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THE FEEDING ECOLOGY
OF THE
BLACK RHINOCEROS
IN
HLUHLUWE-UMFOLOZI PARK

PART 2

1999

PART 2

THE FEEDING ECOLOGY OF THE BLACK RHINOCEROS
(*Diceros bicornis minor*)
IN HLUHLUWE -UMFOLOZI PARK,
WITH SPECIAL REFERENCE TO THE PROBABLE CAUSES OF THE HLUHLUWE POPULATION CRASH

BY

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CHAPTER 9

BLACK RHINO FEEDING PATTERNS IV : RESULTS OF POST-BURN SURVEYS

INTRODUCTION

The objectives of the Post-burn feeding surveys discussed in this chapter were to determine the feeding patterns of black rhino immediately after burns (before vegetation flush); and during the Post-burn vegetation flush.

This chapter addresses the following questions:

* Do black rhino change their habitat or species selection because of burns?

* Do they preferentially seek unburnt patches to feed in, or do they feed more on burnt material?

Particular concern was expressed about the possible negative impact of burning on black rhino at a Natal Parks Board meeting in 1988 (Anon 1988). Burning is an important management tool; and fire may alter the distribution and quality of black rhino food in both the short and long term. Natal Parks Board managers were therefore keen to determine the likely impact of burning on black rhino. However, readers keen to get to the "so-what" section discussing the implications of burning on black rhinos must be patient as this current chapter focuses on the results of the Post-burn surveys. The effects of fire on the vegetation, and the implications of burning for black rhino are discussed in more detail in later chapters (15, 16, 20, 21 & 22).

CAVEAT

Readers should bear in mind that Post-burn feeding patterns also represent late dry season and early spring feeding patterns, so that differences in feeding compared to the Grid and Pilot surveys are not due to the influence of burns alone.

In the Post-burn surveys, the term *burn intensity* is used in a different way to how it is normally used. Burn intensity is usually expressed in KW m^{-1} (Van Wilgen & Wills 1988, Van Wilgen *et al*. 1990). However, in the Post-burn surveys, burn intensity was assessed in terms of how "clean" the burn was (i.e. how much biomass remained unburnt). The Post-burn surveys therefore do not distinguish between cooler back burns and hotter head fires. Both types of fire have the potential to remove all above ground biomass (and be rated as severe using the Post-burn survey method); yet these fires have very different patterns of vertical heat distribution and scorching. In turn these differences in fire behaviour may differentially affect palatability of browse on the plots. Never the less the burn severity scale used in the Post-burn surveys will still crudely reflect fire severity.

Offtake levels recorded in the Post-burn surveys were much lower than in the Grid surveys for a number of reasons:

1) The recorded Post-burn black rhino feeding occurred over a much shorter time period than in the Grid and Pilot surveys.

2) As a result of the need to measure a large number of plots, search effort could not be as great as in the Grid and Pilot surveys.

3) By using a bigger transect width (± 4m either side of the transect line in the Post-burn surveys; compared to ± 2.5m in the Grid survey and +2m in Pilot surveys) the probability of not seeing feeding towards plot edges increased.

Thus one cannot directly compare absolute offtake levels between the Post-burn surveys and either the Pilot or Grid surveys. However, as in the Grid surveys, an effort was made to increase search effort whenever visibility declined. One can therefore compare relative offtake levels in different habitats using the Post-burn data.

GENERAL FEEDING PATTERNS AND SPECIES SELECTION IMMEDIATELY POST- BURN AND DURING THE POST-BURN FLUSH IN HLUHLUWE

GENERAL FEEDING PATTERNS

In the first Hluhluwe Post-burn survey, ten routes were walked in two parts of Hluhluwe north - the Hlaza/Nkwakwa and Manzimbomvu areas (Figure 4.4). The Sisuze, Nhlayinde and Manzimnyama areas of the Grid study area were not covered in this survey:

o Black rhino feeding was more frequent and intensive in burnt than in unburnt patches in the Hlaza/Nkwakwa region. Feeding patterns were similar in burnt and unburnt patches of Manzimbomvu (Table 9.1).

o Overall, during the period soon after the burns, 28% more feeding per hectare occurred in burnt areas (23 bottles/ha) than in unburnt ones (18 bottles/ha). **In the month following burns, Hluhluwe North's black rhino were clearly not being forced to feed only in unburnt areas and forest patches.**

The second and main Hluhluwe Post-burn survey covered the whole study area (Figure 4.6), examining immediate post-burn feeding, and feeding during the later post-burn flush period. Unless otherwise stated, reference to the Hluhluwe Post-burn survey refers to this main survey:

o The distribution of feeding in the Hluhluwe study area changed slightly over time after the burns (Figure 9.1), although the general patterns were similar. Immediately post-burn, black rhino feeding levels in the Manzimbomvu/Hidli Vlei, and the upper parts of Hlaza hill, were higher than during the post burn flush. This may be related to grass interference, as grass length increased rapidly in these areas during the flush period (see also Figure 8.19).

Figure 9.1. Distribution of black rhino feeding at different times after burns (based on feeding data from post burn surveys of N Hluhluwe, interpolated by uncontrolled Kriging).

A: Up to 1 month after burns

B: 1 to 3 months after burns

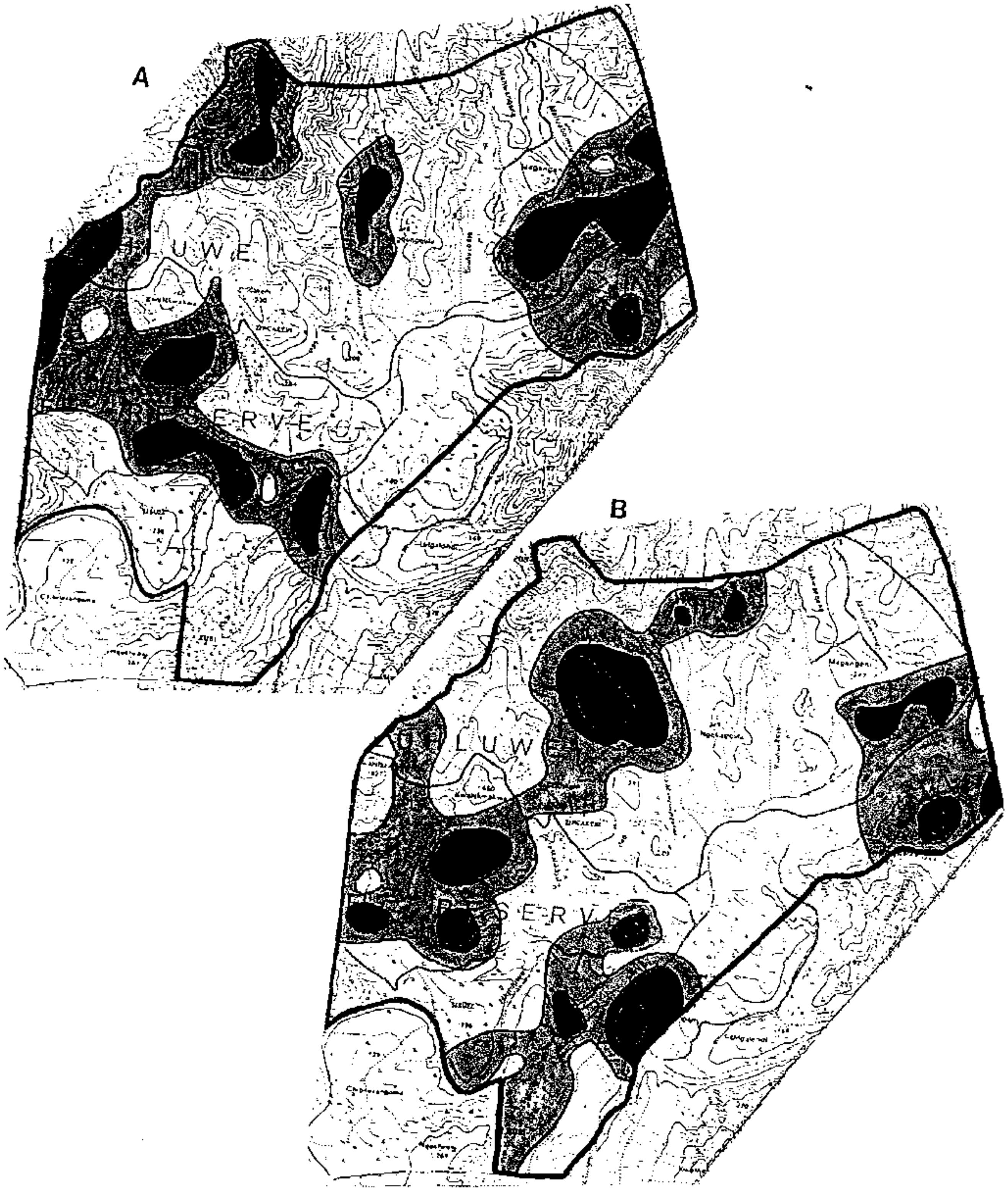


Table 9.1: Summary data for First Hluhluwe Post-Burn Survey.

	HLAZA/NKWAKWA	MANZIMBOMVU
% of plots burnt	60%	68%
% with feeding: BURNT	29%	19%
% with feeding: UNBURNT	16.5%	21%
Bottles eaten / hectare:		
BURNT	26.7	20.6
UNBURNT	16.6	19.9

SPECIES COMPOSITION OF THE POST-BURN DIET COMPARED WITH FEEDING AT OTHER TIMES

Figures 9.2 to 9.6, graphically contrast the proportional composition of the woody diet after burns with other survey periods. All species shown made up at least 1.75% of the woody diet in one of the four periods.

Table 9.2 gives the percentage contribution to the woody diet of species browsed immediately post-burn on the first Hluhluwe Post-burn survey (covering part of the study area only). Tables 9.3 and 9.4 respectively show immediate post-burn, and post-burn flush, dietary composition over the entire study area, based on the results of the second Post-burn survey.

Table 9.5 examines the contribution to Hluhluwe post-burn woody diets of each species, split up according to browsing on *burnt* compared to *unburnt* trees.

The Euphorbiaceae duo *S.africana* (10.01%) and *A.glabrata* (12.45%) were indicated as key post- burn period food species. "*Acacia*" species contributed a further 38.68% of the Hluhluwe study area post- burn diet.

Z.mucronata, D.rotundifolia, L.javanica, D.lycioides, K.floribunda and *E.divinorum* were only eaten in any quantity immediately after the burns (Figure 9.2).

Z.mucronata, was classed as intermediate in acceptance in the Grid survey where it accounted for 1.23% of the total woody diet. Soon after the burns feeding levels on this species increased in importance to account for 7.10% of the total woody diet. Thereafter, it returned to previous levels (1.86%).

Similar brief increases in browsing importance immediately post-burn were recorded for *L.javanica* (Grid 0.41% , Post-burn 4.07% ,Flush 0.66%) , *D.rotundifolia* (Grid 0.81%, Post-burn 3.78%, Flush 1.74%), *E.divinorum* (Grid 0.00%, Post-burn 3.56%, Flush 0.00%), and possibly for *D.lycioides* (Grid 0.84%, Post-burn 1.92%, Flush 0.66%).

FIGURE 9.2

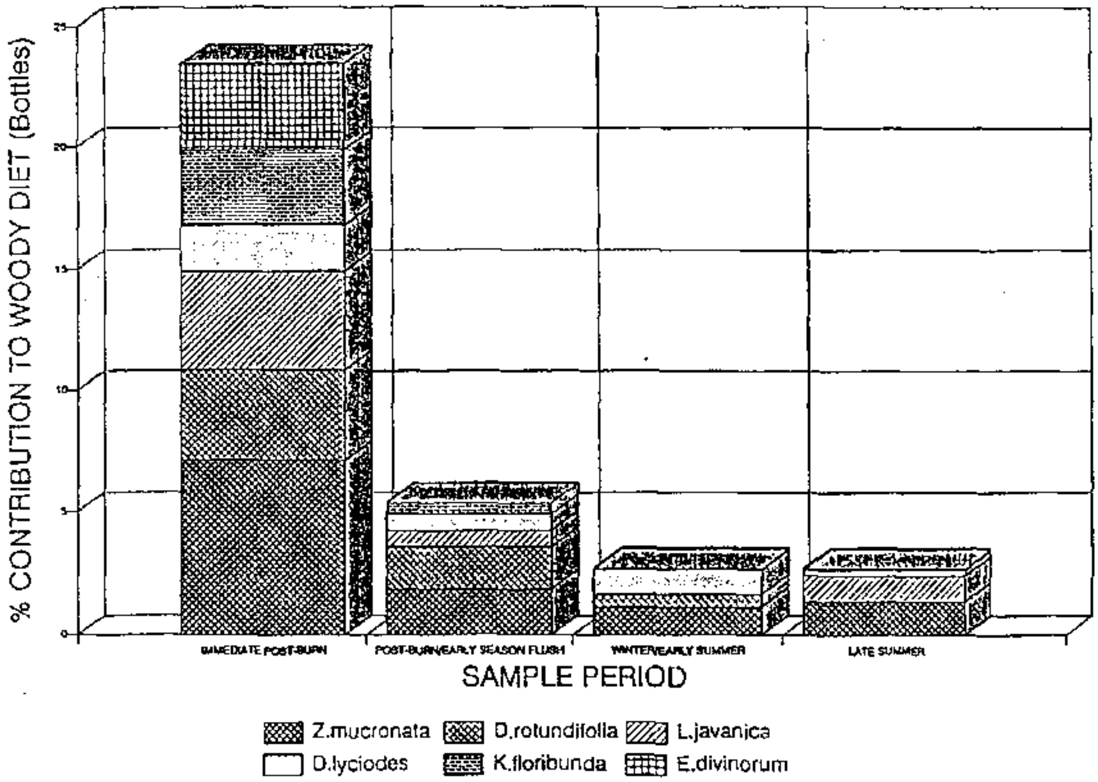


FIGURE 9.3

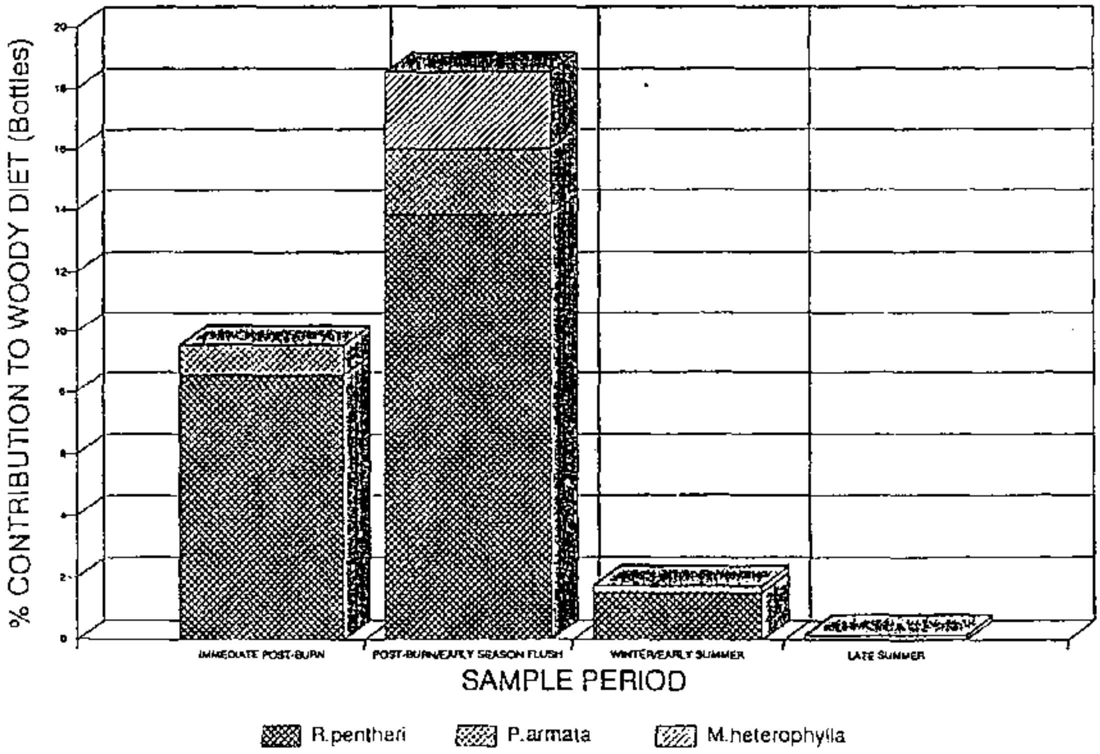


FIGURE 9.4

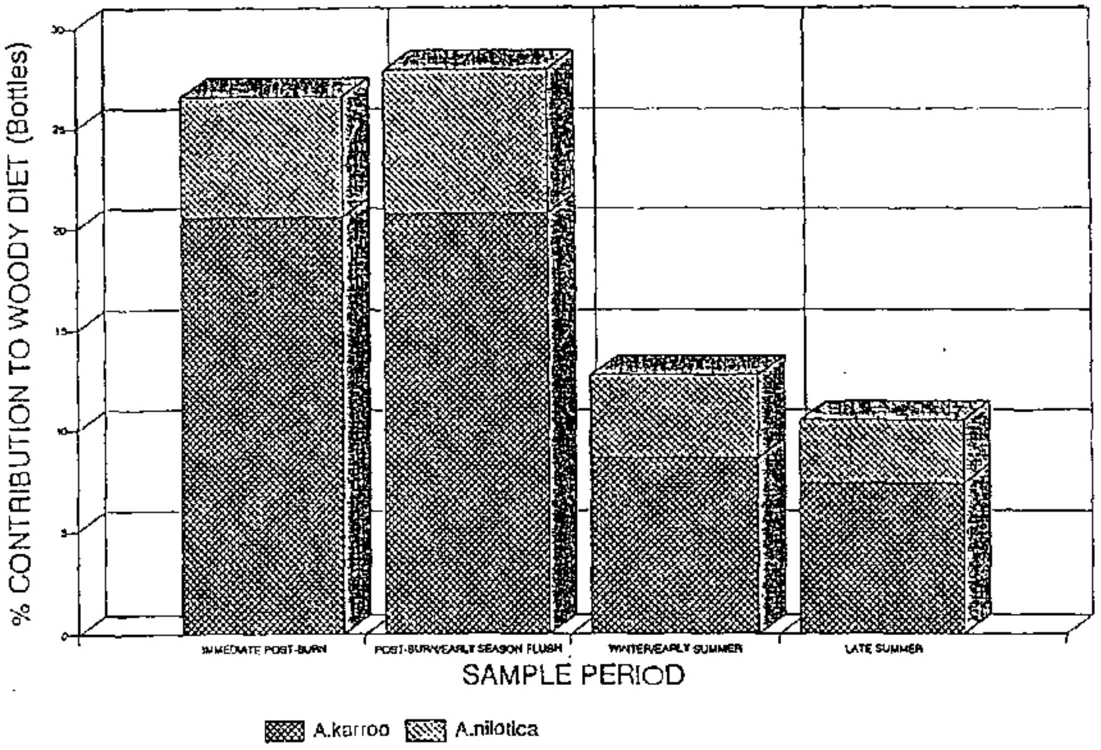


FIGURE 9.5

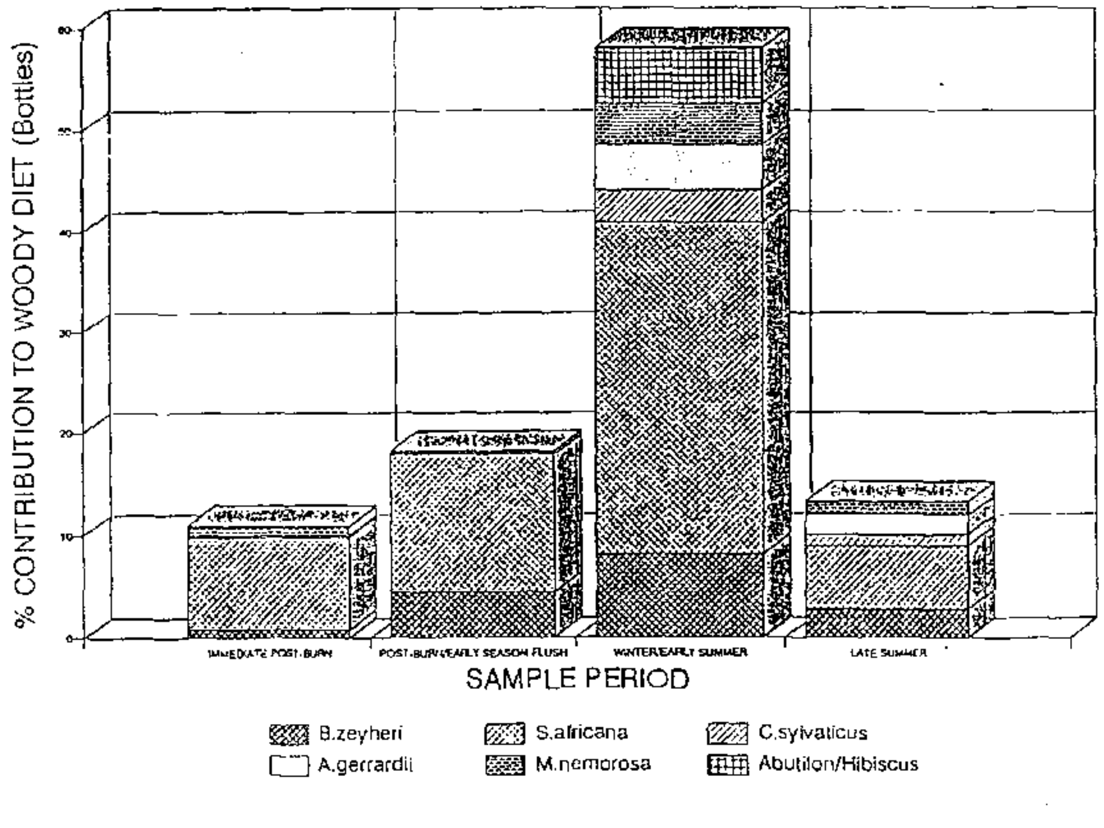


FIGURE 9.6

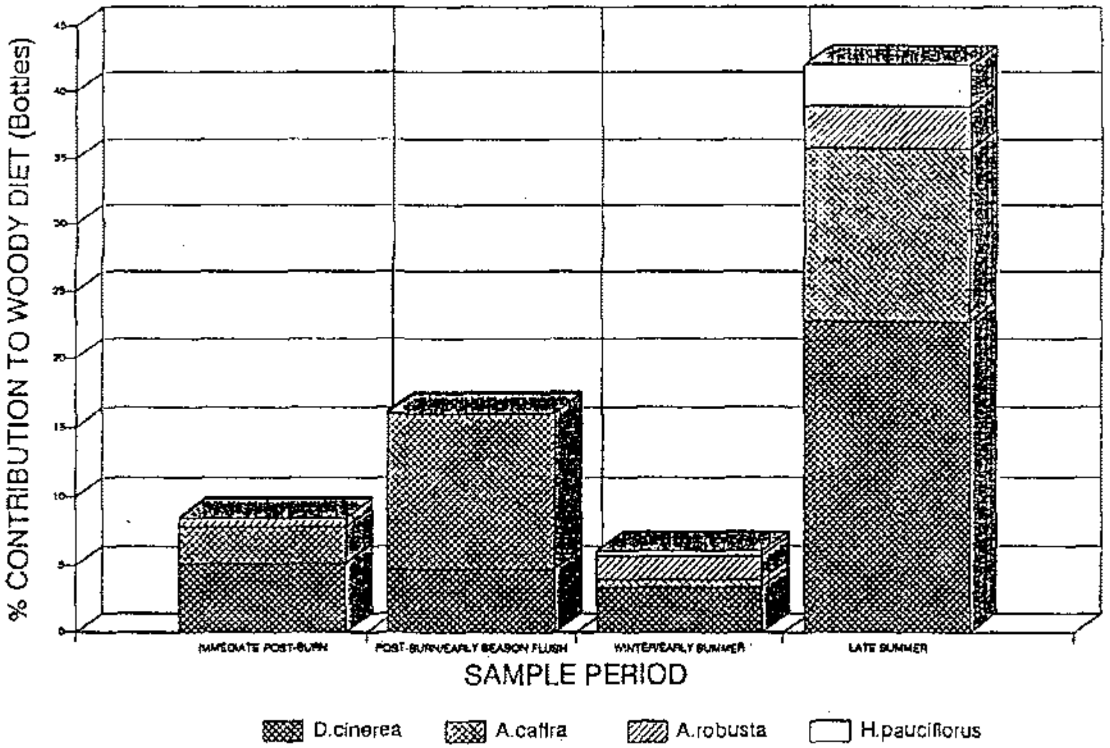

% CONTRIBUTION TO WOODY DIET (Bottles)
45
40
35
30
25
20
15
10
5
0
IMMEDIATE POST-BURN
POST-BURN/EARLY SEASON FLUSH
WINTER/EARLY SUMMER
LATE SUMMER
SAMPLE PERIOD
D.cinerea
A.caffra
A.robusta
H.pauciflorus

