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# DIET OF THE COMMON WARTHOG (*PHACOCHOERUS AFRICANUS*) ON FORMER CATTLE GROUNDS IN A TANZANIAN SAVANNA

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In otherwise nutrient-poor savannas, fertile vegetation patches are particularly attractive to ungulates because of the higher-quality food they provide. We investigated forage plants and diet of the common warthog (*Phacochoerus africanus*) on an abandoned cattle ranch in coastal Tanzania. The forage grasses of highest nutritional quality occurred in former paddock enclosures (bomas) where cattle had been herded at night. In the dry season, grass samples from bomas contained approximately 4 times as much nitrogen and phosphorus as those of the surrounding vegetation. $\delta^{15}N$ values of soil and plants also were highest in bomas and decreased significantly with distance, and high $\delta^{15}N$ values in feces suggest that warthogs preferentially fed in the vicinity of the former bomas. $\delta^{13}C$ values of warthog feces indicate that warthogs ingested on average 83% (77–98%) $C_4$ grasses, with this proportion varying regionally but not seasonally. We conclude that, for medium-sized selective grazers such as warthogs, bomas represent attractive feeding grounds. We also hypothesize that by promoting nutrient turnover in these patchily distributed areas, grazing animals help to maintain them as sources of high-quality forage.

Key words: African savanna, isotopic analyses, livestock, medium-sized grazer, nitrogen, phosphorus

Understanding the nutritional status of plants and animals is essential for wildlife population and habitat management (van der Waal et al. 2003). Compared to dicotyledons and $C_3$ grasses, the dominant $C_4$ grasses of tropical savannas are nutrient-poor, and also vary in nutritional quality both seasonally and between sites (Owen-Smith 1982). Thus, to meet their nutritional requirements, small ungulates must be very selective in their diet (Murray 1993; Wilmshurst et al. 1999). For this reason, some East African grazers undertake long-distance migrations (Dörgeloh et al. 1998), following flushes of new grass growth triggered by rainfall (Durant et al. 1988; Mduma et al. 1999).

The common warthog (*Phacochoerus africanus*) is a medium-sized, nonmigratory ungulate. It is a hindgut fermenter with significant microbial fermentation in parts of the digestive tract (Boomker and Booyse 2003). Warthogs are predominantly grazers and depend on high-quality food. Their wide distribution in African savanna ecosystems can partly be explained by their dietary flexibility (Estes 1991; Kingdon 1997; Rodgers 1984).

The nutrient content of grass depends on rainfall and on the availability of macro- and micronutrients in the soil (Olff et al. 2002). Feedback loops from ungulates to plants, with plant nutrient uptake being stimulated by grazing, can lead to increases in both forage biomass and quality, and thereby in nutrient turnover rates (de Mazancourt and Loreau 2000; Georgiadis et al. 1989). Such facilitation effects (Arsenault and Owen-Smith 2002) are evident in "grazing lawns," where concentrated grazing maintains a high productivity of protein-rich vegetation (McNaughton et al. 1997). Similar nutrient enrichment also can be observed in areas receiving high inputs of excreta from domestic livestock (Augustine 2003).

We studied the diet of warthogs on a former ranch in Tanzania recently abandoned after 50 years of intensive use (Treydte et al. 2005). Warthogs were most abundant around former paddock enclosures (bomas) where cattle had been kept at night (Treydte 2004), and we hypothesized that nutrient enrichment made these areas particularly attractive to recolonizing wildlife. We chose to study the warthog not only because it was one of the most common animals in the area but

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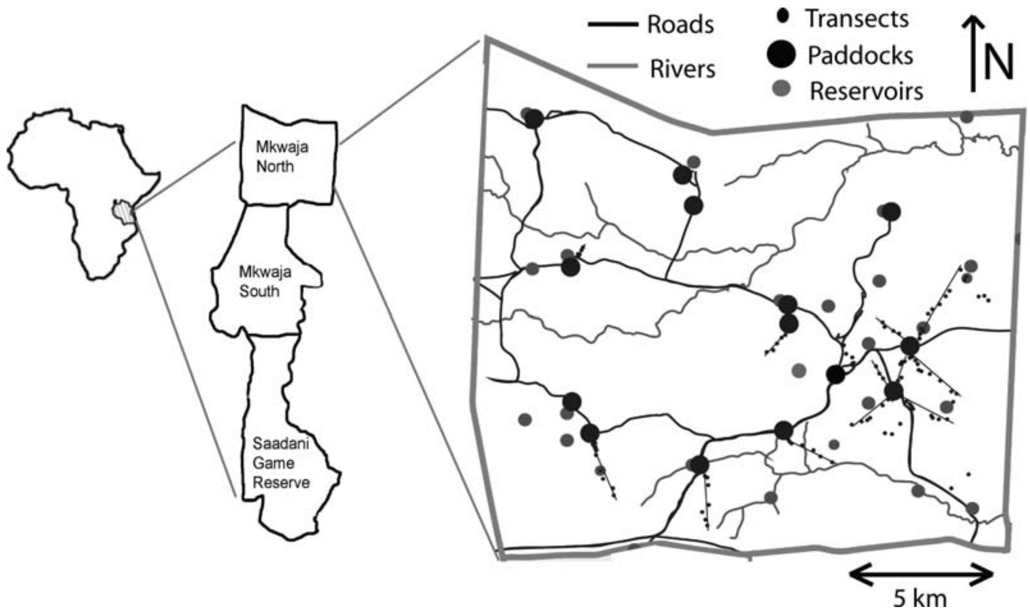


**Fig. 1.**—Study site, Mkwaja North (250 km$^2$), Tanzania, which had been a cattle ranch from 1954 to 2000. Mkwaja South and the former Saadani Game Reserve are adjacent to the south.

also because it leaves numerous signs of its presence, such as feces, scrapings, hoofprints, and rooting-sites; hence, its distribution and habitat preferences could be readily assessed. We had 4 specific hypotheses to be tested. First, grasses and forbs (herb and legume species) in formerly fenced paddock centers (bomas) and, to a lesser extent, in paddock margins show higher nutrient contents than the same species in the surrounding vegetation. Second, any decline in grass nutrient quality during drought periods is less severe in paddock areas than in the surrounding vegetation. Third, warthogs select their food to maximize nutrient intake, that is, crude protein and phosphorus (P). Fourth, for this reason animals feed preferentially in the nutrient-rich boma areas.

