

FEEDING ECOLOGY OF BLACK RHINOS

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INTRODUCTION

This paper summarises the main findings relating to black rhino feeding ecology to come from the Black Rhino 2000 (BR2000) project we undertook in Hluhluwe-Umfolozi Park (For full details see: Chapters 6-11 & 13, BR2000 final report - Volumes 2,3 &4; Emslie & Adcock 1993). We have also compared our findings with those of feeding studies and observations in other areas, to see whether any general principles emerge (Chapter 12 BR2000 final report - Volume 4; Emslie & Adcock 1993).

A BRIEF SYNOPSIS OF METHODS AND ANALYSES

Only a very brief overview of the research and analytical methods used is provided below. Interested technical readers can consult Chapters 3,4 and 5 in Volume 2 of the BR2000 final report (Emslie & Adcock 1993) for full details of the methods and analyses used.

NATURE DETECTIVE APPROACH USED TO STUDY BLACK RHINO WOODY BROWSING

After a review of alternative approaches to study black rhino feeding, we decided to use a plant-based approach to study woody plant browsing. The black rhino's characteristic "pruning" of woody vegetation made this possible. In other words, because black rhinos leave a history of their woody browsing behind on the vegetation, we can measure and contrast this with available browse. More recent browsing can also be distinguished from older browsing by the colour of the wood at point of browsing.

Plant-based methods also had a number of major advantages over other methods. Firstly, they eliminated most of the serious biases inherent with direct observation methods or dung analyses; secondly, they had a potentially greater return per unit effort than direct observation methods or dung analyses; and thirdly, unlike dung analysis, they enabled the size of the browsed plants and their settings to be quantified.

We developed and used a new eye-balling volumetric woody browse measure ("The Browse Bottle") in the BR2000 project. A field trial demonstrated that the method was suitably robust and repeatable between different observers. Kotze (1990) also used our browse bottle method in his study in Itala, facilitating comparison of his results with ours.

PLANT-BASED FEEDING:HABITAT SURVEYS UNDERTAKEN TO STUDY BLACK RHINO WOODY BROWSING

The results presented in this paper are based on an examination of about 764 000 trees for browsing. A total of 3 457 transects were measured during eight Hluhluwe and Umfolozi feeding:habitat surveys undertaken by BR2000 from 1988-90.

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Four distinct types of black rhino feeding:habitat survey were undertaken:

1) *Pilot surveys* (1988) were carried out in both Hluhluwe and Umfolozi.

Available browse, browse offtake, and the degrees of grass, forb and thicket interference of browse were assessed on each of 2 614 individual trees from 57 plots, in different habitat strata in Hluhluwe and Umfolozi.

2) *Grid surveys* (1989) were carried out in both Hluhluwe and Umfolozi. The plots were sampled throughout a 4,900 ha Hluhluwe study area and a 4,675 ha Umfolozi study area using a regular systematic sampling design. A total of 429 (30 x 5m) plots were measured during the two grid surveys. Unless otherwise stated results presented in this paper refer to the grid surveys.

- Braun-Blanquet Cover abundance scores, Tree Densities and Total and Free Browse Bottle availabilities were recorded at a spize (SPecies sIZE class) level to quantify habitat composition and structure in each plot. Mean grass interference of browse was also estimated for each small or medium spize (<2m). The amounts of both new and old black rhino feeding (Browse Bottle Offtake) were assessed for each individual browsed tree. About 32 720 trees were examined for browsing in these Grid survey transects.

- The amount of black rhino feeding seen while walking between plots was also scored using a 5-point scale over every 225m in Hluhluwe and every 250m in Umfolozi. Black rhino dung was also recorded when encountered. A total of about 215 km was assessed for black rhino browsing while navigating between grid survey plots.

3) *Rapid Post-Burn surveys* (1989) were carried out in both Hluhluwe and Umfolozi. Three Rapid Post-Burn Surveys were conducted: one each immediately after burns in Umfolozi and Hluhluwe, and one, (the main survey) during the post-burn vegetation flush in Hluhluwe.

The post burn surveys differed from the grid surveys in that measurement was at a cruder scale, but many more plots were measured. The latter was needed to pick up the limited amount of browsing to have occurred since the burns.

A total of 2 931 (50 x 8m) or 146,55km of contiguous transects were measured while walking along predetermined routes in both study areas. Ca 252 000 trees were assessed in the first post-burn surveys in Hluhluwe and Umfolozi. A further 476 000 trees were then examined for signs of browsing in the main Hluhluwe Post-Burn Survey.

The main Hluhluwe Post-Burn Survey evenly covered the whole of the Hluhluwe Grid Study Area allowing close comparison with earlier Grid Survey results.

- The total amount of black rhino woody browsing was assessed in each 50m transect using an almost linear 6 point categorical browse bottle scale. The proportional contributions of various spizes to total browsing in the plot were then assessed.

- Habitat composition was described by listing up to three key species in each of two size classes.

- Burn intensity, tree density, bush physiognomy, and plot location in relation to paths and drainage lines were also assessed for each plot using categories.

4) In 1990 *Hitchins* 1969-71 plots in a bush-cleared part of N.E.Hluhluwe, were remeasured to assess the changes in black rhino feeding and in woody vegetation structure over 20 years. Peter kindly made his original data available for comparison.

Woody spize density and an index of browse severity were recorded for each of the 40 transects (100 x 6 feet). The plots were not permanently marked and so could not be relocated exactly. To assess the relative effects of slightly different transect location on spize composition and browsing three transects were replicated. In each case, two replicate transects were measured a few metres parallel to each other. The bush clearing and burning history of each transect was also summarised from the maps at Hluhle Game Rserve research centre.

ELECTRONMICROSCOPIC ANALYSIS OF DUNG USED TO BLACK RHINO HERBACEOUS USE

After a trial of direct observation using radio-tracking proved unsuccessful, faecal analysis of dung samples was used to study herbaceous (forb) plant use.

Black rhino 2000 co-operated with Bruce Page of the University of Natal (Durban) in initiating three third year projects that used a Scanning Electron Microscope (SEM) to identify leaf fragments in samples of black rhino dung. The SEM work and projects were undertaken by Craig Haskins, J. Raubenheimer and Keren Pearman (1989).

DATA ANALYSIS

Relational database querying and a range of statistical analyses were used to analyse the various rhino feeding:habitat survey datasets.

- Relational database querying, ANOVA's, Ridge regressions, Exploratory Discriminant Function analyses of Ordination scores, Tukey's Honestly Significant Difference Multiple Comparison Testing, and a TWINSpan analysis were used to analyse the Pilot Survey data.