Table 9.2

PERCENTAGE CONTRIBUTION OF EACH SPECIES TO TOTAL WOODY BROWSE OFFTAKE
IMMEDIATE POST BURN BROWSING - FIRST HLUHLUWE POST-BURN SURVEY
(NB. Not all of Hluhluwe Grid Study Area Surveyed in First Post Burn Survey)

Species	% Browsing
Acacia karroo	37.10
Diospyros lycioides	11.30
Spirostachys africana	7.20
Dichrostachys cinerea	5.80
Acacia robusta	3.40
Dombeya rotundifolia	3.40
Rhus pentheri	3.40
Maytenus nemorosa	3.20
Acalypha glabrata	2.60
Solanum mauritianum/giganteum	2.10
Lippia javanica	1.90
Berchemia zeyheri	1.70
Heteropyxis natalensis	1.50
Diospyros simii	1.40
Dombeya burgessiae	1.40
Zizyphus mucronata	1.40
Acacia nilotica	1.30
Dovyalis caffra	1.30

Table 9.3

PERCENTAGE CONTRIBUTION OF EACH SPECIES TO TOTAL BROWSE OFFTAKE
HLUHLUWE GRID STUDY AREA - IMMEDIATE POST BURN FEEDING
(OLD BOTTLES EATEN IN THE MAJOR 1990 HLUHLUWE POST-BURN SURVEY)

Species	% Browsing
Acacia karroo	20.51
Acalypha glabrata	11.45
Spirostachys africana	9.21
Rhus pentheri	8.57
Ziziphus mucronata	7.10
Acacia nilotica	6.06
Dichrostachys cinerea	5.13
Lippia javanica	4.07
Dombeya rotundifolia	3.78
Euclea divinorum	3.56
Kraussia floribunda	3.10
Acacia caffra	2.72
Solanum spp.	1.96
Diospyros lycioides	1.92
Ozoroa engleri	1.31
Acacia burkei	1.18
Plectrionieila armata	1.03
Acacia spp.	1.01
Maytenus nemorosa	1.00
Acacia robusta	.82
Euclea racemosa	.79
Berchemia zeyheri	.76
Coddia rudis	.59
Vernonia subuligera	.47
Acacia gerrardii	.35
Dombeya burgessiae	.35
Maytenus senegalensis	.35
Crotolaria capensis	.26
Celtis africana	.17
Galpinia transvaalica	.17
Dalbergia armata	.13
Rhoicissus tridentata	.10
Euclea crispa	.03

Table 9.4

PERCENTAGE CONTRIBUTION OF EACH SPECIES TO TOTAL BROWSE OFFTAKE
HLUHLUWE GRID STUDY AREA - POST BURN FLUSH FEEDING
(NEW BOTTLES EATEN IN THE MAJOR 1990 HLUHLUWE POST-BURN SURVEY)

Species	% Browsing
Acacia karroo	20.73
Rhus pentheri	13.84
Spirostachys africana	13.72
Acacia caffra	11.43
Acacia nilotica	7.19
Dichrostachys cinerea	4.76
Berchemia zeyheri	4.48
Acalypha glabrata	4.29
Maytenus heterophylla	2.55
Plectrionielta armata	2.18
Ziziphus mucronata	1.86
Oombeya rotundifolia	1.74
Acacia schweinfurthii	1.50
Adenopodia spicata	1.34
Diospyros simii	1.15
Phyllanthus reticulatus	.92
Diospyros lycioides	.66
Lippia javanica	.66
Solanum spp.	.61
Kraussia floribunda	.51
Maytenus nemorosa	.50
Unknown	.44
Ozoroa engleri	.42
Ochna natalitia	.33
Capparis sepiaria	.25
Ficus spp.	.25
Justicia sufritescens	.25
Maytenus senegalensis	.25
Rhus rehmanniana	.23
Bersama lucens	.19
Dalbergia armata	.19
Dombeya burgessiae	.19
Ormocarpum trichocarpum	.16
Rhoicissus tridentata	.13
Acacia burkei	.09

Table 9.5

HLUHLUWE GRID STUDY AREA - IMMEDIATE POST-BURN AND POST-BURN FLUSH WOODY DIETS (57.99% of recorded eating = Post-Burn Flush; 68.13% of Immediate Post-Burn Offtake on burnt trees 56.97% of Post-Burn Flush offtake on burnt trees; 2.44 times more offtake on paths yet paths only made up an estimated 41.84% of total sample transect length.)

Species/Burn	% Immediate Post-Burn Diet	% Post-Burn Flush Diet
Burnt Acacia karroo	18.42	17.70
Unburnt Acalypha glabrata	11.32	2.52
Burnt Rhus pentheri	7.48	7.88
Unburnt Spirostachys africana	6.94	12.74
Burnt Ziziphus mucronata	6.75	.25
Burnt Acacia nilotica	6.06	6.94
Burnt Dichrostachys cinerea	5.13	2.58
Burnt Dombeya rotundifolia	3.78	1.50
Burnt Euclea divinorum	3.56	
Burnt Lippia javanica	3.19	.25
Burnt Acacia caffra	2.72	11.43
Burnt Spirostachys africana	2.27	.98
Unburnt Acacia karroo	2.09	3.03
Burnt Kraussia floribunda	1.74	.13
Burnt Diospyros lycioides	1.39	.41
Unburnt Kraussia floribunda	1.35	.38
Burnt Solanum spp.	1.31	.16
Unburnt Ozoroa engleri	1.31	.16
Unburnt Acacia burkei	1.18	
Unburnt Rhus pentheri	1.09	5.96
Burnt Acacia spp.	1.01	
Unburnt Maytenus nemorosa	1.00	.50
Unburnt Lippia javanica	.88	.41
Unburnt Berchemia zeyheri	.76	4.23
Burnt Plectroniella armata	.68	.19
Unburnt Solanum spp.	.65	.44
Unburnt Euclea racemosa	.65	
Unburnt Coddia rudis	.59	
Burnt Acacia robusta	.56	
Unburnt Diospyros lycioides	.52	.25
Burnt Vernonia subuligera	.47	
Unburnt Plectroniella armata	.35	1.99
Unburnt Ziziphus mucronata	.35	1.61
Burnt Maytenus senegalensis	.35	.25
Burnt Dombeya burgessiae	.35	.19
Burnt Acacia gerrardii	.35	
Unburnt Acacia robusta	.26	
Unburnt Crotolaria capensis	.26	
Burnt Galpinia transvaalica	.17	
Unburnt Celtis africana	.17	
Burnt Euclea racemosa	.14	
Burnt Acalypha glabrata	.13	1.77
Unburnt Dalbergia armata	.13	.19
Burnt Rhoicissus tridentata	.10	.13
Burnt Euclea crispa	.03	
Unburnt Dichrostachys cinerea		2.19
Burnt Maytenus heterophylla		2.05
Unburnt Acacia schweinfurthii		1.50
Unburnt Adenopodia spicata		1.09
Unburnt Diospyros simii		.99
Unburnt Phyllanthus reticulatus		.66
Unburnt Maytenus heterophylla		.50
Burnt Ochna natalitia		.33
Burnt Adenopodia spicata		.25

Most recorded feeding on *Euclea* species in the Hluhluwe study area took place soon after the burns. *Euclea* species, and especially *E.divinorum*, made up 4.77% of the feeding soon after the burns in Hluhluwe. In contrast *Euclea* species made up only 0.62% of the Hluhluwe Grid Survey diet. *R.pentheri* and *P.armata* browsing increased after the burns to reach a peak during the post-burn/early season flush period - before declining to low levels for the rest of the year (Figure 9.3). The highest level of *M.heterophylla* browsing also occurred during the flush period.

Rhus pentheri became the third most important species eaten in the post burn flush period (14.60% of the diet). Reasons for this may be that this species was one of the first to flush that year, and acted as a stop-gap "filler" till other species flushed. The increasing use of *R.pentheri* after the burns occurred mainly in the southern reaches of the study area (Figure 9.7), where this species averaged 1.5 to 3.5m in size, and was often slightly but not badly burnt. It appeared to be more available to rhino than elsewhere (eg. in the taller woodlands of *A.nilotica*, *E.racemosa* and *B.zeyheri*). By way of contrast, *R.pentheri* only accounted for just less than 1% of total browsing in the Grid survey (summer).

A.karroo and *A.nilotica* were important dietary items throughout the year, but were more heavily browsed during the post burn and post-burn flush period than later in the growing season (Figure 9.4)[#1].

In Hluhluwe, *A.karroo* contributed the most to immediate post-burn and post-burn flush diet. After the burns, black rhino chose to feed more in more open areas where the favoured size classes of this species predominated. *A.karroo* is also one of the first species to flush; and the high feeding levels on this species at this time may in part be function of *A.karroo*'s greater accessibility after burns, as fire had removed grass interference.

A.nilotica showed a similar pattern to *A.karroo* of declining dietary importance as the season progresses. In the study area *A.nilotica* declined in importance from the post- burn flush period (7.58%) to late summer (3.21%).

B.zeyheri, Croton sylvaticus, M.nemorosa, A.gerrardii, Abutilon/Hibiscus species and *S.africana* were eaten less after the burns, but contributed most (over half of recorded eating) to the winter/early summer diet (Grid survey- Old bottles- see Figure 9.5).

High levels of *A.caffra* browsing were recorded during the post- burn/early season flush period, and also during late summer. *A.robusta* and *H.pauciflorus* were also important contributors to the late summer woody diet (Figure 9.6).

D.cinerea was not as important a post-burn dietary item as *A.karroo*, although it did account for 5-6% of the Hluhluwe diet during the post-burn period. This contrasted with late summer where its contribution to the diet increased, and it became more important in the diet than *A.karroo*. A possible explanation is that *D.cinerea* has a very wide ecological tolerance, and is more widespread than *A.karroo*; and is often found and browsed in shorter grass areas (on hill crests and in developing woodlands). It is also one of the latest of the "*Acacias*" to flush.

In the Hluhluwe Grid survey, *A.caffra* was classed as an important dietary item (5.21% of the woody diet) that was intermediate in acceptance (Free Preference Index 0.92). Soon after the burns, feeding levels on this species declined (2.62% of the immediate post-burn woody diet. However, during the post-burn/early season flush period, feeding on *A.caffra* increased substantially, so that it became the fourth most important species making up 11.43% of the diet. *A.caffra* flushed prolifically after the burns, making it one of the most abundant food sources in the northern part of the study area at that stage of the season. This, combined with reduction in grass interference from the burns, may account for its increased importance at that time.

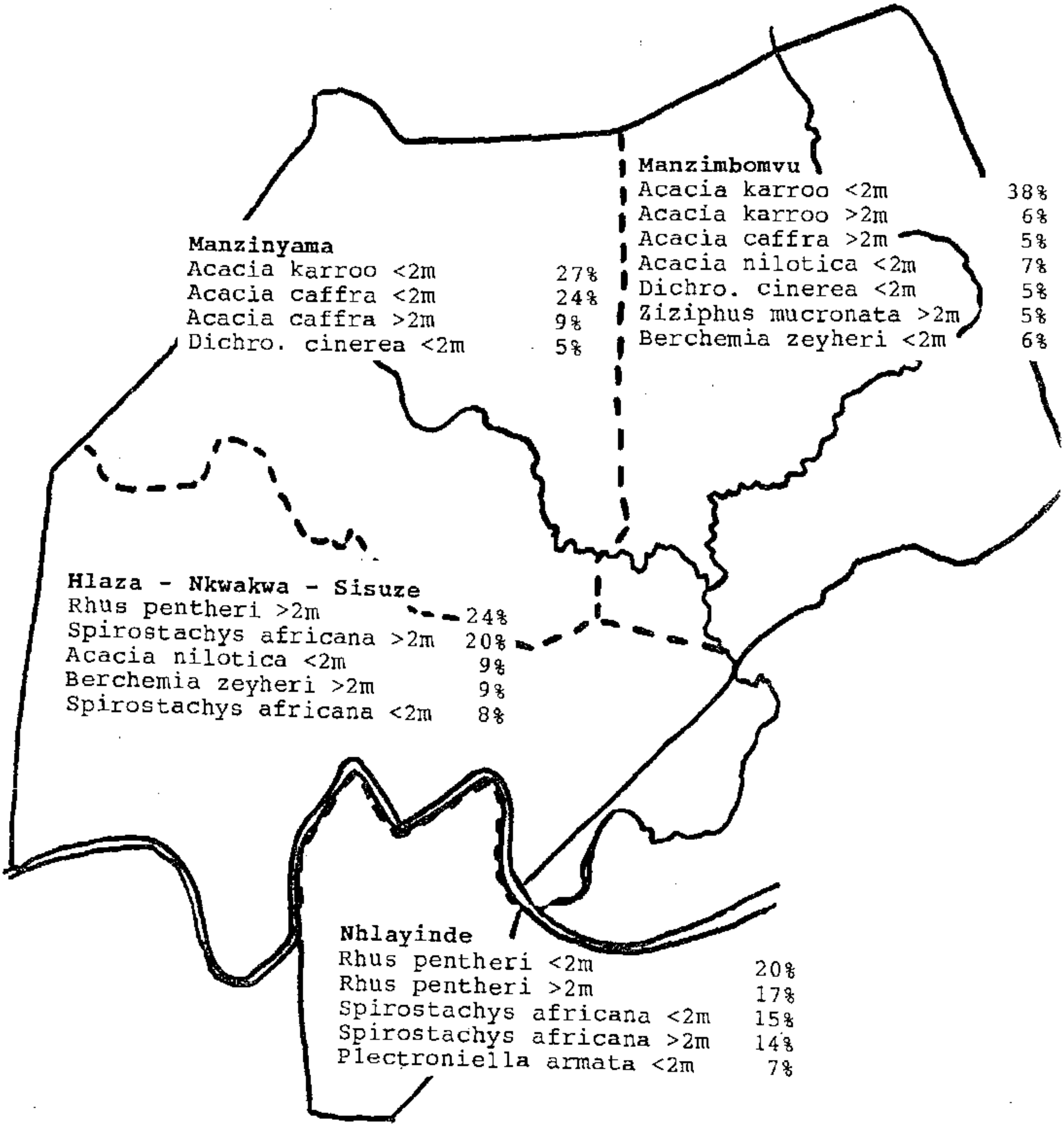
In Hluhluwe a much larger proportion of the post-burn woody diet was made up of species which were classified as rejected at other times of the year. 30.55% of the immediate post-burn woody diet of the Main Post-burn survey was made up of these rejected species (This figure was 25% for the first Post-burn survey. The percentage declined to 17.83% of the post-burn flush diet against only 6.80% of the Grid survey diet. Examples of such species include *R.pentheri, L.javanica, E.divinorum, K.floribunda, D.rotundifolia, D.lycioides, Ozoroa engleri, Plectroniella armata, E.racemosa, Vernonia subuligera, M.senegalensis, Rhoicissus tridentata,* *E.crispa*, *Phyllanthus reticulatus*, *Ochna natalita*, *Rhus rehmanniana* and *Rhoicissus tridentata*.

The question is : Why did browsing of unpalatable species increase during the early growing season post-burn flush period?

> Condensed tannin concentrations tend to be higher in the leaves of unpalatable species than in the foliage of palatable deciduous species, or relatively palatable evergreens (Cooper *et al.* 1985). A threshold concentration of condensed tannins equal to 5% of dry mass appeared to distinguish between palatable and unpalatable species during the mature leaf phase (Cooper *et al.* 1985). Tannins reduce digestibility by forming complexes with proteins which inhibits the action of digestive action of proteolytic enzymes (Owen-Smith 1982). A study of browsing by kudu, impala and goat in a savanna area found that early in the wet season, certain normally unpalatable species became highly acceptable (Owen-Smith & Cooper 1987); yet levels of condensed tannins were no lower than they were in mature leaves of these species (Owen-Smith & Cooper 1988). However, they showed that otherwise unpalatable species were favoured at the start of the wet season because protein levels were elevated in young foliage relative to tannin contents (Owen-Smith & Cooper 1988; Cooper *et al.* 1988). Similar reasons may account for the increased browsing of unpalatable species by black rhino during the early growing season period. (Of the "*Acacias*", *A.karroo* and *A.nilotica* have amongst the highest of condensed tannin levels (Owen-Smith pers. comm.), and it is interesting that feeding on these species increased during the post- burn period).

Figure 9.7 summarises the composition of immediate post-burn and post-burn flush feeding in different parts of the Hluhluwe study area. It shows that *A.karroo* and *A.caffra* dominate the diet in the north of the area, while *R.pentheri* and *S.africana* dominate the diet in the south after burns.

FIGURE 9.7 The percentage contribution to black rhino feeding of the main woody species 0-3 months after burns, in four sections of the Hluhluwe study area. (ie. immediately post-burn and during the post-burn flush period).



IMMEDIATE POST-BURN FEEDING PATTERNS IN UMFOLOZI

GENERAL FEEDING PATTERNS IN UMFOLOZI

Five routes within the Umfolozi study area were surveyed in areas where burns had been put in (Figure 4.5). One of these routes was entirely unburnt (Thobothi-Mbhuzane). Interestingly only 24.8% of plots in areas where burns were put in, were actually burnt in 1989. As relatively little feeding was encountered in the study area, additional plots were surveyed near permanent water sources outside but near the study area, where feeding was more intense. Only 550 Post-burn survey plots and about 55,000 trees were sampled in Umfolozi, compared to the 2,381 plots and about 694,000 trees sampled in the two Hluhluwe Post-burn surveys.

Within the study area, 12.7% of burnt plots contained feeding; while 14.3% of unburnt plots contained feeding. However, in burnt plots, 18 bottles /ha were eaten as opposed to 11.5 bottles/ha in unburnt plots. Thus on average, the feeding intensity was greater in burnt patches. (The bottles eaten at this time of year in Umfolozi were less than those eaten in Hluhluwe, as many black rhino had moved out of the Umfolozi study area during the Post-burn survey due to lack of water).

Feeding intensities on the "burnt" routes were contrasted with the one route that was 100% unburnt. Along burnt routes, 13.9 % of plots had feeding, at an intensity of 13.1 bottles /ha, while 11% of plots had feeding at 6.9 bottles/ha along the unburnt Thobothi-Mbhuzane route.

SPECIES SELECTION IMMEDIATELY POST-BURN IN UMFOLOZI

Table 9.6 summarises the woody species browsed during the first September immediate Post-burn survey:

o *Spirostachys africana* dominated the black rhinos' diet at this time (36% of the diet, compared to about 25% in summer), with microphyllous species receiving correspondingly less feeding attention than at other times of year.

Table 9.6

PERCENTAGE CONTRIBUTION OF EACH SPECIES TO TOTAL WOODY BROWSE OFFTAKE
IMMEDIATE POST BURN BROWSING - UMFOLOZI POST-BURN SURVEY
(NB. Not all of Umfolozi Grid Study Area was surveyed in this survey
Sampling also favoured sites close to and far from permanent water.)

Species	% Browsing
Spirostachys africana	35.70
Schotia capitata	5.80
Pappia capensis	5.60
Maytenus nemorosa	5.30
Solanum mauritianum/giganteum	5.00
Acacia tortilis	4.30
Acacia grandicornuta	3.20
Coddia rudis	2.90
Commiphora neglecta	2.50
Acacia nilotica	2.20
Azima tetracantha	2.20
Ormocarpum trichocarpum	2.10
Acacia karroo	2.00
Dichrostachys cinerea	1.40
Pseudoasparagus spp.	1.30
Acacia borleae	1.10
Acacia gerrardii	1.10
Ehretia rigida/amoena	1.10
Euclea undulata	1.10
Sideroxylon inerme	1.10

o *M.nemorosa, S.capitata, P.capensis* and *E.undulata* accounted for 17.8% of recorded offtake immediately post-burn, which was nearly three times that recorded in the Grid survey (6.75%). This suggests that in Umfolozi, black rhino feed more in thicket and bush-clump vegetation immediately after the burns (or in late winter) than they do at other times of the year.

o Unpalatable *Euclea* species were noted as occasionally being quite heavily eaten in Umfolozi immediately post-burn. West of Mbulunga, *Euclea undulata* contributed 13% of feeding. Browsing was also noted on burnt *E.divinorum* at Sontuli loop; although in this case the browsed trees were outside the survey transects.

EFFECT OF WATER DISTRIBUTION ON POST-BURN FEEDING IN UMFOLOZI

o Feeding intensity and frequency were strongly related to the presence of water at this time of year. Routes adjacent to a permanent water supply (Sontuli, Thobothi stream area) had on average 21.7 bottles/ha eaten, while feeding near water-holes (Nqutshini road crossings; Mpapha hide) was 54.6 bottles/ha. Mean offtake was only 4.7 bottles/ha in areas further from water (eg Gqoyini). Black rhino appeared to have concentrated near water during this survey. **Water distribution (and related spizes composition) in the drier Umfolozi therefore influenced late dry-season habitat suitability more than whether or not plots had been burnt.**

To some extent, the distribution of rhino near to drainage lines at this time of year may also reflect the fact that plants (via the soils) retain more moisture in these areas, and are more succulent and palatable than the same species further from water, providing some "green bite" during the dry season.

FEEDING PATTERNS DURING THE POST-BURN PERIOD IN HLUHLUWE, IN RELATION TO HABITAT STRUCTURE AND COMPOSITION

All parts of the Hluhluwe Grid study area were covered in the main Hluhluwe Post-burn survey. The 1 687 (50x8m) plots were analysed using both Continuous and Categorical Formal Inference-based Recursive Modelling (CONFIRM and CATFIRM, Hawkins 1990). FIRM is a largely assumption-free method of exploring the relationship between a dependent variable and a set of predictors. The data set is partitioned into two to four groups defined by a range of values of one of the predictors. Each of the successor groups is in turn similarly partitioned into two or more groups defined by ranges of values of one of the predictors. The analysis continues until some termination rule indicates that none of the sub-groups can be split further. Each split is designed to create further nodes which are in some sense maximally internally homogeneous. Output is used to create a dendrogram. FIRM is ideally suited to discovering interactive effects in the data. Details of the FIRM methodology and analysis options selected are listed in Chapter 5.

The optional Appendix 9.1 (copy lodged with KZNNCS and available to examiners on request) contains an edited summary of the results (ANOVA tables, sample sizes, standard deviations and standard errors) of the four main FIRM runs.

As an to aid interpretation of the results of the Post burn surveys, interested readers may wish to refer to Chapter 20 for an analysis of the patterns of species associations revealed by the Hluhluwe Post-burn data.

FEEDING PATTERNS IN RELATION TO HABITAT

CONFIRM: RUN 1

Mean browsing levels for each split predictor after analysis of node 1 are shown in Figure 9.8. The dotted line in Figure 9.8 represents average feeding levels per plot. Plots experiencing light/medium intensity fires had higher levels of black rhino feeding than unburnt plots. During the late winter/early spring period black rhino feeding levels were also above average in lower lying communities with *E.divinorum* and *S.africana* as dominants; but were low in forest margin plots. Offtake levels appeared to increase near or on paths. Feeding levels were also above average in *A.caffra* dominated plots; and below average in plots with tall *A.nilotica* and *E.racemosa* as dominants. Physiognomically feeding was above average in plots with higher densities of lower size class trees; while open grassland and closed woodland/forest plots had lower than average levels of feeding.

The CONFIRM dendrogram (Figure 9.9) summarises the results of the analyses where the variables for Burn severity, Tree density and Path were deemed *monotonic*. The bold lines and boxes show the significant splits and nodes when the more conservative 1% raw and Bonferroni significance levels were used (see Chapter 4 for further details of analysis). In Figure 9.9 small squares and bold dotted lines separate the outlier nodes from the other nodes, which are indicated by bigger squares. Mean browsing levels (in mean browsing units or MBU) for each CONFIRM node are listed inside the boxes on Figure 9.8. After excluding three outlier groups which contained 3 or less plots, a total of nine groups were formed using the conservative 1% significance levels. Preference and Importance ratios for the nine key nodes and selected subdivisions from the first CONFIRM run are listed in Table 9.7.

Burn was selected as the best predictor to split node 1 on the first CONFIRM run. However, it should be remembered that fire intensities are strongly influenced by vegetation physiognomy. For example, tall grass *A.caffra* dominated sites are more prone to severe burns than shorter grassed closed woodland dominated by tall *E.racemosa* and tall *A.nilotica*. Therefore, the first predictor here (burn) involves more than simply describing the influence of burn severity on habitat suitability. However, subsequent FIRM analyses confirmed that **burn intensity influences habitat suitability in its own right, in addition to the influence of vegetation physiognomy and spize composition**. **Browsing levels were highest on plots that had experienced low to intermediate intensity burns.** Plots experiencing Light (lightly/poorly burnt) and Medium burn severities (well burnt but with some grass tufts not fully burnt) were lumped together. These plots, on average, had 2.88 times more browsing (0.41 MBU n=261) than unburnt plots. **Browsing on unburnt plots was well below average levels.** Mean browsing on unburnt plots (0.14 MBU, n=450) was only two thirds of average browsing levels.

