons,  $P < 0.0001$ ), with two exceptions. Giraffes in Kruger Park exhibited a decrease in fecal %N from June to January, even though available browse %N increased during this period. Baboon feces in the Waterberg were lower in N during January than during September (mean =  $2.7 \pm 0.7\%$ ,  $n = 126$  for September; mean =  $2.3 \pm 0.5\%$ ,  $n = 159$  for January).

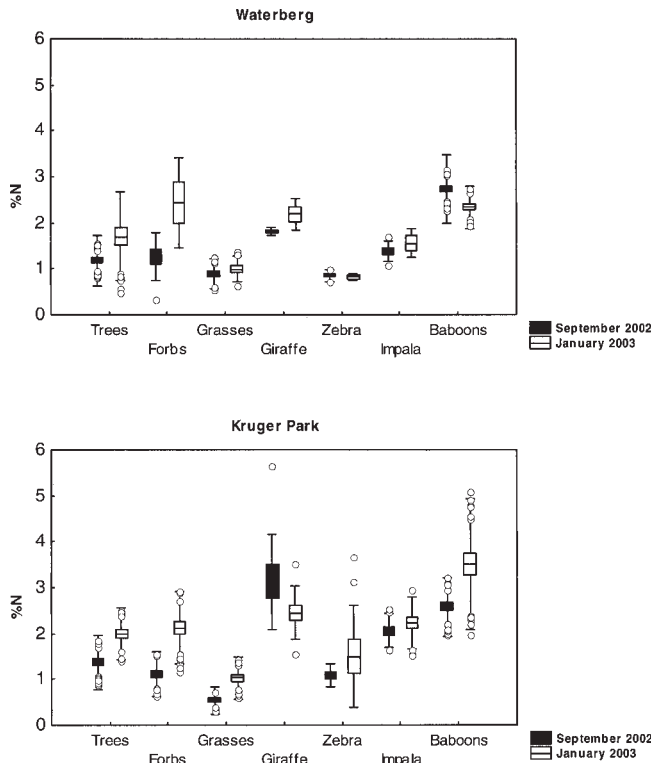


**Fig. 3.** Seasonal comparison of  $\delta^{15}\text{N}$  values of plants and mammal feces in the Waterberg and Kruger National Park. The dry season is represented by September in the Waterberg, and June in Kruger Park, while January represents the wet season. On the graph, the horizontal lines denote the mean values, the box widths indicate standard error from the mean, whiskers the standard deviation, and circles represent outliers.

**DISCUSSION**

Data show that expected trends for  $\delta^{13}\text{C}$  values and percentage N are apparent in the study areas.  $\delta^{13}\text{C}$  values of  $\text{C}_3$  plants (trees and forbs) are distinct from  $\text{C}_4$  plants (grasses), and fecal  $\delta^{13}\text{C}$  values of browsing giraffe and grazing zebra reflect  $\text{C}_3$ - and  $\text{C}_4$ -dominated diets, respectively. Impala fecal  $\delta^{13}\text{C}$  reflects the diet of a mixed feeder. Percentage N (reflecting crude protein content) of available browse was higher than that for grasses, and plants displayed higher N content during the wet season in both regions (Boutton et al., 1988). Mammal fecal N content mirrored the trends observed in plants, with browsing giraffe having the highest %N, grazing zebra the lowest, and impala intermediate (Grant et al., 2000; Sponheimer et al., 2003c). Seasonally, fecal %N followed changes in plants, showing a general dry to wet season increase. These data provide a baseline for interpreting data from baboon feces within the context of sympatric plant and herbivore communities.

