

# How a mega-grazer copes with the dry season: food and nutrient intake rates by white rhinoceros in the wild

A. M. SHRADER\*<sup>†</sup>, N. OWEN-SMITH and J. O. OGUTU<sup>‡</sup>

Centre for African Ecology, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, WITS 2050, South Africa

## Summary

1. Few studies have investigated how free-ranging wild herbivores adjust their food intake rate and nutrient gains during the dry season. Our study focused on the largest extant grazer, the white rhinoceros (*Ceratotherium simum* Burchell 1817). Field measurements were made on changes in bite mass, bite rate and nutrient concentrations of food eaten during the dry season.

2. As the dry season progressed, the quality and availability of food resources declined. During this time white rhinos foraged mainly in high-quality short and woodland grasslands. Late in the dry season they also used flushes of green grass in previously burnt Themeda grasslands.

3. Bite mass increased linearly with increasing sward height, while bite rate declined. Intake rate was determined primarily by bite mass and thus tended to increase linearly with sward height. Maximum bite mass and intake rate was obtained in swards >20 cm.

4. White rhinos did not compensate for seasonal declines in food quality by adjusting their food intake rate or diet breadth. We suggest that white rhinos mobilize fat reserves to help meet their nutritional needs during the dry season.

*Key-words:* body size, *Ceratotherium simum*, feeding ecology, food intake, white rhinoceros

*Functional Ecology* (2006) **20**, 376–384  
doi: 10.1111/j.1365-2435.2006.01107.x

## Introduction

The dormant season for plant growth is a critical time of year for large mammalian herbivores because both the amount and nutritional quality of the food available declines drastically. In southern African savannas the winter period is also the dry season, when grasses cease growth and the leaves of these plants change from green to brown (Grunow, Groeneveld & du Toit 1980). Nutrients within the remaining foliage are largely shifted to underground reserves, while those components of the grassland retaining adequate nutrients are progressively depleted through selective consumption.

To compensate for the reduced nutritional value of the forage available during the adverse season, mammalian herbivores may (1) widen their diet to include less nutritious vegetation components (Owen-Smith &

Cooper 1989; Owen-Smith 1994); (2) increase bite size to maintain an intake rate closer to some target level (Spalinger *et al.* 1988; Laca *et al.* 1994); (3) extend daily foraging time (Illius & Gordon 1991); or (4) mobilize fat reserves to meet shortfalls (Adamczewski *et al.* 1993).

The effectiveness of these responses will vary among herbivore species. Body size and digestive system determine mass-specific metabolic requirements, intake rate and digestive efficiency (Demment & Van Soest 1985; Illius & Gordon 1992). Very large herbivores can potentially meet their nutrient requirements from lower-quality food than smaller herbivores. For ruminants, daily food intake can be restricted by the slow passage rate of fibre (Mertens 1987). Non-ruminants with hindgut fermentation do not experience this limitation, but digest fibre less completely than ruminants (Bell 1971; Janis 1976). Under some circumstances non-ruminants may be better able to obtain their nutritional requirements from poorer quality diets than ruminants. This depends on whether they can achieve an intake rate that compensates for their lower digestive efficiency (Foose 1982; Duncan *et al.* 1990; Illius & Gordon 1992).

The food intake rate of grazing ungulates depends on the sward height and bulk density (weight per unit volume) of grass (Black & Kenney 1984; Laca *et al.* 1992). These factors largely determine bite mass (Hodgson

<sup>†</sup>Author to whom correspondence should be addressed.  
E-mail: adrian.shrader@nmmu.ac.za

\*Present address: Terrestrial Ecology Research Unit, Department of Zoology, Nelson Mandela Metropolitan University, PO Box 7700, Port Elizabeth, 6031, South Africa.

<sup>‡</sup>Present address: International Livestock Research Institute (ILRI), PO Box 30709, Nairobi, Kenya.

1985; Laca *et al.* 1994). To some extent, animals may be able to compensate for reduced bite mass by increasing bite rates (Black & Kenney 1984; Wickstrom *et al.* 1984; Hodgson 1985). Oral morphology (mouth dimensions and structure of the dental arcade) and the mechanics of food consumption (jaw movements involved in cropping and chewing) ultimately limit the food intake rate (Shiple *et al.* 1994).

Most studies focusing on food intake rates and nutritional gains have used domestic ungulates (van Wieren 1996; Menard *et al.* 2002) or artificially confined wild ungulates (Renecker & Hudson 1985; Jiang & Hudson 1992; Murray & Brown 1993). Few studies have been conducted on free-ranging wild herbivores (Vivas & Saether 1987; Owen-Smith & Cooper 1989; Bergman *et al.* 2001). Observations on Wildebeest (*Connochaetes taurinus*) in Serengeti indicated that these animals selected foraging areas that enabled them to maximize long-term energy intake (Wilmshurst, Fryxell & Colucci 1999). In contrast, Bison (*Bison bison*) maximized immediate rates of food intake rather than long-term energy gains (Bergman *et al.* 2001; Fortin, Fryxell & Pilote 2002).

The white rhinoceros (*Ceratotherium simum* Burchell 1817) is the largest extant pure grass-feeder. Males can attain an adult body mass up to 2300 kg, females up to 1700 kg. As non-ruminants, white rhinos should be able to tolerate lower-quality food than other grazing ungulates (Owen-Smith 1988). However, their wide lips enable them to crop high-quality, short grass, their preferred food source for much of the year. Nevertheless, over the course of the dry season, grass height in short grass lawns becomes reduced and consequently the rate of food intake declines, eventually prompting a shift to taller but less nutritious grassland (Owen-Smith 1988).

Our study aimed to establish how changing grass height and greenness determined the selection of grazing areas by white rhinos, and ultimately their movements. The ability to observe these free-ranging animals at close quarters, as well as the dimensions of their large bites, provided a unique opportunity to estimate the food intake rates they obtained under natural conditions. The objectives of our study were to (1) document how bite sizes and biting rates obtained by white rhinos, controlling food intake rate, changed over the course of the dry season; (2) assess how the resulting rates of nutrient gain while foraging were affected; and (3) determine the extent to which white rhinos were able to compensate for reduced food availability and quality.