FIGURE 9.8

MEAN BROWSING LEVELS FOR EACH SPLIT PREDICTOR AFTER ANALYSIS OF NODE 1

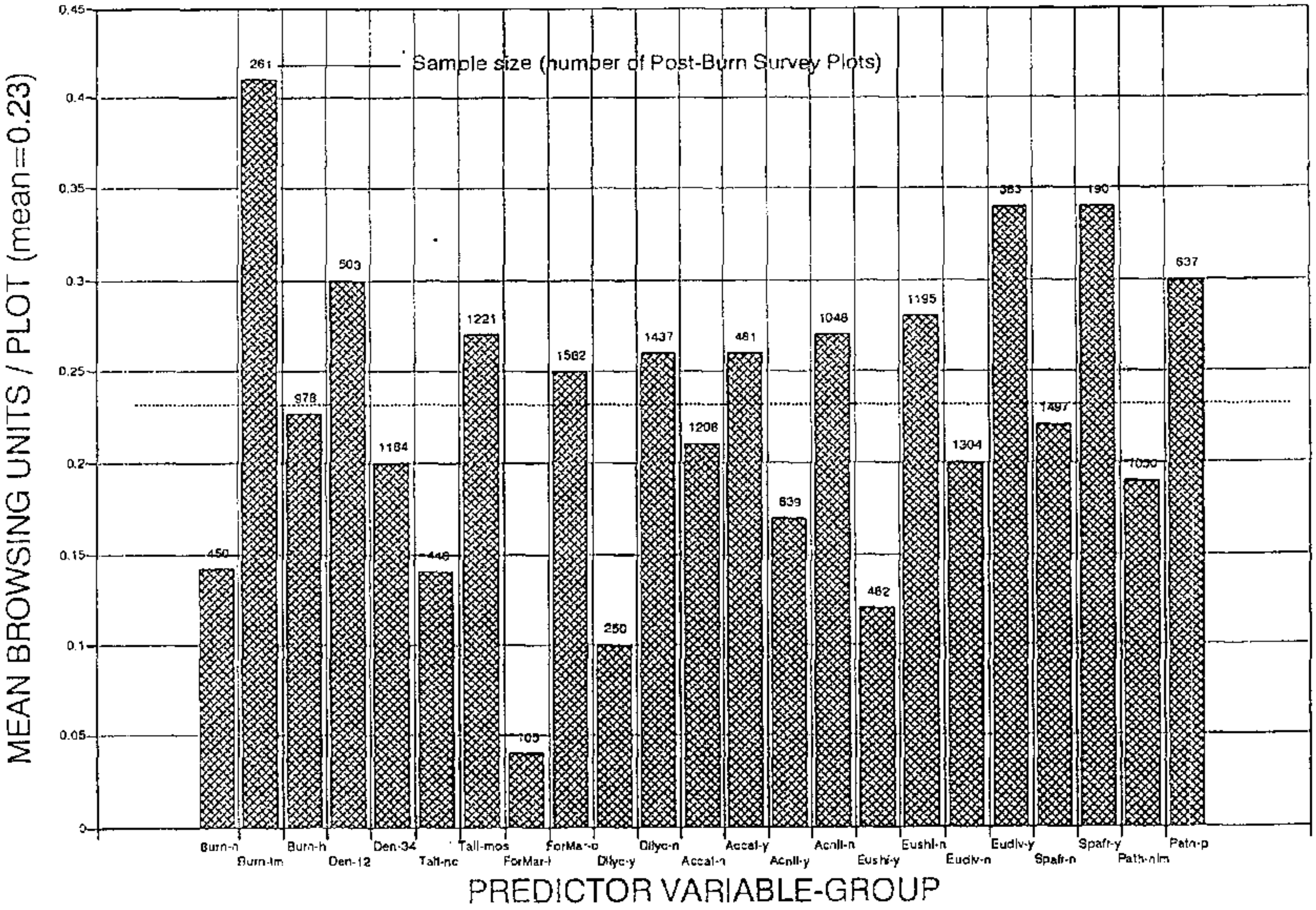


FIGURE 9.9 Dendrogram of the CONFIRM run 1 of the Hluhluwe Main Post Burn Survey data (n=1,687 plots). Mean browsing per plot is expressed in Mean Browsing Units (MBU). The nine key nodes significant at the 1% level (■), and four outlier nodes are shown (▪).

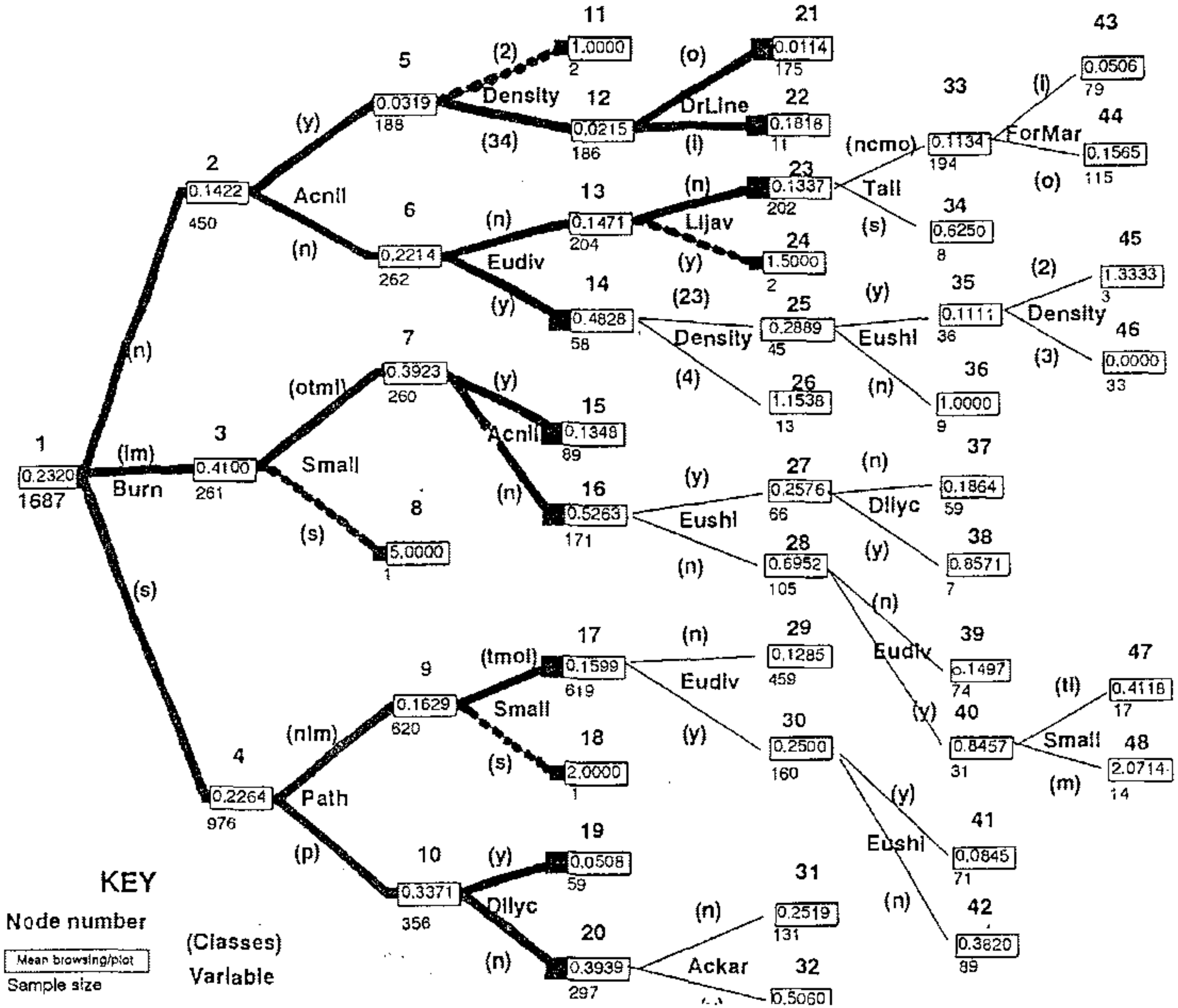


Table 9.7

The nine key nodes and selected subdivisions derived from CONFIRM analysis of the Hluhluwe Post Burn Transects (n=1,687). Mean browsing per plot is expressed in Mean Browsing Units (MBU). The percentage contribution to diet of each node is expressed as the percentage of total BU eaten on all plots. Preference indices and symbols are the same as the rest of Chapter 5. Burn,Density and Path Predictors were monotonic. The nine key nodes were significant at the 1% level.

NODE Predictor Set	PrefIndx		%Diet	MBU	n	%Plots	PrefRANK	ImpRANK	FreqRANK
NO BURN - TALL A.nilotica - DENSITY 34 - OUT OF DRAINAGE LINE	0.05	—	0.51	0.011	175	10.37	14	13.5	3
NO BURN - TALL A.nilotica - DENSITY 34 - IN DRAINAGE LINE	0.78	-	0.51	0.182	11	0.65	8	13.5	14
NO BURN - NO TALL A.nilotica - NO E.divinorum	0.63	-	7.65	0.147	204	12.09	9	7	2
NO BURN - NO TALL A.nilotica - E.divinorum	2.08	**	7.14	0.483	58	3.44	4	8	12
LIGHT/MEDIUM BURN - TALL A.nilotica	0.58	-	3.06	0.135	89	5.28	10	10	6.5
LIGHT/MEDIUM BURN - NO TALL A.nilotica	2.27	**	22.96	0.526	171	10.14			
Sub-division: TALL E.racemosa	1.11		4.34	0.257	66	3.91	6	9	10
Sub-division: NO TALL E.racemosa	2.99	***	18.62	0.695	105	6.22			
Sub-Sub-division: NO E.divinorum	2.15	**	9.44	0.500	74	4.39	3	3	8
Sub-Sub-division: E.divinorum	5.00	***	9.18	1.161	31	1.84	1	4	13
SEVERE BURN - <67% OF PLOT ON PATH	0.70	-	25.77	0.163	620	36.75			
Sub-division: NO E.divinorum	0.55	-	15.05	0.129	459	27.21	11	2	1
Sub-division: E.divinorum	1.08		10.20	0.250	160	9.48			
Sub-Sub-division: NO E.racemosa	1.64	*	8.67	0.382	89	5.28	5	5	6.5
Sub-Sub-division: E.racemosa	0.36	–	1.53	0.085	71	4.21	12	11	9
SEVERE BURN - >67% OF PLOT ON PATH - D.lycioides	0.22	—	0.77	0.051	59	3.50	13	12	11
SEVERE BURN - >67% OF PLOT ON PATH - NO D.lycioides	1.70	*	29.85	0.394	297	17.61			
Sub-division: NO A.karroo	1.08		8.42	0.252	131	7.77	7	6	5
Sub-division: A.karroo	2.18	**	21.43	0.506	166	9.84	2	1	4
OUTLIERS					3				

The remaining 58% of plots experienced severe burns where all visible biomass was burnt. Browsing in these plots (0.23 MBU, n=976) was close to average levels.

Post-burn browsing was 50% higher in plots with low densities of small trees (Densities 1,2 0.30 MBU, n=503), compared to plots with higher small tree densities, where visibility and movement were often impeded (Densities 3,4, 0.20 MBU, n= 1184).

Subsequent predictors chosen after Burn, clearly showed that species/spize composition uniquely affected post-burn habitat suitability (ie by accounting for more variation not already explained by burning severity).

Communities with *D.lycioides* and tall *E.racemosa*'s as dominants had markedly less feeding in them than other communities. Woodland communities dominated by tall *A.nilotica*'s were also strongly rejected after the burns.

Communities dominated by *A.caffra* had slightly higher than average post-burn browsing levels.

Communities where *E.divinorum* and/or *S.africana* were dominant species, were especially favoured. This indicates that low lying areas near rivers are important feeding areas in the late winter/early growing season post-burn period. The favouring of *Euclea divinorum* dominated communities may reflect the feeding on *A.nilotica, R.pentheri, D.cinerea* and *S.africana* which occurred in these communities.

Within each of the three "burn" nodes 2, 3 and 4; habitat preferences were strongly related to which species and spizes were dominant.

On Unburnt plots (Node2 mean 0.142 MBU) plots with *D.lycioides* (0.03 MBU), *D.cinerea* (0.05 MBU), tall *A.nilotica* (0.03 MBU) and tall *E.racemosa* (0.10 MBU) as dominants had lower than average feeding levels. Feeding in unburnt Forest Margin plots was also low (0.04 MBU). By way of contrast, feeding levels on unburnt plots with *E.divinorum* (0.30 MBU) and *S.africana* (0.30 MBU) as dominants were approximately double mean unburnt plot offtake levels, and about a third higher than mean feeding levels over all plots.

In tall *A.nilotica* dominated plots with a high density of trees less than two metres, feeding levels were substantially higher in plots which included a drainage line (0.182 MBU) than those without (0.011 MBU). Such plots with drainage lines were only slightly rejected; while **unburnt tall *A.nilotica* dominated woodland plots away from drainage lines were strongly rejected. The latter habitat made up 10.4% of sampled plots, and feeding levels were only 4.9% of the average feeding levels on all plots.**

A similar pattern of habitat selection was shown on Light/Medium burnt areas, with feeding levels again being significantly higher here than on unburnt plots: *D.cinerea* (0.17 MBU), tall *A.nilotica* (0.13 MBU) and tall *E.racemosa* (0.23 MBU), *E.divinorum* (0.56 MBU) and *S.africana* (0.76 MBU). Light/Medium burnt plots with *E.divinorum* (but not tall *A.nilotica* and *E.racemosa*) as a dominant were highly preferred (Preference Index 5.00 ***). Feeding levels in these plots (1.161 MBU) were over a hundred times greater than in unburnt tall *A.nilotica* dominated woodland away from drainage lines. This in part reflects the seasonal preference for feeding in areas near drainage lines in late winter.

Even on Light/Medium burnt plots, tall *A.nilotica* dominated communities had below average feeding levels (0.135 MBU). **Tall *A.nilotica* dominated areas were therefore rejected by black rhino during the post- burn period irrespective of their burning history.**

Average feeding levels were almost 60% higher on paths (0.30 MBU, n=637) than off them (0.19 MBU, n=1050). Interestingly, **paths were still favoured feeding areas in severely burnt areas** (0.34 MBU). For example, feeding levels on severely burnt plots with *A.karroo* as a dominant, were almost four times higher on paths (0.41 MBU) than off or only partly on paths (0.11 MBU).

Slight preference was shown for severely burnt plots with *A.caffra* as a dominant species (0.28 MBU). *A.caffra* often occurs in more open communities with tall grass on hillslopes, and so it is not surprising that 89% of all plots with *A.caffra* as a dominant experienced severe burns in 1989. Feeding in plots with *A.caffra* as a dominant was also highest on paths in severely burnt areas (0.41 MBU).

Severely burnt plots with *D.lycioides* (0.09 MBU) and tall *E.racemosa* (0.07 MBU) as dominants were again strongly rejected.

Physiognomically, shrubland with scattered tall trees had the most browsing. Opposite ends of the tall tree density continuum (No tall trees, Closed Woodland/Forest) had mean browsing levels (0.14 MBU; n=466) which were about half that recorded for the intermediate tall tree density classes (Scattered trees-Open woodland-Medium Woodland; 0.27 MBU; n= 1221). Although analysis of Node 1 did not significantly separate out the small tree categories, the densest category, thicket, had the smallest mean browsing levels (0.17 MBU).

Interestingly, forest margins were largely avoided during the post-burn period with an average of only 0.04 browse units (n=105) compared to the 0.36 for true evergreen forest (n=66). This finding contrasts with the Grid survey conclusion that forest margins appeared to be more important feeding areas than true forest later in the growing season.

Severely Burnt Plots on Paths (>67% on a Path) without *D.lycioides* but with *A.karroo* as a dominant species represented both important and preferred habitat (Table 9.3). These plots accounted for 21.48% of all feeding, but only 9.84% of all sampled plots (Preference Index 2.18 **). The absence of *A.karroo* as a dominant from these Severely burnt path sites without *D.lycioides*, reduced browsing preference indices from preferred to close to average preference levels (Preference Index = 1.08). This finding was expected, as *A.karroo* was the most important contributor to post-burn black rhino woody plant diets.

Severely burnt plots on paths with *D.lycioides* as a dominant were strongly rejected.

Severely Burnt plots not, or only partially on a Path, and not dominated by *E.divinorum* made up the second most important habitat grouping (15.05% of total recorded post-burn woody browsing). The primary reason for the high importance value was that it was by far the biggest node (n=459) which could not be further sub-divided. This habitat type was slightly rejected with mean browsing levels 40% below average (Preference Index = 0.55 -).

By way of contrast, Severely burnt plots, not or only partially on a Path, with *E.divinorum* but not tall *E.racemosa* as a dominant, were slightly preferred (Preference Index 1.64 *).

Unburnt dense bush with *Euclea divinorum* but not tall *A.nilotica* as a dominant accounted for 7.14% of total post-burn woody-browsing and was a preferred habitat type.

The results for communities with *R.pentheri* as a dominant were variable. *R.pentheri* dominated Post-burn plots had average feeding levels (0.24 MBU). *R.pentheri* was identified as an important contributor to the post-burn woody diet of black rhinos, although the Grid survey revealed it to be strongly rejected as a food item for much of the year. In unburnt plots with no tall *A.nilotica* (node mean 0.221 MBU), feeding was substantially greater on plots dominated by *R.pentheri* (0.62 MBU) and *E.divinorum* (0.48 MBU) but not *D.cinerea* (0.17 MBU). However on severely burnt plots with paths (node mean 0.337 MBU) feeding levels were lower on plots with *R.pentheri* as a dominant (0.10 MBU).

CONFIRM: RUN 2

In the second main CONFIRM analysis, all variables were classed as *free* predictors. Once again significance levels were set at the conservative 1% level to minimise the chance of spurious divisions. The use of *free* rather than *monotonic* predictors is perhaps more appropriate when one is primarily interested in determining which habitats are most important to black rhino during the post-burn period. Lumping together of predictor extremes when variables are classed as *free* is not a problem when intermediate predictor values happen to be the most preferred by black rhino. However if the primary aim of analysis is to quantify feeding levels for all habitat types, the use of *monotonic* predictors is more appropriate.

Table 9.8

The seven key nodes and selected subdivisions derived from CONFIRM analysis of the Hluhluwe Post Burn Transects (n=1,687). Mean browsing per plot is expressed in Mean Browsing Units (MBU). The percentage contribution to diet of each node is expressed as the percentage of total BU eaten on all plots. Preference indices and symbols are the same as the rest of Chapter 5. All predictors were free.
The seven key nodes were significant at the 1% level.

NODE Predictor Set	Preference Index		%Diet	MBU	n	%Plots	PrefRANK	ImpRANK	FreqRANK
TALL E.racemosa - TALL A.nilotica	0.13	--	1.79	0.029	241	14.29	7	6.5	4
OUT OF DRAINAGE LINE : 0.02 MBU									
IN DRAINAGE LINE : 0.13 MBU									
A.karroo : 0.09 MBU									
E.divinorum : 0.06 MBU									
TALL E.racemosa - NO TALL A.nilotica	0.93		13.78	0.215	251	14.88	4	4	3
OPEN/MEDIUM CLOSED WOODLAND : .34 MBU									
NO OR SCATTERED TALL TREES or CLOSED WOODLAND/FOREST : 0.05 MBU									
E.divinorum : 0.29 MBU									
NO E.divinorum : 0.08 MBU									
NO TALL E.racemosa - NO E.divinorum - <67% OF PLOT ON PATH - UNBURNT, LIGHT or SEVERE BURN	0.57	-	18.37	0.132	546	32.37	5	3	1
NO TALL E.racemosa - NO E.divinorum - <67% OF PLOT ON PATH - MEDIUM BURN	1.79	*	5.10	0.417	48	2.85	2	5	7
NO TALL E.racemosa - NO E.divinorum - >67% OF PLOT ON PATH - D.lycioides	0.43	--	1.79	0.100	70	4.15	6	6.5	6
NO TALL E.racemosa - NO E.divinorum - >67% OF PLOT ON PATH - NO D.lycioides	1.70	*	39.03	0.395	387	22.94	3	1	2
NOT FOREST MARGIN : 0.43 MBU									
FOREST MARGIN : 0.11 MBU									
NO TALL E.racemosa - E.divinorum	2.36	**	20.15	0.549	144	8.54	1	2	5
SEVERE BURN : 0.25 MBU									
UNBURNT or LIGHT/MEDIUM BURN : 0.98 MBU									

Excluding final splits, which only identified outlier plots, the second main CONFIRM run identified seven main nodes (Table 9.8). **Although the ordering of split predictors differed from the first run, similar patterns of habitat use were revealed. Once again plots dominated by tall *A.nilotica* and *E.racemosa* were strongly rejected while plots dominated by *E.divinorum* were preferred.** In plots without *E.racemosa* and *E.divinorum* as dominants, feeding was again higher on paths. On paths, areas with *D.lycioides* as a dominant were again rejected.

In plots off paths, medium burnt plots (burnt well but some grass tufts not fully burnt) were selected for.

Although Burn was not selected as the best first predictor, Light/Medium burnt plots were again significantly preferred, with mean browsing levels just over double those recorded in severe and unburnt plots.

Burn was still selected as a significant predictor after some of the variation in habitat preferences had been explained by vegetation physiognomy and species composition. This indicates that burning severity itself effects black rhino habitat suitability.

Severe burning of *E.divinorum* dominated communities without tall *E.racemosa* significantly reduced habitat suitability during the post burn period (F=8.39 df 1,142 p=0.00437).

Medium burning increased habitat suitability of path plots where neither *E.divinorum* or tall *E.racemosa* were dominants. Feeding levels were three times higher on medium burnt path plots, than on plots receiving other burn treatments (F=13.39 df 1,592 p=0.00027). The trinomial CATFIRM run brought out the same pattern.

Table 9.9

The eleven key nodes and selected subdivisions derived from CATFIRM analysis of the Hluhluwe Post Burn Transects (n=1,687). Browsing levels per node are expressed as the percentage of plots eaten per node. The contribution to diet of each node is the number of plots eaten/node expressed as the percentage of all 223 eaten plots. Preference Indices and symbols are the same as the rest of Chapter 5. All predictors were free. The eleven key nodes were significant at the 1% level.

NODE Predictor Set	Preference Index		%Diet	%PlotsEat	n	%Plots	PrefRANK	ImpRANK	FreqRANK
NO TALL E.racemosa - <33% OF PLOT ON PATH - NO E.divinorum - NOT FOREST	0.59	-	13.90	7.8	398	23.59	8	2	2
NO TALL E.racemosa - <33% OF PLOT ON PATH - NO E.divinorum - FOREST	2.04	**	3.14	26.9	26	1.54	1	5.5	10
NO TALL E.racemosa - <33% OF PLOT ON PATH - E.divinorum	1.44	*	8.97	19.0	105	6.22	3	4	5
NO TALL E.racemosa - >33% OF PLOT ON PATH - NO D.lyciodes - NOT FOREST MARGIN	1.78	*	53.81	23.5	510	30.23	2	1	1
NO TALL E.racemosa - >33% OF PLOT ON PATH - NO D.lyciodes - FOREST MARGIN	0.41	–	1.35	5.4	56	3.32	9	7.5	6
NO TALL E.racemosa - >33% OF PLOT ON PATH - D.lyciodes - NO OR SCATTERED TALL TREES	1.02		3.14	13.5	52	3.08	4	5.5	7
NO TALL E.racemosa - >33% OF PLOT ON PATH - D.lyciodes - OPEN-MEDIUM WOODLAND	0.00	—	0.00	0.0	45	2.67	11	11	8
TALL E.racemosa - NO TALL A.nilotica	0.81		12.11	10.8	251	14.88	6	3	3
MEDIUM BURN : 18.6%									
NO,LIGHT or SEVERE BURN : 8.9%									
OPEN-MEDIUM WOODLAND : 14.9%									
NO/SCATTERED TALL TREES or CLOSED WOODLAND/FOREST : 5.5%									
R.pentheri : 17.2%									
E.divinorum : 13.8%									
TALL E.racemosa - TALL A.nilotica - NOT DRAINAGE LINE - NO,LIGHT or SEVERE BURN	0.04	—	0.45	0.5	189	11.20	10	10	4
TALL E.racemosa - TALL A.nilotica - NOT DRAINAGE LINE - MEDIUM BURN	0.61	-	1.35	8.1	37	2.19	7	7.5	9
TALL E.racemosa - TALL A.nilotica - DRAINAGE LINE	1.01		0.90	13.3	15	0.89	5	9	11
OUTLIERS					3				
SAMPLE AVERAGE				13.2					

able 9.10

ıe seven key nodes and selected subdivisions derived from CATFIRM analysis of the Hluhluwe Post Burn ansects (n=1,687). Browsing levels per node are expressed as the percentage of plots eaten per node, and e proportion of eaten plots with more than just a little feeding (MTALF:offtake levels > 1 BU). ıe seven nodes were significant at the 1% level. All predictors were free. The categorical dependent variable ıd 3 classes: No feeding, A little feeding (l BU) and More than a little feeding (>1 BU). The Preference dex was calculated as the % of plots eaten (irrespective of offtake) / % of total sample size.