Previous studies of baboon diet, especially those using direct observations, focused mainly on plant forms (e.g., trees, shrubs, or forbs) or plant parts (e.g., leaves, fruits, flowers, or roots) utilized (e.g., Dunbar and Dunbar, 1974; Barton et al., 1993; Byrne et al., 1993). To compare our results with those of other studies, we converted data from the literature to represent average percent  $\text{C}_3$ ,  $\text{C}_4$ , or CAM plants consumed (Table 5). We assumed that all trees, shrubs, and forbs in the respective study areas were  $\text{C}_3$  (as well as items such as fruits and flowers), grasses were  $\text{C}_4$ , and succulents (e.g., *Euphorbia* spp. and *Aloe* spp.) were CAM. Moolman and Breytenbach (1976)



**Fig. 4.** Seasonal comparison of %N of plants and mammal feces in the Waterberg and Kruger National Park. The dry season is represented by September in the Waterberg, and June in Kruger Park, while January represents the wet season. On the graph, the horizontal lines denote the mean values, the box widths indicate standard error from the mean, whiskers the standard deviation, and circles represent outliers.

reported diet in terms of proportions of dicots to monocots. For our purposes, we took dicots to represent  $C_3$  plants, and monocots  $C_4$  grasses. Sedges may be either  $C_3$  or  $C_4$  (Sage et al., 1999), making it difficult to interpret sedge-feeding based on carbon isotopic data alone; thus, reported consumption of sedges was excluded from this comparison.

### Comparison of baboon diets between Waterberg and Kruger Park

$\delta^{13}C$  values of baboon feces reflected significantly different diets between the two study areas. Feces from Kruger Park were heavily  $^{13}C$ -depleted compared to those from the Waterberg. Conversely, giraffe, zebra, and impala did not show significant dietary differences (as reflected by fecal  $\delta^{13}C$ ) between these two study areas.

Baboon feces from Kruger Park had  $\delta^{13}C$  values reflecting  $C_3$ -dominated diets (~80–90%); thus, grasses did not constitute important dietary items on this reserve. Baboons from other savanna environments in both East and southern Africa reportedly consume between ~10–20% grass (Table 5); thus the Kruger population displays similar feeding patterns to general observations for baboons across Africa. However, the higher mean  $\delta^{13}C$  values of baboon feces from the Waterberg suggest a much greater utilization of grasses (~30–50%), likely advocating the presence of some alternative resource not common in

their diets elsewhere. Baboons in Welgevonden were observed feeding on a CAM-photosynthesizing succulent, *Euphorbia ingens*, and feces collected from beneath this tree had a  $^{13}C$ -enriched signal. While grass-feeding may account for some of the  $^{13}C$ -enrichment of baboon feces from the Waterberg, in Welgevonden at least, some proportion of *E. ingens* (and possibly other CAM-photosynthesizing succulent plants) was certainly selected for. *Euphorbia ingens* was reported previously to be an important dietary item for some East African baboon populations (Lock, 1972; Barton et al., 1993). In the Eastern Cape of South Africa, where succulents abound, baboons are often observed feeding on *Euphorbia* spp. (Trollope, personal communication).

Another possibility is that baboons in the Waterberg utilized large amounts of  $C_4$  animal matter, such as grass-feeding insects. Yet, insects are relatively scarce in the Waterberg, especially during the dry season (Burger, personal communication). An analysis of stomach contents of baboons from the Loskop Dam Nature Reserve, also situated in the Limpopo “sourveld,” revealed that insects made up less than 10% of the bulk diet (Moolman and Breytenbach, 1976). Thus, significant levels of faunivory by baboons in the Waterberg seem unlikely. In addition, the low  $\delta^{15}N$  values of baboons compared to other species further indicate that animal matter is not a major component of their diet in either the Waterberg or Kruger Park.

At present, the most likely explanation for the  $^{13}C$ -enrichment of baboons in the Waterberg is that a combination of grasses and CAM-photosynthesizing succulent plants (especially *E. ingens*) contributed significantly to their diets. In Zoetfontein, where baboon feces reflected diets averaging ~80%  $C_3$ , succulents do not appear to have been utilized to any great degree.