## Methods

### STUDY SITE

The study was conducted in the western iMfolozi section of the Hluhluwe-iMfolozi Park in KwaZulu-Natal, South Africa (28°20' S, 31°51' E). The rainy season in the Hluhluwe-iMfolozi Park extends from

September or October to March, followed by a dry season from April or May through to August or September. Annual rainfall recorded in the study area was below average (545 mm) during the first seasonal cycle (October 1998–September 1999), and above average (791 mm) during the second seasonal cycle (October 1999–September 2000), compared with the long-term mean of 690 mm (1981–98). In both years, portions of the study area were burnt during July and August, providing flushes of new growth after the rains commenced in September 1999 and October 2000. Based on these patterns, months were grouped into the following seasonal subdivisions: early dry, April–May 2000; late dry, June–August 1999 and June–September 2000; transitional, September–October 1999 and October 2000. The mean white rhino density in iMfolozi was 2.6 animals km<sup>-2</sup> at the time of the study.

### FIELD OBSERVATIONS

Radio telemetry was used so that feeding data could be recorded from specific individuals on a regular basis. MOD-125 radio transmitters from Telonics were implanted in the anterior horns of five sub-adult males, two sub-adult females and three adult females (body mass 1000–1600 kg) (Shrader & Beauchamp 2001). Feeding observations were made in the morning and late afternoon when rhinos were active. Rhinos were located using radio telemetry, approached on foot from downwind, and observed from distances of 10–40 m. Data were collected from both transmitter-equipped individuals and other rhinos associated with them.

Bite rate was recorded using a Psion Organizer II programmed to record the number of bites taken per step and the number of bites per second. Each observation spanned 10 consecutive feeding steps and started with the movement of one of the front feet. A feeding step was defined as a step with one of the front legs where the rhino took at least one bite. Observations of bite rate could include non-feeding steps. Bite rate was calculated by dividing the total number of bites by the time taken during 10 feeding steps. The mean duration of these observations was 58 s (range 34–83 s,  $N = 374$  observations). Consecutive observations of bite rate were not taken from the same individual at less than 10-min intervals, to eliminate or reduce the serial autocorrelation of the observations.

Once the rhino had moved a safe distance away, measurements were made of the dimensions of 10 bites. The length ( $L$ ) and width ( $W$ ) of each bite were measured as the furthest distances between the severed ends of grass leaves or stems (typically 20 × 10 cm). The height above ground level of the grass at the point of severance was measured in five places within the bite area and averaged ( $H_b$ ). Five height measurements were also taken from unbitten grass of the same species in close proximity to the bite ( $H_{unb}$ ). The depth of each bite was then estimated as  $H_{unb} - H_b$ , and the bite volume as  $L \times W \times (H_{unb} - H_b)$ .

For each observation, the bulk density of the upper and lower strata of the grass sward was categorized subjectively as high, medium or low. The lower stratum was defined as the portion of the sward below 20 cm before grazing, and the upper stratum as above 20 cm. Bulk density categories were used to reduce the need to cut, dry and weigh bulk density estimates for each of the 6950 bites measured during the study. Bulk density estimates were determined for each grassland type by clipping 820 grass samples, which were representative of the different bulk density categories. Each clipping approximated the volume of a rhino bite ( $20 \times 10 \text{ cm} \times \text{height of grass removed}$ ). All clippings were air-dried out of direct sunlight in paper bags for over a month before being weighed. The bulk density of each clipping was determined by dividing its dry weight (g) by the bite volume (Hodgson 1985). From these clippings, median bulk density was determined for the different bulk density categories of the strata in the different grasslands. Median values were used, as the data were not symmetrically distributed.

For each bite, the bite mass (g dry matter) was calculated as the product of bite volume and median bulk density (Hodgson 1985; Laca *et al.* 1992) for the grassland type and stratum. Consecutive bites overlapped to some extent. In order to correct for this, 79 observations were subsequently made of the mean overlap within sets of 10 consecutive bites. The median overlap of 0.2 did not differ significantly among grassland types, hence bite volumes for all grassland types were corrected by multiplying them by 0.8 ( $1 - 0.2$ ). The dry matter intake rate was then determined as the product of the corrected bite mass estimate and the corresponding bite rate.

The predominant grassland type [short, woodland, Themeda or other, following Downing (1972) and Owen-Smith (1973)]; grass greenness [categorized as a percentage using Walker's (1976) eight-point scale: 0, 1–10, 11–25, 26–50, 51–75, 76–90, 91–99, 100%]; and prevalent sward height (<10, 10–30, >30 cm) were recorded in the region of each bite mass estimate. Estimates of grass greenness were then combined into four categories: very brown (0–10% green); mainly brown (11–50%); mainly green (51–90%); very green (91–100%). The ungrazed sward height was calculated by dividing the summed mid-points of the different height categories by the total number of bites for each observation ( $N = 10$  bites).

Monthly changes in grass greenness and sward height were recorded towards the end of each month along four transects 5 km long and 1 km apart within the central 50-km<sup>2</sup> region of the study area. Observations were made every 50 m within two 70 × 70-cm quadrates thrown randomly near each point. The prevalent grassland type was noted, general grass greenness categorized as above, and mean sward height categorized as short ( $\leq 10$  cm), intermediate (11–30 cm) or tall ( $> 30$  cm). The relative monthly use of grassland types was obtained by recording the grassland type

occupied by white rhinos observed during the morning and afternoon sampling sessions ( $N = 221$  in 1999; 223 in 2000).