)DE Predictor Set	Preference Index		%Eaten =MTALF	%Node Plots Eaten	%Eaten Plots	% LF Plots	% MTALF Plots	PLOT n	%Sample	n LF	n MTALF
) TALL E.racemosa - NO E.divinorum - NONE or 33-67% OF PLOT ON PATH	0.804		25	10.6	21.1	27.1	12.8	442	26.20	35	12
) TALL E.racemosa - NO E.divinorum - <33% OF PLOT ON PATH	0.747	-	67	9.9	6.7	3.9	10.6	152	9.01	5	10
NO,LIGHT or SEVERE BURN			73	8.8				139			
MEDIUM BURN			50	30.8				13			
) TALL E.racemosa - NO E.divinorum - >67% OF PLOT ON PATH	1.606	*	37	21.2	43.5	47.3	38.3	457	27.09	61	36
) TALL E.racemosa - E.divinorum	1.629	*	68	21.5	13.9	7.8	22.3	144	8.54	10	21
NO,LIGHT or MEDIUM BURN			80	32.6				46			
SEVERE BURN			56	16.3				98			
D.cinerea			47	20.8				82			
NO D.cinerea			93	22.6				62			
.LL E.racemosa - NO TALL A.nilotica	0.814		52	10.8	12.1	10.1	14.9	251	14.88	13	14
ND/SCATTERED TALL TREES or CLOSED WOODLAND/FOREST			0	5.5				110			
OPEN/MEDIUM WOODLAND			66	14.9				141			
R.pentheri			47	17.2				87			
NO R.pentheri			59	7.3				164			
.LL E.racemosa - TALL A.nilotica - NOT DRAINAGE LINE	0.134	—	24	1.7	1.8	2.3	1.1	226	13.40	3	1
NO,LIGHT or SEVERE BURN			0	0.5				189			
MEDIUM BURN			12	8.1				37			
A.karroo			0	1.0				192			
NO A.karroo			50	5.8				34			
LL E.racemosa - TALL A.nilotica - IN DRAINAGE LINE	1.009		0	13.3	0.9	1.6	0.0	15	0.89	2	0

CATFIRM RUNS 1 AND 2

Generally, the two CATFIRM runs revealed similar patterns to those in the two CONFIRM runs and so details have been relegated to the Notes section [#2]. Some key points to emerge from these runs are listed below and key nodes described in Tables 9.9 and 9.10.

Binomial CATFIRM run 1

Unburnt plots were eaten in less frequently (8.9%) than burnt plots (14.8%). The highest proportion of plots with eating occurred in medium burn plots (18.4%).

Excluding final splits which only identified outlier plots, the first binomial CATFIRM run identified eleven main nodes which were significant at the 1% level (Table 9.9). Only 1.7% of plots away from drainage lines with both *E.racemosa* and tall *A.nilotica*'s as dominants contained black rhino feeding signs. The average proportion of plots eaten in this study (13.2%) was almost eight times higher than this.

Trinomial CATFIRM run 2

The findings from this run concurred with those of the initial CONFIRM run that light/medium burns were more preferred than severely burnt plots; with unburnt plots being least preferred. In general Light/medium burnt plots were not only browsed in more frequently (17.6%); but the level of feeding in them was also higher than other burn treatments (17.6% of such plots had feeding, 61% of which had more than just a little feeding (> 1 BU). This contrasts with the 8.9% of unburnt and 14.0% of severely burnt plots which were browsed. Only 35% and 38% of unburnt and severely burnt plots had more than just a little feeding. Thus black rhino generally ate more per plot in the more frequently browsed habitats.

Excluding final splits which only identified outlier plots, the final trinomial CATFIRM run identified seven main nodes which were significant at the 1% level (Table 9.10).

A.caffra dominated plots were more frequently eaten in than the average frequency of feeding in other plots (17.4% vs 11.5%). However, in contrast to other post-burn feeding areas the frequency of plots with more than just a little feeding was close to average levels irrespective of whether *A.caffra* was a dominant or not (6.0% vs 5.4%). This indicates that although the frequency of post- burn feeding in *A.caffra* dominated areas was above average, these areas should probably not be classed as prime post-burn habitat. One can speculate that the severe burns in *A.caffra* areas may have reduced habitat suitability.

CHAPTER 9 NOTES

#1 : This may because of increased grass interference late in the season. Alternatively it could be because of changing ratios of leaf concentrations of protein and condensed tannins as these two species have amongst the highest recorded tannin levels of "Acacias" (R.N. Owen-Smith pers.comm.). One can speculate that as growth plant slows later in summer, the changing carbon:nitrogen balance in the plants may result in a more unfavourable ratio of leaf tannins to protein reducing palatability. The latter ratio has been found to be related to browse palatability (Cooper *et al.* 1988). I have also noticed greatly reduced acceptance levels of *A.karroo* in the dystrophic Zimbabwe midlands (Emslie 1995), and this to may be related to less favourable tannin:protein ratios. Future chemical reseach is needed to investigate this hypothesis and better understand the factors governing woody plant palatability to browsers.

CHAPTER 10

BLACK RHINO FEEDING PATTERNS V : RE-MEASUREMENT OF HITCHINS' 1969-1971 TRANSECTS IN THE BUSH-CLEARED AREAS OF HLUHLUWE NORTH

CHAPTER SUMMARY

o The 1990 re-survey of Hitchins' 1969-71 transects (with the 1989 Hluhluwe Grid survey) provided comparative data on black rhino feeding in N.E.Hluhluwe between 1969-71 and 1989-90. Although black rhino numbers in Hluhluwe North were high in 1969-71, the population density in the area had already declined by about half from the peak level of 1.64/km^2 recorded in 1961 (before the die-off). Black rhino densities in N Hluhluwe continued to decline, and by the time of the remeasurement of the plots in 1990, were about a third of 1970 levels. This chapter concentrates on comparing feeding patterns between 1969-71 and 1989-1990 with a view to indicating whether or not nutritional factors were implicated in the decline.

o The amount of black rhino browsing recorded in NE Hluhluwe was far lower in recent times (1990) than in 1969-71. The drop in feeding more than corresponded to the three-fold difference in black rhino densities in NE Hluhluwe between these times (0.80 - 0.26/km^2). The very high grass interference levels prevailing in the area of Hitchins' plots at the time of remeasurement in 1989/90 are likely to have forced the black rhinos in Hluhluwe North to make increasing use of other areas with lower grass interference levels (see Chapter 8).

o Two reasons can be advanced why "*Acacia*"s formed nearly half the diet in 1969-71, yet they only formed just over a quarter of the diet in 1989-90:

- The greatly increased grass interference following the wet period 1987-90 (compared to the dry period 1965-71 prior to Hitchins' original measurements).

- Acacias made up 28% of all trees available in the Hitchins' plots around 1970, compared to only 21.7% in 1990. In turn, this is probably a function of both the recent bush clearing in the area; and self thinning as the size structure of Acacias has changed with a higher proportion of trees occurring in taller less palatable size classes in 1990 (Chapter 16).

This evidence indicates that the carrying capacity of Hluhluwe North has declined since 1969-71.

o Unpalatable species (i.e. currently rejected *E.crispa, M.senegalensis, L.javanica, Diospyros* species, *Rhus* species and *K.floribunda*) formed 15.3% of the rhinos' diet in 1969-71 , but 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.

o The proportion of individual trees of a number of species which showed signs of black rhino browsing was exceptionally high in Hitchins' time, when compared to recently collected data in Hluhluwe, Umfolozi and Itala (this project & Kotze 1990). The higher browsing pressure in Hitchins' time may have induced the increased production of secondary plant chemicals in certain palatable and unpalatable species, lowering their digestibility and nutritional value.

> One can speculate that in 1969-71, the much higher contribution of unpalatable species to the diet, along with 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.

o To conclude, the remeasurement of Hitchins' plots revealed that the black rhino diet in Hitchins' time comprised a greater amount of low-quality food than their present-day diet. This indicates that black rhino in Hluhluwe North were still under nutritional stress in 1969-71, even though their densities in the area had declined by half from peak levels in only a decade.

The indications that carrying capacities have declined in Hluhluwe North since 1970 supports the "poor nutrition as the major cause of the population decline" hypothesis. However, the higher contribution of the more palatable species in the 1989/90 black rhino diet indicates that the decline in carrying capacity may be starting to, or has already bottomed out. Apart from high levels of grass interference in 1989-1990, and the less favourable distribution and density of "Acacia" spizes in the habitat; the feeding data indicated black rhino were worse off in 1970.

We can be thankful Hitchins had the foresight to measure these plots twenty odd years ago. However, it is a great pity that nobody thought to do the same thing thirty years ago (just before the big die-off when black rhino densities in Hluhluwe were the highest ever recorded at 1.64/km^2), not to mention sixty, fifty and forty years ago when population densities were high (compared to current RMG area densities) but the population was still increasing in size.

The possible influence of bush clearing and fire treatments on habitat changes on Hitchins' transects are discussed in later chapters (Chapters 16 & 18)

CHAPTER 11

BLACK RHINO FEEDING PATTERNS VI : FORB USE

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CHAPTER 12

BLACK RHINO FEEDING PATTERNS VII : COMPARISON OF HLUHLUWE-UMFOLOZI RESULTS WITH OTHER AREAS

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CHAPTER 13

BLACK RHINO FEEDING PATTERNS VIII : BOMA FEEDING OBSERVATIONS

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THE FEEDING ECOLOGY OF THE BLACK RHINOCEROS (*Diceros bicornis minor*) IN HLUHLUWE -UMFOLOZI PARK, WITH SPECIAL REFERENCE TO THE PROBABLE CAUSES OF THE HLUHLUWE POPULATION CRASH

PART III

THE INFLUENCE OF ENVIRONMENTAL FACTORS AND MANAGEMENT ACTIONS ON BLACK RHINO HABITAT QUALITY

CHAPTER 14

HLUHLUWE WOODY SPECIES: ENVIRONMENT RELATIONSHIPS

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CHAPTER 15

THE EFFECTS OF MANAGEMENT ACTIONS ON BLACK RHINO HABITAT QUALITY I: SHORT TERM EFFECTS OF FIRE

INTRODUCTION

In eight previous chapters (6-13) black rhino feeding patterns were examined in detail to determine what constitutes good, intermediate and poor black rhino habitat. **This chapter is the first of five chapters which aims to unravel the effects of different management actions on black rhino habitat suitability.**

This chapter examines the shorter term effects of fires on black rhino (from immediately following fire up to eight years). The following chapter (16) continues the study of fire, but focuses instead on the longer term effects of fire on black rhino.

MANAGEMENT CONCERNS AND KEY QUESTIONS

At a Natal Parks Board Management Recommendations meeting in 1988, Peter Hitchins expressed concern that palatable young browse plants were being selectively removed by hot burns (Anon 1988). Hitchins (Hitchins & Brooks 1986, Hitchins 1988) also suggested that more black rhinos may have been burnt in veld fires than generally thought. At the start of this project, Park Management were therefore concerned that the more frequent burning in the 1980s, may have had a negative impact on the black rhino population (Anon 1988).

Given the above concerns, the key questions which needed to be addressed were:

- **Does fire reduce black rhino habitat quality?**
    - **Are palatable young plants being selectively removed by fire as suggested by Peter Hitchins?**

- Are black rhinos being forced to restrict their feeding to unburnt patches immediately after fires?

- How does burn severity affect black rhino habitat preferences in the short term?

● What are the chances that veld fires burn a significant number of black rhinos to death?

RESEARCH APPROACHES USED

In most of the chapter a two step approach is used - attempting to elucidate the short term effects of fire on the vegetation; and then interpreting any fire induced short-term vegetation changes in the light of knowledge of rhino feeding patterns and preferences (chapters 6-13).

To determine the short term effects of fire on the vegetation:

○ This chapter briefly summarises the key results of the Post-burn surveys which studied black rhino feeding patterns, both immediately after, and a few months after burning (discussed in detail in chapter 9).

○ In an attempt to shed light on the browsing of burnt browse, limited chemical analyses were undertaken of samples of burnt and unburnt plants from the post-burn period.

○ The fire literature was also examined. In particular papers from the 1979 Hluhluwe-Umfolozi vegetation dynamics symposium, and local Hluhluwe-Umfolozi theses and reports were inspected for any references to short term effects of fire on woody habitat structure and composition. Konstant's (1990 *in litt*) documented short to medium term (1-5year) changes in densities of key woody spizes in Hluhluwe in response to experimental fire and bush clearing treatments were also interpreted in the light of knowledge of black rhino feeding preferences.

o The results the partial fire-constrained ordination analysis of Hluhluwe Grid survey data are discussed in detail in the next chapter (16) as they primarily examine the longer term influences of fire on habitat structure and composition. However, this chapter discusses the influence of two short term fire variables (a dummy variable for burning in 1988 - the year prior to measurement; and fire frequencies from 1980-1988) on habitat composition and structure revealed by this analysis.

o The direct mortality risk from fire was quantified using data in the annual (confidential) Rhino Management Group of Southern Africa (RMG) Status Reports (from South Africa and Namibia) over the period April 1989 to March 1995.

o The relationship between fire frequencies from 1980-88, and densities of the "problem" species *Maytenus senegalensis* was also examined using an exploratory Formal Inference-based Recursive Modelling (FIRM) analysis of the Hluhluwe Grid survey data.

HLUHLUWE-UMFOLOZI POST-BURN SURVEYS

The Post-burn surveys (chapter 9) indicated that in the short term - both immediately after burns and later during the post-burn flush period - fire was on the whole beneficial to black rhino. This conclusion is the antithesis of what had been proposed by Peter Hitchins at the NPB meeting in 1988 (Anon 1988).

The following sections briefly summarise the key findings to emerge from the Post-burn surveys, firstly in the period soon after fire, and then later during the post-burn flush period. (see chapter 9 for full details).

IMMEDIATE POST-BURN PERIOD

FEEDING LEVELS IN BURNT AND UNBURNT PLOTS

The Post-burn surveys (chapter 9) showed that black rhino were clearly not being forced to restrict their feeding to unburnt areas immediately after burns. In both Hluhluwe and Umfolozi, feeding levels were **greater in burnt than in unburnt plots.** This was a function of both the **higher proportion of burnt plots which had been browsed,** and the **higher mean offtake levels/plot in browsed burnt plots compared to unburnt browsed plots.**

FEEDING LEVELS ON BURNT "*Acacias*"

In Hluhluwe, burnt "*Acacias*" were important in the immediate post-burn diet. During this period, burnt *A.karroo*, *A.nilotica* and *D.cinerea* trees made up 29.6% of the woody diet; while other burnt *Acacias* made up a further 4.6% of the diet. By way of contrast, unburnt "*Acacias*" only contributed 3.5% of the woody diet during this period. Given that **almost ten times more of the immediate post-burn diet came from burnt compared to unburnt "*Acacias*"**, it is probable that burnt "*Acacia*" trees were preferred in addition to being important food items[#1]. Figure 17.2b shows burnt "*Acacias*" regrowing on a recently bush cleared site that have been heavily browsed in southern Hluhluwe. Other authorities have also recorded heavy selective browsing of burnt "*Acacias*" by black rhino (Marchant and Pullen 1995, Broomhall 1997, see also chapter 12). However the limited chemical analyses undertaken indicated that burnt twigs were very low in crude protein (averaging <6%).

Black rhinos in Umfolozi also browsed stands of burnt small "*Acacias*", although in Umfolozi "*Acacias*" were less important than Hluhluwe, accounting for only 13.5% immediate post-burn browse offtake. This was probably because in the drier Umfolozi, black rhinos favoured areas nearer water during the immediate post-burn (pre flush) period resulting in a reduced "*Acacia*" component in the diet[#2].

FEEDING LEVELS ON BURNT AND UNBURNT *S.AFRICANA* & *A.GLABRATA*

Although in general black rhinos fed more on burnt rather than unburnt trees, this was not the case for all species. 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 finding may simply reflect the low proportion of trees of these species which were burnt in 1989.

BROWSING OF BURNT AND UNBURNT INDIVIDUALS OF NORMALLY UNPALATABLE SPECIES

Increasing use was made of normally unpalatable spizes during the post-burn period. Just over a third of the immediate post-burn diet in Hluhluwe was made up of the following normally intermediate or rejected species: *Rhus pentheri, Ziziphus mucronata, Dombeya rotundifolia, Euclea divinorum, Lippia javanica, Kraussia floribunda, Diospyros lycioides, Plectroniella armata, Vernonia subuligera, Maytenus senegalensis, E.racemosa, Rhoicissus tridentata* and *E.crispa*. A total of **85.1% of the offtake from these unpalatable species during the immediate post-burn period came from burnt individuals. It was noted that in the southern part of the Hluhluwe study area, the black rhinos preferred to browse on lightly burnt individuals of *R.pentheri*.**

In Umfolozi, increasing use was also made of normally unpalatable species during the immediate post-burn period[#3]. Notably, black rhino in Umfolozi fed more in low-lying thicket and bush-clump vegetation immediately after the burns, than at other times of the year, avoiding the drier, more open areas at this time of year. Feeding levels on a number of species commonly found in thick bush clump areas increased in late winter. *Scotia capitata, Pappea capensis, Maytenus nemorosa, Coddia rudis, Azima tetracantha, Ehretia rigida/amoena, Euclea undulata* and *Sideroxylon inerme* together made up 25.5% of the immediate post-burn woody offtake (compared to 13.1% during summer).

POST-BURN/EARLY GROWING SEASON FLUSH PERIOD

CONTRIBUTION OF BURNT TREES TO TOTAL WOODY OFFTAKE

In Hluhluwe, burnt trees made up a slightly reduced contribution to the postburn/early season flush woody diet. **During this flush period, 58.2% of all woody offtake came from burnt trees.** Again, one would hardly expect burnt trees to make up such a high component in the diet if burning detrimentally affected browse quality.

BROWSING OF BURNT "*ACACIA*"S

The importance of regenerating burnt "*Acacias*" in Hluhluwe increased to account for 41.8% of the black rhino post-burn flush woody diet with 86.1% of the post-burn flush "*Acacia*" diet coming from burnt trees. By way of contrast, browsing on unburnt "*Acacias* only contributed a further 6.72% of the woody diet.

Rather than "pruning" big diameter twigs, black rhinos were seen to nibble the slender, freshly coppicing shoot tips of "*Acacias*" in both Hluhluwe (especially *A.karroo* and *A.caffra*) and Umfolozi during the early summer flush period. As a result **browse bottle based "*Acacia*" offtake estimates during the post-burn/early growing season flush period are likely to have underestimated true offtake levels. Therefore in all probability, "*Acacias*" contributed at least half of all woody browse eaten in Hluhluwe during this period. Limited chemical analysis of coppicing *Acacias* after burns indicated that new basal coppice growth was very high in Crude Protein (average 18.85%) as well as phosphorus (average 0.23%) and potassium (average 1.30%).**

EFFECTS OF FIRE ON BLACK RHINO HABITAT IN OPEN, GRASSY AREAS

During the post-burn flush period in Hluhluwe, black rhinos fed more often on open *A.karroo* and *A.caffra* dominated sites. These two species are among the first "*Acacias*" to flush. Observations showed they made increasing use of forbs and the soft new coppice on burnt areas during the post-burn flush period, and it was noticeable that the consistency of the dung became less coarse during this period as a result.

A comparison between Figures 8.19 and 9.1 shows that feeding levels increased substantially in N.E. Hluhluwe (Magangeni, Hidli, Manzimbomvu and Oncobeni valleys) following the burns. Figure 8.19 also shows that modal grass heights were high over most of this area during late summer. Without fire having removed grass interference, these areas would have been largely avoided by rhino (see chapters 6,8 and 12). **Thus, the application of extensive control burns during above average rainfall periods temporarily increases the area of suitable black rhino habitat in Hluhluwe.** In the short term, burning also creates conditions conducive to the growth of palatable early season ground forbs.

During the Grid Survey, parts of the Umfolozi study area were covered by tall dense stands of *Themeda triandra* dominated grasslands. By removing the grass biomass, fire stimulated subsequent forb growth and made browse accessible to the animals leading to increased use of this area during the flush period[#4].

After the rains, and during the post-burn flush period, black rhinos made increased use of the more open areas in the Gqoyini basin in Umfolozi. Black rhinos were observed spending considerable time feeding at ground level in this area. Examination of fresh feeding sites revealed that they were browsing freshly coppicing shoots of *A.borleae* and *A.karroo*[#5].

As in Hluhluwe, the high amount of topkill achieved by some burns in 1989 in Umfolozi was beneficial to black rhinos by maintaining "*Acacias*" in the preferred lower size classes, reducing grass competition, and creating suitable conditions for forb growth.

BROWSING OF NORMALLY UNPALATABLE SPECIES

The increasing use by browsers of some normally unpalatable species during the late winter "crunch" period has been demonstrated for other species and other areas (Owen-Smith & Cooper 1987; Owen-Smith 1988, 1993; Fabricius and Mentis 1990, 1991). Unpalatable woody species have been shown to be highly acceptable to browsers in the new-leaf phase even though condensed tannin levels in leaves were still above 5% (Owen-Smith 1993). Owen-Smith (1993) interprets this as meaning that animals are responding to the relative balance between nutrient levels as indexed by protein, and anti-feedent chemicals represented by condensed tannins. One can hypothesise that the stimulation of new leaf growth of normally unpalatable species during the early growing season and following fire may favourably alter the ratio of crude protein to these secondary chemicals (if crude protein levels increase and/or if levels of secondary anti-feedent chemicals decline (as less spare carbon may be available during periods of rapid growth). Therefore the increased browsing of "stop-gap" food resources during this period is to be expected; and to a large measure could be independent of fire. The findings of this study reflect the general conclusion reached by Owen-Smith (1988, 1993) that unpalatable species are eaten during restricted periods of the seasonal cycle, either in the dry season when foliage of the more favoured species is less available, or during the new-leaf phase. **Therefore, the observed increase in use of unpalatable spizes during this period is not necessarily a negative consequence of burning.**

BURN INTENSITY AND FEEDING LEVELS

The Post-burn survey data showed that **burn intensity significantly influenced habitat suitability in its own right** (ie. in addition to the influences of vegetation physiognomy and spize composition - see chapter 9):

- Average black rhino feeding in light/medium burnt plots was almost three times greater than in unburnt plots. The highest proportion of plots with feeding occurred in the medium burnt plots.

- Browsing levels in severely burnt plots (clean burn - no visible fuel left) were close to average levels, but were still 65% higher than average feeding levels in unburnt plots.

- **Light/medium burnt plots also experienced the most intense browsing levels.** *A.caffra* dominated plots proved to be the exception to this rule, as feeding on these plots was greatest in severely burnt plots. However this was not surprising as almost 90% of *A.caffra* dominated plots experienced severe burns in 1989 [#6]. On the other hand, severe burning of lowland communities dominated by *E.divinorum* (but not *E.racemosa*) significantly reduced black rhino feeding levels.

BROWSING IN TRUE FOREST AND FOREST MARGIN PLOTS

Black rhino selected for forest plots during the post-burn flush. However, this selection contributed very little to the diet compared to non-forest plots (where "*Acacias*" probably made up at least half of the woody diet during this period).

CONCERN THAT PALATABLE BROWSE PLANTS WERE BEING SELECTIVELY REMOVED BY FIRE

At a Natal Parks Board Management Recommendations meeting in 1988, **Peter Hitchins expressed concern that palatable young browse plants were being selectively removed by hot burns to the detriment of rhinos** (Anon 1988). At the time Hitchins did not specify which palatable species he considered were being negatively affected.

The evidence presented in this study shows this was clearly not the case with regard to favoured "*Acacias*". Indeed the opposite was true - burning improved habitat conditions in the short term by removing thorns, keeping "*Acacias*" in more preferred size classes for longer, removing grass interference, and stimulating coppice regrowth.

Indeed if fire was as detrimental to black rhinos as postulated by Hitchins (Anon 1988), then surely one would not have expected the outcome of evolution to result in fire adapted "*Acacias*" being such preferred and important items in diet of black rhino?

The FIRM analyses (chapter 9) also clearly showed that in most habitats fire increased both the proportion of plots which black rhinos browsed and the offtake levels from these plots.