The inferred high utilization of succulents in Welgevonden is higher than in previous reports based on observational data (5%, or less, of total foods consumed; Table 5). Why baboons utilize a toxic plant species such as *E. ingens* is unclear, though they appear to be immune to the poisonous effects of this species. In the Waterberg, baboons seem to feed on this plant as a dietary supplement in an otherwise homogeneous landscape. Barton et al. (1993) presented phytochemical data for *Euphorbia* from Laikipia, Kenya, where the plant comprised 5.2% of total forage time for baboons. The nutritive quality (protein/fiber + tannin) ratio) of these plants was reportedly lower than that of other dietary tree species and parts. However, *Euphorbia* does have a high water (89.9% of fresh weight) and lipid (9.0% of dry weight) content. In Welgevonden, water is freely available in the form of seasonal rivers and perennial water from artificial boreholes, and hence it seems unlikely that baboons should turn to such poisonous, thorny plants as *E. ingens* as a water source in this region. Whiten et al. (1991) concluded that lipids are important determinants of diet selection for baboons, especially during winter. Thus, the reportedly high lipid content of *Euphorbia* (Barton et al., 1993) may explain the utilization of this plant.

### Intrahabitat dietary variations

Within the respective study areas, baboon fecal  $\delta^{13}C$  values reflected almost no spatial differences in diet. Although individuals' diets varied widely (~25–95%  $C_3$  in the Waterberg and ~60–100%  $C_3$  in Kruger Park), no differences, apart from the  $^{13}C$ -enrichment of the six samples collected at Nalana in Welgevonden, were

TABLE 5. Diet of *Papio* spp. in African savannas, with previously published data converted to represent average percentage  $C_3$  and  $C_4$  consumed (averages are rounded), on premise that all trees, forbs, shrubs, and herbs are  $C_3$ , and all grasses are  $C_4$ <sup>1</sup>

| Method of analysis           | Region                             | % $C_3$ plants | % $C_4$ plants | %CAM plants | % Sedges | % Animal matter | Reference                      |
|------------------------------|------------------------------------|----------------|----------------|-------------|----------|-----------------|--------------------------------|
| Forage time                  | Bole Valley, Ethiopia              | 70             | 23             | 3.0         |          |                 | Dunbar and Dunbar (1974)       |
|                              | Laikipia Plateau, Kenya            | 58             | 23             | 5.0         | 14.0     |                 | Barton et al. (1993)           |
|                              | Giant's Castle, Kwazulu-Natal, RSA | 84             | 11             | 0.3         | 0.3      | 4               | Byrne et al. (1993)            |
| Stomach content              | Loskop Dam NR, Limpopo, RSA        | 81             | 11             |             |          | 8               | Moolman and Breytenbach (1976) |
| Bone collagen $\delta^{13}C$ | Various reserves, Kenya, Tanzania  | 80             | 20             |             |          |                 | Ambrose and DeNiro (1986)      |
|                              | Drakensberg, Kwazulu-Natal, RSA    | 90             | 10             |             |          |                 | Thackeray et al. (1996)        |
|                              | Limpopo, RSA                       | 72             | 18             |             |          |                 | Thackeray et al. (1996)        |

<sup>1</sup> CAM plants are represented by *Aloe* spp. and *Euphorbia* spp. Both sedges and animal matter may be either  $C_3$  or  $C_4$ , and are thus treated separately.

found between mean  $\delta^{13}C$  values of feces collected at various sampling sites within each region. It seems likely that the relatively homogeneous landscapes of the Waterberg result in low intertroop dietary variations. It is also possible, however, that feces sampled from different sleep sites in Welgevonden may be representative of the same troop utilizing more than one sleep site. In Kruger Park, the low level of spatial variation is more surprising, given the diversity of landscapes between our sample sites, ranging from semideciduous woodland to open grassland savanna (Venter and Gertenbach, 1986).