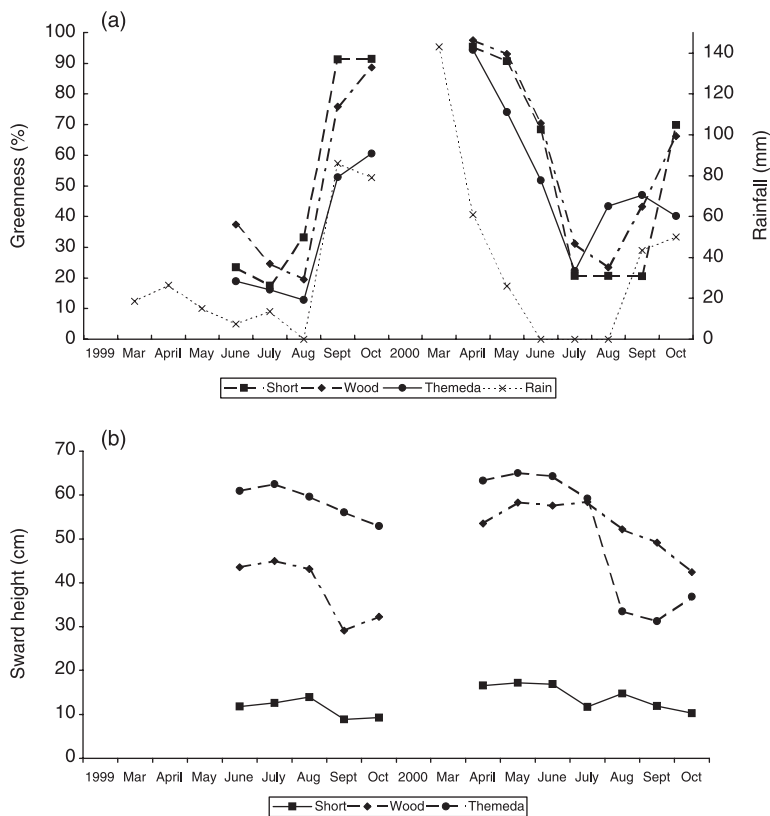
#### CHEMICAL ANALYSIS

Concentrations of nitrogen, phosphorus and sodium were determined from the analysis of 101 grass clippings representing three grassland types (excluding 'other') in each of the four grass greenness categories by the Institute of Commercial Forestry Research, University of Natal. Analyses for fibre contents and digestibility were impractical because of the range of plant species, greenness categories and period covered. There is generally a close correlation between the crude protein ( $N \times 6.25$ ) content of grasses and their digestible energy yield, and protein levels drop as leaves senesce and lose their greenness (Skarpe & Bergstrom 1986). Availability of P is recognized as a widespread limitation on herbivore performance in South African grasslands (du Toit *et al.* 1940), while recent findings suggest that Na could be a particularly important need for white rhinos (H. Olf, personal communication). Clippings were collected during the first year of the study. These were taken from areas where white rhinos had previously been observed feeding, and constituted a mix of species. Forty-eight clippings comprising *Panicum coloratum*, *Sporobolus nitens* and *Digitaria argyrograpta* were collected in short grassland; 32 clippings of *Panicum maximum* plus *Enteropogon monostachyus* in woodland grassland; and 21 clippings of *Themeda triandra* in Themeda grassland. All clippings were air-dried out of direct sunlight in paper bags for over a month before being milled and analysed. Crude protein was calculated by multiplying percentage N by 6.25.

For short grassland, estimates of all three nutrients differed significantly among the three grass species. Hence species-specific concentrations were used for each of these grass species. For bites in this grassland type made up of grass species not analysed chemically, the mean nutrient concentration of the three species analysed for the respective greenness category was assigned. For woodland grassland there was no significant difference in nutrient levels between *P. maximum* and *E. monostachyus*, hence mean concentrations for these two species were used. For Themeda grassland, nutrient concentrations of clippings of *T. triandra* were used. From these results, mean nutrient concentrations were assigned to each of the 528 feeding observations based on the prevalent grass species and greenness, and converted to a nutrient intake rate by multiplying by the estimated food intake rate.

#### DATA ANALYSIS

A general linear mixed model was used to analyse the variation in mean bite mass, bite rate and intake rate with grassland type, seasonal period, sward height and



**Fig. 1.** Monthly trends in the availability of (a) grass greenness; (b) grass sward height in the three main grassland types recorded along four transects through the centre of the study area. Data are shown with monthly rainfall pattern.

grass greenness. Categorical fixed effects in the model included the three seasonal stages, three grassland types, three sward height categories, and four grass greenness levels. Akaike's Information Criterion established that a model without the random effect of individual rhinos was better supported by the data, thus this effect was not included. As the data were unbalanced due to unequal observations among rhinos, we synthesized the denominator degrees of freedom using the Satterthwaite approximation. Bite rate was normally distributed, whereas bite mass and intake rate were log-transformed. Two-way ANOVA was used to analyse the effect of grass species and greenness on nutrient concentrations. Estimates of crude protein, P and Na as percentage of dry mass were arcsine square root-transformed for normality. Wald-type *F* tests were used to test for significance of all fixed effects. All models were fitted in SAS PROC MIXED.

Functional response relationships for bite mass, bite rate and intake rate were derived using the ungrazed sward height near the bites as a measure of the amount of food on offer. A drawback of using mean values was that the data tended to bunch at certain sward heights. ANCOVA was used to compare the slopes and intercepts of the seasonal trends. All analyses were performed using SAS ver. 8.2 (2001). Mean values are reported with standard deviations.

## Results

### ENVIRONMENTAL CONDITIONS AND GRASSLAND USE

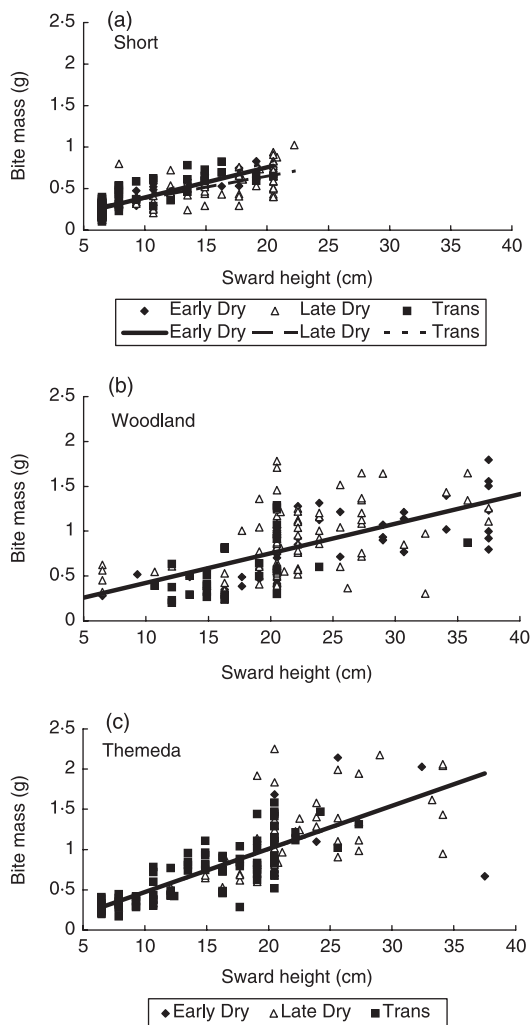
In 1999 the dry season (monthly rainfall < 20 mm) started during March, whereas in 2000 March and April were wet (Fig. 1a). Small amounts of rain fell during the late dry season in 1999, but in 2000 it did not rain in June–August. The dry season ended in 1999 when substantial rain fell during early September, but in 2000 persisted for most of September. Grass remained somewhat greener in 2000 than in the corresponding dry-season months of 1999, but greenness during the transitional period was greater during 1999 than in 2000. Woodland grassland tended to remain green longer than other grassland types. Short grassland greened up earliest during the transitional season in 1999, but in 2000 green growth was extensive in tall grassland areas that had been burnt. Mean sward height remained generally higher during the dry season of 2000 than in 1999 (Fig. 1b). Burning caused a lowering of the mean height of Themeda grassland late in the 2000 dry season.