Obtaining detailed information about wild herbivore diet is difficult if feeding animals cannot be observed directly. However, indirect observations based on fecal analyses can deliver a wealth of information about diet. Thus, microhistological studies of plant fragments can reveal which plant species are consumed (Stewart 1967), whereas inferences about possible nutrient deficiencies can be made from fecal nutrient content (e.g., nitrogen [N] and P). Fecal ash content can provide information on the amount of soil ingested and thus about the relative importance of grazing and rooting. Also, because $C_3$ and $C_4$ plants discriminate differently between the C isotopes—and because most savanna grasses are $C_4$ plants—the isotope ratio $^{13}C/^{12}C$ ($\delta^{13}C$) of fecal material reveals the relative proportions of these metabolic types in the diet (Lajtha and Michener 1994; Sponheimer et al. 2003). Finally, the plant N isotope ratio $^{15}N/^{14}N$ ($\delta^{15}N$) can be used to indicate spatial differences in soil and plant resources (Högberg 1997). Here we used all of these techniques to study warthog diet in relation to soil nutrient conditions and plant nutritional quality at different distances from paddock centers and at different times of year. Examination of the data on diet, preferred feeding sites, and nutritional status of warthogs allowed us to draw conclusions about the importance of the former bomas for wildlife. Our results have implications for wildlife management and we discuss the potential long-term persistence of nutrient-enriched areas on former cattle pastures.

## Materials and Methods

*Study area.*—Mkwaja Ranch (5°43′S, 38°47′E), established in 1954, occupies approximately 480 km$^2$ of coastal savanna and forest north of the former Saadani Game Reserve in northeastern Tanzania. Until it was abandoned in 2000, up to 13,000 cattle were kept on the ranch. It has now been incorporated into Tanzania's 13th national park together with the adjacent Saadani Game Reserve (Tanzania National Parks 2002). The mean annual temperature is 25°C; annual rainfall has varied between 500 and 1,700 mm over the last 50 years with a mean of 900 mm (Tobler et al. 2003). There are 2 rainy seasons, one with little rain from October to December and one with high rainfall from March until May. September and February tend to be the driest months.

Until the ranch was established, the region was a mosaic of open savanna and coastal forest. Long-term vegetation monitoring started in the 1970s in response to increasing bush encroachment caused by high cattle densities (Klötzli 1995; Tobler et al. 2003). In 2001, when all remaining cattle were removed and measures to control illegal poaching were introduced, the area was available for recolonization by wildlife.

During operation of the ranch, the northern part (Mkwaja North, 250 km$^2$), was divided into 14 paddocks, and more than 20 reservoirs were built to provide water for cattle (Fig. 1). Up to 1,500 cattle were herded in the fenced core (boma) of each paddock at night, whereas herdsmen let the cattle graze away from bomas during the day. These paddock centers were barely covered with vegetation and their surroundings were modified by the effects of trampling, grazing, and excreta. With increasing distance from the boma, the impact of livestock declined.

*Vegetation types.*—We recognized 4 vegetation zones along a transect running from a paddock into the unmodified savanna (Treydte 2004). First, after the last cattle were removed, the former bomas or paddock centers remained very distinct from the surrounding vegetation and soon developed a dense cover of short stoloniferous grasses, mainly *Cynodon dactylon*, *Paspalum*, and *Brachiaria*. Second, the paddock margins, comprising the immediate surroundings of the paddock centers, consisted of heavily modified savanna vegetation in which invasive weeds such as *Agathisanthemum bojeri* were abundant. Third, the *Acacia* scrub zone usually commenced about 1,000 m from the paddock and was dominated by tree species such as *Acacia zanzibarica*, *Dichrostachys cinerea*, and *Terminalia spinosa*. Fourth, the least impacted or "unmodified" savanna was typically $\geq$2 km away from a paddock and contained tall grasses such as *Heteropogon contortus*, *Diheteropogon amplectens*, and *Echinochloa haploclada*. We also studied a savanna area south of Mkwaja Ranch in the neighboring Saadani Game Reserve. There has been no recent cattle grazing in this area but it supports large populations of several wildlife species including warthog.

The $C_4$ grasses *C. dactylon* and *Paspalum dilatatum* were the most abundant species in paddock centers, where they were more common than in any other zone. Prominent grasses in the other vegetation zones outside of the paddock center and in the game reserve included *Digitaria milanjiana*, *Eragrostis superba*, *Aristida adscensoris*, *H. contortus*, and *Panicum infestum* (Tobler et al. 2003). Taller grass species (>100 cm) such as *D. amplectens*, *H. contortus*, *Themeda triandra*, *Sporobolus pyramidalis*, *Cymbopogon caesius*, and *E. haploclada* (Klötzli 1995) increased with distance from the paddock center.

Vegetation in the game reserve was dominated by grasses, and cover by trees, bushes, and forbs was less than 10% each (Treydte 2004). The average height of the grass layer was 21 cm $\pm$ 4 *SE*. Abundant species included the grasses *P. infestum*, *E. superba*, *Andropogon gayanus*, *E. haploclada*, *C. caesius*, and the sedge *Fimbristylis triflora*.

*Plant, soil, and fecal sampling*.—Vegetation and feces were sampled on Mkwaja Ranch in each of the 4 vegetation zones described above. In a previous study of warthog habitat use we had established 116 plots of 300 $m^2$ each in and around 7 paddock systems (Treydte 2004). For the plant and soil sampling we selected 3 of these paddocks; these included 27 plots, 10 of which were located in paddock centers, 7 in paddock margins, 3 in *Acacia* scrub, and 7 in the surrounding unmodified savanna. To allow comparison with savanna unaffected by cattle, we also selected 11 plots in the Saadani Game Reserve in areas where we knew warthogs to be present.

We sampled the dominant grass and herb species in the 5 zones and also a few less-abundant plant species reported to be important in the diet of warthog (Cumming 1975; Field 1970; Kingdon 1997; Rodgers 1984). Plant material was collected monthly from May until September 2002, starting immediately after the long rainy season, and in February 2003, the driest month of the year. At least 2 individuals per species were collected in each plot. The material sampled included roots or rhizomes, stems, and leaves. Soil samples (0–10 cm) were taken from 4 different plots per vegetation zone.

During a 6-month period we collected warthog feces from 71 of the 116 plots in 7 paddock systems; 21 of these were in the paddock center, 18 in paddock margins, 8 in *Acacia* scrub, 12 in the surrounding vegetation, and 12 plots in the game reserve. From each fecal pellet group at least 3 pellets were stored in a paper bag. Only samples estimated to be <2 weeks old were collected (based on previous observations of the disappearance rate of warthog feces—Irwin et al. 1993; Treydte 2004). Additionally, 3 warthog bone samples found in the study area were collected and their stable isotope ratios were investigated.