- Relational database querying, ANOVA's, Multiple Decomposition of Correlation Coefficients and Ridge regression were the standard statistical techniques used to analyse the Grid survey data. To study and separate out the effects of environmental, fire and bush-clearing variables on Hluhluwe species composition and structure (ie rhino habitat quality); a sequence of partial constrained ordination analyses was used.

- Woody plant succession was studied using a Static Ordination approach based on RESOURCE-processed spize-based data. Successional pathways were revealed using three dimensional interpolated maps of spize abundances in ordination space (drawn using an inverse distance squared algorithm). These topographical maps were then in turn related to a three dimensional map of black rhino feeding levels throughout the same ordination space. This directly linked successional trends with rhino habitat suitability.

Woody plant changes and the Whateley-Wills successional model for Hluhluwe were evaluated using a number of alternative approaches. These included ..

- A review of key papers by Bews (1917), Bayer (1933,1938) and Attwell (1948) relating to vegetation ecology in Zululand in the 1930's and 1940.

- A close examination of the communities in Hluhluwe-Umfolozi described by Whateley & Porter (1979)

- A review of key recent papers on processes of vegetation succession in Hluhluwe (Whateley & Wills in prep.) and Mkuzi (Smith & Goodman 1986,1987).

- A review of selected key papers relating to models and processes of vegetation succession.

- A review of Nick King's (1989) study of past aerial photographs

- A spize-based TWINSpan analysis of Hluhluwe Grid data.

- A Median cluster analysis of Hluhluwe Grid data.

- Interviews

- Looking at old photos of the area.

- An examination of partial fire constrained ordination biplots.

Short-term effects of bush clearing and fire were examined using the results of studies by King (1987) and Konstant (in prep). The impact of any habitat changes on black rhino was then inferred in the light of known rhino feeding patterns and preferences revealed by these studies. Black rhino use of burnt areas following burns was also studied in the Post burn surveys. Short-term effects of bush clearing were also ascertained by looking at recently cleared sites. Biplots of partial constrained ordinations of the Hluhluwe Grid data were examined to ascertain the effects of recent bush clearing and fire treatments on the vegetation.

The post-burn survey data were analysed using relational database querying; while more detailed patterns of feeding in relation to burns, paths and vegetation types were investigated using Continuous and Categorical Formal Inference-based Recursive Modelling (CATFIRM & CONFIRM). Attempts were made at cross-validating the derived models.

The Hitchins' plot data were examined to determine the long-term effects of bush clearing, and changes in black rhino feeding patterns between 1969/70 and 1990. Results for plots grouped according to frequency of bush-clearing and topographical position were compared between the two time periods. As feeding on the Hitchins plots in 1990 was infrequent, a subset of the 1989 Grid survey from the plots in Hitchins' study area was used to provide additional comparisons between black rhino feeding patterns of c. 1970 and 1990.

Standard chemical analyses of limited numbers of browse and plant samples were also undertaken, involving crude protein, nitrogen, calcium, phosphorus, zinc, manganese and other minerals.

SOME DEFINITIONS USED IN THIS PAPER

"ACACIAS"

Unless otherwise stated the term "*Acacias*" (i.e. in inverted commas) is defined as including the *Acacia*-like *Dichrostachys cinerea* (a member of the sub family Mimosoideae of the family Leguminosae along with true *Acacias*).

DIETARY IMPORTANCE, PREFERENCE AND REJECTION

An *important* species is one which contributes a high proportion of the total diet.

A *preferred* species occurs in the diet in a greater proportion than it occurs in the habitat; while a *rejected* species occurs in the diet in a lower proportion than it occurs in the habitat.

Preference Indices (PI's) were always calculated as the percentage contribution of species or spize X to the diet divided by the percentage contribution of X in the habitat (i.e. an importance:abundance ratio).

Highly preferred items (***) had PI's greater than or equal to 2,75.

Preferred items (**) had PI's greater than or equal to 2, but less than 2,75.

Slightly preferred items (*) had PI's greater than or equal to 1,25, but less than 2.00.

Intermediate items which were likely to be neither preferred nor rejected were defined as having PI's greater than or equal to 0,80, but less than 1,25.

To facilitate comparison, rejection class boundaries were simply defined as the reciprocals of preference class boundaries:

Highly rejected items (---) were defined as those with PI's less than 0,36.

Rejected items (--) had PI's greater than or equal to 0,36, but less than 0,50.

Slightly rejected items (-) had PI's greater than or equal to 0,50, but less than 0,80.

NO AND YES PLOTS

NO plots are plots where no black rhino feeding signs were found while *YES plots* had signs of black rhino browsing. NO and YES plots were used to study patch selection.

FIRE SEVERITY

In the post-burn survey fire severity was assessed using a four point categorical scale; Unburnt, Light, Medium and Severe Burns. *Light* burns were poorly burnt; *Medium* burns had burnt well, but some tufts had not been fully burnt; while on *Severe* burns all visible grass biomass had been burnt.

GRID SURVEY SIZE CLASSES

Four size classes were used: **1: Small** (<1m) **2: Medium** (1-2m) **3: Intermediate** (2-4m) and **4: Tall** (>4m)

RESULTS AND DISCUSSION

ONLY A SMALL PROPORTION OF AVAILABLE BROWSE REPRESENTS BLACK RHINO FOOD

The first popular misconception of laymen that needs to be debunked is that the greater amount of bush you have on a property the higher the carrying capacity for black rhino. For example, Hluhluwe-Umfolozzi currently has one of the highest densities of black rhino in the RMG region (Namibia and South Africa). Despite this, total offtake levels over a period of 5-6 months by the grid surveys only represented a very small proportion of the standing crop of total available browse bottles in the habitat - 3,62% in Umfolozzi and 1,11% in Hluhluwe. (The intensity of the grid and post burn sampling was therefore vindicated).

BLACK RHINOS ARE HIGHLY SELECTIVE FOR BOTH SPECIES AND SIZE CLASS

Although black rhinos selected their food at a hierarchy of scales, they were highly selective for both species and for size class. Therefore when assessing habitat suitability it is important to work at a *spize* level rather than simply a species level. In other words black rhinos are not simply botanists selecting only for latin binomials! Seen through the eyes of a hungry black rhino a 75cm *A. nilotica* bush is a completely different resource to a 4m mature *A. nilotica* tree.