White rhinos concentrated their feeding mainly on short grasslands (40–50% of feeding observations throughout most of the dry season, declining to a minimum of 25% in September 2000). Woodland grasslands were second in importance, constituting 20–40% of feeding observations. Use of Themeda grassland increased from 10–20% of feeding observations during the early part of the dry season to 30–45% through September–October, with greater use apparent in 2000 than in 1999. Use of 'other' grassland also increased in the late dry season, to a maximum of 20% of feeding observations.

### FUNCTIONAL RESPONSES TO SWARD HEIGHT

Bite mass increased linearly with increasing sward height (Fig. 2). The mean bite mass relative to sward height did not differ significantly among grassland types ( $F_{3,477} = 1.02$ ,  $P = 0.39$ ) or among seasons for woodland grassland (slope,  $F_{2,164} = 3.01$ ,  $P = 0.05$ ; intercept,  $F_{1,164} = 1.21$ ,  $P = 0.27$ ) and Themeda grassland (slope,  $F_{2,153} = 0.85$ ,  $P = 0.43$ ; intercept,  $F_{1,153} = 0.71$ ,  $P = 0.40$ ). In short grassland, bite mass obtained at the different grass heights was similar across all seasons ( $F_{2,187} = 1.63$ ,  $P = 0.20$ ). Nevertheless, the upper envelope to the scatter of points suggests that the maximum bite mass for each grassland type could be obtained from a sward height of 20 cm. Because Themeda and woodland grasslands reached taller heights, white rhinos obtained a mean bite mass approximately twice that in short grassland (woodland  $\bar{x} = 0.75$  g,  $SD = 0.43$ ; Themeda  $\bar{x} = 0.72$  g,  $SD = 0.34$ ; short  $\bar{x} = 0.37$  g,  $SD = 0.18$ ).

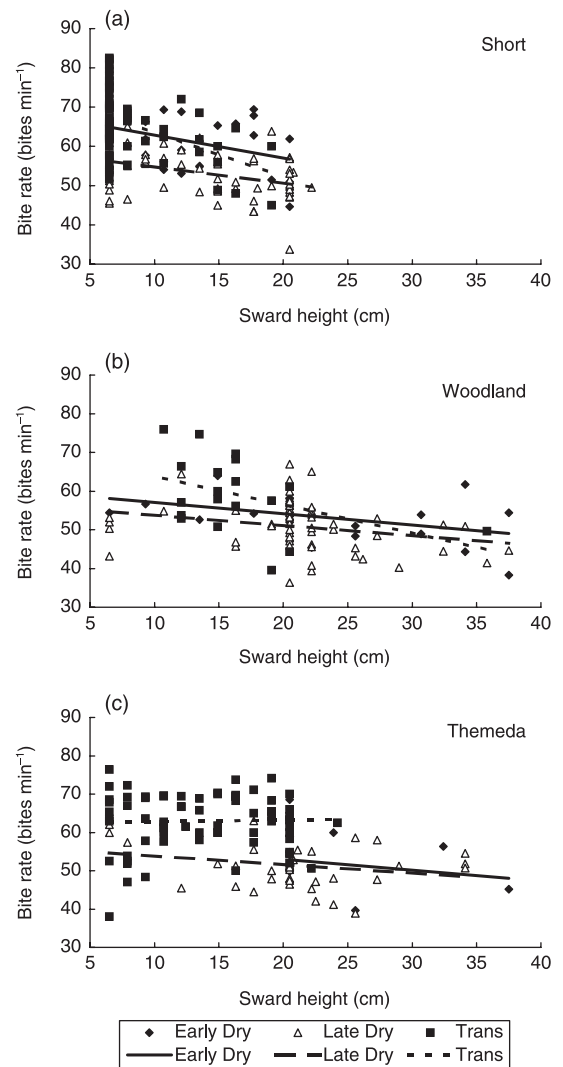
Bite rate declined significantly as sward height increased ( $F_{2,326} = 5.03$ ,  $P < 0.01$ ), although the actual



**Fig. 2.** Functional relationship of bite mass in relation to sward height of (a) short; (b) woodland; (c) Themeda grasslands in the different seasons. Similar bite masses were obtained in (b) woodland and (c) Themeda grasslands throughout the three seasonal periods, so a single line was fitted to these data.

decrease was relatively small (Fig. 3). Within each grassland type, bite rate differed significantly between seasons independently of grass height differences (short grassland: slope,  $F_{2,155} = 27.60$ ,  $P < 0.0001$ ; intercept,  $F_{1,155} = 2051.41$ ,  $P < 0.0001$ ; woodland: slope,  $F_{2,92} = 6.95$ ,  $P = 0.002$ ; intercept,  $F_{1,92} = 768.20$ ,  $P < 0.0001$ ; Themeda: slope,  $F_{2,117} = 24.40$ ,  $P < 0.0001$ ; intercept,  $F_{1,117} = 587.70$ ,  $P < 0.0001$ ). Overall, bite rates on grass of the same height in all three grassland types were similar, and bite rates relative to grass height did not differ seasonally ( $F_{4,326} = 0.57$ ;  $P = 0.69$ ). Maximum bite rates  $\approx 75$  bites  $\text{min}^{-1}$  were exhibited in each grassland type on grass up to 20 cm high.