While the evidence strongly ruled out Hitchins' hypothesis in terms of favoured "*Acacias*": Could other species of palatable young browse plants have been selectively removed by hot burns?

- *Dombeya burgessiae* often occurs in forest margins and is a preferred food species. However this palatable species also occurs in more open areas which experience high fire frequencies, and this was confirmed by the partial fire constrained ordination in chapter 16 (Figure 16.5)

- The partial fire constrained ordination in chapter 16 (Figure 16.5) also indicated that *Hippobromus pauciflorus* and small (<1m) *Berchemia zeyheri* were associated with recently burnt sites. These species also increased on Hitchins' plots despite the higher fire frequencies in N.E. Hluhluwe.

- Other preferred non-"*Acacia*" species (*Spirostachys africana*, *Acalypha glabrata*, *Abutilon/Hibiscus*, *Maytenus nemorosa*, and *Dovyalis caffra*) primarily occur in areas which experience low fire frequencies.

These observations are not consistent with fire in Hluhluwe removing palatable non-*Acacia* browse plants negatively affecting black rhino food quality.

As will be discussed later, some of the unpalatable later-successional evergreen species (eg. *E.racemosa*, *K.floribunda*, and *S.myrtina*) appear to be more sensitive and prone to be killed by fire (Konstant 1990 *in litt*).

CHEMICAL ANALYSIS OF POST-BURN BROWSE SAMPLES AND HYPOTHESES TO INVESTIGATE THE FAVOURING OF BURNT BROWSE BY BLACK RHINO

A limited number of pooled browse sample were chemically analysed #7 to investigate the quality of post-burn diets and to look for gross differences between burnt and unburnt samples. The raw data and a more detailed discussion of the results were included in the final BR2000 report. Unfortunately, due to the small sample sizes that could be analysed in this pilot study, the results should only be treated as preliminary. These preliminary analyses suggested that:

> Crude Protein levels of burnt sticks were below maintenance levels, averaging only 5.0% (n=7).
>
> Burnt twig "*Acacia*" preference appeared to be positively correlated with calcium content, and calcium levels in burnt *Acacia* twigs were high (averaging 1.27%).
>
> In contrast to the burnt twigs, the **post-burn early growing season basal coppice of burnt "*Acacias*" was high in nitrogen with average crude protein levels of 18.85% (n=6).**
>
> While the data suggested that effective phosphorus uptake from a diet made up solely of burnt twigs is likely to be very deficient (especially for lactating females); the **post-burn early growing season basal coppice of "*Acacias*" appeared to be high in both phosphorus and potassium.** Average levels of phosphorus recorded in the samples were similar to that estimated for Addo vegetation (Koen et al. unpublished) and Hluhluwe's black rhino should therefore be able to obtain sufficient phosphorus from the diet.

The apparent selection for calcium has been corroborated by a recent study of browsing in Weenen Nature Reserve (Vickery 1997) which concluded that there was a strong correlation between soil calcium levels and levels of browsing of woody species in the reserve, and that this may reflect a real need for calcium in the herbivores diet.

McNaughton (1990) also found that wildebeest migrating through the Serengeti actively selected for the nutrients calcium, magnesium and phosphorus rather than a rainfall gradient. However, the high calcium levels may simply reflect the high proportion of wood (ie structural tissue) in the burnt twigs.

While burnt browse may superficially appear to be a low quality food, heat may increase digestibility and palatability of burnt browse by either reducing levels of secondary plant anti-feedent chemicals (such as condensed tannins), or by changing more complex carbohydrates to more digestible simple sugars. While further research is needed to test the above hypotheses, supportive evidence for the beneficial effect of heat on browse chemistry can be found in the literature. Levels of secondary plant metabolites were also found to be significantly lower in burnt compared to unburnt lodgepole pine bark, and neutral detergent fibre in the burnt bark was at least four times as digestible as bark from live trees (Jakubas *et al* 1994). Heat treating milled dried cut browse (from encroaching thorn bush) was also a factor which made browse pellets more acceptable to wild browsers (van Hoven *et al* 1998). According to the manufacturer of these browse pellets, varying the temperature during pelleting influenced their acceptability (K.Adcock pers.comm.). Interestingly the Post-burn surveys (chapter 9) also found that fire severity significantly influenced black rhino feeding levels.

FIRE, *ACACIA* THORNS AND BROWSING

Observations in Pilanesberg indicated that black rhino selectively fed on lightly burnt *A.tortilis* branches that had their thorns burnt off, in preference to other unburnt branches with thorns. Broomhall (1997) also found that fire reduced thorn length on smaller *Acacias* in Weenen Nature Reserve. Thus, avoidance of physical defence may in part explain the observed heavy browsing of burnt "*Acacia*" twigs in Hluhluwe and Umfolozi by black rhino[48].

From the limited research undertaken on the responses of plants to different fires[#9], there is at least a basic understanding of the characteristics and some of the effects of different fires. **The role of fire in preventing favoured "*Acacias*" growing into taller less preferred size classes is of particular relevance to assessing the short term influence of fire on black rhino habitat.** In the short term fire will benefit black rhino if it results in topkill keeping *"Acacias"* in favoured small size classes (especially <1m), and preventing them maturing and becoming less palatable.

EFFECT OF FIRE INTENSITY AND FLAME HEIGHT ON LEVELS OF TOPKILL

The literature indicates that it is necessary to have more intense fires with high flame heights to achieve high levels of topkill once "*Acacias*" grow to above 1.5 to 2m (Trollope 1974; Macdonald 1982; Frost 1984; Trollope & Tainton 1986; Trollope *et al* 1988 and van Wilgen et al. 1990):

- Frost (1984) using data of Trollope (1974) and Macdonald (1982) describes a pattern where bigger topkill rates on taller *A.karroo* trees were only recorded after hot fires.

- In Hluhluwe, Macdonald (1980) observed that a 100% topkill of *A.karroo, A.davyii* and *E.divinorum* was only achieved when flame height exceeded plant height.

- In the Eastern Cape fireline intensities of 2500 kW/metre were necessary for topkill rates of over 40% on shrubs 1.5 to 3 m tall, and increases in the levels of topkill of *A.karroo, R.lucida, E.rigida* and *G.occidentalis* were significantly related to increases in fireline intensity (Trollope and Tainton 1986).

- In the Kruger National Park as fire intensities increased, increased topkill rates and reduction in the height of bush were recorded (Trollope *et al* 1988). However, the bush became more resistant to fire as its height increased. As trees got over about 1.5m tall, the level of height reduction after fire in Kruger dropped sharply (Trollope et al, 1988).

However, fires with low flame heights may still produce significant topkill rates on small trees preventing them escaping to taller size classes where they become more resistant to the effects of fire.

- In Kruger National Park, even when fire intensities were as low as 500 kW/m the percentage height reduction on trees less than a metre was similar to intense fires of 3000 kW/m (Trollope et al, 1988). It is significant that height reductions of over 95% were recorded in Kruger on small 0.5 m trees after low intensity fires (500 kW/m).

By placing a high emphasis on build ups of sufficient fuel, fire frequencies will tend to be lowered, allowing small (<1m) trees time to grow taller and become less influenced by fires. Thus the general conclusion that managers should aim to apply intense fires to produce significant topkill rates (van Wilgen et al. 1990) perhaps needs the rider "unless most trees are small, when frequent cooler fires will be sufficient" to be added.

SHORT TERM EFFECT OF FIRE ON TREE MORTALITY LEVELS

The key point to emerge from savanna fire research to date, is that while burning may achieve significant rates of topkill, documented rates of "*Acacia*" mortality after single fires have been low ((Trollope 1974; Macdonald 1982, Wills and Phelan 1983, Frost 1984).

- For example, while the 1983 control burns in Hluhluwe did not achieve great success in killing whole trees, the extent of *D.cinerea, A.karroo, A.caffra* and *A.nilotica* topkill was considered quite adequate for controlling bush encroachment (Wills and Phelan 1983). The range of recorded tree mortalities in three areas of Hluhluwe following the 1983 control burns were as follows: *D.cinerea* 0% - 1.2% ; *A.karroo* 1.4% - 10.0%; *A.nilotica* 0% - 10.7% ; *A.caffra* 0% ; *M.senegalensis* 0% - 18.2% (Wills and Phelan 1983).

- Data collected by Trollope (1974) and Macdonald (1982) illustrated in Frost (1984) indicated that while *A.karroo* topkill rates following fire were highest on small trees; peak mortality rates of *A.karroo* following fire occurred on medium sized trees 1.75m tall (Frost 1984). While mortality levels peaked at only 17% on 1.75m *A.karroo* trees, both smaller and taller trees showed reduced mortality levels (Frost 1984). Mortality levels around 11% were recorded for both 1.25m and 2.25m *A.karroo* trees falling to 8% and 6% for 2.75m and 0.75m *A.karroo*'s respectively. Very low mortalities of about 1% were recorded for 0.25m and 3.25m tall *A.karroo*'s (Frost 1984).

- Trollope (1974) also demonstrated that mortality of *A.karroo* trees following complete topkill increased with increasing stem diameter and age. It was hypothesised that this probably reflects a progressive decline in the viability of buds in the root collar region (Trollope 1974).

However one area requiring further research is the possible interactive effect of heavy browsing and fire together on mortality of *Acacias* (see chapter 22).

EFFECTS OF FIRE ON "*S.AFRICANA*"

While past literature has referred to the highly favoured *S.africana* as fire tolerant (Bayer 1938), in Umfolozi I have seen a small patch of favoured two to four metre high *S.africana* trees surrounded by tall grass that was completely destroy by fire. The results of the Hluhluwe FIRM analyses (chapter 9) also indicated that black rhino feeding levels were lower following severe burning of areas dominated by *E.divinorum* (commonly associated with *S.africana*).

However, fire generally only affects small pockets of *S.africana* thicket, because in more extensive areas of this habitat there is usually little grass fuel, and fire appears to be largely excluded from such areas. *S.africana* accounted for 13.7% of the Hluhluwe postburn flush woody diet with 93% of this coming from unburnt trees (reflecting the low fire frequencies in areas dominated by *S.africana)*. The low grass biomass in *S.africana* communities was confirmed by the TWINSPAN analysis in Hluhluwe (chapter 8). This analysis also showed that *S.africana* dominated lowland communities had experienced the lowest recorded fire frequencies since 1955 of any of the communities examined. In contrast to small isolated pockets of *S.africana* thicket surrounded by taller grass, burns that penetrate extensive *S.africana* communities are also likely to be cool.

PRELIMINARY FINDINGS OF KONSTANT'S PROJECT

T. Konstant investigated changes in woody plant populations on experimental *A.nilotica* woodland plots in northern Hluhluwe that had experienced factorial fire and bush clearing treatments (see chapter 18 for further details of experimental design). This section reviews her main findings and their implications for black rhino [#10].

Konstant (1990 *in litt.*) found that fire reduced *M.senegalensis* densities in Hluhluwe. Exploratory Continuous Formal Inference-based Recursive Modelling of the Hluhluwe Grid Survey data provided corroborative evidence to support this[#11]. Similarly, repeated fire in a five year period was found to reduce *E.crispa* densities by half (Konstant 1990 *in litt.*). Both *M.senegalensis* and *E.crispa* are highly rejected by black rhino, and **in the case of these two species, control burning may therefore benefit black rhino in the short term.**

Konstant's (1990 *in litt*) results also indicated that fire on cleared plots appeared to stimulate the germination of *A.karroo* - an important black rhino food species.

Konstant's (1990 *in litt.*) results also showed that in uncleared control plots, *D.cinerea, H.pauciflorus* and to a lesser extent *L.javanica* and *D.lycioides* increased in density following fire. The first two species are important black rhino food plants, while the latter two are unimportant, and are rejected by black rhino for most of the year.

She noted that over a three to four year period the important black rhino food plant *D.cinerea* was stimulated by fire.

In her *E.divinorum* dominated site, Konstant (1990 *in litt.*) recorded that fire reduced numbers of unpalatable *E.divinorum* by over 80%. Combined bush clearing and fire at this site appeared to favour black rhino as *K.floribunda, M.heterophylla* and to a lesser extent *E.racemosa* and *R.pentheri* declined in numbers; while *A.karroo* and *D.cinerea* germinated rapidly after fires to become dominant species. Large numbers of seedlings of *A.robusta* also emerged. Therefore **in this plot, combined clearing and subsequent fires favourably altered spize composition in the short term for black rhino.** However, in areas with cool fires some germination of *E.divinorum* was recorded.

In a cleared *A.nilotica* woodland plot, Konstant (1990 *in litt*) found that fire had little effect on tree densities, although it altered the size structure, reducing tree heights as compared to unburnt cleared control plots - once again benefiting black rhino in the short term.

Konstant (1990 *in litt.*) found that later successional *S.myrtina* was sensitive to any kind of disturbance, only becoming very common in the unburnt uncleared *A.nilotica* woodland treatment. This species was particularly vulnerable to fire as even the cool, and incomplete burns experienced by the *A.nilotica* closed woodland removed almost all *S.myrtina* seedlings. Konstant (1990 *in litt.*)showed that germinating *E.racemosa* individuals were also very susceptible to cool undercanopy fires. Small size classes of *D.lycioides* were also vulnerable to undercanopy burning. Given adequate fuel loads *Kraussia floribunda* was also fire sensitive. Hot fires also reduced the densities and average size of *R.pentheri*. **These short term fire induced reductions in densities of these unpalatable generally later successional species will also not be to the detriment of black rhinos.** However, in this case, the longer term effects of burning appear more important, as Konstant's results indicate that frequent cool fires could retard or prevent the succession of *A.nilotica* closed woodland through to *E.racemosa/B.zeyheri* dominated dry forest which has a lower carrying capacity for black rhino (see chapters 16 and 20). The fire constrained biplot in chapter 16 is consistent with this.

INFLUENCE OF SHORT TERM FIRE VARIABLES ON PARTIAL FIRE- CONSTRAINED ORDINATION OF HLUHLUWE GRID DATA

Chapter 16 presents the results of a partial fire constrained spize-based ordination which found that the fire variables significantly explained some of the residual variation in black rhino habitat composition and structure (after the influence of a suite of environmental variables had been partialled out)#12.

While a longer term axis dominated by fire frequencies from 1955-64 had the biggest influence on habitat composition and structure, the fire-constrained biplot (Figure 16.5) showed that **a largely independent secondary fire frequency axis in part reflected the influence of the two short term fire variables** (Fire frequencies in the period 1980-88, and a dummy variable for whether or not plots were burnt in 1988 - the year prior to measurement)#13. The biplot indicated that frequent recent fires appear to have maintained *A.nilotica*'s in the most preferred small size class. The biplot also suggested that small (<1m) *A.karroo* was also associated more with recent frequent fires than medium (1-2m) trees. These findings were consistent with the observation that although the 1983 control burns in Hluhluwe did not kill many trees, topkill of encroaching species (namely *D.cinerea, A.karroo, A.caffra, M.senegalensis* and *A.nilotica*) was considered "quite adequate for controlling bush encroachment" (Wills and Phelan 1983).

While the biplot suggested that frequent recent fires reduced the size of medium (1-2m) *A.karroo* trees, tall (>4m) and to a lesser extent intermediate (2-4m) *A.karroo* were associated with frequent recent fires indicating that *A.karroo* is likely to be resistant to fires once it has grown taller. Other palatable species associated with frequent fires included *A.caffra* and *H.pauciflorus*.

The biplot indicated that taller individuals (>2m) of the unpalatable *M.senegalensis* were more associated with lack of recent fires, suggesting that in the short term fire may be preventing this unpalatable species growing taller.

Given that, in previously grassland areas, spizes associated with more frequent recent fires were generally more readily eaten by black rhinos, and the most favoured small spizes of some important and preferred "*Acacias*" were associated with recent fires, the results of the partial fire constrained ordination (Figure 16.5) were also consistent with fire being beneficial to black rhino in the short term.

DIRECT MORTALITY RISK DUE TO FIRE

Hitchins reports two instances where a total of three black rhinos were burnt to death in Hluhluwe-Umfolozi (Hitchins & Brooks 1986). These records were the first reported cases of Hluhluwe-Umfolozi black rhinos being killed by fires since 1952. Hitchins speculated that other black rhinos may have suffered the same fate without being found (Hitchins & Brooks 1986), and that the increased fire frequencies in the 1980s may have negatively affected black rhino populations in Hluhluwe-Umfolozi Park.

However, **a review of Southern African Rhino Management Group (RMG) data indicated that the risk of black rhino being trapped and burnt alive by large advancing fire fronts was small. In South Africa and Namibia only one death reported to the RMG over the period 1989-95 was due directly to fire out of a sample of 6,619 black rhino years. Fire is a management tool used throughout much of the RMG region, and if fire was a major mortality factor we could have expected the fire risk to be substantially higher than the recorded 0.015% fire mortality risk per animal per year over the period 1989-95.**

Regular fires in Kruger, Pilanesberg, Mkuzi and Umfolozi have also not affected population performance. The change to a more frequent fire regime therefore cannot be invoked as a major cause of the Hluhluwe decline.

The greatest risk to the animals is probably when very intense large runaway fires occur, and the change to more frequent burning should reduce the risks of such fires occurring. By implementing a policy of frequent cool spot burns (rather than promoting the application of hot fires along a large fire front) the risk of rhino mortalities can be kept to a minimum.

CONCLUSIONS

Hitchins' hypotheses that burning may be detrimental to black rhino in the short term (Anon 1988) is not supported by the evidence from the Post-burn surveys, fire-constrained ordination of the Grid survey data, Konstant experimental study or the literature. The opposite appears to be the case. In general burning favours black rhino in the short term, and RMG data indicated that the direct mortality risk to rhinos from fire was small.

In particular:

- Fire in more open areas appears to be beneficial to black rhino in the short term by keeping "*Acacias*" in the most preferred small size classes and removing grass interference.

- Black rhinos were also clearly not being forced to restrict their feeding to unburnt patches. Rather they selected to feed in burnt patches, regularly choosing to browse on burnt plants of both palatable and unpalatable species. Further chemical analysis of burnt and non-burnt browse, and especially the study of the effect of heat on browse palatability may explain the heavy feeding on burnt plants by black rhino.

- Basal coppice on regrowing burnt *Acacia* trees during the early growing season flush period appears to have a very high crude protein content and high levels of phosphorus and potassium.

- Unless *Acacia* trees have grown above 1.5 to 2m, the literature indicates that fires do not have to be hot to benefit black rhino. Indeed the Post-burn surveys (chapter 9) indicated that areas receiving low to medium intensity fires were generally more preferred than areas receiving severe burns.

- Cool undercanopy fires in closed woodland are also likely to benefit black rhino by removing seedlings of unpalatable evergreen species that could otherwise become canopy dominants.

CHAPTER 15 NOTES

#1: "*Acacias*" grow in more open areas which not surprisingly experience the highest fire frequencies, and a high proportion of "*Acacias*" were burnt in 1989. Thus even if there had been no selection for burnt trees, offtake from burnt "*Acacia*" trees would still have been greater (than from unburnt trees). Given the nature of the post-burn surveys (where abundance levels of burnt and unburnt browse was not accurately measured) it was not possible to calculate accurate preference values for burnt and unburnt "*Acacia*" trees. However despite this, the scale of the selection for browsing burnt twigs indicates these were in all probability preferred as well as important dietary items. If burning reduced palatability of "*Acacias*", one would have expected unburnt trees to have made up a far higher proportion of the diet.

#2 With the exception of *A.grandicarnuta* and *A.rabusta*, *Acacia*s are generally not dominant in riverine and alluvial areas near to water. *A.grandicornuta* is strongly associated with *S.africana*, and the favouring by black rhino of lower lying alluvial areas near permanent water at this time of year, was reflected in the increased contribution of the normally rejected *A.grandicornuta* to the Umfolozi immediate post-burn diet (3.2% vs 0,32%). By way of contrast late winter feeding levels in plots far from water in the drier Umfolozi were very low (chapter 9).

While *A.nigrescens* is also a dominant on dolerite derived shortlands soils near the river, this species is generally tall and all but the smallest spize is rejected by black rhino. .

#3: With Umfolozi being drier than Hluhluwe, one would expect more of a dry season crunch period in Umfolozi (when plant moisture and nutrient content is poor and dietary quality drops to potentially sub-maintenance levels). Rhino may simply be seeking out "green bite" in late winter by eating in low lying areas where the higher moisture and nutrient status keeps plants "succulent" for longer, or by increasing browsing on evergreen or semi-evergreen species ("stop-gap" species) in the bush clump vegetation.

#4:For example, black rhinos were seen to browse the leaves of bulbous *Crinum graminicola* during early summer. The majority of plants of this species showed signs of browsing in some areas. *C.graminicola* is summer growing and requires full sun (Du Plessis & Duncan 1989), and removal of above ground grass biomass by late winter burning appears to favour its growth. The majority of *Crinum*'s are "heavy feeders" (Du Plessis & Duncan 1989), and one can speculate that ash from the burns may have improved soil nutrient status around these plants.

#5: Limited chemical analysis of browse samples revealed that fresh coppice during the post-burn flush period was very high in crude protein, phosphorus and potassium. However, burning was not the only reason for increased use of the Gqoyini basin area by black rhino during early summer. The most important factors governing use of this area appear to be water availability and accessibility of favoured small and flushing *Acacia* browse. After the first rains, black rhinos made frequent use of the numerous pans in the area that had filled up suggesting that the availability of surface water was also influencing habitat use levels. During the dry years from 1980 to 1983, black rhinos were also commonly seen in this area following the first rains during the early season growth flush period. During these dry years, because grass biomass was low there were no control burns (as there was insufficient fuel) browse plants grew more slowly and remained readily accessible to black rhino.

#6: *A.caffra* appears to be particularly able to withstand repeated severe fires (chapter 16; Bruce Brockett personal communication). Repeated hot burns may result in *A.caffra* increasing at the expense of other less fire tolerant species. While this has negative implications for game viewing it is not a detrimental change in terms of black rhino habitat suitability as *A.caffra* is a favoured black rhino food.

#7: All browse samples were very kindly analysed by Richard Eckhart of Cedara. Each sample consisted of a pooled sample of browse from at least three trees. One problem with this work was that published data on large non-ruminant megaherbivores was very limited, and interpretation all too often has to rely on inappropriate standards developed for domestic grazing animals (Koen 1992). Results are presented and discussed in more detail in the BR2000 final report.

#8: P.S. Goodman (pers comm) also reports having witnessed elephants also favour browsing on burnt Acacias that had their thorns burnt off.

#9: Almost fifty years ago, Attwell (1948) wisely had the foresight to propose that scientific ecological research be undertaken into the effects of fire on savanna vegetation. Sadly his advice was not adequately heeded as a disproportionately small part of research budgets and effort has gone towards the study of applied plant ecology and plant population biology (compared to large animal accountancy and glamorous "big & hairy" research). This criticism has been echoed by van Wilgen et al (1988). Hopefully future research effort will focus more on determining woody plant responses to different fire characteristics (including fire:animal interactions). The results of such research would undoubtedly be of great applied value to managers who would have increased predictability of the effects of their burning on vegetation.

Van Wilgen & Wills (1988) highlighted the limitations of most current post fire monitoring which simply records topkill rates of shrub species following management burns. Topkill is defined as the killing of above ground parts of resprouting plants without killing the roots. They argued that such monitoring does not provide answers to the major questions as to how fire should be used to achieve conservation management goals. By way of contrast, post-burn tree mortality rates have rarely been recorded.

#10: Although Konstant never completed her thesis write-up, some of her preliminary findings were written up and submitted to the Natal Parks Board as a draft chapter in 1990 (Konstant 1990 *in litt.*). She is thanked for giving me permission to discuss this unpublished work.

#11: Konstant's (1990 *in litt.*) findings that *M.senegalensis* densities can be reduced by fire were corroborated by exploratory Continuous Formal Inference-based Recursive Modelling of the Hluhluwe Grid Survey data. The effect of recent fire frequencies (1980-88) on *M.senegalensis* densities was an interactive one with altitude and underlying geology. In lower lying altitudes (75m-200m) where the soils were derived from Lower-Middle Beaufort sediments, *M.senegalensis* densities were significantly higher (F 5.768 DF 1,152 p 0.0175 Grouping was significant at the 3.51% conservative level). Densities were about double those on Non Lower-Middle Beaufort plots. However on the lower lying Non Lower-Middle Beaufort sediment plots fire significantly affected densities. Plots which had experienced the most frequent burning (5 or 6 burns in 9 years compared to plots burnt only 2-4 times) had significantly lower densities of *M.senegalensis* (F 6.806 DF 1,79 p 0.0109 Grouping was significant at the 4.35% conservative level). Densities on the less frequently burnt plots were approximately double those on the frequently burnt plots.