*Plant, soil, and feces analyses*.—All plant, soil, and fecal samples were oven-dried at 70°C for 24 h. The microhistological method of determining diet from feces (Putman 1984; Stewart 1967) is based upon differences among plant species in the shape and arrangement of epidermal cells (Barthlott and Martens 1979; Liversidge 1970). We compiled a reference collection of the 30 most common grass species in our study area. Their epidermal layers—both abaxial and adaxial leaf sides—were separated by maceration, and reference slides were prepared and photographed (Stewart 1967). Fecal samples were prepared according to Stewart (1967) and de Jong et al. (1995). To reduce the samples to a manageable number, material was pooled within vegetation zones. Thus, 12 composite fecal samples were analyzed, including 2 in the paddock centers (in February 2003), 4 in paddock margins (1 in July 2002 and 3 in February 2003), and 6 in the surrounding vegetation (3 in July 2002 and 3 in February 2003). The material was examined under a microscope, using a $10 \times 10$-$mm^2$ grid for counting and measuring epidermal fragments (Putman 1984).

Plant samples for nutrient and isotopic analyses were milled using a Cyclotech 1093 sample mill (Cyclotech, Höganäs, Sweden), and soil samples were ground in a mortar. The Kjeldahl method (Bradstreet 1965) was used to digest subsamples of plant, soil, and fecal material, and total N and P contents were then determined in a FIAstar 5000 flow-injection analyzer (Foss Tecator, Höganäs, Sweden). Further subsamples were ignited in a muffle furnace at 600°C for 4 h to determine their ash contents (Vogtmann et al. 1975).

Nitrogen and carbon (C) isotope compositions of plant, soil, and feces samples were determined using a Carlo-Erba elemental analyzer (NCS 2500; Carlo-Erba, Milan, Italy) coupled in continuous flow to a MICROMASS-Optima ion ratio mass spectrometer (IRMS; Micromass, Manchester, United Kingdom). Sample material was ignited in the presence of $O_2$ in an oxidation column at 1,030°C, combustion gases were passed through a reduction column (650°C), and $N_2$ and $CO_2$ gases were separated chromatographically and transferred to the IRMS via an open split for on-line isotope measurements. Isotope ratios are reported in the conventional notation with respect to atmospheric $N_2$ (AIR) and Vienna Pee Dee Belemnite standards, respectively. The methods were calibrated with standards from the International Atomic Energy Agency, IAEA-N1 and IAEA-N2, for $\delta^{15}N$ values and from the National Bureau of Standards, NBS22, for $\delta^{13}C$ values. Reproducibility of the measurements was better than 0.2‰ for both N and C.

*Data analysis*.—Data on N, P, and ash contents of plants, feces, and soils are presented as total dry matter percentages. Crude protein content was calculated as N $\times$ 6.25 (Association of Official Analytical Chemists 1980); to keep units identical, results are presented as N in tables and figures. $\delta^{13}C$ data did not fit a normal distribution and were log-transformed. The significance of variation in nutrient concentrations and stable isotope ratios among vegetation zones was tested using 1- and 2-way analysis of variance (ANOVA) and paired *t*-tests followed by a post hoc Bonferroni test (Sokal and Rohlf 1995). Because variation among paddock systems was not significant the data were pooled for multiple comparisons among means between vegetation zones and for seasonal differences. The statistical software JMP for Mac OX (SAS Institute Inc. 2002) was used for all analyses. Values are presented as mean $\pm$ *SE*.

## Results

*Diet based on microhistological analyses*.—From the leaf cuticle fragments in feces we identified 63 plant taxa to the level of species or genus or, in case of Cyperaceae, to family. We distinguished fragments of root and rhizome material, which made up 5% of all fragments, ranging from 1% to 8%, with highest amounts found in paddock margin and surround-

**Table 1.**—Cuticular plant fragments in warthog feces from Mkwaja Ranch, Tanzania. Numbers represent the size of all fragments summed as a percentage of the entire fragment surface encountered in each fecal sample from 3 vegetational zones (paddock center, paddock margin, and surrounding vegetation). Dry season = February 2003, Wet season = July 2002. Only fragments that accounted for ≥0.3% in the fecal sample are shown.

| | Dry season | | | Wet season | | |
|---|---|---|---|---|---|---|
| | Paddock center | Paddock margin | Surrounding vegetation | Paddock center | Paddock margin | Surrounding vegetation |
| *Andropogon gayanus* | 0.1 | 0 | 0 | 0 | 0.7 | 5.1 |
| *Brachiaria* | 2.6 | 11.5 | 9.7 | 11.2 | 1.9 | 16.8 |
| *Cynodon dactylon*, *Chloris gayana* | 8.6 | 12.7 | 0.9 | 11.4 | 6.6 | 3.3 |
| Cyperaceae | 4.1 | 17.7 | 21.1 | 0 | 4.2 | 4.8 |
| *Diheteropogon amplectens* | 0 | 1.7 | 2.1 | 0.1 | 0.9 | 1.6 |
| *Echinochloa haploclada* | 0 | 2.4 | 12.7 | 0.8 | 1.7 | 2.0 |
| *Eragrostis* | 16.0 | 8.1 | 5.5 | 37.0 | 15.0 | 17.5 |
| *Heteropogon contortus* | 0.1 | 0 | 0 | 0 | 0 | 1.4 |
| *Leersia hexandra* | 0 | 0.4 | 0 | 2.7 | 1.7 | 1.2 |
| *Panicum* | 0.3 | 8.9 | 0.5 | 0 | 1.7 | 2.6 |
| *Paspalum dilatatum* | 0.9 | 1.3 | 0 | 1.7 | 5.9 | 5.5 |
| *Sporobolus pyramidalis* | 0.9 | 0.3 | 3.1 | 0 | 1.2 | 0.4 |
| *Themeda triandra* | 0 | 0 | 0 | 1.3 | 0.5 | 2.9 |
| Other species | 3.6 | 3.0 | 2.1 | 2.5 | 4.6 | 1.3 |
| Unidentified | 43.5 | 18.0 | 22.0 | 20.6 | 41.4 | 20.7 |
| Roots, rhizomes | 1.9 | 5.3 | 6.8 | 1.3 | 7.9 | 4.9 |
| Stems | 16.4 | 7.8 | 8.2 | 8.3 | 3.6 | 5.0 |

ing vegetation samples (Table 1). Leaf cuticle of grasses and Cyperaceae accounted for a mean of 58% and stems for a further 8% of recorded fragments. This left a mean of 28% of mainly leaf cuticle fragments that could not be identified. An average of 21 grass and sedge species was recorded per fecal samples, with no marked seasonal variation in this number. With a mean of 17% of fragments, *Eragrostis* was the most abundant taxon overall, and was especially common in paddock center samples. *C. dactylon* and *Chloris gayana* cuticle (these species could not be distinguished), both being more abundant close to the center, accounted for 7% of fragments. *Brachiaria* accounted for 9% of fragments. Cyperaceae cuticle also represented 9% of fragments, but there was wide variation among samples; it was more common in the dry season (14%) than in the wet (3%), and was notably scarce in paddock center samples at all times. We found very few dicotyledonous plant fragments and no insect remains.