Food intake rate was determined largely by bite size, and thus tended to increase linearly with sward height (Fig. 4). However, the data suggest that a maximum limit to the intake rate was reached at a sward height of  $\approx 20$  cm. This was  $\approx 50$  g  $\text{min}^{-1}$  in short grassland; 70 g  $\text{min}^{-1}$  in woodland grassland; and 100 g  $\text{min}^{-1}$  in

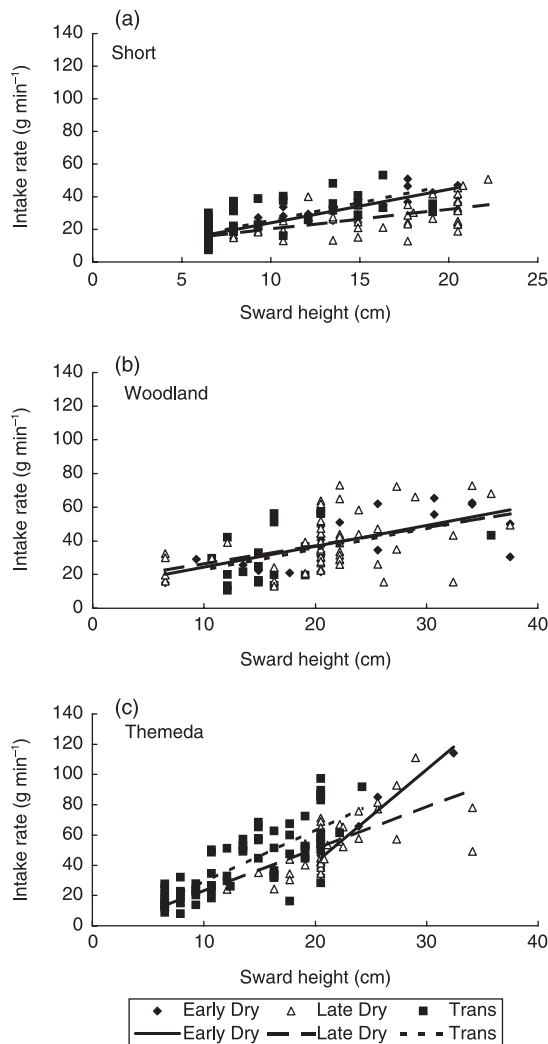


**Fig. 3.** Functional relationship of bite rate in relation to sward height in (a) short; (b) woodland; (c) Themeda grasslands in the different seasons.

Themeda grassland. A seasonal difference in the intake rate achieved on similar grass heights within grassland types was evident (short grassland: slope,  $F_{2,155} = 10.92$ ,  $P < 0.0001$ ; intercept,  $F_{1,155} = 21.02$ ,  $P < 0.0001$ ; woodland: slope,  $F_{2,92} = 0.40$ ,  $P = 0.67$ ; intercept,  $F_{1,92} = 7.36$ ,  $P = 0.008$ ; Themeda: slope,  $F_{2,117} = 6.58$ ,  $P = 0.002$ ; intercept,  $F_{1,117} = 3.17$ ,  $P = 0.08$ ). Nevertheless, overall the seasonal intake rate relative to sward height remained similar ( $F_{4,326} = 1.78$ ,  $P = 0.13$ ). Overall, the geometric mean intake rate in short grassland ( $\bar{x} = 22$  g  $\text{min}^{-1}$ ,  $\text{SD} = 10$ ) was approximately half that obtained in Themeda ( $\bar{x} = 40$  g  $\text{min}^{-1}$ ,  $\text{SD} = 22$ ) and woodland grasslands ( $\bar{x} = 34$  g  $\text{min}^{-1}$ ,  $\text{SD} = 15$ ).

#### SEASONAL TRENDS IN FEEDING MEASURES

Bite mass averaged 0.63 g from April–July in both years (Fig. 5a). Thereafter, mean bite mass decreased to  $\approx 0.35$  g in 1999, after the first rains, whereas in 2000



**Fig. 4.** Functional response of white rhinos in relation to sward height in (a) short; (b) woodland; (c) Themeda grasslands in the different seasons.

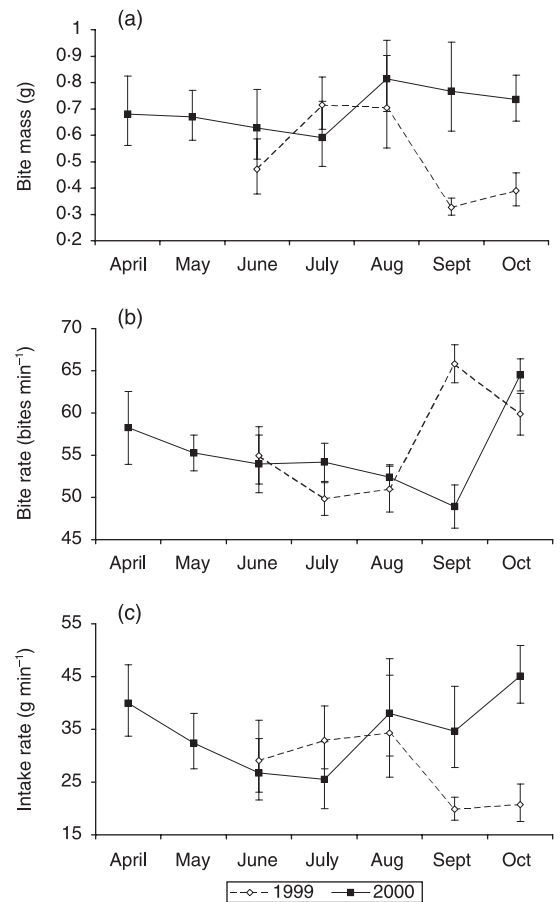
it rose to  $\approx 0.75$  g when the rhinos fed on green regrowth from burns in Themeda grassland.

Mean bite rate remained between 50 and 58 bites  $\text{min}^{-1}$  from April to August in 1999 and 2000 (Fig. 5b). It then rose to over 60 bites  $\text{min}^{-1}$  when white rhinos fed on green regrowth during the transitional period in 1999. In 2000, bite rate rose to over 60 bites  $\text{min}^{-1}$  only in October.