#12: This was a two step process. The first step was to identify a small set of key environmental variables which significantly explained variation in species canopy cover abundances in Hluhluwe (chapter 14). The next stage of the analysis was to determine whether fire frequency variables since 1955 significantly explained any more of the variation in the data not already accounted for by the set of key environmental variables (see chapter 5). The rationale behind this approach, was that if fire frequencies directly influenced habitat conditions in their own right, and provided sites with similar environmental conditions had not all experienced identical fire regimes; then fire variables should still significantly explain some of the residual habitat variability (i.e. variation in the habitat data not already accounted for by the environmental variables).

Tree size is a function of successional stage, which can be influenced by management actions such as bush clearing and burning. Therefore the constrained polynomially detrended correspondence analyses undertaken were based on RESOURCE processed spize based cover abundance data.

As the analysis sought to investigate how fire had influenced woodland succession in Hluhluwe, 49 plots were excluded from the data set prior to analysis. The dropped plots were either aberrant (identified by RESOURCE) or contained riverine forest or mature *Celtis africana* evergreen forest.

#13: The angle between biplot arrows indicated that the effect of the two short term fire variables was largely independent from the general longer term fire frequency 1955-64 axis. The importance of recent fires was indicated by another run that included the dummy variable for fires in 1988. In this run the Fire1988 dummy variable had the highest second axis inter set correlation and biplot score.

CHAPTER 16

THE EFFECTS OF MANAGEMENT ACTIONS ON BLACK RHINO HABITAT QUALITY II: LONG TERM EFFECTS OF FIRE

INTRODUCTION

This chapter discusses the longer term effects of fire on habitat quality for black rhino, and is the second of five chapters examining the effects of management actions on black rhino habitat suitability.

Hluhluwe Grid study area's past fire history is determined as best as possible by both reviewing local literature and analysing the past fire maps for the area (drawn up annually by the Natal Parks Board since 1955).

An attempt is then made, within the limitations of the data, to examine how rates of underlying black rhino population change varied in relation to periods of low and higher fire frequencies.

Past fire histories derived from the fire maps at Hluhluwe Research are then examined to see if there was any relationship between past fire regimes and observed timing of major changes in Hluhluwe vegetation physiognomy revealed by King's (1987) study of aerial photographs and local literature.

The influences of fire frequencies at different times since 1955 on woody spize composition in the Hluhluwe Grid study area are then examined using a partial fire-constrained ordination analysis of Grid survey data (excluding riverine, mature evergreen forest and aberrant plots)[#1], and the results interpreted in the light of knowledge of rhino feeding preferences. The statistical significance of the results was tested using non-parametric Monte-Carlo permutations testing.

The data from the remeasurement of Hitchins' plots were examined for any indications of the longer term effects of fire on vegetation, and hence black rhino habitat quality. The proceedings from a Hluhluwe-Umfolozi vegetation dynamics workshop, Konstant's (1990 *in litt*) findings and King's (1987) thesis were also reviewed (along with other local literature) for references to the likely longer term effects of past fire regimes on habitat structure and composition. The possible longer term interactive effects of animals and fire are also briefly discussed.

HLUHLUWE'S PAST FIRE HISTORY

SOURCES OF INFORMATION

Fire maps lodged at Hluhluwe Research were used to determine the history of fires in the Hluhluwe Grid study area since 1955[#2] when maps were first produced. Additional sources of information included King's (1987) review of the literature on fire and past vegetation changes in Hluhluwe and Zululand, papers from the 1979 workshop and symposium on vegetation dynamics in Hluhluwe-Umfolozi, and Brooks and Macdonald's (1983) historical review paper.

EARLY HLUHLUWE FIRE HISTORY

A review of the literature indicated that prior to 1911, frequent annual or biennial winter burning maintained extensive areas in a sub-climax pyrosere of open grasslands (Bews 1912, Aitken & Gale 1921, Henkel 1937, Bayer 1938, Feeley 1978, Blakeway 1985)[#3]. After the appointment of a Game Conservator in 1911, there probably was a decrease in fire frequencies, although according to Capt. Potter's annual reports burning in Hluhluwe was carried out "*whenever and wherever it was necessary*" up till 1932 (whatever that means !). Notes from the 1979 vegetation dynamics workshop in Hluhluwe indicated that Hluhluwe North became more woody during this period (Cowles 1959 referring to Capt. Potter's reports). Nevertheless by 1936, much of Hluhluwe's vegetation was still woodland and parkland savanna with large expanses of open grassland (Henkel 1937, Brooks & Macdonald 1983). Almost no burning was undertaken in the 1930s to avoid damaging the wooden tsetse fly traps that had been placed throughout Hluhluwe-Umfolozi (Henkel 1937). However, after removal of the fly traps there was some winter burning between 1943-46 (Vincent 1970). There were no records of fire from 1947 to 1954, and in 1954 an order was given that no burning should take place, although this was later modified to allow burning of peripheral firebreaks (King 1987). Thus there appears to have been an eight year period without fire before fire mapping began in 1955. Figure 16.4 shows this was a very "dry" below average rainfall period with only 1949 being a "wet" year.

HLUHLUWE FIRE HISTORY SINCE 1955

Annual fire maps at Hluhluwe Research were used to compile Figure 16.1 which shows fire regimes in the Grid study area over five period from 1955-1987[#4].

Figures 16.2 and 16.3 illustrate changes in fire frequencies and fire return periods since 1955 when fire records were kept and annual fire maps started to be produced.

Fire frequencies shown in Figure 16.2 were calculated in two ways.

- In the first method, the average fire return periods were calculated for the 193 Grid survey plots after excluding 49 aberrant and true forest and riverine plots that would not have been burnt (shaded black on Figure 16.2).

- In the second method, the Hluhluwe Grid study area fire regimes shown in Figure 16.1 were quantified using a 470 point sampling overlay (shaded with a dot pattern on Figure 16.2). This method uses a bigger sample size of points (470 vs. 193) but has the disadvantage that true evergreen forest and riverine plots are not excluded.

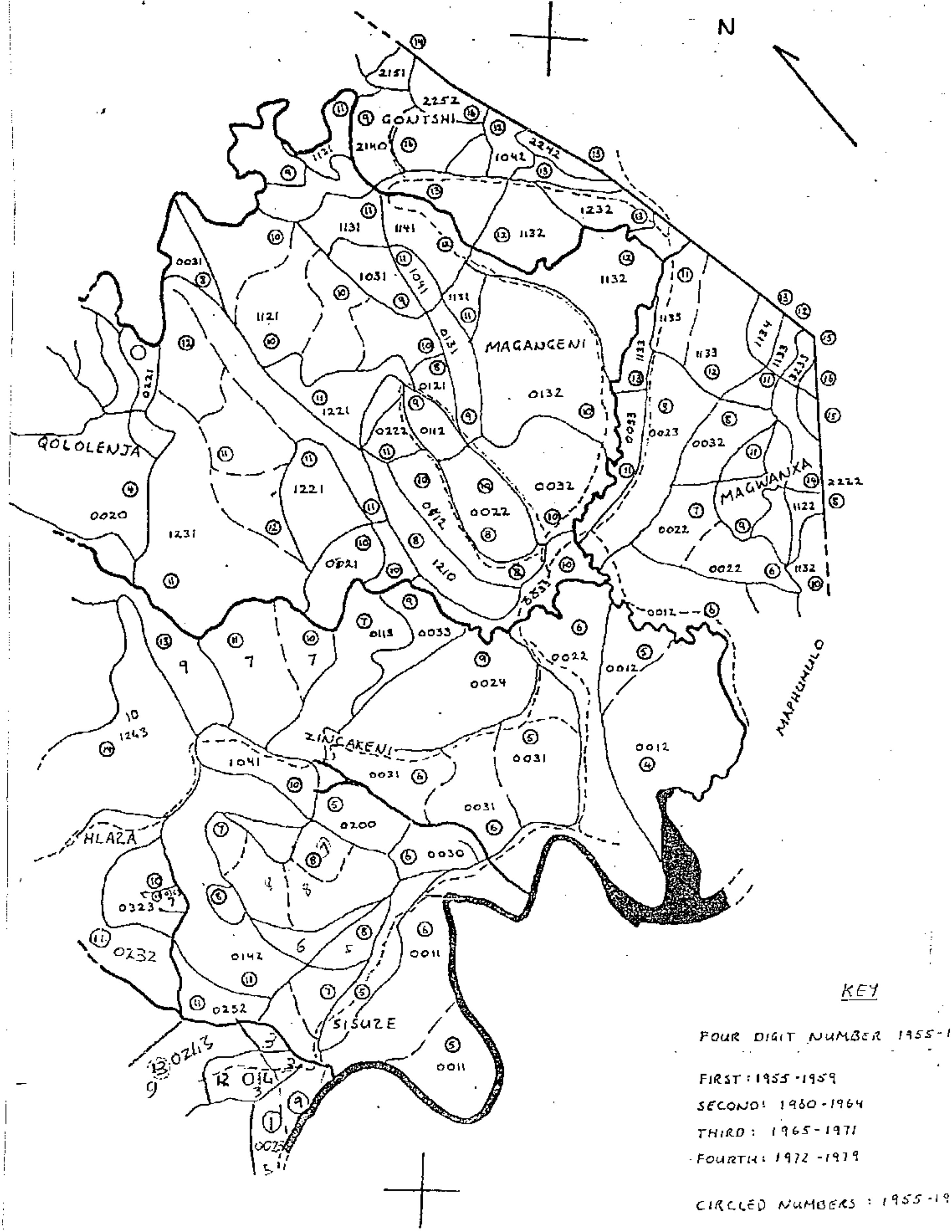
Figure 16.2 shows that while there were differences between the results from the two methods, the same general patterns emerged. For this reason, the average of the two estimated fire return periods are given below in the text and notes at the end of the chapter unless otherwise stated.

FIGURE 16.1

DISTRIBUTION OF BURNS 1955-1987

HLUHLUWE STUDY AREA

1:50 000



KEY

FOUR DIGIT NUMBER 1955-1

FIRST: 1955-1959
SECOND: 1960-1964
THIRD: 1965-1971
FOURTH: 1972-1979

CIRCLED NUMBERS: 1955-19

Figure 16.2 The burning history of NE Hluhluwe, showing average fire return times calculated from 193 non-forest/riverine grid plots (left axis,black) and summarised over grid study area from Figure 16.1 (left axis, grey); and the mean % of the area burnt per year in different time periods from 1955 to 1987 summarised over grid study area from Figure 16.1 (right axis, striped) .

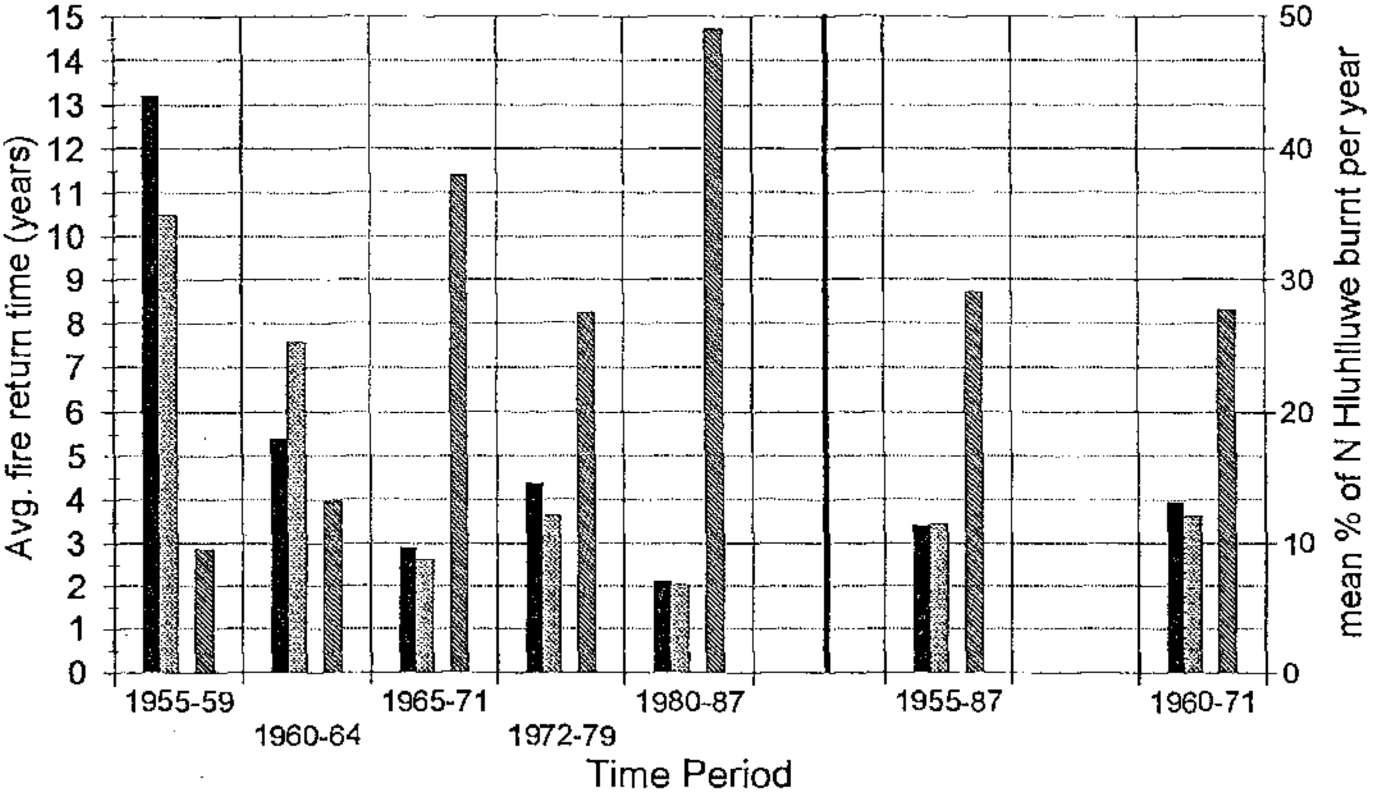


Figure 16.3 Burning history of NE Hluhluwe grid study area showing the proportion of the area burnt at different frequencies, in different time period from 1955-1987 based on data in Figure 16.1 . Shading gets darker as fire frequency increases from white (burnt once) to black (burnt 6 times). For example, 64.5% of the area was burnt from once to four times over the period 1980-87.

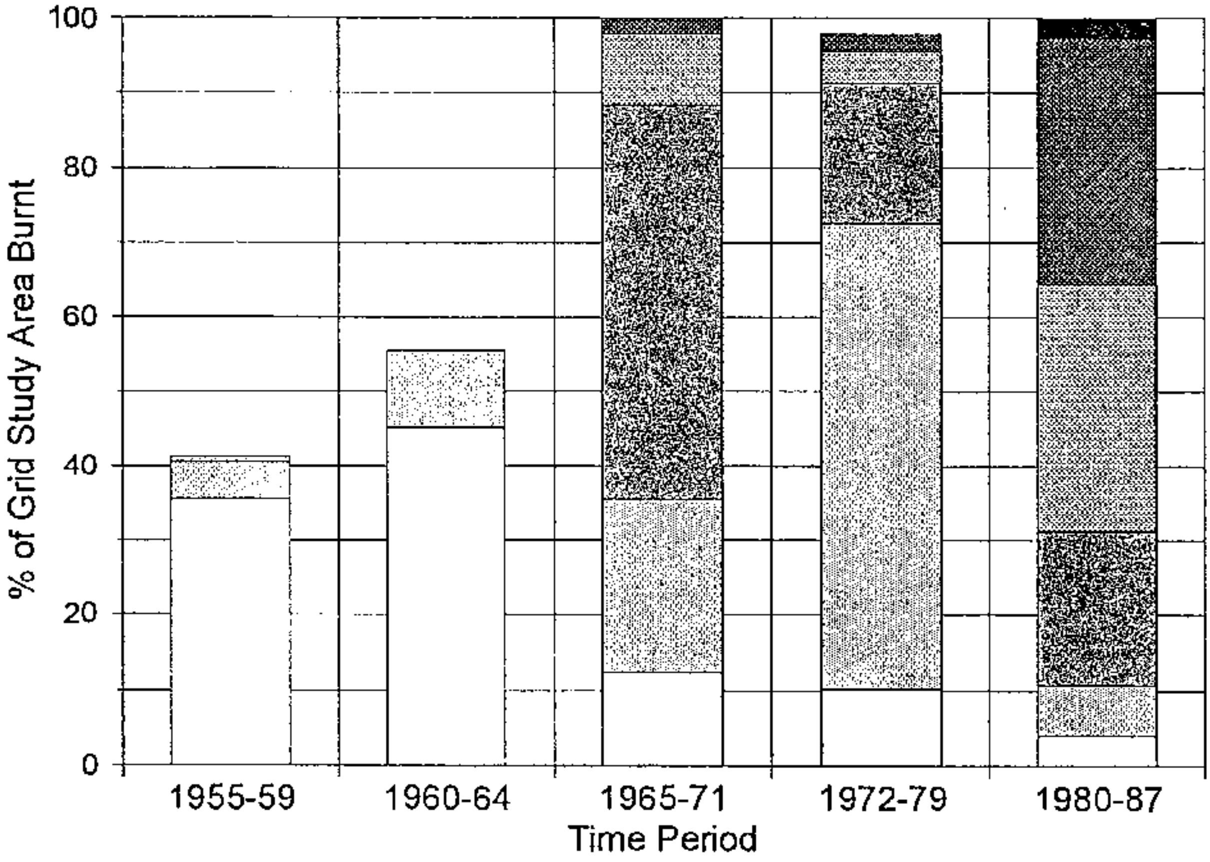


Figure 16.4. Variation in annual Hluhluwe rainfall over the period 1933-1990 (based on Egodeni data supplied by M.Pattenden)

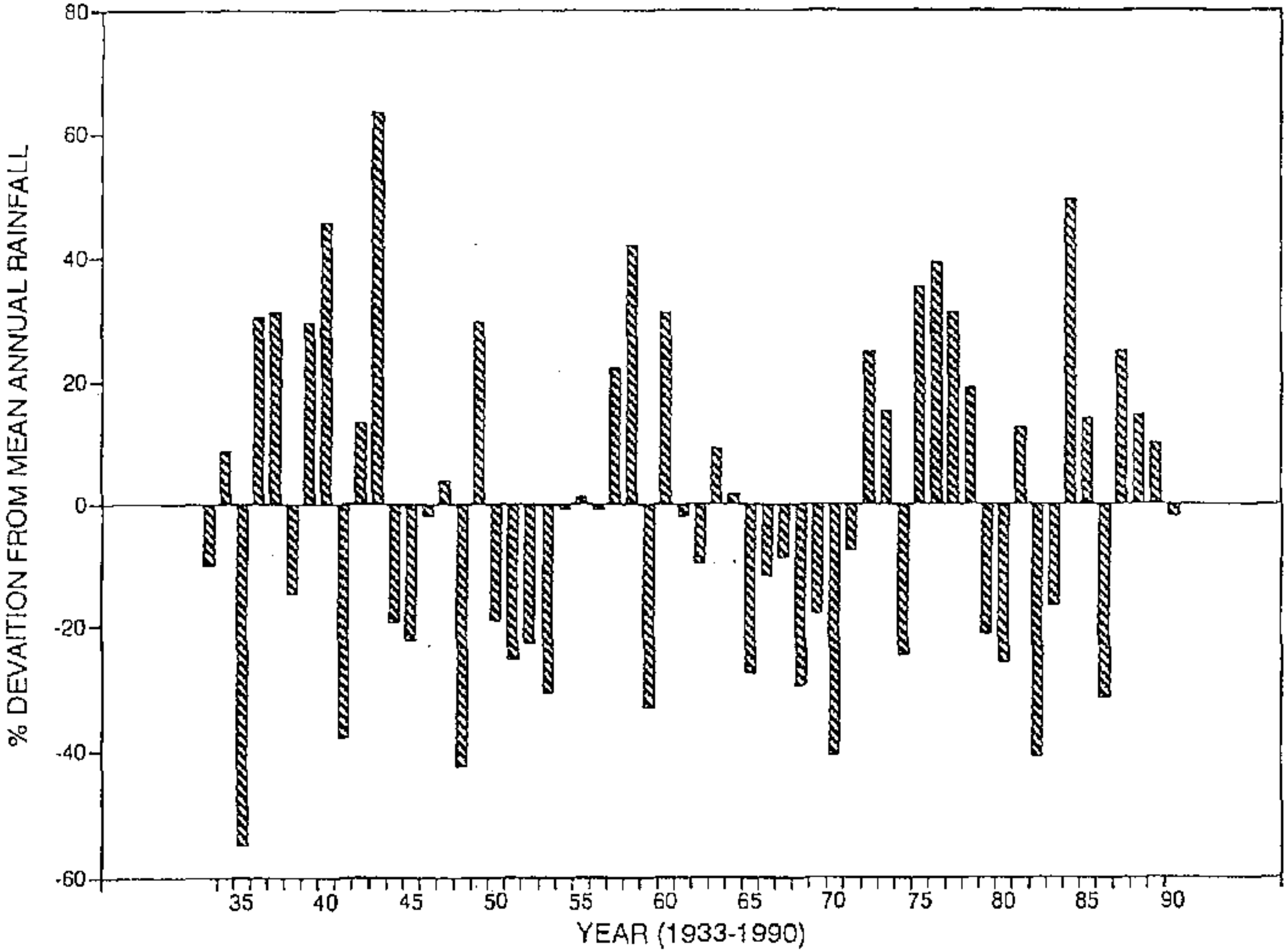


Figure 16.3 was derived using only the second method (quantifying Figure 16.1 using the 470 point sampling overlay), and shows the proportion of the Grid study area burnt at different frequencies in different time periods from 1955-1987. It shows how a large proportion of the study area was never burnt from 1955-64, and that fire frequencies during this period were low. By way of contrast, Figure 16.3 shows that after 1964 all or almost the whole Grid Study area was burnt.

Figures 16.2 and 16.3 show that the increase in area burnt since 1964 coincided with increased fire frequencies and reduced fire return periods. This was particularly the case in the periods 1965-71 and 1980-87 (period with the highest fire frequencies) which were the only periods where the average fire return period fell below three years. Fire frequencies were lower in the intervening period 1972-79. For a more detailed description of the Hluhluwe fire history since 1955 readers should consult note [#5] at the end of this chapter.

For comparative purposes Figure 16.4 shows above- and below-average rainfall years since 1933.

RELATIONSHIP BETWEEN BLACK RHINO POPULATION CHANGES AND PERIODS OF BOTH LOW AND HIGH FIRE FREQUENCIES

Since the start of fire records (1995) and prior to the Grid survey (1989) there have only been two periods with high fire frequencies, 1965-71 and 1983-89. The obvious question is how have rates of population change varied in relation to periods of both lower and higher fire frequencies ? Unfortunately black rhino population estimates have only been updated annually since 1990, with the result that the intervals between past population estimates do not necessarily correspond exactly to the time periods with different fire frequencies. Over time, area boundaries for many of the population estimates have also changed. Translocations from Hluhluwe also occurred in some years, but exactly which area animals were removed from in the reserve was not always known. The accuracy of a few of the population estimates (eg 1982) that were not primarily based on ID data is also lower. These factors make it difficult to accurately relate the rates of black rhino population decline/increase to the different time periods with differing fire frequencies. This has however been attempted within the limitations of the available data in this chapter and Table 1.1.

- The increase in densities of black rhino in Hluhluwe from 1948 to 1961 coincided with a period of low fire frequencies and rapid bush encroachment (chapter 20, King 1987, Attwell 1948, Cowles 1959, Deane 1966, Bourquin & Hitchins 1979, Watson & Macdonald 1983).

- Fire frequencies were also low from 1960-64. In 1961, the population crashed in northern Hluhluwe with numbers declining over a few months from an estimated 146 to 100 (a decline of 32.2%). Much of this decline however was probably related to the extensive clearing of *Acacia* scrub in northern Hluhluwe just prior to the die off and the increase in grass growth that occurred following recent heavy culling of grazers and high rainfall (see chapter 17). Over the post "die-off" period till 1967 the northern Hluhluwe population declined by a further 25 animals (average annual decline in densities of 3.5% per annum). No animals were translocated from Hluhluwe over this period (Brooks & Macdonald 1983).

- Fire frequencies increased between 1965 and 1971, despite all seven years having below average rainfall. From 1967 to 1972 estimated densities of black rhino in northern Hluhluwe only declined slightly from an estimated 0.842 to 0.752 black rhino/km^2. However, 28 black rhino were removed from Hluhluwe in 1971 (equivalent to an average density reduction of 0.121 rhino/km^2), and after allowing for translocations, numbers of rhino therefore remained relatively stable over this period of frequent fires.