"ACACIAS" ARE VERY IMPORTANT AND HIGHLY PREFERRED DIETARY ITEMS

"*Acacias*" make up about 46% of all black rhino woody browsing in the Umfolozi, and 34% in the Hluhluwe.

In Umfolozi the seven most highly preferred species were all "*Acacias*"; and at a finer level 16 of the 23 preferred spizes were "*Acacias*" less than 4m. In Hluhluwe three out of the four most highly preferred species were "*Acacias*".

Although "*Acacias*" are generally very important food items, their role in the diet varies according to the plant size, species, season, and whether or not the trees have been burnt:

"*Acacia*" size selection patterns

One clear point to emerge from BR2000 was that as "*Acacias*" get taller they become less palatable to black rhino. Unless grass interference levels are high, the smaller "*Acacias*" (<1m) are invariably the most highly preferred, and may also be the most important size class in the diet. For example, in Umfolozi "*Acacias*" less than 1m (Size 1) were both very important and highly preferred. *D. cinerea*1, *A. karroo*1, *A. nilotica*1, *A. gerrardii*1, *A. tortilis*1 and *A. borleae*1 were among the 10 most important spizes, and are rated as highly preferred. These spizes made up only 3.49% of available free bottles in Umfolozi; yet contributed to 23% of total woody browse offtake. The smallest size class (size1 = <1m) was most the preferred size for 11 of the 12 "*Acacia*" species in Umfolozi. The odd man out in this trend was *A. luderitzii*, which was both rare and apparently rejected.

Conversely, tall "*Acacias*" are invariably highly rejected as food items. While most browse on such tall trees is unavailable, what there is usually rejected. Even tall, spindly *A. karroo* (>4m) which are occasionally pushed over and browsed by black rhinos in Hluhluwe are rejected. While size 1 "*Acacias*" made up 25,8% of all black rhino woody plant browsing in Umfolozi, size classes' 2,3 and 4 made up 14,74%, 5,39% and 0,05% respectively.

Interestingly, in Umfolozi more bottles were also removed per tree from the more preferred "*Acacia*" size 1 and 2 spizes, than from the less preferred ones. Thus habitat selection occurred at a hierarchy of scales.

The differences in size class preferences were even more pronounced if one only looked at the important palatable "*Acacia*" species in Umfolozi (Umfolozi Size1:6,51 *** Size2: 2,84 *** Size3: 2,21 ** Size4: 0,00 ---).

"*Acacia*" size selection patterns in Hluhluwe are modified by grass interference.

Although "*Acacia*" spizes were still preferred in Hluhluwe (accounting for 9 of the 22 common preferred spizes), "*Acacia*" spize selection patterns differed from those in Umfolozi. These differences between study areas were primarily related to the increased grass interference recorded in Hluhluwe. After pooling the data for all "*Acacias*", a similar size preference ordering emerged in Hluhluwe and Umfolozi, although preference indices were generally lower than in Umfolozi (Umfolozi Size1:4,68 *** Size2: 2,30 ** Size3: 1,35 * Size4: 0,08 --- Hluhluwe Size1:2,48 * Size2: 1,73 * Size3: 1,52 * Size4: 0,00 ---). However, while 6 different "*Acacias*" were rated as highly preferred, and contributed more than 0,25% of free (available) bottles in Umfolozi, only one size 1 "*Acacia*" in Hluhluwe (*A. karroo*1) did so in Hluhluwe.

In Hluhluwe *A.karoo*, *A.robusta*, *D.cinerea* and *A.caffra*, size 1 trees (<1m) were still the most preferred sizes of the common "Acacias". However, size 2 (1-2m) *A.nilotica* and *A.gerrardii* trees were the most preferred. Size 3 (2-4m) trees were also the second most preferred size class for *A.caffra*, *A.nilotica* and *A.karoo*.

In contrast to Umfolozi, medium-sized "Acacias" between 1 and 2m (size2) were the most important in Hluhluwe. Taller size 3 "Acacias" (2-4m) contributed about the same proportion to total browsing as size 1's. Thus in Hluhluwe, size 1 "Acacias" made up only about a third as much of the total woody diet as in Umfolozi, but size class 3 "Acacias" made up about 70% more.

Differences in preference and importance ratings for different "Acacia" species

Although as a group "Acacias" were generally preferred, in both Hluhluwe and Umfolozi palatability varied between species and size classes.

A.gerrardii, *A.borleae*, *A.nilotica*, *A.caffra*, *A.tortilis* and *A.senegal* were the most preferred species.

The more ubiquitous *D.cinerea* and *A.karoo* were less preferred, but very important dietary items. Each species accounted for about 8-10% of the woody diet.

A.luderitzii, *A.grandicornuta* and *A.nigrescens* were generally rejected. Only small *A.nigrescens* trees (<1m) were preferred out of these heavily defended spizes.

The most highly preferred spize in Umfolozi was *A.nilotica* size 1 plants (<1m). Taller medium to intermediate sizes of *A.nilotica*'s were still preferred (1-2m) or slightly preferred (3-4m). However, in Hluhluwe, tall *A.nilotica*'s (>4m) were highly rejected. This finding is particularly important when one comes to assess the likely effects of past habitat changes in Hluhluwe on black rhino, where previously dense stands of this species has undergone self thinning and growing out to mature woodland.

"Acacias" and patch selection

As a general rule, whether or not black rhinos fed in a patch depended on the species, sizes and density of plants available. Black rhino also selected to feed in patches of vegetation with high densities of "Acacia" spizes less than 2m. Also, in Umfolozi, patches without feeding had a greater proportion of "Acacias" which were over 2m tall compared to feeding patches. In both reserves, availability of preferred spizes was generally higher in plots with feeding than in those without.

In Umfolozi the densities of the preferred spizes 1, 2 and 3 of *A.nilotica* in Umfolozi, were up to 3,4 times greater in plots with feeding than those without. On the other hand, rejected tall *A.nilotica*'s occurred at a higher density and canopy cover in plots with no feeding (NO plots). A similar pattern emerged in Hluhluwe.

- Absolute canopy cover of tall *A.karoo*'s in Hluhluwe plots without feeding was almost double that in plots which had feeding, indicating that mature *A.karoo* woodlands were less preferred.

- In Hluhluwe, total canopy cover and densities of *A.caffra* were higher in plots with browsing. The density of free bottles on *A.caffra*'s 2-4m high was 2,23 times greater in plots with feeding, indicating black rhinos select scrubby *A.caffra* dominated areas in Hluhluwe.