*Ash and nutrients in soil and plants.*—The average ash content in plant samples was 9.8% ± 1.3%. Crude protein and P contents varied considerably among species and also according to the plant part sampled (Table 2). The highest P contents measured in shoots (i.e., leaves and stems) were in 2

**Table 2.**—Phosphorus, nitrogen, and carbon contents (as percentage dry weight; mean ± *SE*) of plants, soil, and feces on Mkwaja Ranch, Tanzania. Plant parts were analyzed separately as shoots (leaves and stems), and roots.

| | Phosphorus | | Nitrogen | | Carbon |
|---|---|---|---|---|---|
| | Shoots | Roots | Shoots | Roots | Shoots |
| *Andropogon gayanus* | 0.04 | 0.03 | 0.8 | 0.5 | 42.3 ± 0.9 |
| *Brachiaria leucacrantha* | 0.08 ±0.04 | 0.14 | 0.4 ±0.1 | 0.4 | 38.4 ±1.5 |
| *Chloris gayana* | | | 1.6 | | 42.4 |
| *Cymbopogon caesius* | 0.04 ± 0.004 | 0.03 ± 0.003 | 0.5 ± 0.1 | 0.5 ± 0.1 | 41.3 ± 0.5 |
| *Cynodon dactylon* | 0.23 ± 0.02 | 0.12 ± 0.03 | 1.0 ± 0.2 | 0.8 ± 0.3 | 40.9 ± 0.6 |
| Seedheads | 0.41 | | 2.4 | | |
| *Dactyloctenium aegypticum* | 0.05 ± 0.01 | 0.05 ± 0.002 | 0.6 ± 0.1 | 0.7 ± 0.1 | 41.9 |
| *Digitaria milanjiana* | 0.10 ± 0.02 | 0.07 ± 0.01 | 0.5 ± 0.1 | 0.6 ± 0.1 | 37.8 ± 0.9 |
| *Echinochloa haploclada* | 0.05 | 0.03 | 1.0 | 0.7 | 32.2 ± 5.3 |
| *Eragrostis superba* | 0.14 ± 0.02 | 0.08 ± 0.01 | 0.6 ± 0.1 | 0.5 ± 0.1 | 36.1 ± 1.4 |
| *Fimbristylis triflora* | 0.06 ± 0.01 | 0.07 ± 0.01 | 0.6 ± 0.1 | 0.5 ± 0.1 | 39.0 ± 1.1 |
| *Panicum infestum* | 0.14 ± 0.02 | 0.08 ± 0.01 | 0.7 ± 0.1 | 0.6 ± 0.1 | 39.5 ± 1.0 |
| *Paspalum dilatatum* | 0.18 ± 0.04 | 0.10 ± 0.03 | 1.1 ± 0.2 | 1.2 ± 0.2 | 40.3 ± 3.2 |
| Cyperaceae | 0.06 ± 0.01 | 0.11 ± 0.02 | 0.6 ± 0.2 | 0.5 ± 0.1 | 42.8 ± 0.04 |
| Leguminosae | 0.11 ± 0.03 | 0.07 ± 0.02 | 1.4 ± 0.3 | 1.1 ± 0.5 | 42.7 ± 0.09 |
| *Agathisanthemum bojeri* | 0.07 ± 0.01 | 0.05 ± 0.01 | 1.0 ± 0.1 | 0.6 ± 0.1 | 42.1 ± 1.1 |
| Soil | 0.04 ± 0.01 | | 0.2 ± 0.1 | | 1.2 ± 0.3 |
| Feces | 0.27 ± 0.03 | | 1.5 ± 0.1 | | 38.5 ± 1.3 |

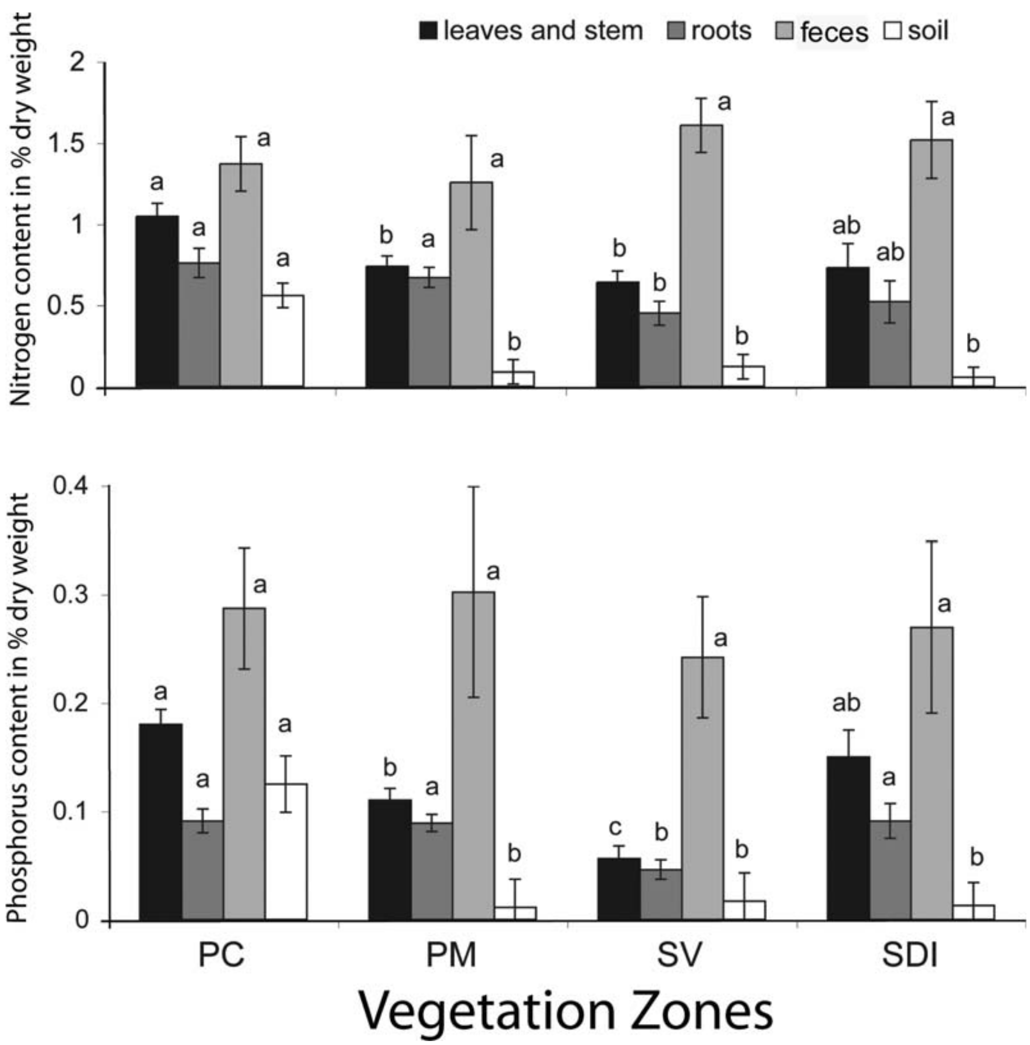


**FIG. 2.**—Nutrient content (± 1 *SE*) in plants, feces, and soil within 4 vegetation zones on Mkwaja Ranch, Tanzania. Columns with different letters indicate significant differences between vegetation zones (post hoc Bonferroni test). Zones are described in text: PC = paddock center, PM = paddock margin, SV = surrounding vegetation, and SDI = Saadani Game Reserve plots where direct observations of foraging warthogs were possible.