- Fire frequencies declined from 1972-82 as did black rhino densities in Hluhluwe Game Reserve which decreased from an estimated 0.863 to 0.545 black rhino/km^2 (from 1973-82). The actual decline in density was probably greater than this, as the 1982 estimate (not based on ID monitoring) is believed to be an overestimate (as more accurate and intensive 1985 ID monitoring data analysed using Bayesian Mark-Recapture techniques estimated the density in Hluhluwe at only 0.377 black rhino/km^2). Even after allowing for these translocations (five rhinos were removed from Hluhluwe in both 1977 and 1978 with a further sixteen removed in 1981), the underlying population trend during this low fire frequency period was sharply downwards. The end of this period coincided with a bad drought as four of the five years from 1979-83 had below average rainfall (Figure 16.4).

- Fire frequencies increased markedly from 1983 onwards (post drought period). From 1985-1991 (a time of frequent burning) densities continued to decline in Hluhluwe from 0.377 to an estimated 0.268 black rhino/km^2 by 1991, although one can hypothesise that this decline may in part have been due to a die-off of a cohort old animals born during the increase in population up to peak levels. Unfortunately failure of Park staff to keep and age all the skulls from animals that died during this period meant it was not possible to confirm whether this was the case.

- However, following increased elephant activity, the build up in grazer densities, continued bush clearing and continued more frequent fires, estimated densities of black rhino have apparently increased rapidly in northern Hluhluwe from an estimated 0.261 black rhino/km^2 in 1991 to 0.402 black rhino/km^2 by 1996 (Howison *et al* 1997). Interestingly kudu numbers have also increased during this period.

Thus in summary, while the increase of black rhinos in Hluhluwe up to peak levels coincided with a period of low fire frequencies (but also rapid bush encroachment), after the 1961 population crash, the only periods without underlying population declines (after allowing for translocations) were associated with the two periods of more frequent fires (average fire return periods less than three years).

HLUHLUWE BUSH ENCROACHMENT IN RELATION TO FIRE FREQUENCIES

King's (1987) thesis quantified physiognomic changes on aerial photographs of Hluhluwe from 1937-82[#6] pin-pointing the time of accelerated bush thickening.

Prior to 1954, "*scrub*" encroachment on the aerial photographs was relatively insignificant, averaging only an increase of 0.12% per annum between 1937-1954. This was a period of low fires frequencies

The biggest increase in "*scrub*" on the aerial photographs occurred in the late 1950s - also a period of low fire frequencies and above average rainfall. In just six years (1954-60), the area of "*scrub*" increased by 73.9% to cover 20.5% of the reserve. The start of the decline in black rhino numbers in 1961 followed the rapid increase in "*scrub*" on the aerial photographs.

As King's "*scrub*" category refers to later stages of bush thickening [#7] the initial establishment of large numbers of small "*Acacias*" in the grasslands (favouring black rhino [#8]) will, most probably, have taken place earlier than 1954, with the increase in "*scrub*" on the aerial photographs reflecting increased canopy cover (tree height and size) of established encroaching *Acacias* in response to the continued low fire frequencies and wetter conditions in the mid-late 1950s.

King (1987) also noted that while fire and bush clearing have controlled scrub encroachment in Hluhluwe in the short term, it has not done so in the long term. Watson & Macdonald (1983) noted that bush encroachment has proceeded throughout Hluhluwe-Umfolozi despite 23% of the Park being burnt each year, concluding that to control scrub encroachment, fires should occur at least every three years. From 1955-89 there have been only two periods in the Grid study area with average fire return periods less than three years. However, even this frequency of burning may not be enough to slow woody plant thickening, as the results from burning experiments conducted in the drier Kruger Park since 1954 indicated that the most desirable burning frequency (for the control of bush encroachment) was annual or biennial, depending on grazing or fuel conditions (Gertenbach 1979). While annual and biennial burning in late winter during a wet period reduced woody cover in Kruger Park, triennial burns only slowed the rate of increase (Gertenbach & Potgeiter 1979).

Although fire frequencies increased after 1964, bush thickening continued up to 1982. By 1982 King's "*scrub*" covered 32.2% of the reserve - an area 3.27 times greater than in 1937, and between 1937 and 1982 the total area covered by forest and "scrub" increased from 22.0% to 48.5%. It is also clear from a close examination of the 1982 aerial photograph in Kings' thesis (Plate 3) that extensive areas classified as "open grassland/parkland" were also progressing rapidly towards what King termed "*scrub*". An examination of King's map (King's Figure 7) reveals a correspondingly **marked decline in areas of "open grassland/parkland"**. Indeed, by 1989, the Post-burn survey revealed that open grassland only accounted for 7.6% of Hluhluwe North.

King (1987) noted that the areas most frequently burnt corresponded well to those least affected by bush encroachment. The corollary was also true. From repeatedly covering the ground in the Pilot, Grid, Post-burn and Hitchins surveys, it was apparent that by 1989/90 much of area of extensive "scrub" in the 1982 aerial photograph of the central Hluhluwe Grid study area (see Plate 3 - King 1987) consisted of *A.nilotica* closed woodland in transition to lowland forest dominated by *E.racemosa, B.zeyheri,* and *R.pentheri*. By mentally overlaying the fire frequency map (Figure 16.1) it was apparent that most of these areas of *A.nilotica* dominated "*scrub*" were not burnt from 1955-1964. Given that there was no evidence of fire from 1947 to 1954 (King 1987) these areas are likely not to have been burnt for at least 17 years (and probably far longer than that).

Man and elephant had been absent from Hluhluwe since proclamation in 1897. Historical annual or biennial winter burning probably stopped around 1911, and from 1930 till 1960 fire frequencies appear to have been significantly reduced. If fire was solely responsible for keeping areas open one would have expected bush thickening to have taken place earlier. The question is why did rapid bush encroachment (early phases of which would have benefited black rhino allowing densities to increase to record levels) take place in the 1940s and 1950s, and not before?

> - **A key factor may have been that it was not until the 1950s that game numbers began to build up appreciably in Hluhluwe reducing tree:grass competition.** In the predominantly wet period from 1930 to 1944 grazer stocking rates in Hluhluwe ranged from an estimated 7.3 to 11.0 A.U./km^2. Thus during this period, fire frequencies were low, grass biomass is likely to have accumulated and reduced light availability for developing woody seedlings. However, in the 1950s with game numbers building up, viable *Acacia* seed would have been well dispersed by browsers, been able to germinate and establish in favourable conditions with few fires and reduced grass competition (due to below average rainfall and high grazer stocking densities).

- Although there is no direct evidence, the use of DDT to kill tsetse flies in the reserve at this time, may have increased *Acacia* seed survival rates if the DDT reduced populations of brucchid beetles (*Acacia* seed predators). However other authorities have argued that seed predation is not that important to recruitment of long-lived perennials (TM Smith and SE Taylor quoted in Smith and Goodman 1986; Anderson 1989 [#9])

In summary, the period of initial bush encroachment coincided with a dry period with little fire and the subsequent development of "scrub" on the aerial photographs coincided with a wet period with little fire. The timing of the initial establishment of encroaching species was also associated with a build up game and followed DDT spraying of the reserve.

Although fire frequencies increased after 1964, woody plant thickening in Hluhluwe continued. King (1987) hypothesised that the change in season of burn from winter to early spring may have favoured woody savanna species at the expense of fire tolerant grasses like *Themeda triandra* (King 1987).

Areas of *A.nilotica* closed woodland in transition to lowland forest dominated by *E.racemosa, B.zeyheri,* and *R.pentheri* appear to have been associated with lack of fire from 1955-64.

PARTIAL FIRE-CONSTRAINED ORDINATION TO EXAMINE THE EFFECTS OF FIRE FREQUENCIES SINCE 1955 ON HLUHLUWE GRID STUDY AREA HABITAT COMPOSITION AND STRUCTURE

The partial fire-constrained ordination analysis of the non-forest/riverine plot data[#10] provides an objective test of the hypothesised key role of fire in longer term woody plant dynamics as it is highly improbable that the fire-constrained ordination analysis would generate statistically significant canonical axes and spize patterns consistent with those hypothesised simply by chance.

If fire has had a major influence on woody species composition, size structure and successional development as hypothesised by King (1987) and Whateley and Wills (1996), then past fire frequencies should significantly explain some of the residual variation in habitat structure and composition that cannot already be explained by physical and environmental variables[#11]. If lack of fire in the past was a key factor governing vegetation changes in Hluhluwe, the first fire constrained canonical axis and canonical trace should be statistically significant, and the variable for fire frequencies from the mid 1950s to early 1960s should end up with one of the longest arrows on the biplot. In addition, the relationship between the different spizes on the ordination biplot should reflect hypothesised (Whateley & Wills 1996) successional patterns in *A.nilotica* dominated areas with rejected later successional spizes associated with the development of lowland forest (eg *A.nilotica4, E.racemosa4, B.zeyheri4, R.pentheri4,* and *S.myrtina3*) being associated with low fire frequencies in both the short and long term.

MAIN CANONICAL FIRE AXES

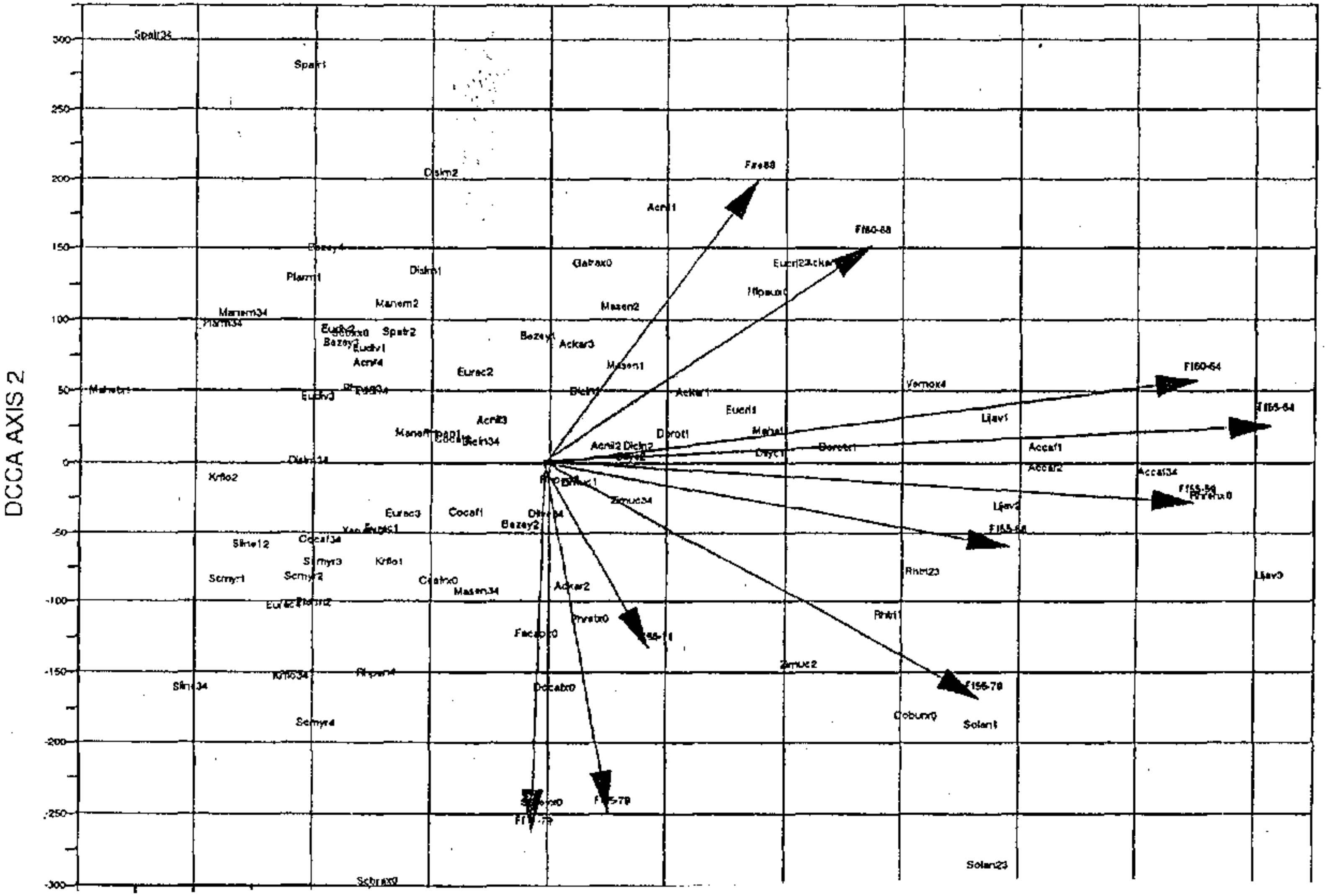
A total of four runs were undertaken to pick the best subset of fire variables and ensure that each variable contributed independently to the final model[#12].

Fire significantly explained some of the residual variation in spize canopy covers (Canonical axis 1 $p \leq 0.01$). Only two fire axes were revealed ($\lambda 1 = 0.084$ $\lambda 2 = 0.064$). **The biplot[#13] (Figure 16.5) shows that the first fire axis was a general fire frequency axis, with fire frequencies from 1955-64 having the biggest influence on spize composition[#14]. This axis was statistically significant ($p<0.01$) providing objective corroboration that lack of fire thirty to forty years ago had a major influence on current Hluhluwe woody composition and structure.**

The second fire frequency axis primarily differentiated between recent high fire frequencies in the period 1980-88 and high fire frequencies in the intermediate period 1965-1979.

The similarity in the main groupings of spizes to emerge in both the fire constrained biplot (Figure 16.5) and a straight unconstrained Detrended Correspondence Analysis (used to produce the 3D plots of spize abundance in

Figure 16.5. Hluhluwe spize plot (non forest grid plots) Axes 1 and 2 from Partial Canonical Correspondence Analysis - Fire run 3



ordination space in chapter 20) was also consistent with fire having had a major influence on the Hluhluwe woody vegetation structure and composition[#15].

The following common species and spizes were favoured by high fire frequencies (First Axis scores in brackets - in order of increasing height classes where applicable): *A.caffra*[#16](210,210,258), *L.javanica* [#17](189,194,306), *Rhus macowani* (now renamed *R.rehmanniana*) (281), *Solanum* species (184,187), *Vernonia subuligera* (160), *R.tridentata* (144,159) *D.burgessiae* (156), *D.rotundifolia* (52,122), *H.pauciflorus* (92), *E.crispa* (81,101) and tall *A.karroo* (>4m 115). Taller individuals of these fire tolerant species were associated with more frequently burnt patches.

A number of species and spizes showed the opposite trend being more associated with low fire frequencies since 1955 (First Axis scores in brackets - In order of increasing height classes where applicable): *S.africana* (-102,-64,-170), *S.inerme* (-126,-152), *M.nemorosa* (-56,-65,-130), *P.armata* (-105,-100,-139) *E.divinorum* (-77,-90,-99,-76) *Cassine aethiopica* (-86) and *Canthium inerme* (-118). These species are associated with low lying more alluvial areas nearer the Hluhluwe river in thicker habitat which are infrequently burnt.

RELATIONSHIP OF KEY LOWLAND FOREST PRECURSOR AND LOWLAND FOREST SPIZES TO THE MAIN CANONICAL FIRE AXES

The fire constrained biplot (first and second canonical axes scores) were then examined to see if fire regimes were strongly related to spize succession in *A.nilotica* dominated areas towards lowland forest as hypothesised by Whateley and Wills (1996).

The spizes mentioned by Whateley and Wills (1996) were ordered along axis 1 in approximately the correct order hypothesised in their successional model (ie. *A.karroo, D.cinerea, A.nilotica, M.senegalensis, R.pentheri, B.zeyheri, C.africana, E.racemosa, M.heterophylla, Scolopia zeyheri, Zanthoxylum capense*). The fire-constrained ordination was based on a far larger data set (number of plots and species) than the study of Whateley and Wills

(1996), and indicated that *Kraussia floribunda, Scutia myrtina, Sideroxylon inerme* and *Cordia caffra* were also key indicator species associated with later stages of the Whateley-Wills successional pathway.

As fire frequencies decreased between 1955and 1964 (i.e. proceeding leftwards on axis 1 Figure 16.5 from 50 through to -150) the spizes showed the following pattern.

> Small-medium (<2m) *A.nilotica*'s, *D.cinerea*'s and *M.senegalensis*'s → → → → Small-medium *B.zeyheri*'s and *C.caffra*'s, and taller *A.nilotica*'s (2-4m) *D.cinerea*'s and *M.senegalensis*' → → → → Tall (>.4m) *A.nilotica*'s, *R.pentheri*'s, intermediate (2-4m) *B.zeyheri's* and small-intermediate *E.racemosa*'s and *K.floribunda*'s → → → → *S.myrtina*'s, *S.inerme*'s and tall (>4m) *E.racemosa*'s, *B.zeyheri*'s and *C.caffra*
>
> .

Thus mature *E.racemosa/B.zeyheri/S.myrtina/S.inerme* lowland forest was associated with the lowest fire frequencies from 1955-1964 (probably no fires). *A.nilotica*'s role as a key species was also apparent with smaller individuals being associated with higher fire frequencies, and mature tall individuals > 4m with developing lowland forest.

The second canonical axis indicated that favoured small *A.nilotica* trees were associated with higher recent fire frequencies in the 1980s (second axis scores in order of increasing height classes 180,12,30,-70).

Other key species in the succession to lowland forest showed similar patterns, with generally reducing Axis 2 scores as tree size increased indicating that later successional spizes were also associated with lack or recent fire (*D.cinerea* (50,12,15); *B.zeyheri* (89,-44,84,-150), *E.racemosa* (-47,63,-36,-103), *K.floribunda* (-71,-11,-153), *M.senegalensis* (68,110,-92), *R.pentheri* (21,-12,52,-150), *S.myrtina* (-84,-82,-71,-186), *S.inerme* (-58,-160), *Cordia caffra* (-35,17,-55) *Celtis africana* (-85) *Fagara capensis* (-122) and *D.lyciodes* (7,4,-36).

Tall individuals of hypothesised later successional species (*B.zeyheri, E.racemosa, K.floribunda, S.myrtina*, and *S.inerme*) also had lower axis 2 scores (ie were not associated with recent fires) than earlier successional more fire tolerant successional species (*D.cinerea, D.lycioides* and *A.nilotica*).

R.pentheri, *B.zeyheri* and *M.senegalensis* axis 2 scores ranged from positive scores for small trees to large negative scores for mature trees over 4 metres. The ranges of axis 2 scores from small trees less than a metre tall to mature trees were *R.pentheri* (171), *B.zeyheri* (239) and *M.senegalensis* (160). Of the three species, *M.senegalensis* (-92) had a lower mature spize score compared to *B.zeyheri* and *R.pentheri* (both -150). This can be contrasted with *K.floribunda*, *S.myrtina*, and *E.racemosa*. The smallest spizes of these unpalatable later successional more fire intolerant species received a negative score in Axis 2, and the range of scores from smallest to tallest spizes were lower (*K.floribunda* (82), *S.myrtina* (102), and *E.racemosa* (56)). This indicates that *intermediate* species *R.pentheri*, *B.zeyheri* and *M.senegalensis* were earlier successional species than *K.floribunda*, *S.myrtina*, and *E.racemosa*. However the bigger range in scores, with high negative score for mature trees, indicates that *R.pentheri* and *B.zeyheri* are long lived remaining in the community, and are probably more fire tolerant than other apparently more fire sensitive forest dominants like *E.racemosa* and *S.inerme*. The axis 2 scores are consistent with Konstant's (1990 *in litt.*) observation that *S.myrtina* is particularly susceptible to fire.

Although there was insufficient data to subdivide *C.africana* and *F.capensis* according to size class, the negative axis score for these species suggest they are also later successional forest species.

The transition from intermediate size classes to the tallest mature spize produced the greatest Axis 2 score differentials for *B.zeyheri*, *C.caffra*, *E.racemosa*, *K.floribunda*, *R.pentheri*, and *M.senegalensis*. The difference in Axis 2 scores between *S.inerme* trees less than and greater than 2m was also large. Thus the growth of these species seems to have been associated with lower fire frequencies in the 1980s. This makes biological sense, because as canopy cover in closed *A.nilotica* woodland increases, grass species composition changes under trees towards either the less flammable *Panicum maximum* or short *Dactyloctenium australe* (Whateley and Wills 1996) further reducing the ability of fire to spread. As closed woodland develops into forest, fire is effectively excluded.

In the case of *A.nilotica*, there were large jumps in score from intermediate (2-4m) trees to tall mature individuals which is consistent with the maturation of this species being critical to the subsequent development of lowland forest as hypothesised by Whateley and Wills (1996).

The biggest jump in Axis 2 scores was between small (<1m) and medium (1-2m) trees for both *A.nilotica* and *D.cinerea* indicating that fire is likely to have been keeping these species in the most preferred lower size classes (through topkill or by stimulating germination). **The highly favoured small *A.nilotica*'s were particularly associated with high fire frequencies in the 1980s** (axis 2 score 180) confirming the conclusion in chapter 15 that frequent fires can benefit black rhino.

The results of the fire-constrained ordination were therefore on the whole consistent with Whateley and Wills' (1996) hypothetical successional pathway in *A.nilotica* dominated areas:

- Initially lower fire frequencies between 1955-1964 allowed large numbers of small *A.nilotica, D.cinerea,* to develop and then grow out of the reach of fire (reducing black rhino carrying capacity)

- In time and in the absence of fire, extensive areas of *A.nilotica* dominated closed woodland (further reducing black rhino carrying capacity) developed. Intermediate species *B.zeyheri* and *R.pentheri* also increased in density and size.

- More shade tolerant and fire sensitive (generally unpalatable) evergreen species like *E.racemosa, S.myrtina, K.floribunda, C.caffra, C.africana,* and *S.inerme* then became established within the closed woodland

- Following continued protection from fire, individuals of these species then grew up within the closed woodland to create a lowland forest with *E.racemosa, B.zeyheri* and *R.pentheri* as canopy dominants (further reducing black rhino carrying capacity as the palatable *B.zeyheri* and stop gap late winter/early summer food R.pentheri grow out of rhino reach). Highly palatable regenerating small *Acacias* are not associated with these later successional stages. Instead, more unpalatable later successional species establish and develop.

- Eventually some of the older shade intolerant *A.nilotica* and *D.cinerea* trees are likely to be over-topped by the taller growing *E.racemosa, S.inerme* and *B.zeyheri* trees. In time some of the old *A.nilotica* and *D.cinerea* trees die leading to reduced representation of mature *"Acacias"* in older *E.racemosa/B.zeyheri* dominated lowland forest. In time the slower growing *C.africana* trees may grow up to become dominant or co-dominant canopy trees in the forest.

Given knowledge of black rhino feeding preferences, the development of lowland forest in *A.nilotica* dominated areas of northern Hluhluwe following long-term protection from fire will have resulted in greatly reduced black rhino carrying capacity for black rhino (see chapter 20).

ROLE OF FIRE IN *A.karroo* AND *A.caffra* DOMINATED AREAS

Although *A.karroo* was included in the proposed successional sequence by Whateley and Wills (1996) its axis scores did not show the same trend as other Whateley-Wills species. In chapter 20, it is hypothesised that succession in *A.karroo* dominated areas represents a different successional pathway and system compared to the Whateley-Wills successional model for closed *A.nilotica* woodland succession.

A.karroo areas are prone to build ups of tall grass, and tree canopy cover is much lower than in *A.nilotica* woodland. As a result frequent hot fires can more readily spread through such woodlands. It is therefore harder for fire sensitive later successional evergreen forest species to develop in *A.karroo* dominated woodlands.

The same is true for *A.caffra* dominated areas which experience even higher fire frequencies. Given *A.karroo* and *A.caffra*'s association with tall grass areas (chapter 8) it is not surprising that Figure 16.5 indicates that these two species appear fire tolerant. Small *A.caffra*'s represent good black rhino food.

While other Whateley-Wills species scores declined on both axes as tree size increased, if anything, *A.karroo* did the opposite with tall *A.karroo* (>4m) receiving the highest score on both axes (1:115, 2:140). The next highest axis 1 score was attained by small *A.karroo* trees (1:60). *A .karroo* has a tall spindle form in Hluhluwe and the results suggest this species is therefore very fire tolerant once it has matured.

As with *A.nilotica*, it appears that more frequent recent fires were keeping small/medium *A.karroo*'s in the most favoured small size class (Axis2: *A.karroo1* 49, *A.karroo2* -88). Whateley and Porter (1983) also postulated that the height of the woody plants (*D.cinerea*, *A.karroo* and *A.nilotica*) varied from grass height to 4m depending on the interval between burns. They noted this habitat type was the most frequently burnt in the reserve, especially during above average rainfall periods; and used the term "induced" to describe this thicket community because of the effects of man made fires on its physiognomy. Frequent fires in this community should therefore benefit black rhino by keeping plants in the most preferred small size classes.

Thus in the short term frequent recent fires were also likely to be favouring black rhino in *A.karroo* and *A.caffra* dominated areas.