- Besides *A.nilotica*, the canopy covers of taller individuals (>2m) of five key *E.racemosa*/*B.zeyheri* lowland forest species in Hluhluwe were also higher in plots with no feeding (*B.zeyheri*, *C.caffra*, *E.racemosa*, *S.inerme* and *R.pentheri*). These findings have an important bearing on the effects of habitat changes in Hluhluwe on black rhino.

Conclusion on "Acacias"

The above emphasises the need to not just to consider "*Acacia*" densities when assessing black rhino habitat, but also the size and species of "*Acacias*", the mix of species, and the degree of grass interference.

The high preference for "*Acacias*" is one of the reasons "sweetveld" areas like Umfolozi have a higher carrying capacity for black rhinos than mixed or sourveld areas like Pilanesberg or Lapalala. As "*Acacias*" are subject to leaf drop after frost, frost-prone areas tend to have a more extreme dry season crunch period and therefore have lower carrying capacities compared to frost free areas.

In terms of black rhino habitat suitability the marked size selection preferences for "*Acacias*" indicates how important it is to maintain these species in a short growth stage and prevent them maturing into taller trees.

MANY MEMBERS OF THE EUPHORBIACEAE FAMILY REPRESENT VERY IMPORTANT AND HIGHLY PREFERRED BLACK RHINO FOODS

Intermediate size Spirostachys africana - a key and preferred resource

In Hluhluwe-Umfolozi, *Spirostachys africana* (Tambohi) was found to be the most important woody species in the diet, accounting for 22,9% and 24,6% of total woody browsing in the two reserve study areas respectively. Young *S.africana* thicket was also the most preferred habitat patch sampled in the Umfolozi Pilot Survey. Despite its dietary importance, there does appear to be an upper limit to the amount of this species black rhinos will eat.

Unlike "*Acacias*", the most preferred *S.africana*'s were intermediate in size. *S.africana* size's 3 (2-4m) and 2 (1-2m) were the two most important sizes in the diet in both Hluhluwe and Umfolozi study areas. Tall *S.africana* trees were highly rejected. In Umfolozi, plots without feeding contained less *S.africana* overall, but more taller *S.africana* individuals than those with feeding.

Acalypha glabrata - an important food in Hluhluwe

In Hluhluwe, *Acalypha glabrata* was also the second most important woody species in the diet, and patch selection was particularly strong for patches dominated by this species. *A.glabrata* accounted for about 13% of the Hluhluwe study area diet. Medium (1-2m) and to a lesser extent Intermediate (2-4m) *A.glabrata* sizes were the most important and preferred size classes.

Euphorbiaceae species - conclusions.

Apart from *S.africana* and *Acalypha* species other members of the *Euphorbiaceae* family also contributed to the black rhino diet, with *Croton sylvaticus* making up a further 2.5% of the Hluhluwe diet and *C.menyhartii* accounting for 2,27% of the Umfolozi woody diet.

Once again in terms of black rhino habitat suitability the marked size selection preferences favouring medium (1-2m) and especially intermediate (2-4m) *S.africana*, indicates how important it is to prevent these plants from maturing into taller trees. As with "*Acacias*" it is therefore very important not to think statically about habitat suitability; but be aware how vegetation dynamics, and especially structural changes, can affect habitat suitability and hence black rhino carrying capacities. We must not forget that vegetation changes can greatly alter carrying capacity as has happened over the last 30 years in Hluhluwe and Umfolozi.

IF THICKETS GET TOO DENSE BLACK RHINO FEEDING DECLINES

Study results show that amounts of black rhino feeding increased as the density of trees below 2,5m tall increased. However, black rhino feeding levels declined if the bush density got so high that it became difficult to walk inside the plots (High impenetrability index).

THICK BUSH CAN REPRESENT POOR BLACK RHINO FEEDING HABITAT

There is a general perception amongst laymen that thick bush = good black rhino habitat. This is not necessarily so. We saw above how the density of "Acacia" thickets can get so dense that they become sub-optimal habitats. Furthermore the spize composition of some dense thicket/bush communities may mean such areas represent poor black rhino food. For example, *Croton menyhartii* thicket areas in Umfolozi were highly rejected by black rhino.

Of eight common species in dense donga-dissected bush clump communities in Umfolozi, *M.nemorosa*, and *S.capitata* were intermediate in preference. *Rhoicissus rhomboidea* was rejected, and *Euclea undulata*, *Brachylaena ilicifolia*, *Olea europea*, *Pyrostria hystrix*, and *Carissa bispinosa* were all highly rejected.

Although such dense bush areas did not represent prime black rhino habitat in terms of food, such areas appear to be important for rhino by providing shelter, and a place to keep cool during the heat of the day (thermoregulation).

RIVERINE AREAS PROVIDE IMPORTANT BLACK RHINO HABITATS

In the Hluhluwe pilot survey dense riverine forest was the most preferred habitat patch surveyed. Areas near water also tended to provide "green bite" later in the season after more open sites have dried out. This in part explains the increasing use of riverine areas by black rhino during the dry season. Thicker bush along the banks of semi-permanent and occasional streams also provided very important dry season habitats. Following severe floods, individuals of some species such as *Ficus sycamorus* (Nigel Kemper pers.comm, pers obs.) and *S.africana* which grew up were highly favoured by black rhino.

FOREST MARGINS PROVIDE GOOD BLACK RHINO HABITAT

Although true evergreen forest patches in Hluhluwe appear to have been rejected for woody plant feeding by black rhino, evergreen forest margins appear to be preferred summer habitats. Although the main Hluhluwe post-burn survey indicated that true evergreen forests in Hluhluwe may be used more during the crunch dry-season period, these areas did not contribute a high proportion of the late dry season / post-burn diet. Such habitats could also be expected to provide some late winter "stop gap" foods for rhino.

In Hluhluwe patches in various states of transition from mature closed *A.nilotica* woodland towards a dry evergreen forest dominated by *Euclea racemosa*, *Berchemia zeyheri* and *Rhus pentheri* were highly rejected by black rhinos. In this case, the development of extensive areas of closed *A.nilotica* woodland facilitated the development of this dry forest. By way of contrast, in the past, the "bush encroached" short *A.nilotica* scrub savanna would have provided ideal habitat. However due to infrequent burning and the absence of elephants this later matured into the rejected closed *A.nilotica* dominated woodland, and dry *E.racemosa/B.zeyheri* forest of today with disastrous consequences for Hluhluwe's black rhino carrying capacity.

SUMMARY OF SPECIES PREFERENCES IN THE STUDY AREAS

Preferred species

S.africana, *A.karoo*, *A.gerrardii* and *A.nilotica* were preferred species in both study areas.