grasses, *C. dactylon* and *P. dilatatum*, that occurred mainly in the paddock center; P concentrations of *P. infestum* and *E. superba* also were high. The highest shoot crude protein contents were found in Leguminosae, although various grasses (*A. gayanus*, *C. dactylon*, *E. haploclada*, and *P. dilatatum*) also contained >5% crude protein. However, by far the highest crude protein and P concentrations were measured were in the seedheads of *C. dactylon* (15.0% crude protein; 0.41% P).

The mean concentrations of crude protein and P in shoots (pooled for all plant species) were twice as high in paddock centers as in the surrounding vegetation (for crude protein, $F = 4.1$, *d.f.* = 3, 126, $P = 0.008$; for P, $F = 16.6$, *d.f.* = 3, 126, $P < 0.0001$; Fig. 2), and roots showed a similar trend (for crude protein, $F = 2.5$, *d.f.* = 3, 64, $P = 0.07$; for P, $F = 7.6$, *d.f.* = 3, 64, $P = 0.0002$). Most species, including 3 important fodder species of the warthog (*D. milanjiana*, *E. superba*, and *P. infestum*) contained significantly more P in paddock centers and margins than in the surrounding vegetation (Fig. 3). Soil nutrient contents in paddock centers were more than 3 times that of the other zones (for N, $F = 12.1$, *d.f.* = 4, 19, $P < 0.0001$; for P, $F = 7.7$, *d.f.* = 4, 19, $P = 0.001$).

Crude protein contents in both grass roots and shoots (pooled for all species) varied seasonally (ANOVA: $F = 4.7$, *d.f.* = 5, 188, $P = 0.0005$), with the lowest concentrations being measured in February 2003 (dry season). For 3 species (*D. milanjiana*, *F. triflora*, and *P. dilatatum*), this seasonal variation was significant ($P < 0.02$); similar but not significant trends of reduced crude protein during dry periods also were evident in *P. infestum*, *E. superba*, and *C. dactylon*. In the latter species, mostly confined to paddocks, the crude protein content remained about 4 times higher than that of any other grass species even in the driest month (February 2003).

*Ash and nutrients in feces.*—The average crude ash content of warthog feces was 26.2% ± 11.6% but some samples contained >50% total ash (data not shown). Fecal ash contents in paddock centers and margins were 10% lower than in the surrounding vegetation and in the game reserve ($F = 2.4$, *d.f.* = 4, 93, $P = 0.06$) but did not differ significantly between

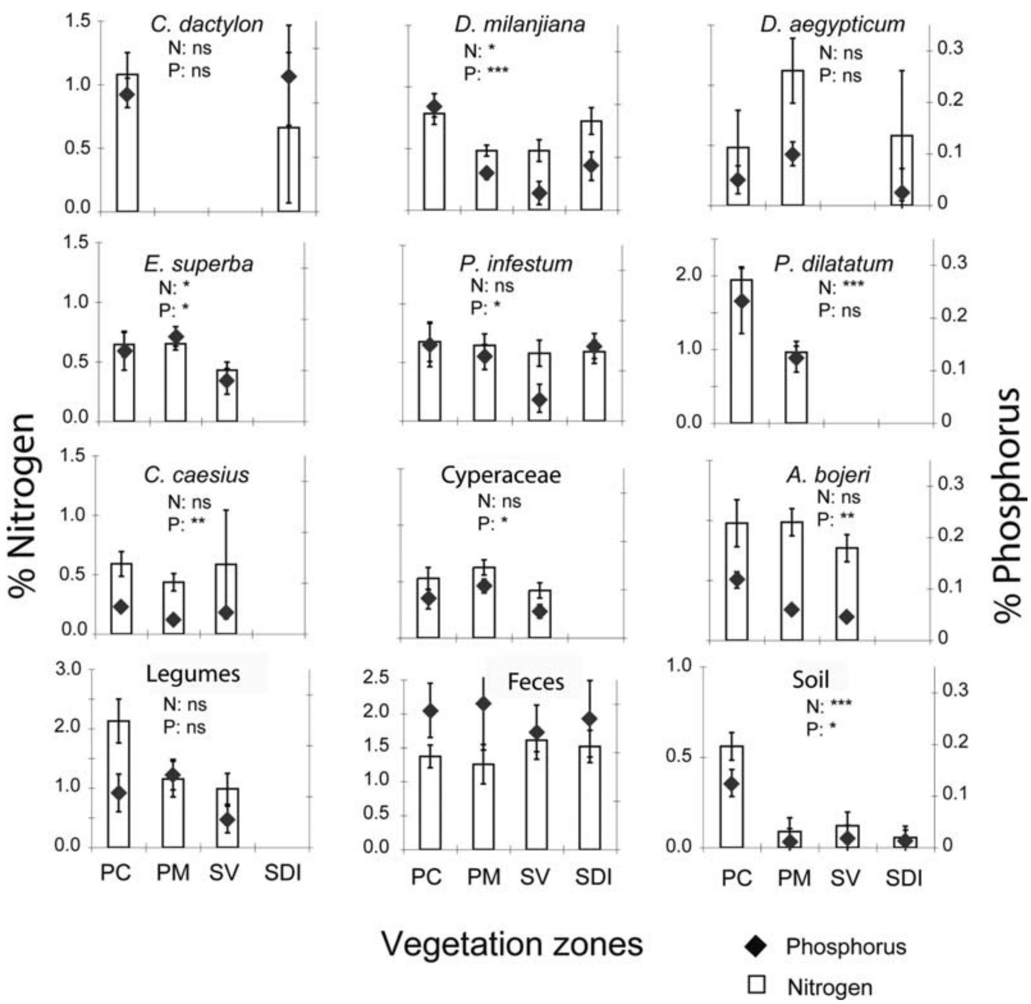


**FIG. 3.**—Nitrogen (N) and phosphorus (P) contents (± 1 *SE*) in plants, soil, and feces across 4 vegetation zones on Mkwaja Ranch, Tanzania. PC = paddock center, PM = paddock margin, SV = surrounding vegetation, and SDI = Saadani Game Reserve plots where direct observations of foraging warthogs were possible. Significant differences between zones are indicated by ns, nonsignificant; *, $P < 0.05$; **, $P < 0.01$; or ***, $P < 0.001$ (post hoc Bonferroni test). Note the different y-axis scale for *Paspalum dilatatum*, legumes, feces, and soil. Full names of plants are given in the text.

seasons. The mean fecal P and N contents were 0.28% ± 0.03% and 1.5% ± 0.1%, respectively, with no significant variation among vegetation zones (Fig. 2).