The mean food intake rate remained between 29 and 34  $\text{g min}^{-1}$  from June to August in 1999, whereas in 2000 it decreased from 40  $\text{g min}^{-1}$  in April to 26  $\text{g min}^{-1}$  by July (Fig. 5c). In 1999, food intake rate fell to  $\approx 20$   $\text{g min}^{-1}$  during the transitional months of September and October. In 2000, the larger mean bite mass made possible by the burns led to an increase in the mean food intake rate to over 35  $\text{g min}^{-1}$  from August to October.

#### NUTRIENT GAINS

The six grass species used in the chemical analysis formed  $\approx 75\%$  of the grass eaten during the dry-season

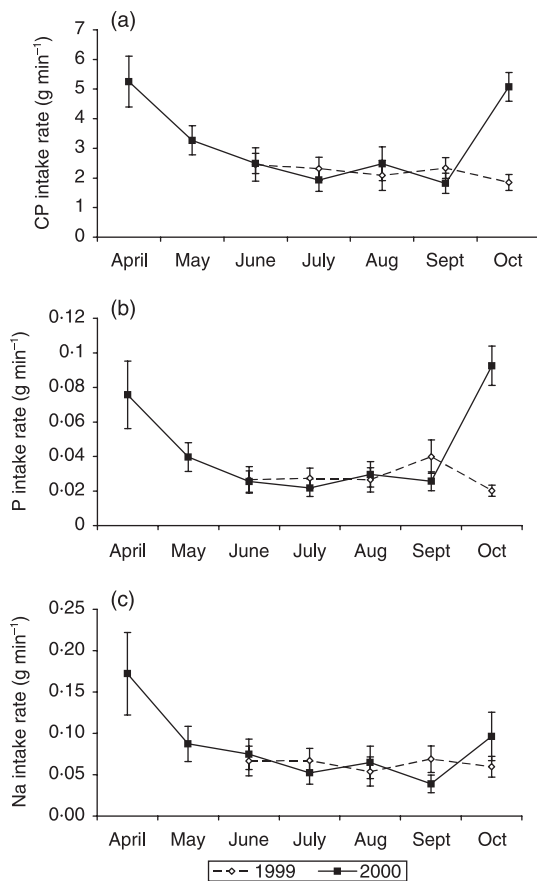


**Fig. 5.** Monthly changes ( $\pm 95\%$  CI) in (a) geometric mean bite mass; (b) mean bite rate; (c) geometric mean intake rate by white rhinos.

months and 82% during the transitional period. As grass greenness decreased through the dry-season months, the crude protein content in the food consumed declined from 13 to 6% of dry matter, P from 0.19 to 0.06% of dry matter, and Na from 0.45 to 0.14% of dry matter. Following the start of rains and the initiation of grass regrowth, the crude protein increased to 12%, P to 0.22% and Na to 0.34% of dry matter.

Despite fluctuations in the food intake rate achieved, the intake rate of all three nutrients (N, P and Na) by white rhinos remained remarkably constant from June to September (Fig. 6). These rates of nutrient gain, however, were less than half those attained at the beginning of the dry season in April 2000, and in October 2000 when the rhinos fed extensively on the somewhat taller regrowth in burnt Themeda grasslands at the start of the wet season. Through September–October 1999, the increase in nutrient contents in grass regrowth after the early rains, coupled with an increase in the bite rate, was only just adequate to compensate for the substantial reduction in bite size.

While curvilinear trends have been fitted for the rate of crude protein gain relative to grass height for each grassland type in Fig. 7, a linear trend was equally well supported statistically in most cases, irrespective of whether the curve was fitted through the mid-point

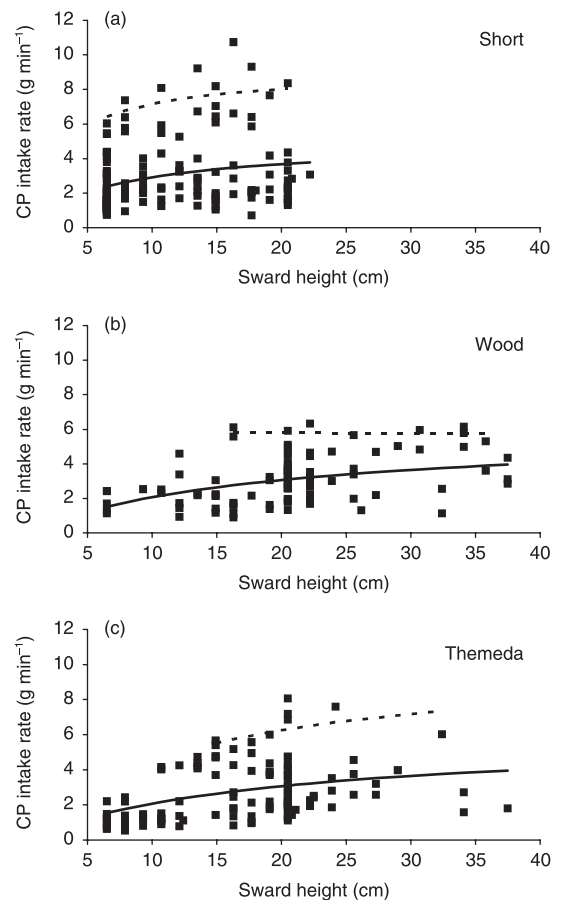


**Fig. 6.** Monthly variation ( $\pm 95\%$  CI) in the intake rate by white rhinos of (a) crude protein; (b) phosphorus; (c) sodium.

of the scatter (short grassland: curvilinear  $RSS = 572$ ,  $R^2 = 0.76$ , linear  $RSS = 585$ ,  $R^2 = 0.76$ ; woodland: curvilinear  $RSS = 153$ ,  $R^2 = 0.58$ , linear  $RSS = 151$ ,  $R^2 = 0.59$ ; Themeda: curvilinear  $RSS = 270$ ,  $R^2 = 0.70$ , linear  $RSS = 283$ ,  $R^2 = 0.69$ ), or as a quantile regression through the upper 10% of the data (short grassland: curvilinear  $RSS = 24$ ,  $R^2 = 0.47$ , linear  $RSS = 24$ ,  $R^2 = 0.46$ ; woodland: curvilinear  $RSS = 1.4$ ,  $R^2 < 0.01$ , linear  $RSS = 1.4$ ,  $R^2 < 0.01$ ; Themeda: curvilinear  $RSS = 9$ ,  $R^2 = 0.22$ , linear  $RSS = 10$ ,  $R^2 = 0.11$ ). For Themeda grassland, the protein intake rate appeared to decline for grass heights  $> 25$  cm, but there were too few data points in this region to support this trend because the rhinos rarely fed on such tall grass.