Berchemia zeyheri and *Abutilon/Hibiscus* species were other important dietary components in Hluhluwe. However, *B.zeyheri* is only available while small, and within rhino reach. As a canopy dominant it provides no food.

In Umfolozi, other important dietary species were *Ehretia rigida/amoena*, *Schotia capitata*, and five *Grewia* species.

A. glabrata, *B. zeyheri*, *Abutilon/Hibiscus*, *Hippobromus pauciflorus*, *Dovyalis caffra*, and *Dombeya burgessiae* were preferred species in Hluhluwe but were less common in Umfolozi.

Similarly *A. borleae*, *A. tortilis*, *Ehretia rigida/amoena*, *Grewia flava*, *G. occidentalis*, *Commiphora neglecta*, *Capparis tomentosa*, and *Azima tetraantha* were preferred species in Umfolozi, but less common in Hluhluwe.

Maytenus nemorosa was the only *Maytenus* to be preferred. Like *S. africana* and (to a lesser extent) *A. glabrata*, the most preferred spize of *M. nemorosa* was intermediate in height (2-4m). Of the other *Maytenus* species *M. heterophylla* was more readily eaten than *M. senegalensis*.

A number of palatable evergreens such as *E. rigida/amoena*, *S. capitata*, *B. zeyheri*, and *Pappia capensis* occur as understorey plants in bush clumps growing on termite mounds. Such clumps can provide important dry season foods, and the density of such clumps has been correlated with estimated carrying capacity in some conservancies in Zimbabwe (Raoul du Toit pers.comm.).

Intermediate preference species

Most people believe *Zizyphus mucronata* is a preferred black rhino browse species because Kudu and Nyala prefer it. However for black rhino it was only intermediate in acceptance in Hluhluwe, and slightly rejected in Umfolozi (where it formed a greater proportion of the available browse bottles). The low preference rating of *Z. mucronata* by black rhino was corroborated by the Pilot surveys.

Rejected species

With the exception of *Maytenus nemorosa*, *Maytenus* species were relatively unimportant dietary items. *Rhus* and *Euclea* species were also mostly unimportant, and highly rejected, contributing only 1,65% and 0,96% to the Hluhluwe and Umfolozi Grid diets.

Tarchonathus camphoratus, *Sideroxylon inerme* and *Plectroniella armata* were also strongly rejected in both study areas. The physically defended *Acacia grandicornuta* and *A. luderitzii* were rejected in Umfolozi; while in Hluhluwe *Cordia caffra* and *Kraussia floribunda* and the abundant *Lippia javanica* and *Diospyros lyciodes* were rejected in Hluhluwe.

The three species with the greatest grass interference in Hluhluwe (*Euclea crispa*, *Rhoicissus tridentata* and *Rhus rehmanniana*) were all highly rejected.

Although *C. menyhartii* was the eleventh most important species in the Umfolozi diet it was highly rejected. Of eight common species in dense bush clump communities in Umfolozi, *Rhoicissus rhomboidea* was rejected, and *Euclea undulata*, *Brachylaena ilicifolia*, *Olea europea*, *Pyrostria hystrix*, and *Carissa bispinosa* were all highly rejected.

In Umfolozi, *C. menyhartii* thickets were obviously avoided by black rhino. This one species accounted for a third of all available browse in Umfolozi Grid plots with no feeding; but less than 10% in plots where black rhinos browsed.

The least important communities in Hluhluwe, were low lying and dominated by either *D. lyciodes* or *L. javanica*. These two communities had the tallest grass heights and substantially higher levels of past "Acacia" bush clearing.

THERE ARE LIMITS TO THE AMOUNT OF ANY ONE SPECIES A BLACK RHINO WILL EAT

The proportional contributions to the diet of the six species which occurred in both Hluhluwe and Umfolozi "top 10" most important woody browse species lists were strikingly similar between study

areas. Proportional differences in their contribution to available browse in the habitat were however noticeably less similar.

A corollary of this observation is that species were generally less preferred in the study area where they were more abundant (eg. *A.caffra*, *S.africana*, *A.robusta* and *M.nemorosa*). This suggests that there probably is a limit to the amount of a certain species a black rhino may choose to eat, irrespective of its abundance in the habitat (e.g. *S.africana*). This has important implications for habitat assessments, and the feeding of cut browse to boma'ed black rhino. Intuitively this could be expected to be a function of the negative consequences of build ups of specific secondary plant chemicals; and a need to eat a variety of plants to obtain all the minerals, micro-nutrients and essential fatty acids required for healthy metabolism.

BURNS AND BLACK RHINO FEEDING ECOLOGY

During the post-burn period, black rhinos in both Umfolozi and Hluhluwe were clearly not forced to restrict their feeding to unburnt areas. In most habitats, fire increased both the proportion of plots in which black rhinos browsed, and the offtake levels from these plots.

In the majority of habitat types which are potentially exposed to frequent fires, fire severity influenced short term habitat suitability. Light to medium severity burning appeared to be more beneficial to black rhino than severe burning (where all visible biomass was burnt). With the exception of *S.africana* and *A.glabrata* (which were infrequently burnt in HGR North), burnt trees contributed substantially more to the immediate post-burn woody diet than unburnt trees. Just over two thirds of the immediate post-burn woody diet came from burnt trees. During the early growing season in Hluhluwe 58,2% of total woody browsing also occurred on trees that had been burnt.

Findings in Hluhluwe were similar to those in Umfolozi. However, in the drier Umfolozi, water distribution and spize composition influenced black rhino habitat suitability more than whether or not plots had been burnt. Black rhinos were observed to particularly favour browsing burnt "*Acacia*" twigs. In Hluhluwe during the immediate post burn period 34,2% of the diet was made up of burnt "*Acacia*" twigs compared to only 3,5% from unburnt "*Acacias*".

The importance of regenerating burnt "*Acacias*" increased to account for 41,8% of the Hluhluwe black rhino post-burn flush woody diet. Given the uncharacteristic nibbling of coppicing shoot tips during this period by black rhino, this figure is probably an underestimate. By way of contrast, browsing on unburnt "*Acacias*" only contributed a further 6,72% of the Hluhluwe post-burn flush woody diet.