*Stable C isotope ratios.*—The overall mean $\delta^{13}C$ of grasses was −12.8‰ ± 0.1‰, with values varying significantly among species ($F = 6.4$, $d.f. = 18, 147$, $P < 0.0001$; Table 3). There was no significant variation in the $\delta^{13}C$ of grasses (all species combined) among vegetation zones ($F = 1.4$, $d.f. = 4, 147$, $P = 0.3$) but there was seasonal variation, with slightly higher values from June to September 2002 than in February 2003 ($F = 3.56$, $d.f. = 5, 109$, $P = 0.005$).

The $\delta^{13}C$ values of individual fecal samples ranged from −11.9‰ to −24.1‰, with a mean of −15.0‰ ± 0.3‰. The frequency distribution of these values showed 2 peaks, a large one at −13.5‰ and a smaller one at −19.5‰ (Fig. 4). Using the average $\delta^{13}C$ values of grasses (−12.8‰ ± 0.1‰) and forbs (−26.4‰ ± 1.0‰) as reference points, we calculated that the average percentage of $C_4$ grasses in the diet was 83.5% (99% confidence interval between 79.2% and 89.0%). However, there was some variation among zones; the diet consisted of 97.6% $C_4$ grasses in the game reserve, but only 76.9% in the paddock margins ($F = 2.6$, $d.f. = 4, 125$, $P = 0.04$). The proportion of $C_4$ grasses in the paddock margin samples was significantly higher in the wet season than in the dry season (94.0% versus 70.3%; $t = -2.5$, $d.f. = 24$, $P = 0.02$); in other zones differences between seasons were not significant.

*Stable N isotope ratios.*—The overall mean $\delta^{15}N$ in grasses was 4.8‰ ± 0.3‰ but values for individual samples were as high as 16‰ (for *C. dactylon*). The mean $\delta^{15}N$ value for all plant species in the paddock center was more than 2‰ higher than in any other vegetation zone (Table 4). The $\delta^{15}N$ values of *D. milanjiana* and *P. infestum* were 3 times higher in paddock centers than in the surrounding vegetation (Table 4). At 10.1‰ ± 1.5‰, soil $\delta^{15}N$ values in the center were twice those of any other vegetation zone ($F = 17.9$, $d.f. = 4, 40$, $P < 0.0001$).

The $\delta^{15}N$ values in feces ranged from −2.6‰ to 15.3‰, with a mean of 6.7‰ ± 0.3‰. There was considerable

**TABLE 3.**—$\delta^{13}C$ and $\delta^{15}N$ values (mean ± *SE*) of grasses and forb species on Mkwaja Ranch, Tanzania. *n* = number of samples analyzed.

| | $\delta^{13}C$ (‰) | $\delta^{15}N$ (‰) | *n* |
|---|---|---|---|
| *Aristida adscensoris* | −14.8 ± 0.4 | 5.3 ± 0.5 | 2 |
| *Andropogon gayanus* | −12.7 ± 0.5 | 1.4 ± 1.0 | 3 |
| *Brachiaria leucacrantha* | −13.6 ± 0.5 | 1.5 ± 1.1 | 5 |
| *Brachiaria pilosa* | −11.8 ± 0.0 | 5.1 ± 0.2 | 2 |
| *Cymbopogon caesius* | −12.8 ± 0.1 | 1.2 ± 0.7 | 11 |
| *Cynodon dactylon* | −13.2 ± 0.2 | 9.4 ± 0.8 | 15 |
| *Chloris gayana* | −14.4 | 4.4 | 1 |
| *Dactyloctenium aegypticum* | −12.6 | 3.9 | 1 |
| *Dichanthium bladhii* | −12.8 ±0.0 | 3.8 ± 0.6 | 2 |
| *Digitaria milanjiana* | −11.9 ± 0.2 | 3.8 ± 0.6 | 14 |
| *Echinochloa haploclada* | −12.6 ± 0.1 | 3.3 ± 1.2 | 3 |
| *Eragrostis superba* | −13.2 ± 0.1 | 4.9 ± 0.5 | 24 |
| *Hyparrhenia rufa* | −12.8 ± 0.0 | 4.2 ± 1.0 | 2 |
| *Paspalum dilatatum* | −13.4 ± 0.7 | 8.4 ± 0.9 | 8 |
| *Panicum infestum* | −13.0 ± 0.3 | 3.0 ± 0.4 | 32 |
| *Sporobolus pyramidalis* | −12.1 | 2.5 | 1 |
| *Urochloa* | −12.6 ± 0.0 | 10.2 ± 0.0 | 2 |
| Cyperaceae | −12.3 ± 0.3 | 5.2 ± 1.2 | 25 |
| Leguminosae | −20.5 ± 2.8 | 0.1 ± 1.2 | 7 |
| *Agathisanthemum bojeri* | −28.2 ± 0.3 | 1.6 ± 0.4 | 12 |
| Other forb species | −28.7 ± 0.5 | 5.1 ± 1.9 | 8 |

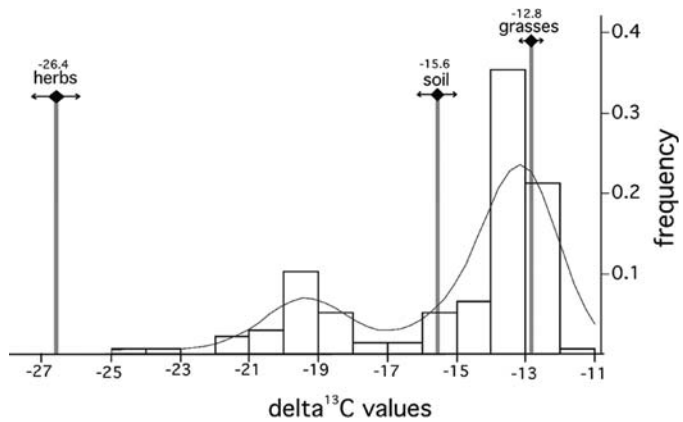


**FIG. 4.**—Frequency curve (dark line) of $\delta^{13}C$ fitted to $\delta^{13}C$ values in feces (open columns) of 124 samples collected on Mkwaja Ranch, Tanzania. "Frequency" indicates how often specific $\delta^{13}C$ values were encountered in fecal samples. Vertical gray lines show average $\delta^{13}C$ values (± 1 *SE*) for herbs (excluding legumes), soil, and grasses. Frequency curves are fitted to the 2 peaks.

variation among zones, with values declining with increasing distance from the paddock center ($F = 8.8$, $d.f. = 4, 125$, $P < 0.0001$; Fig. 5). The average $\delta^{15}N$ value for our 3 samples of warthog bone was 8.38‰. There were no significant differences in $\delta^{15}N$ across seasons either for the pooled grass samples or for forbs, feces, and soil samples.