Anderson (1982) argued that baboons living in environments that experience extreme seasonal changes, such as southern Africa, would show correspondingly variable diets. Byrne et al. (1993) found a strong seasonality in the plants eaten by chacma baboons in the Kwazulu-Natal Drakensberg, with the widest range of plants and plant parts being incorporated during the spring months. Our fecal  $\delta^{13}C$  data reflect no seasonal changes in the isotopic composition of baboon diets (and thus in the amounts of grasses and succulents consumed) in the study areas. Similarly, a 5-year study of baboons in Mikumi, Tanzania, revealed very little seasonality in their feeding behavior (Norton et al., 1987). In that study, staple foods did not change throughout the seasonal cycle, and only perimeter food items varied. Thus, our fecal data are consistent with the findings of Norton et al. (1987) for baboons in Mikumi. Carbon isotopic data, however, do not necessarily reflect all dietary changes that may have occurred, since several different plant foods may have similar isotopic compositions. Moreover, we sampled during only small parts of two seasons, and thus our fecal sampling very likely did not capture the full extent of dietary variation in these groups. The study period was also characterized by unusually low rainfall (data from the South African Weather Bureau for 2002 and 2003), possibly resulting in low seasonal changes in primary production, and hence reducing temporal dietary variability in baboons. Thus, while our data indicate no temporal changes in South African chacma diets, these do not necessarily preclude the possibility that baboons may indeed forage for different foods during different seasons.

### Patterns of food selection

Fecal  $\delta^{13}C$  values do not provide insights into dietary variability in terms of plant species utilized, but the carbon isotopic compositions of their diets have implications for understanding patterns of food selection in baboons.

For example, baboon populations throughout Africa reportedly consume varying amounts of grasses, generally dependent on overall grass availability. In East Africa, where savanna grasslands dominate, baboons were observed to consume significant amounts of grass (>20% of bulk diet), whereas grasses seem to make up only about 10% of their diets in southern Africa (Table 5). In an extreme case, East African *Papio* spp. devoted as much as 90% of forage time to grass-feeding (DeVore and Hall, 1965). However, carbon isotopic data for baboon bone collagen from East Africa suggested that  $C_4$  grasses comprise only between ~5–20% of their diet in this region (Ambrose and DeNiro, 1986). This finding of Ambrose and DeNiro (1986) is more consistent with our findings for South African baboons, suggesting that even though baboons (at least in East Africa) may devote much of their foraging time to grass consumption, this resource does not necessarily make a very large contribution (less than 20%) to bulk intake.

Carbon isotopic data for baboon bone collagen from various southern African environments suggest that grass intake is positively correlated with regional grass biomass (Thackeray et al., 1996). Open grasslands abound on the eastern basaltic soils of Kruger Park (Venter and Gertenbach, 1986). The low utilization of grasses in these regions suggests that grass availability does not necessarily lead to increased grass intake by baboons. Indeed, fecal samples collected on basaltic landscapes had  $\delta^{13}C$  values similar to those from the more densely wooded western granites. In the Waterberg, it is difficult to quantify  $C_4$  grass and CAM plant intake from fecal  $\delta^{13}C$  values. Nevertheless, the higher January  $\delta^{13}C$  values of impala feces from this region, as compared to September, may be suggestive of a seasonal change in grass availability. Baboon feces from the Waterberg showed no seasonal changes in  $\delta^{13}C$  values, again indicating that their diets did not vary according to overall grass availability.

A number of authors have concluded that baboons are selective foragers, well-equipped to adapt their feeding behavior in order to obtain maximum nutritional benefit from their immediate environment (e.g., Norton et al., 1987; Barton et al., 1993; Jolly, 2001). Overall, fecal  $\delta^{13}C$  data for baboons agree with this interpretation. Although baboons have flexible diets, varying considerably between the two study areas, the consistency of their feeding patterns within each region suggests selective feeding. The strongest evidence for intense diet selectivity is evinced in the fecal %N data. Baboon feces had consistently higher N levels than zebra, impala, and giraffe, indicating that baboons had higher-quality diets, at least in terms of

crude protein content, than the other savanna species. These data are in accordance with baboons being highly selective feeders in comparison with contemporary savanna herbivores.