In attempting to shed some light on the reasons for the browsing of burnt "*Acacias*", limited chemical analyses of browse samples were undertaken in cooperation with Richard Eckhart of Cedara. However, in terms of plant chemistry and nutrition the reasons for eating burnt twigs still remained unclear. One can speculate that burning may alter the taste and/or smell, or denature chemicals that inhibit digestion. Further more extensive chemical analysis of secondary plant compounds in burnt and non-burnt twigs (and especially condensed tannin levels) may shed some light on this behaviour. Observations in Pilanesberg indicated that black rhino selectively browsed lightly burnt *A.tortilis* branches that had their thorns burnt off, in preference to other unburnt branches with thorns. Thus avoidance of physical defence may explain some of this curious behaviour.

Individuals of normally unpalatable species were increasingly eaten after the burns. A large proportion of browsed trees of these species had been burnt. One can again speculate that burning may have denatured some secondary plant chemicals and increased the palatability of these species. The stimulation of the new leaf growth phase following burning should also increase palatability. However, increased browsing of generally unpalatable species is to be expected during the crunch dry season and early flush period (Owen-Smith 1993). To a large extent browsing of such "stop-gap" species will be independent of fire. The increasing use of unpalatable species during the post burn period should therefore not be interpreted as a negative consequence of burning.

Burnt trees did not always form the bulk of black rhino browsing on every species during the immediate post burn period. In the case of the favoured Euphorbiaceae duo, *S.africana* and *A.glabrata*; burnt trees only contributed 11.6% of immediate post-burn offtake on these two species. However this simply reflects the low proportion of trees of these species which were burnt in 1989.

The removal of tall grass interference was clearly a major advantage of burning during above average rainfall periods. In Hluhluwe, burning during above average rainfall periods clearly increased the effective area of suitable black rhino habitat. Burning also created conditions conducive to the early season growth of palatable ground forbs.

Light burning of *S.africana* seems better for black rhinos than severe burning. If Tambothi thickets are to be managed for black rhino with fire, a balance between keeping the plants within the favoured intermediate height classes with fire, and not burning too severely, is needed.

While the evidence strongly rules out the hypothesis of fire selectively removing palatable food plants in terms of favoured "*Acacias*"; the data were examined to determine if other species of palatable young browse plants may have been selectively removed by hot burns.

The palatable *Dombeya burgessiae* often occurs in forest margins. However this species also occurs in more open areas which experience high fire frequencies; and even appears to be favoured by fires. Other preferred non "*Acacia*" species (*S.africana*, *A.glabrata*, *B.zeyheri*, *Abutilon/Hibiscus*, *M.nemorosa*, *H.pauciflorus*, and *D.caffra*) occur primarily in areas which experience low fire frequencies or cool fires. Thus it does not appear that fire in Hluhluwe selectively removes palatable young browse plants by hot burns.

Rather it is the reverse. In most cases while palatable species are affected little by fire; many unpalatable species (eg. *E.racemosa*, *K.floribunda*, and *S.myrtina*) are more sensitive and prone to being killed by fire.

This study has demonstrated how important "*Acacias*" are to the Hluhluwe-Umfolozi black rhino diet. The many advanced adaptations to fire of "*Acacias*" also leaves little doubt that the occurrence of frequent fires played a major role in the evolution of these species (Jackson 1974). If fire was as detrimental to black rhinos as postulated a 1988 NPB meeting (Anon 1988), then surely one would not have expected evolution to result in fire adapted "*Acacias*" being such preferred and important items in diet of black rhino?

In conclusion, burning on the whole benefits black rhino. Infrequent burning on the other hand, will largely be negative for black rhino by 1) allowing "*Acacias*" to grow into taller less preferred size classes; 2) allowing emerging seedlings of unpalatable fire sensitive later successional evergreen species to establish and grow; 3) not removing grass interference in wet years; and 4) not creating conditions conducive to the early season growth of palatable ground herbs.

THE ROLE OF LACK OF FIRE IN THE HLUHLUWE BLACK RHINO DECLINE

The ground truthed interpretation of Nick King's (1987) analysis of Hluhluwe vegetation changes from 1933 to 1982 indicated that the period of bush encroachment and development of closed woodland areas coincided with the long period with very little fire.

The partial constrained ordination analysis provided a good objective test of the theory that lack of fire was a key factor governing vegetation changes in Hluhluwe. The results strongly supported the hypothesised Whateley-Wills successional model with less preferred and rejected tall spizes (*A.nilotica*⁴, *E.racemosa*⁴, *B.zeyheri*⁴, *R.pentheri*⁴, *S.myrtina*⁴, *K.floribunda*³, and *S.inerme*⁴) being significantly associated with low fire frequencies from 1955-1964. Lack of fire therefore played a key role in the development of areas of sub-optimal black rhino habitat (closed woodland and lowland forest).

The remeasurement of Hitchins's plots and a derived biplot indicated that the increase in densities of the unpalatable *L.javanica* was not primarily the result of competitive release after bush clearing, but rather a function of high fire frequencies, and possibly also a response to the above average rainfall period in the mid to late 1980's. However *L.javanica* grows in areas predisposed to tall grass growth in wet periods; and therefore fire will at least have increased access for rhinos to other more palatable species growing in these areas (by removing grass interference).

In conclusion, the evidence gained from BR2000 strongly supported the *habitat change as a major cause of the Hluhluwe black rhino decline* hypothesis. Lack of fire in the past was identified as a key factor in these changes. We could not support the arguments advanced at the 1988 NPB meeting (Anon 1988) that fire is detrimental to black rhino by selectively removing their favoured food species. The evidence presented in this chapter (and Chapter 20) clearly shows it was rather lack of fire in the past that contributed to the marked vegetation changes that have reduced Hluhluwe's carrying capacity for black rhino.

MONITORING THE CONTRIBUTION OF "UNPALATABLE" SPECIES TO SUMMER BROWSING CAN BE USED AS AN INDICATOR OF WHETHER BLACK RHINOS MAY BE UNDER NUTRITIONAL STRESS

On Hitchins' plots, unpalatable species (i.e. currently rejected *E.crispa*, *M.senegalensis*, *L.javanica*, *Diospyros* species, *Rhus* species and *K.floribunda*) made up 15,3% of the black rhinos' woody diet in 1969-71. These same species only accounted for 1,3% of 1989-90 feeding. The high feeding levels on unpalatable species in 1969-71 could not be accounted for by season of measurement alone.

One can speculate that in 1969-71, the much higher contribution of unpalatable species to the diet, and the possibility of heavy browsing inducing secondary plant chemical defence; may have resulted in secondary chemical levels in the diet exceeding the threshold amounts that a black rhino's metabolism can cope with. This would increase the possibility of liver damage, which may have reduced the fitness of the animals. In addition, condensed tannin concentrations tend to be higher in the leaves of unpalatable species; and as tannins reduce digestibility by binding with proteins such as digestive enzymes, the heavy browsing of unpalatable species in 1969-71 probably reduced food digestibility.