## DISCUSSION

Although the effect of cattle enclosures upon vegetation and soil conditions in African savannas has been well studied (Augustine 2003; Stelfox 1986), less is known about how wild species use areas no longer occupied by humans or cattle (Young et al. 1995). Examination of the data presented here clearly shows how the former use of Mkwaja Ranch for cattle has affected the diet and patterns of habitat use of the warthog. As in other studies with tropical ungulates (Field 1972), the microhistological analyses of feces provided the most detailed information about the plant species selected. The results indicate that warthogs at Mkwaja obtained most of their food by grazing, supporting observations from Zimbabwe (Cumming 1975). Although the fecal samples contained many plant species, a few grasses—notably *C. dactylon* and *Eragrostis*—were particularly abundant, and other studies also have shown these to be important plants in the diet of warthogs (Field 1970; Rodgers 1984). *C. dactylon*, which was dominant in paddock centers but scarce in other vegetation zones, occurred mainly in feces collected close to the paddocks. This suggests that warthogs distribute their feces close to their feeding sites, so that the distribution of feces can be taken as a guide to patterns of habitat use for feeding.

The high ash content of plant material ($\bar{X} = 9.8\%$) can be attributed mainly to the silica phytoliths present in $C_4$ grass leaves (Georgiadis and McNaughton 1990). Assuming a mean ingested food digestibility of 50% (Halsdorf 2002), we would expect to find approximatley 20% ash in feces, and this rough estimate is not far from the mean value of 26.2% ash actually recorded in feces. The lowest ash contents were found in feces collected close to paddocks where the high herbage quality may decrease the need to ingest soil. In contrast, samples collected in the surrounding vegetation and in the game reserve had high ash contents, and animals feeding in these areas might supplement the poor-quality food available aboveground by digging for more nutritious roots and young shoots, thus increasing their intake of soil. Although Cumming (1975) suggested that warthogs feed more on roots in the dry season, we found little evidence either from the microhistological analyses or from fecal ash contents for such seasonal variation.

Nitrogen and P concentrations of soil and vegetation were high within and close to former night enclosures, indicating that there has been a significant nutrient transfer by livestock from the feeding areas, up to 3 km away, to the paddocks. Similar patterns also have been observed in other extensive grazing systems, although on a smaller spatial scale (Jewell 2002). *C. dactylon* and *P. dilatatum*, the dominant grass species in paddock centers, had the highest crude protein and P contents of any plants analyzed and the decline in nutrient concentrations in these species during the dry season was smaller than in grasses growing at some distance from the paddock. Similar effects of soil nutrient status upon seasonal variation of herbage quality in savannas have been reported by Robbins (1983) and Skerman and Riveros (1990). During the dry periods, crude protein contents of *C. dactylon* and *P. dilatatum* were up to 6 times higher than in other grass species of the surrounding vegetation but similar to those reported by Augustine (2003) for *Cynodon plectostachys* growing in cattle bomas abandoned 12–24 years ago.

As reported elsewhere (Hess et al. 2002, 2003; Owen-Smith 1982), the crude protein contents of forbs and herbaceous

**TABLE 4.**—$\delta^{13}C$ and $\delta^{15}N$ values (mean ± *SE*) in plants, soil, and feces. Shown are values and their associated significance level (analysis of variance) for each vegetation zone (paddock center, paddock margin, *Acacia* scrub, and surrounding vegetation). "Game Reserve" refers to the plots in the former Saadani Game Reserve. Asterisks indicate significance level: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.[a]

| | Paddock center | Paddock margin | *Acacia* scrub | Surrounding vegetation | Game reserve | *F* | *P* | *d.f.* |
|---|---|---|---|---|---|---|---|---|
| $\delta^{15}N$ values (‰) | | | | | | | | |
| All forbs | 7.5 ± 1.5a | 3.0 ± 1.1b | 0.7 ± 3.1ab | 0.3 ± 0.9b | 1.2 ± 2.2b | 4.4 | * | 26 |
| All grasses | 7.5 ± 0.4a | 5.3 ± 0.4b | 4.9 ± 1.1b | 2.6 ± 0.3c | 1.7 ± 0.9c | 26.8 | *** | 147 |
| *Cymbopogon caesius* | 2.7 ± 1.1 | 0.5 ± 1.6 | | −0.01 ± 1.1 | | 1.7 | 0.25 | 9 |
| *Cynodon dactylon* | 10.0 ± 1.0 | 9.1 ± 1.5 | | | 4.4 ± 3.1 | 1.6 | 0.24 | 15 |
| Cyperaceae | 5.9 ± 0.7a | 5.8 ± 0.4a | | 3.6 ± 0.3b | | 13.8 | ** | 21 |
| *Digitaria milanjiana* | 6.4 ± 1.1a | 4.1 ± 0.6ab | | 2.3 ± 0.7b | | 5.1 | ** | 14 |
| *Eragrostis superba* | 6.9 ± 1.2a | 5.4 ± 0.6ab | | 3.6 ± 0.7b | | 3.7 | ** | 22 |
| *Panicum infestum* | 6.0 ± 0.5a | 4.6 ± 0.4b | | 2.0 ± 0.3c | 1.1 ± 0.4c | 31.7 | *** | 30 |
| *Paspalum dilatatum* | 9.2 ± 0.9 | 6.0 ± 1.5 | | | | 3.6 | 0.11 | 7 |
| Feces | 8.2 ± 0.4a | 7.8 ± 0.6a | 5.7 ± 0.8b | 5.6 ± 0.7b | 4.3 ± 0.7b | 8.3 | *** | 127 |
| Soil | 10.6 ± 0.6a | 5.8 ± 0.5b | 4.9 ± 0.6b | 5.7 ± 0.5b | 4.9 ± 0.6b | 17.9 | *** | 40 |
| $\delta^{13}C$ values (‰) | | | | | | | | |
| Feces | −14.1 ± 0.4ab | −15.9 ± 0.6b | −15.0 ± 0.8ab | −15.1 ± 0.7ab | −13.8 ± 0.7a | 1.5 | 0.21 | 127 |
| Soil | −14.4 ± 1.1 | −16.6 ± 0.9 | −16.1 ± 1.1 | −14.4 ± 0.9 | −13.4 ± 1.2 | 1.7 | 0.17 | 40 |

[a] Different letters indicate significantly different groups.

legumes were higher than those of grasses throughout the year and particularly in the dry season. Hence, we might expect a flexible grazer such as the warthog to eat more forbs during times of nutrient limitation. According to Kingdon (1997), warthogs switch to more browse, fruits, and roots during dry seasons. However, we found only a slight tendency toward more $C_3$ plants in the diet during the dry season, this being most evident in feces collected from paddock margins, where forbs were particularly abundant (Treydte 2004).