### Discussion

Illius *et al.* (2002) suggested that foraging can be seen as a trade-off between quality and quantity. However, white rhinos did not compensate for decreasing grass quality during the dry season by increasing their mean food intake rate. Furthermore, the wide scatter in the data points for foraging measures and resulting nutrient intake rates suggest that, for most of the time, white rhinos were accepting intake rates well below the maximum possible for the grassland type and grass height of the feeding area.



**Fig. 7.** Functional response of white rhinos ( $\bar{x} \pm 95\%$  CI) in relation to sward height for crude protein in (a) short; (b) woodland; (c) Themeda grasslands.

A mean food intake rate of  $\approx 40$  g  $\text{min}^{-1}$  during the dry season translates to a daily food intake of  $\approx 2\%$  of body mass for a 1300-kg white rhino (mid-point of body mass range for the animals observed). This assumes that the animals foraged for 50% of the diel cycle (as found by Owen-Smith 1988) and fed for  $\approx 90\%$  of their foraging time. This daily intake is considerably higher than the daily food intake of just over 1% of body mass per day documented for zoo-kept rhinos fed a grass hay diet (Foose 1982). The crude protein content of the hay used by Foose (1982) ranged between 5 and 7% of dry mass, which is lower than the quality of the forage consumed by the free-ranging white rhinos we observed.

While our study design did not allow for round-the-clock observations on the daily activity of the animals, our impression was that white rhinos foraged for no more than  $\approx 4$  h during daylight, much less than the 6 h previously recorded by Owen-Smith (1988). At the time of Owen-Smith's (1988) study, food availability was restricted both by low rainfall and by the much higher rhino density. Hence it seems unlikely that the rhinos increased their daily feeding time to compensate for a reduced food intake rate during the time of our study.

Assuming no seasonal change in daily foraging time, the rhinos incurred a 40% drop in rates of protein and sodium intake, and a 50% reduction in phosphorus intake, over the course of the dry season. Either they did not need to compensate nutritionally, or the passage rate of poor-quality food prevented them from eating more food per day.

Shipley *et al.* (1994) found that the maximum intake rate of mammalian herbivores scales allometrically with body mass raised to the power 0.71. Thus the maximum intake rate of a 1600-kg adult female white rhino should be 119 g min<sup>-1</sup>. Our highest estimated intake rate of 114 g min<sup>-1</sup> was close to this maximum, although only 3% of the records exceeded 80 g min<sup>-1</sup>. Free-ranging domestic ungulates also commonly feed below their maximum rate (Kenney & Black 1984; Distel *et al.* 1995; Illius *et al.* 1999). This may be due to (1) imperfect feeding decisions; (2) sampling to update information of food quality and availability; or (3) the need to ingest different species to obtain a broad range of nutrients (Illius & Gordon 1993; Van Soest 1994; van Wieren 1996; Illius *et al.* 1999).

Hence the white rhinos did not compensate for the seasonal decline in food quality by adjusting either their dry matter intake, daily foraging time or diet breadth. Instead, they tolerated declining rates of gain of dietary protein, P, Na, and presumably also metabolizable energy. Very large animals with relatively low mass-specific metabolic rates lose body condition at a slower rate than smaller animals (Bell 1971). Selous (1899); Cave & Allbrook (1958) noted that white rhinos can show quite large amounts of subcutaneous fat at certain times of year. Our findings suggest that white rhinos used fat and other body reserves to overcome the deficits in nutritional gains that they incurred while foraging during the dry season, and thus did not need to compensate behaviourally.

### Acknowledgements

We thank Ezemvelo KZN Wildlife for permission to conduct the study within Hluhluwe-iMfolozi Park. Peter Hartley (Conservator iMfolozi), Paul Havemann (Section Ranger Mbuzane) and Dave Balfour (Regional Ecologist Northern Zululand) provided logistical support. Godfrey Zondo assisted with the field work. John Fryxell, Joel Brown, Charles Fox and two anonymous reviewers provided constructive comments on earlier versions of the manuscript. Experimental procedure was consistent with the University of the Witwatersrand and South African animal ethics protocols (clearance certificate 99-32-5).

### References

Adamczewski, J.Z., Hudson, R.J. & Grates, C.C. (1993) Winter energy balance and activity of female caribou on Coats Island, Northwest Territories: the relative importance of foraging and body reserves. *Canadian Journal of Zoology* **71**, 1221–1229.

Bell, R.H.V. (1971) A grazing ecosystem in the Serengeti. *Scientific American* **225**, 86–93.

Bergman, C.M., Fryxell, J.M., Gates, C.C. & Fortin, D. (2001) Ungulate foraging strategies: energy maximizing or time minimizing? *Journal of Animal Ecology* **70**, 289–300.

Black, J.L. & Kenney, P.A. (1984) Factors affecting diet selection by sheep. II Height and density of pasture. *Australian Journal of Agricultural Research* **35**, 565–578.

Cave, A.J.E. & Allbrook, D.B. (1958) Epidermal structures in a rhinoceros *Ceratotherium simum*. *Nature* **182**, 196–197.

Demment, M.W. & Van Soest, P.J. (1985) A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist* **125**, 641–672.

Distel, R.A., Laca, E.A., Griggs, T.C. & Demment, M.W. (1995) Patch selection by cattle: maximization of intake rate in horizontally heterogeneous pastures. *Applied Animal Behaviour Science* **45**, 11–21.

Downing, B.H. (1972) A plant ecological survey of the Umfolozi Game Reserve, Zululand. PhD thesis, University of Natal, Pietermaritzburg, South Africa.

Duncan, P., Foose, T.J., Gordon, I.J., Gakahu, C.G. & Lloyd, M. (1990) Comparative nutrient extraction from forages by grazing bovids and equids: a test of the nutritional model of equid/bovid competition and coexistence. *Oecologia* **84**, 411–418.

Foose, T.J. (1982) Trophic strategies of ruminant vs non-ruminant ungulates. PhD thesis, University of Chicago, Chicago, IL, USA.