Thus if monitoring of black rhino browsing over time picks up that normally "unpalatable" species are making up a greater part of the summer diet; this will be a good indicator that the animals are likely to be overstocked. It is likely that failure to rest stop-gap unpalatable foods may further reduce habitat quality by leading to an increase in secondary plant chemicals in some browsed plants (Norman Owen-Smith pers comm.). In such cases you should greatly reduce your stocking rate by removing some black rhino.

BLACK RHINO HABITAT ASSESSMENTS SHOULD BE BASED ON KEY SPIZES RATHER THAN ON PLANT "COMMUNITIES"

The findings of spize-based constrained and unconstrained polynomial Detrended Canonical Correspondence Analyses carried out in Hluhluwe using a range of spize abundance measures indicated that black rhinos primarily viewed their habitat in terms of the composition and volume of browse available 1) within reach and 2) not interfered with by grass.

This finding is reasonable, as tall *A.nilotica*, *S.africana* or *B.zeyheri* (key spizes in canopy cover-based habitat descriptions) are all of almost no effective food value to black rhino; yet smaller sizes of the same species are of markedly better food value.

During black rhino habitat assessments, rather than assessing the abundance of different habitat types, all one needs to do is to assess the abundance of unhindered key preferred spizes in an area. This approach is vindicated by 1) the observations that the bulk of a black rhinos woody diet is

made up of a limited number of key species and 2) the difficulty of allocating vegetation plots to discrete habitat types in the field.

Thus armed with a list of key species, size class selection patterns, and the rule of thumb about what constitutes unhindered browse, a manager can assess black rhino habitat suitability while walking through an area.

GRASS HEIGHT AND INTERFERENCE AFFECTS BLACK RHINO FEEDING LEVELS

Black rhino feeding levels were negatively related to grass height and especially to grass biomass.

At a broad, patch level, very tall grass areas with "*Acacia*" were rejected by black rhino during the Grid Surveys. Black rhinos clearly chose to feed in plots where less of their preferred small "*Acacias*" were hidden by grass. When black rhinos in Hluhluwe used more open patches, they also favoured areas with lower grass interference.

Grass height had a greater influence on feeding levels than the percentage grass interference. Grass height primarily affected browsing levels by influencing 1) the probability of black rhinos feeding in plots; and 2) if browsing occurred in plots, the proportion of available trees eaten. The mean offtake per browsed tree however, was primarily influenced by grass interference levels rather than grass height. Black rhinos thus selectively fed at a hierarchy of scales.

Analysis showed that in Hluhluwe-Umfolozi 75cm was the critical modal grass height; with little small/medium "*Acacia*" browsing occurring in plots with grass over a metre high. Seen through the eyes of a black rhino, trees could be defined as *unhindered* by grass when:

- 1) Plot modal grass is less than or equal to 75cm, and
- 2) Grass interference is less than 25% on medium (1-2m) trees, and less than 50% on small (<1m) trees.

Grass interference levels on many common size 2 trees (1-2m) was a better indicator of whether a plot was fed in or not by black rhino than grass interference levels on size 1 individuals (<1m).

A comparison of summer modal grass height and grid black rhino browsing contour maps in the Hluhluwe Grid Study area clearly illustrated the negative effect of tall grass. Contour maps of post burn feeding however showed that previously little used areas (which had tall grass) no had higher levels of browsing.

Superficially, it appeared that habitat conditions in Hluhluwe should be more suitable for black rhino than in Umfolozi, as the density of total available bottles of food "*Acacia*" (all sizes) was 2,83 times greater. However, on closer examination, shorter grass with resultant reduced grass interference levels, and a more favourable mix of "*Acacia*" species made the Umfolozi habitat more suitable.

Although there was an average of 7 870 total food "*Acacia*" bottles/ha in Hluhluwe, only 6,93% of these bottles (545) were on unhindered small-medium Top8 "*Acacias*". The corresponding percentage for Umfolozi was 31,97% (888/2 777).

Only 1,46% of total food "*Acacia*" bottles/ha occurred on the most preferred unhindered small (<1m) Top8 food "*Acacias*" in Hluhluwe, compared to 12,54% in Umfolozi. The unhindered free available bottle amounts on small Top8's which was three times greater in Umfolozi than Hluhluwe.

The proportion of total bottles on small-medium Top8 "*Acacias*" that was available (unhindered and free), was also much higher in Umfolozi (70,2% available versus 26,9% in Hluhluwe).

Browse was more equitably distributed between a range of food "*Acacia*" species in Umfolozi, rather than predominantly being made up of the two important but generally less preferred dominants *A.karoo* and *D.cinerea*.

The importance of grass in influencing black rhino feeding levels was emphasised by the analysis of the factors influencing mean offtake per food "*Acacia*" spize per "*Acacia*" plot. The sums of squares accounted for by modal grass height class was 5,58 times greater than that explained by the covariable dummy variable set for the different food "*Acacia*" species. Clearly, measuring "*Acacia*" densities alone when assessing black rhino habitat suitability is not enough. In order of importance, "*Acacia*" size class, grass height/interference and "*Acacia*" species (including mix of species) also needs to be considered.

Fieldwork for this study was undertaken during a period of above average rainfall. We therefore could expect habitat conditions to improve for Hluhluwe black rhinos in drier years as grass interference levels will decline.

FORBS (HERBACEOUS PLANTS) ARE IMPORTANT FOOD ITEMS

Due to their ephemeral nature, forb species may vary substantially in abundance between years. Conclusions about the dietary importance of individual species may therefore in part reflect the environmental conditions prevailing during the time of study. The BR2000 studies occurred during a period of above average rainfall; and the findings may therefore not hold for below average rainfall periods.

The pilot and grid surveys indicated that the "hard" forbs *Indigofera natalensis/cylingorica*, *Justicia sufrutescens*, *Abutilon/Hibiscus* species and *Sida* species were important and preferred dietary items.

The electronmicroscopic analysis of black rhino dung by Raubenheimer (1989), Pearman (1989) and Haskins (1989) revealed that *Amaranthus vividus* (Amaranthaceae), *Ipomoea ficifolia* (Convolvulaceae), *Tephrosia* species (Leguminosae), *Abutilon* species (Malvaceae), *Xanthium* species (Compositae) and *Datura stramonium* (Solanaceae) were eaten by black rhino. The browsing of *D.stramonium* was interesting as this species was routinely observed growing in rhino dung piles, and its seeds are narcotic.