Higher fecal %N of baboons in Kruger Park is likely due to greater utilization of N-rich C<sub>3</sub> vegetation in this reserve, whereas C<sub>4</sub> grasses and CAM plants (both relatively low in N content) contributed more heavily to their diets in the Waterberg. Additionally, the higher %N of browse vegetation in Kruger Park certainly contributed to the higher fecal %N of baboons in this region.

As was the case with fecal  $\delta^{13}\text{C}$  values, fecal N content of baboons, although varying widely between individuals, was not significantly different between any of the sampling localities within each region. This low intrahabitat variability advocates selection for a relatively consistent level of crude protein intake throughout each study region. Several authors have argued for selection of foods with high protein/fiber ratios and lipid-rich foods, or selection against plant secondary compounds (Norton et al., 1987; Whiten et al., 1991; Barton et al., 1993). Barton et al. (1993) asserted that because baboons lack the specialized foregut of folivorous colobines, and do not rely on body size to compensate for low dietary quality as gorillas do, they are forced into selecting diets of high quality and low in digestion-inhibiting secondary compounds. Indeed, our data show that, regardless of the items constituting the bulk diet, selective foraging enables baboons to maintain a high level of crude protein intake, at least relative to sympatric savanna ungulate species, in any savanna environment.

### Ecological significance of $\delta^{15}\text{N}$ in baboons

Previous models of  $^{15}\text{N}$ -abundances in mammals relied largely on bone collagen data (e.g., Sealy et al., 1987; Ambrose, 1991). In mammals, urea is  $^{15}\text{N}$ -depleted relative to the diet (Steele and Daniel, 1978). The loss of  $^{15}\text{N}$ -depleted urea leads to greater amounts of  $^{15}\text{N}$  remaining in the body nutrient pool, in turn resulting in body tissues (as well as feces) exhibiting  $\delta^{15}\text{N}$  values higher than that of the diet (Steele and Daniel, 1978; Ambrose, 1991). Feces and bone collagen should thus display similar trends in  $\delta^{15}\text{N}$  values, even though fecal values may be affected by the presence of excreted gut microbes and sloughed endogenous tissues (Sponheimer et al., 2003d). We therefore compared nitrogen isotopic data from feces with the predictions of previous models for  $^{15}\text{N}$ -abundances in mammals based on bone collagen.

$\delta^{15}\text{N}$  values in terrestrial plants and animals are reportedly higher in areas that receive less rainfall, or at least where water is less available (Heaton, 1987; Sealy et al., 1987; Ambrose, 1991; Muzuka, 1999). Indeed, this trend was reported for chacma baboon bone collagen  $\delta^{15}\text{N}$  values across southern Africa, although in very high rainfall areas (<1,000 mm per annum), baboons exhibited low collagen  $\delta^{15}\text{N}$  values (Thackeray et al., 1996). In both regions included in our study, plants and mammal feces (except only giraffe in the Waterberg) had higher  $\delta^{15}\text{N}$  values in the wet season compared to the dry. The urea mass-balance model for nitrogen isotope abundances in mammals proposes that drought-tolerant species (usually browsers) are  $^{15}\text{N}$ -enriched compared to obligate drinkers (grazers) (Ambrose, 1991). We observed no significant differences in  $\delta^{15}\text{N}$  values between zebra and giraffe feces in either of the two study areas, while the highest fecal  $\delta^{15}\text{N}$  values were observed for mixed-feeding impala.