Fortin, D., Fryxell, J.M. & Pilote, R. (2002) The temporal scale of foraging decisions in bison. *Ecology* **83**, 970–982.

Grunow, J.O., Groeneveld, H.T. & du Toit, S.H.C. (1980) Above-ground dry matter dynamics of the grass layer of a South African tree savanna. *Journal of Ecology* **68**, 877–889.

Hodgson, J. (1985) The control of herbage intake in the grazing ruminant. *Proceedings of the Nutrition Society* **44**, 339–346.

Illius, A.W. & Gordon, I.J. (1991) Prediction of intake and digestion in ruminants by a model of rumen kinetics integrating animal size and plant characteristics. *Journal of Agricultural Science, Cambridge* **116**, 145–157.

Illius, A.W. & Gordon, I.J. (1992) Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. *Oecologia* **89**, 428–434.

Illius, A.W. & Gordon, I.J. (1993) Diet selection in mammalian herbivores: constraints and tactics. *Diet Selection: an Interdisciplinary Approach to Foraging Behaviour* (ed. R.N. Hughes), pp. 157–181. Blackwell Scientific, Oxford, UK.

Illius, A.W., Gordon, I.J., Elston, D.A. & Milne, J.D. (1999) Diet selection in goats: a test of intake-rate maximization. *Ecology* **80**, 1008–1018.

Illius, A.W., Duncan, P., Richard, C. & Mesochina, P. (2002) Mechanisms of functional response and resource exploitation in browsing roe deer. *Journal of Animal Ecology* **71**, 723–734.

Janis, C. (1976) The evolutionary strategy of the Equidae and the origins of rumen and cecal digestion. *Evolution* **30**, 757–776.

Jiang, Z. & Hudson, R.J. (1992) Estimating forage intake and energy requirements of free-ranging wapiti. *Canadian Journal of Zoology* **70**, 675–679.

Kenney, P.A. & Black, J.L. (1984) Factors affecting diet selection by sheep. I. Potential intake rate and acceptability of feed. *Australian Journal of Agricultural Research* **35**, 551–563.

Laca, E.A., Ungar, E.D., Seligman, N. & Demment, M.W. (1992) Effects of sward height and bulk density on bite dimensions of cattle grazing homogeneous swards. *Grass and Forage Science* **47**, 91–102.

Laca, E.A., Ungar, E.D. & Demment, M.W. (1994) Mechanisms



- of handling time and intake rate of a large mammalian grazer. *Applied Animal Behaviour Science* **39**, 3–19.
- Menard, C., Duncan, P., Fleurance, G., Georges, J.Y. & Lila, M. (2002) Comparative foraging and nutrition of horses and cattle in European wetlands. *Journal of Applied Ecology* **39**, 120–133.
- Mertens, D.R. (1987) Predicting intake and digestibility using mathematical models of rumen function. *Journal of Animal Science* **64**, 1548–1558.
- Murray, M.G. & Brown, D. (1993) Niche separation of grazing ungulates in the Serengeti: an experimental test. *Journal of Animal Ecology* **62**, 380–389.
- Owen-Smith, N. (1973) The behavioural ecology of the white rhinoceros. PhD thesis, University of Wisconsin, Madison, WI, USA.
- Owen-Smith, N. (1988) *Megaherbivores*. Cambridge University Press, Cambridge, UK.
- Owen-Smith, N. (1994) Foraging responses of kudus to seasonal changes in food resources: elasticity in constraints. *Ecology* **75**, 1050–1062.
- Owen-Smith, N. & Cooper, S.M. (1989) Nutritional ecology of a browsing ruminant, the kudu (*Tragelaphus strepsiceros*), through the seasonal cycle. *Journal of Zoology, London* **219**, 29–43.
- Renecker, L.A. & Hudson, R.J. (1985) Estimation of dry matter intake of free-ranging moose. *Journal of Wildlife Management* **49**, 785–792.
- Selous, F.C. (1899) The white or square-lipped rhinoceros. *Great and Small Game of Africa* (ed. H.A. Bryden), pp. 52–67. Rowland Ward, London.
- Shiple, L.A., Gross, J.E., Spalinger, D.E., Hobbs, N.T. & Wunder, B.A. (1994) The scaling of intake rate in mammalian herbivores. *American Naturalist* **143**, 1055–1082.
- Shrader, A.M. & Beauchamp, B. (2001) A new method for the implantation of radio transmitters into the horns of white and black rhinoceroses. *Pachyderm* **30**, 81–86.
- Skarpe, C. & Bergstrom, R. (1986) Nutrient content and digestibility of forage plants in relation to plant phenology and rainfall in the Kalahari, Botswana. *Journal of Arid Environments* **11**, 147–164.
- Spalinger, D.E., Hanley, T.A. & Robbins, C.T. (1988) Analysis of the functional response in foraging in the sitka blacked-tailed deer. *Ecology* **69**, 1166–1175.
- du Toit, P.J., Louw, J.G. & Malan, A.I. (1940) A study of the mineral content and feeding value of natural pastures in the Union of South Africa. *Onderstepoort Journal of Veterinary Science and Animal Industry* **14**, 123–327.
- Van Soest, P.J. (1994) *Nutritional Ecology of the Ruminant*, 2nd edn. Cornell University Press, Ithaca, NY, USA.
- Vivas, H.J. & Saether, B.-E. (1987) Interactions between a generalist herbivore, the moose, and its food resources: an experimental study of winter foraging behaviour in relation to browse availability. *Journal of Animal Ecology* **56**, 509–520.
- Walker, B.H. (1976) An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. *South African Journal of Wildlife Resources* **6**, 1–32.
- Wickstrom, M.L., Robbins, C.T., Hanley, T.A., Spalinger, D.E. & Parish, S.M. (1984) Food intake and foraging energetics of elk and mule deer. *Journal of Wildlife Management* **48**, 1285–1301.
- van Wieren, S.E. (1996) Do large herbivores select a diet that maximizes short-term energy intake rate? *Forest Ecology and Management* **88**, 149–156.
- Wilmschurst, J.F., Fryxell, J.M. & Colucci, P.E. (1999) What constrains daily intake in Thomson's Gazelles? *Ecology* **80**, 2338–2347.

Received 4 October 2005; revised 9 January 2006; accepted 30 January 2006

Editor: C. Fox