Out of the 48 species/sample combinations identified in the dung, 21% were forbs (Raubenheimer 1989; Pearman 1989; Haskins 1989). Similarly, of the 116 species/observer/sample combinations recorded, 23% were forbs. However, as many key woody species in the diet were for an unknown reason omitted from the students' reference key, the forb frequency is likely to have been overestimated. Nevertheless, forbs clearly were important dietary items. *Sida* species (Malvaceae) appeared particularly important.

The electronmicroscopy confirmed the frequent presence of smaller individuals of *Hippobromus pauciflorus* and *Celtis africana* (spizes on which black rhino browsing is difficult to distinguish using the Browse Bottle) in the diet.

Of the species listed by Peter Hitchins (1968) as having been eaten by black rhino, 13% were forbs.

In general the key forb families eaten by black rhino in Hluhluwe include the Leguminosiae, Malvaceae, Acanthaceae, Compositae and Solanaceae.

COMPARISON OF BR2000 RESULTS WITH OTHER AREAS

The comparison of the observed feeding patterns in Hluhluwe-Umfolozi with feeding studies in other RMG areas and East Africa, supplemented by our observations in other areas revealed a number of consistent findings (For full references and details of other studies see Emslie & Adcock BR2000 report Volume 4 1993):

- "*Acacias*" consistently emerged as key dietary items. "*Acacia*" species and size selection patterns appeared similar to those documented in this study.
- A few woody species (ca 10) invariably account for the bulk of a black rhino's woody diet.
- Members of the Euphorbiaceae family are often preferred and important food items (including *Securinega* and *Phyllanthus reticulatus*).
- *Grewias* routinely make up a small proportion of the diet; although in drier or more nutrient poor areas they can become both very important and highly preferred food items.
- *Euclea* species and most *Rhus* species (with the exception of *R.guenzii* and *R.marlothii*) are rejected.
- *E.rigida*, *Coddia rudis* and *Maytenus nemorosa* are generally highly preferred black rhino food plants.
- *L.javanica* is a rejected black rhino food plant.
- *Z.mucronata* is not a highly preferred black rhino food plant.
- *B.zeyheris* between 1 and 2,5 metres are preferred food items.
- In summer, black rhino favour browsing in forest margins.
- In Itala, tall grass reduced habitat suitability for black rhino in *A.karoo/A.nilotica* woodland.
- Burning is, overall, beneficial to black rhino.
- Closed tall *A.nilotica* woodlands and *Combretum* dominated communities are relatively poor black rhino habitats.
- Vegetation with a higher moisture content is sought after by black rhino in the dry season: i.e. palatable broadleaf evergreens, and plants growing along drainage lines.
- We observed that in Ndumo and Pilanesberg, black rhinos also preferentially feed along paths.
- Kes Hillman's radiotracking study in Pilanesberg confirmed our opinion that black rhinos make increasing use of open areas at night; and that using a daytime direct observation method to study feeding would have biased our results.
- The majority of browsing on unpalatable species usually occurs early in the early growing season (flush period).
 - Bush clumps on termitaria contain spizes much sought after by black rhino.
 - Generally, feeding levels are greater lower down on the catena, i.e. in "sweeter", more fertile areas which are not steep, and which have more microphyllous and less broadleafed vegetation.
 - In drier areas, *Rhyzogum* species are favoured and important food species.
 - Forbs form a varying proportion of the diet, depending on the area; and are most important during the early wet season flush period. The forbs *Justicia*, *Hibiscus*, *Abutilon* and *Indigofera* are widely eaten by black rhino.
 - Under conditions of nutritional stress black rhinos may graze.
- Apart from the double rainy season and rich volcanic soils, the main difference between East and Southern Africa is the abundance of leguminous forbs in some areas, leading to higher black rhino carrying capacities in East Africa.

In conclusion; the similarities and degree to which many general principles on black rhino feeding behaviour emerged from the different areas was striking.

POSSIBLE COMPETITION WITH OTHER BROWSERS

See paper of managing black rhinos by Emslie & Adcock in this volume.

GEOLOGY, SOILS AND RAINFALL AND CARRYING CAPACITY

Soils derived from acidic, granitic, or sandstone tend to be poorer in nutrients (Sour). Plants growing on such soils (eg *Faurea saligna*, *Combretum* species) also tend to have a higher fibre content, and as a rule are less palatable compared to sweetveld areas. At annual rainfalls over 700mm leaching of nutrients exacerbates the influence of this geology.

On the other hand basic, basaltic or alluvial derived soils generally have a higher clay content and are richer in nutrients than sourveld. Plants growing on such soils (eg most "*Acacias*") have a lower fibre content and are more palatable. On average levels of secondary plant chemicals (such as condensed tannins) which can interfere with digestion, are also likely to be lower in sweetveld than sourveld. These factors result in sweetveld having higher carrying capacities for black rhino than sourveld. In general, as rainfall increases on such soils carrying capacity increases, unless grass interference becomes excessive.

At rainfalls below 300mm soil nutrients are less relevant.

This paper has focused on bushveld and savanna areas. However it should be remembered that the Eastern Cape Valley Bushveld also contains some excellent black rhino habitat (eg Andries Vosloo and Addo).

WE MUST ALSO CONSIDER SOCIAL LIMITATIONS OF CARRYING CAPACITY

While habitat conditions, rainfall, topography and soil nutrient status are the primary determinants of carrying capacity one must also be aware of the role that social factors can have in limiting carrying capacity (see paper by Adcock in this volume).

IN AREAS WITH LOW RAINFALL AND/OR FROST BLACK RHINO POPULATIONS ARE LIKELY TO BE DRY-SEASON LIMITED

In assessing carrying capacity is important to determine whether populations are likely to be primarily dry season crunch limited or wet season limited. Drier mixed/sourveld areas in the North Western Transvaal such as Pilanesberg National Park or Lapalala are primarily dry season limited. Dry season crunch periods can be exacerbated in areas subjected to occasional frosts.

On the other hand Hluhluwe and Umfolozi (in Zululand sweetveld) are more wet season limited. In the case of Hluhluwe its moist climate and extensive river frontage means that there is sufficient stop gap dry season browse to tide the rhinos over winter. However the habitat changes in areas away from rivers have resulted in a big decline in carrying capacities. Conversely the increase in "*Acacia*" scrub in adjoining Umfolozi has resulted in an increase in carrying capacities.

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