The fecal N concentration is affected by the non–N fraction digestibility of the plant, influencing the N dilution by other undigested matter. For ruminants, fecal N can be used as an indicator of nutritional status (Grant et al. 1995; van der Waal et al. 2003), although it provides only a relative measure suitable for local or seasonal comparisons (Wrench et al. 1997). Secondary compounds such as tannins also can reduce plant digestibility, and because concentrations of these compounds generally are higher in shrub and tree leaves, fecal N content serves as a better nutritional indicator for grazers than for browsers (Hobbs 1987). Our nutrient analyses of warthog feces showed values ranging between 1% and 2% for N. Because these concentrations are considerably higher than the threshold value for ruminants of 0.8% N (5% crude protein—Kinyamario and Macharia 1992), we conclude that warthogs in our study area did not suffer from nutrient deficiency, even during the dry season. The suggested critical value of 5% crude protein for ruminants feeding on tropical grasses during the dry season (Kinyamario and Macharia 1992) was exceeded in the foliage of several grasses growing in and close to paddocks (*A. gayanus*, *C. dactylon*, *E. haploclada*, and *P. dilatatum*). With 14 paddock systems distributed across the northern part of the ranch, high-quality paddock vegetation was always accessible to warthogs when the general forage quality declined during the dry season.

The $\delta^{13}C$ value of feces has often been used to estimate the proportion of $C_4$ grasses in the diet of livestock (Hess et al. 2002) and wildlife (Ambrose and DeNiro 1986; Gagnon and Chew 2000). Our results indicate that warthogs in Saadani fed almost exclusively on $C_4$ plants (98%), whereas grasses made up a smaller proportion of the diet (about 83%) for warthogs on Mkwaja Ranch. The high variance in the proportion of $C_4$ grasses clearly demonstrates that these animals select their food according to the fodder resources available (Cerling et al. 2003).

In general, $\delta^{15}N$ values of herbivore feces are higher than those of the plant material upon which the animals feed (Lajtha and Michener 1994). In addition, $\delta^{15}N$ tends to increase in areas contaminated with excreta because of higher losses of the

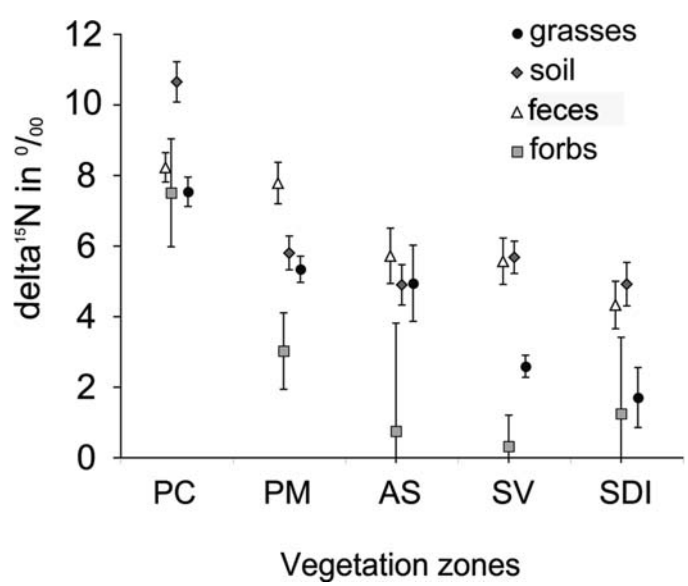


**FIG. 5.**—$\delta^{15}N$ values (± 1 *SE*) in plants, soil, and feces across vegetation zones on Mkwaja Ranch, Tanzania. PC = paddock center, PM = paddock margin, AS = *Acacia* shrub, SV = surrounding vegetation, and SDI = Saadani Game Reserve plots where foraging warthogs were observed.

$^{14}N$ isotope through denitrification and ammonia volatilization (Frank and Evans 1997). Thus, $\delta^{15}N$ values were higher in and around the bomas than in the less-modified savanna. Warthog feces collected in paddock centers and margins also had higher $\delta^{15}N$ values than average, providing further evidence that animals deposit their feces close to their feeding grounds. Similarly, Cerling and Viehl (2004) showed that $\delta^{15}N$ values in the hair of forest hogs in Uganda reflected regional variation in the $\delta^{15}N$ values in plants. However, we found higher than expected $\delta^{15}N$ values in feces from the surrounding vegetation and the game reserve, suggesting that even these animals were selectively feeding in patches of vegetation with a high $\delta^{15}N$. The $\delta^{15}N$ in warthog bones reflects food intake over a longer period than those in feces (Cerling et al. 2003). The average bone $\delta^{15}N$ value of 8.38‰ was similar to that in feces, confirming that warthogs in savannas are highly selective in their food intake.

Treydte (2004) found that warthog feces were more abundant in paddock centers and margins than in the other vegetation zones, which agrees with Stelfox (1986), who recorded a high manure input in bomas dominated by *Cynodon nlemfurensis* in Kenya. Augustine (2003) showed that nutrient-enriched bomas persisted for a long time period after ranching was terminated. In the southern part of Mkwaja Ranch, where paddocks were abandoned $>10$ years ago, the vegetation remains similar to that of the more recently abandoned paddocks in the north and very different from the surrounding savanna. If wild ungulates concentrate their feeding in the former paddocks, they may enhance nutrient turnover and herbage quality in these areas and so help to maintain their higher fertility (McNaughton et al. 1997). Accordingly, then the local nutrient enrichment of former paddocks may persist for a long period.

In conclusion, our results show that paddocks are "honey-pots" of highly nutritious plant resources for wildlife, and are especially important during the dry season. We hypothesize that warthogs and other native ungulate species, once they have encountered these habitats, use them intensively and thereby enhance nutrient turnover. This resulting positive feedback upon their food resource helps to maintain the patchy mosaic produced by 50 years of cattle ranching. National Park management should therefore take account of the vegetation structure, composition, and nutritional quality to predict habitat choice and resource use by wild ungulate populations. Once the feeding ecology of resettling wildlife is known, predictions can be made about further plant composition development and wildlife population dynamics. Important feeding grounds can then be maintained or increased in size to attract additional wildlife to the park.

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