$\delta^{15}\text{N}$  values in animals are generally accepted to show a stepwise enrichment along trophic levels within a food chain (Sealy et al., 1987). Feces from baboons, a noted omnivore, were lower in  $\delta^{15}\text{N}$  than were the herbivorous species in the Waterberg, and the same trend is evident in Kruger Park if feces collected in areas where human foods are utilized are excluded from the analysis. This observation supports our suggestion that baboons in the study areas do not utilize significant proportions of animal matter. However, the absence or at least negligible levels of faunivory do not explain why baboon feces are  $^{15}\text{N}$ -depleted compared to other herbivores.

Ambrose and DeNiro (1986) suggested that low bone collagen  $\delta^{15}\text{N}$  values in baboons from East Africa are due to a high consumption of  $^{15}\text{N}$ -depleted nitrogen-fixing plants, such as *Acacia* spp. and other legumes. However, legumes are not consistently depleted in  $^{15}\text{N}$  compared to other plants (Muzuka, 1999; Schmidt and Stewart, 2003). In both study areas, leguminous trees were  $^{15}\text{N}$ -depleted compared to other trees, but not consistently so. Additionally, many other mammal species (giraffe in this study), which do not display such low fecal  $\delta^{15}\text{N}$  values, also consume high proportions of *Acacia* and other legumes (Skinner and Smithers, 1990).

In the Waterberg, two geophyte corm samples were heavily  $^{15}\text{N}$ -depleted compared to other plants (mean  $\delta^{15}\text{N} = -2.8 \pm 1.5\text{‰}$ ). These data provide evidence that utilization of underground storage organs by baboons in the Waterberg may contribute to low fecal  $\delta^{15}\text{N}$  values. Dental microwear evidence showed that baboons in the Waterberg rely heavily on ground-level and subterranean food items (Daegling and Grine, 1999). However, in Kruger Park, geophytes did not display particularly low  $\delta^{15}\text{N}$  values (mean =  $4.7 \pm 0.9\text{‰}$ , n = 5). Thus, ascribing low  $\delta^{15}\text{N}$  values in baboons to terrestrial foraging is, at best, only partially satisfactory.

Intensive foraging on legumes or subterranean items can at best only partially account for low fecal  $\delta^{15}\text{N}$  values in baboons compared to other mammals. Low levels of faunivory by baboons in the study areas likely result in low  $^{15}\text{N}$ -levels in their feces, but this does not reveal why baboons have even lower fecal  $\delta^{15}\text{N}$  values than contemporary herbivore species. It is possible that rudimentary differences in the digestive physiology of primates and ungulates also play a role, particularly since differential internal pathways of urea-recycling likely influence mammalian  $\delta^{15}\text{N}$  values (Sponheimer et al., 2003d; Sealy et al., 1987). Further information on fecal  $\delta^{15}\text{N}$  values for other primate species will be required to fully test these hypotheses.

### CONCLUSIONS

We examined inter- and intrahabitat variations in chacma baboon (*Papio ursinus*) feeding ecology in the context of sympatric plant and mammal species using  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and %N measured from plants and feces. Baboons had distinctly different diets in two South African savanna habitats, the Waterberg and Kruger Park. In the Waterberg, baboons consumed a large proportion (~35% on average) of C<sub>4</sub> (grasses)- and CAM (succulent plants)-based foods. In Kruger Park, only ~10% of the bulk diet consisted of grasses or CAM plants. Furthermore, baboon diets within Kruger Park did not differ between different savanna landscapes (woodland savanna, mountain bushveld, and open grassland). Baboons also did not vary their diets isotopically in response to season. On present evi-

dence, we cannot reliably predict the environmental mechanisms responsible for  $^{15}\text{N}$  abundances in savanna primates. Comparative analysis of fecal N content revealed that baboons consistently consume foods of greater nutritional value, at least in terms of crude protein content, than do sympatric ungulates.

Overall, these data indicate that chacma baboons are highly selective feeders, concentrating largely on protein-rich foods. Nevertheless, they are capable of selecting different types of foods to optimize nutritional uptake in different savanna landscapes.

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