SUMMARY

The results of the fire constrained ordination analysis were consistent with fire playing a key role in governing woody plant succession and community composition and structure over much of Hluhluwe. The results indicated that:

- Lack of fire from 1955-1964 (actually 1947-1964) had played a key role in the development of thicket to *A.nilotica* woodland to mature *E.racemosa/B.zeyheri* dominated lowland forest in areas of NE. Hluhluwe (as hypothesised by Whateley-Wills 1996)[#12] reducing habitat quality for black rhino (see also chapter 20).

- In contrast to *A.nilotica* dominated areas, plots dominated by palatable *A.caffra* and *A.karroo* were associated with more frequent fires and fewer fire-sensitive unpalatable later-successional evergreen forest species.

- **The results also confirmed the short term benefit of recent fires in keeping favoured "*Acacias*" in the most favoured small size classes (chapter 15).**

Knowledge of rhino feeding preferences indicated that, with the exception of some favoured species in thicker alluvial/more forested habitats in low lying areas which are infrequently burnt (eg *A.glabrata, M.nemorosa,* and *S.africana*), in both the shorter and longer-term, lack of fire was associated with poorer quality black rhino habitat (more taller and rejected spizes), whereas more frequent fires were associated with favoured smaller spizes of *A.nilotica, A.karroo* and *A.caffra,* and reduced levels of generally unpalatable later successional broadleaved species.

These results are consistent with past and recent fire being beneficial to black rhino in previously or currently more open *Acacia* dominated habitats, leading one to reject the hypothesis that fire has negatively affected black rhino by removing favoured food plants. Indeed, the earlier examination of black rhino population changes in Hluhluwe since the 1961 die off, indicated that the only periods without underlying population declines were associated with the two periods of more frequent fires (average fire return periods less than three years).

RE-MEASUREMENT OF HITCHINS' 1969-71 PLOTS

Since Hitchins' plots were first measured, his study area was more frequently burnt than the rest of the Grid study area with fire return period for burnt plots ranging from a fire every 1.8 to 2.6 years over the period 1972-89. Unfortunately, the remeasurement of Hitchins' plots only provided weak circumstantial evidence to support or refute particular hypotheses about the influence of frequent fires for the following reasons:

- lack of any unburnt or less frequently burnt control plots in more open habitats;

- from 1965, the period prior to the initial measurement of Hitchins' plots was one of high fire frequencies, so initial spize composition on the plots will also have reflected a period of frequent fires.

- from 1965, the period prior to the initial measurement of Hitchins' plots was one of below average rainfall in contrast to the above average rainfall prior to the re-measurement of the plots in 1990, and some differences between measurements may in part be due to the probable increased grass growth in 1989-90 relative to 1969-71 (chapter 10).

- recorded declines in densities of some species on Hitchins' plots may be the result of self-thinning rather than fire if the trees have grown taller;

- Hitchins' plots were long and very thin (100 x 2 yards) with a very low area to plot boundary distance ratio (0.98 compared to 3.03, 2.14 and 3.45 for the Pilot, Grid and Post-burn plots) which increased the chances that differences between observers in the two surveys in deciding whether plants were "in" or "out" of the plot significantly biasing density estimates in the two surveys (although in this case one can at least examine the relative scale of differences in densities between species).

- plots were subjected to a multitude of frequent and different bush-clearing treatments (chapter 18);

- given the resolution of burn maps, patches of thicker closed woodland/developing forest on plots may have not been burnt within a mapped burnt area;

- Hitchins' plots in particular were located in the NE section of the Grid study area, with the result that lower lying heavily bush cleared sites on black clay soils dominated by *A.karroo, D.cinerea, E.crispa, M.senegalensis, H.pauciflorus D.lyciodes* and *L.javanica* were well represented, but other communities dominated by *A.caffra, A.nilotica, E.racemosa* lowland forest, riverine or alluvial habitats were under-represented in Hitchins' study area (compared to the whole of the bigger Grid study area); and

- other (unrecorded) factors in the intervening two decades may have significantly affected tree densities (e.g. a number of tall *A.karroo* trees in Hitchins' study area were pushed over by the reintroduced elephants and A.J. Wills and L.Wills [pers.comm.] observed that during the early 1980 drought, baboons [under nutrient stress] noticeably increased basal de-barking of medium tall *A.karroo* in NE Hluhluwe, and that these trees in turn were then easily killed by subsequent fires[#18]).

DECLINES IN DENSITIES OF MANY SPECIES IN OPEN HABITATS

While average densities of *A.karroo* (1,022 to 441 /ha) and *D.cinerea* (384 to 260 /ha) declined on Hitchins's plots from 1969-71 to 1990, so did average densities of many other species found in more open areas pre-disposed to regular burning (and frequent clearing) such as *Diospyros species* (708 to 168/ha)[#19], *E.crispa* (890 to 375/ha), *M. senegalensis* (413 to 136/ha)[#20] and *H. pauciflorus* (480 to 281). Interpretation is confounded as Adcock's analysis of the raw data indicated that the size structure of these species also changed with more taller and fewer smaller trees on the re-measured plots (although the majority of individuals of the species were still less than 2 m tall). Thus in part the reductions in densities of these species may have been the result of self-thinning as individual trees grew taller, and this in part may also reflect that the period prior to remeasurement of the plots was a wetter period. Interpretation is further complicated by bush-clearing on the plots, and in particular lack of unburnt control.

Of the species associated with more open habitats, it is possibly noteworthy that, although their average height increased, *L.javanica*[#17] increased in density (159 to 242/ha) and *A.caffra*[#16] (although less common on Hitchins' plots) showed the smallest relative decline in density of the "*Acacias*" on the plots, (108 to 92/ha). The constrained ordination indicated that these two species were strongly associated with frequent fires.

Adcock's graphical analysis of the Hitchins plot data in the BR2000 report indicated that *L.javanica* densities increased between 1970 and 1990, irrespective of the frequency of bush clearing. *L.javanica* densities also increased the most on uncleared transects, and so the increase in *L.javanica* cannot primarily be ascribed to a competitive release following clearing of *"Acacias"* and *M.senegalensis*. This species may rather be favoured either the high fire frequencies, and/or the above average rainfall in years prior to remeasurement. However, although *L.javanica* is unpalatable, the removal of grass interference of associated more palatable spizes (eg small/medium *A.caffra)* by frequent fires should at least be beneficial to black rhino).

In contrast to *A.caffra, A.karroo* densities declined markedly on the plots although average tree height increased. However, chapter 8 showed that the *A.caffra* dominated hillslope community on average only experienced marginally higher (8% higher) fire frequencies, than the mixed *A.caffra/A.karroo* dominated hillslope communities, and *A.karroo* dominated communities. *A.karroo* dominated areas in all probability were more frequently bush-cleared than *A.caffra* dominated sites, although densities of *A.karroo* declined irrespective of clearing frequencies. This could be due to a greater susceptibility to more frequent fires (and possibly a fire:browsing interactive effect), but it may simply reflect either self thinning as existing trees have matured and grown taller or that increased grass interference is negatively affecting re-establishment of this species on burnt sites[#21].

Although densities of small *D.cinerea* densities declined over the period in most areas, Adcock's graphical analysis indicated that overall densities remained similar or increased slightly on the more frequently cleared sites (2-4 times cleared). Thus a frequent disturbance regime coupled with frequent fires was apparently not detrimental to this species.

Although generally less common, densities of intermediate and later-successional species in general (eg. *B.zeyheri, R.pentheri, E.racemosa, K.floribunda, S.inerme, S.myrtina, C.caffra* and *C.africana*) remained similar or increased on the plots, as well as generally increasing in size. This is consistent with an increase in forest development over the twenty year period. Although general fire frequencies in Hitchins's study area were high, (in the absence of very detailed fire maps), individuals of these later successional species on Hitchins's plots may have grown up on more forested sites that may have been largely protected from fire. Interestingly, while densities of small/medium *M.senegalensis* trees (<6') declined in many areas, densities of taller (>6') *M.senegalensis* trees (a spize often associated with the development of lowland forest in *A.nilotica* dominated closed woodland areas) increased. The partial polynomially detrended canonical correspondence analysis (Fig 16.5) indicated that *B.zeyheri* was an intermediate successional species that was more fire tolerant compared to later successional forest species like *E.racemosa, S.myrtina, S.inerme,* and *K.floribunda*. With the exception of western facing slopes, small *B.zeyheri* (<6') increased in density over the period on Hitchins' plots. This is consistent with *B.zeyheri* having a degree of fire tolerance#22.

LONGER TERM ANIMAL : FIRE INTERACTIONS

Although not a specific focus of this study, it is well known that browsers and fire can have significant interactive effects on savanna woody plant dynamics while grazer densities influence the build up of fuel loads.

In the Eastern Cape, for example, the combination of goat browsing and fire depressed densities of *A.karroo* which fire alone did not (Trollope 1980)#23. De-barking by porcupines (A.J. Wills and L.Wills pers.comm.; Yeaton 1988) ,baboons (A.J. Wills and L.Wills pers.comm.) together with fire can be a major determinant of woody plant succession #24.

High elephant densities together with very frequent fires can also contribute to the opening up woodland and savanna and the maintenance of grassland (Eg. Masai-Mara - Dublin 1993, Southern Garamba National Park - Kes Hillman-Smith *in litt* and pers.obs.). The corollary is that reductions in elephant densities as a result of heavy poaching may quickly result in marked habitat changes (e.g. The Northern area of Garamba National Park (Kes Hillman-Smith *in litt* and pers.obs.). It has been hypothesised that the past lack of elephants in Hluhluwe together with the low fire frequencies in the past, contributed to the development of extensive areas of *A.nilotica* closed woodland and subsequently lowland forest (Owen-Smith 1989, chapter 19)#25.

To better understand the longer term effects of fire on woody vegetation and black rhino habitat quality in Hluhluwe, plant population biology research is needed to study the interactive impacts of fire with elephants and other browsers.

CONCLUSIONS

- **The results of the polynomially detrended partial canonical correspondence analysis provided strong evidence to support the hypothesised Whateley-Wills successional model (see chapter 20) that** low fire frequencies (especially from 1955-1964) facilitated the maturation of *A.nilotica* woodlands and their subsequent transformation to lowland forest dominated by *E.racemosa* and *B.zeyheri* resulting in a marked decline in black rhino carrying capacity in these areas. Chapter 8 and the fire constrained biplot also indicated that the palatable *A.caffra* and *A.karroo* were associated with taller grass areas and higher fire frequencies, but that with low fire frequencies these plants were likely to grow up in height and become less palatable for black rhino.

- The **evidence presented in this and the previous chapter does not support the hypothesis advanced by Peter Hitchins at the 1988 NPB meeting (Anon 1988) that past fire frequencies in Hluhluwe have been detrimental to black rhino by selectively removing their favoured food species either in the short or long term. Indeed the evidence indicates that Hluhluwe's black rhino carrying capacity is likely to have been higher today had fire frequencies been higher thirty five years ago.**

- As knowledge of how fire frequency and intensity (and browsing) interact and affect the population biology of key species improves, so will our ability to interpret the longer term impacts of alternative burning regimes on black rhino habitat suitability.

CHAPTER 16 NOTES

#1: See chapter 4 for details of analyses and Appendix 4.1 for a layman's guide to the methods.

#2 The NPB fire maps were useful in studying the effects of fire return periods and time since last fires on vegetation. However, readers should be aware that there are limitations when using data from past fire maps. Firstly, not all the areas shaded as burnt on a burn map may actually have been burnt (eg forest patches or some open areas when burns were patchy). Secondly, simply shading an area on a map gives no information on the characteristics of that fire. That there is little information about past fire behaviour on many of the burn maps is due in large measure to logistic problems.

#3: Evidence to support this comes from:

- Whateley's observation that annual burning on the fire breaks around Hluhluwe maintained areas of open grasslands (Whateley & Wills 1996).
- Photographs taken during the Zululand war towards the end of the last century.
- The finding that annual burning increased grass cover in a high rainfall (>1000mm p.a.) savanna in Nigeria (Sharma 1986).
- Frost's (1984) demonstration that repeated burning, and particularly successive burns at short intervals, adversely affected the survival of resprouting woody individuals.

The following sections give additional historical information on fire regimes prior to 1955.

In 1938, Bayer wrote "*that as long as the usual annual grass fires are allowed to pass through, thornveld remains open. The effect of fires is to retard the succession and to prevent the development of thickets. There is no doubt that in the absence of fire thorn veld would close up to form a closed woodland. It would seem that typical open thorn veld does not represent a climatic climax type of vegetation, but is virtually a fire sub-climax. Exactly what the composition of a true climatic climax would be cannot be determined, since no thorn veld vegetation which is immune from the effects of fire exists in Zululand, and it seems quite impossible to provide permanent protection from fire for any portion of the vegetation*".

While lightning caused many fires, man has been regularly introducing fire into the more open areas of southern Africa for more than 150,000 years (Hall 1984, Blakeway 1985). King (1987) argued that it is important to see anthropogenic fires as a central component in the ecology of grassland communities rather than as an extraneous factor. Hall (1977) and Feely (1978) have also proposed that the increased frequency of fires associated with human occupation which dates back to Palaeolithic times, served initially to reduce the proportion of woody communities present in Hluhluwe-Umfolozi, and thereafter to maintain the dominance of grassland communities.

Watson & Macdonald (1983) also concluded that "*the reduced frequency with which vegetation was burnt and the removal of other human influences following the reserves' proclamation is seen as a fundamental factor responsible for the recent increase in the Complex's woody plant communities*".

#4: A similar map was drawn up for the Umfolozi study area and included in the BR2000 report.

#5: The following sections describe fire regimes in different time periods:

1955-59: Due to lack of control in the early days, some areas (usually adjoining fire breaks) were also burnt. In the Hluhluwe Grid study area (which has been burnt more frequently than the rest of Hluhluwe-Umfolozi) the fire return period from 1955-59 averaged 11.8 years. This period was predominantly an average to "wet" period with two of the five years being "wet", two "average" and only 1959 being a "dry" year. On the assumption that no fires took place between 1947 to 1954, then the average fire return period from 1947-59 increased to 30.8 years.

1960's: From 1961 there was a change in policy with large areas of the reserve again being burnt. From 1960-64 the average fire return period was estimated at 6.5 years, although a high proportion of the area still remained unburnt (Figure 16.3). On the 193 non-forest/riverine Grid study plots the fire frequencies varied from nought to three fires in the five year period, and fire return periods ranged from 1.7 to ∞ years. The period started with a "wet" year with the remaining four years being close to average rainfall levels (Figure 16.4). Since 1965, progressively larger areas of the reserve were burnt at increasing frequencies using natural barriers and roads as firebreaks. Between 1965 and 1971 the average fire return period in the Grid study area dropped to 2.8 years despite the fact that the period had seven consecutive years with below average rainfall. On the 193 non-forest/riverine Grid study plots the fire frequencies varied from nought to five fires in the seven year period.

1970s: Although rainfall levels increased from 1972-79 with six of the eight years having above average rainfall, fire frequencies declined, with an average fire return period of 4.0 years from 1972-79. On the 193 non-forest/riverine Grid study plots the fire frequencies varied from nought to four fires in the eight year period.

1980s: Fire frequencies increased markedly during the 1980s to average a fire every 2.1 years in the Hluhluwe Grid study area from 1980-1987. On the 193 non-forest/riverine Grid study plots the fire frequencies varied from nought to six fires in the eight year period. Four of the five years from 1979-1983 were "dry" years followed by a "wet" period with five of the next six years (1984-89) having above average rainfall (Figure 16.4). Fires were more frequent in the wetter mid-late 1980s and between 1983 and 1989 the average fire return period on the 193 non-forest/riverine Grid study plots was 1.3 years. Although this is probably the first time since proclamation that fire frequencies may have been equivalent to historical fire frequencies during above average rainfall periods; not all areas in Hluhluwe will have experienced such a high fire frequency. This is because extensive areas which were marked as burnt on the burn maps, will contain unburnt patches (especially closed woodland and forest areas).

In summary, average fire frequencies have increased significantly since 1959 with an increased proportion of the total area burnt. Only two periods (65-71 & 83-89) had average fire frequencies of less than three years.

#6: King analysed the aerial photographs of Hluhluwe taken in 1937, 1954, 1960, 1975 and 1982. The timing of the photographs fortuitously allowed the timing of the major bush thickening to be identified.

#7: Readers should be aware that King's "scrub" category is somewhat misleading as the term "scrub" is used in a different way than it is normally used. Ground truthing indicated that King was really classifying thicket and nearly closed woodland as "scrub". In addition many areas which were classified as "open grassland/parkland" by King on the 1982 photograph (Plate 3 in his thesis) were bush encroached in 1989/90.

For example, the slope to the west of the Ngunqulu drainage line was an *A.nilotica* dominated closed woodland developing into a lowland forest in 1989/90. On the 1982 aerial photograph King classified this area as "parkland/open woodland". On closer examination, the photograph shows there was already a substantial woody biomass present in this area. Most of the areas classified as open grassland/parkland on the 1982 aerial photograph are more textured and a darker grey than known open grass areas in the study area such as the old landing strip or hilltop ridges.

To be classed as "scrub", the vegetation therefore had to be a dense thicket or almost closed-closed woodland. Indeed many of the areas classified by King as "scrub" on the 1982 aerial photograph of central north Hluhluwe are now lowland forest dominated by tall *E.racemosa* and *B.zeyheri*. In the case of dense thicket, the trees are unlikely to be the most preferred smaller size classes.

Therefore prime rhino habitat in terms of densities and size class of "*Acacias*" is likely to occur at the medium to denser end of King's "open grassland/parkland". By the time the area had become "scrub" it is likely to be sub-optimal for black rhino. King also noted that the areas designated "scrub" have progressively appeared more dense; and that by 1982 areas classified as "scrub" supported closed to almost closed canopy vegetation.

Given knowledge of black rhino feeding preferences (chapters 6-13); one can expect that the rapid increase in "scrub" in Hluhluwe from 1955-1982 to have reduced habitat quality for black rhino. King's observation that the areas of "scrub" seem to have got denser (i.e. became more closed) over time also points to a further decline in habitat quality.

#8: Conditions would undoubtedly have been most favourable for black rhino during this period as densities of favoured small *A.nilotica, A.karroo, D.cinerea* and *A.caffra* will have been high prior to their growing up and bush encroachment becoming noticeable*.

*Based on personal interviews, it appears that people really only notice when bush encroachment has progressed to a stage where visibility has decreased, canopy cover has increased, and/or the bush becomes more impenetrable and harder to walk through. Given human nature one would therefore expect more mention to be made of the rapid expansion of areas of "scrub" (as defined by King in his analysis of aerial photographs) rather than the establishment of small "*Acacias*" (so favoured by black rhino).

#9: Although there is no hard evidence, it has been speculated that the aerial spraying of DDT (from 1947-1952) to control tsetse fly might have contributed to increased *Acacia* seed viability (and higher germination rates) by reducing bruccid beetle damage of *Acacia* seeds (Bourquin & Hitchins 1979, Macdonald 1979, A.J. Wills pers.comm.).

However, argument against DDT being a major factor comes from T.M.Smith and S.E.Taylor (unpublished quoted in Smith & Goodman 1986) who concluded that neither seed predation in under canopy environments, or lack of germination appeared to be a factor limiting *Acacia* establishment under canopies. Rather it was the high seedling mortality of "*Acacia*'s" under canopies that was responsible for the *Acacia*'s establishing in open areas. Anderson (1989) has also argued that seed predation is not that important to recruitment of long-lived perennials. Even when insect seed predators destroyed 95% of seeds, Anderson (1989) concluded that these losses did not necessarily have an important impact on population recruitment, because in most years, recruitment appeared to be more limited by a rarity of safe sites and not seed supply. Ernst et al. (1990) also indicated that seed predation by brucchid beetles on *A.nilotica* seed was variable from year to year depending on the quantity of seed produced. In years of good seed production seed survival was higher.

#10: As the aim of the constrained ordination was to determine how fire had influenced woodland succession in Hluhluwe, 49 plots were excluded from the data set prior to analysis. The dropped plots were either aberrant (identified by RESOURCE) or contained riverine forest or mature *Celtis africana* evergreen forest which would not have been burnt. Tree size is a function of successional stage; and therefore the four partially constrained polynomially detrended correspondence analyses undertaken were based on RESOURCE-processed spize-based cover abundance data.
King (1987) also determined that true evergreen forest favoured higher moist locations, and had been spreading downwards; and its expansion being favoured by wetter periods. The differing responses of forest compared to "scrub" noted by King (1987) indicates that the removal of forest plots from the dataset prior to partial constrained ordination was highly desirable.

#11: As fire effects are partially confounded with environmental variables, determining the effects of fire frequencies since 1955 (the start of official fire records) on black rhino habitat composition and structure was a two stage problem. The first step was to identify a small set of key environmental variables which significantly explained variation in species canopy cover abundances in Hluhluwe (chapter 14). The next stage of the analysis was to determine whether fire frequencies since 1955 significantly explained any more of the variation in the data not already accounted for by the set of key environmental variables (this chapter). The rationale behind this approach, was that if fire frequencies directly influenced habitat conditions in their own right, and provided sites with similar environmental conditions had not all experienced identical fire regimes, then fire variables should still significantly explain some of the residual habitat variability (i.e. variation in the habitat data not already accounted for by the environmental variables).

#12: Run 3 was selected as the best model.

#13: For a non-technical explanation of what biplots show and how to interpret them interested readers should read Appendix 4.1.

#14: In another run (4) where only three fire frequency variables (1955-64; 1965-79 and 1980-88) were used to constrain the ordination (after partialing out the 14 key environmental variables), and the canonical correspondence analysis was detrended by fourth order polynomials only one highly significant canonical axis was derived ($\lambda 1$ 0.0829 $p<0.01$) and the Species:Environment correlation (in this case really a spize:fire frequencies correlation) was 0.632. The scores of the fire variables again indicated that fire frequencies from 1955-64 (185) again had the biggest influence on community structure, followed by fire frequencies from 1980-88 (83); with fire frequencies from 1965-1979 having the least effect (20). The t-values of the regression coefficients and inter set correlations showed the same pattern. When other fire frequency variables were included as passives the longest biplot arrow still was for fire frequencies from 1955-64. Similar species:fire relationships were revealed to the main run.

- *A.caffra*, *Rhus rehmanniana*, tall *A.karroo*, *Solanum* species, *Vernonia*, *Rhoicissus tridentata*, *Lippia javanica*, *Dombeya rotundifolia*, *Dombeya burgessiae* and *Hibiscus* species being associated with high fire frequencies.

- On the other hand *A.glabrata*, tall *A.nilotica*, tall *B.zeyheri*, *Cassine aethiopica*, *Canthium inerme*, *Cordia caffra*, *Adenopodia spicata*, *Diospyros simmii*, *E.rigida/amoena*, *E.divinorum*, *E.racemosa*, *K.floribunda*, *M.nemorosa*, *Plectroniella armata*, *S.myrtina*, *S.inerme* and *S.africana* were associated with lower fire frequencies at the other end of the canonical axis.

- While taller *L.javanica's* were associated with more frequent fires (Axis 1 scores by increasing height classes 184,193,292) *D.lycioides* (91,30,-23) and *M.senegalensis* (41,37,-29) showed the opposite trend.

Once again clear support is provided for both the existence of the Whateley-Wills successional pathway (see chapter 20), the important role of fire in governing succession, and the negative consequences for black rhino of the development of closed *A.nilotica* woodland and especially lowland forest dominated by *E.racemosa* and *B.zeyheri*. The results of this analysis show that overall food quality of the habitat for black rhino will have declined as a consequence of lack of fire (especially 1955-64 - actually 1947-64).

The following key Whateley-Wills (1996) spizes have been ordered according to their position on axis 1 - the more negative the score the lower the fire frequencies since 1955 The symbols in brackets give the spize dietary importance rating calculated during the Grid survey: *D.lycioides1* 91 (---), *A.nilotica1* 48 (**, ***in Umfolozi), *M.senegalensis1* 41 (---), *M.senegalensis2* 37 (—), *D.cinerea2* 35, (*, **in Umfolozi),*D.lycioides2* 30 (--), *A.nilotica2* 22 (***), *D.cinerea1* 14 (**, ***in Umfolozi), *R.pentheri2* 9 (—), *B.zeyheri1* -5 (*), *A.nilotica3* -14 (**, *in Umfolozi). *B.zeyheri2* -15 (**), *D.lycioides34* -23 (—), *D.cinerea34* -25 (---), *M.senegalensis34* -29 (---), *E.racemosa2* -33 (—), *C.caffra2* -39 (—), *R.pentheri1* -50 (—), *C.caffra1* -52 (—), *E.racemosa3* -53 (---), *K.floribunda1* -61 (---), *R.pentheri4* -64 (—), *E.racemosa1* -64 (—), *R.pentheri3* -74 (---), *A.nilotica4* -75 (---), *B.zeyheri4* -75 (—), *B.zeyheri3* -79 (*), *C.caffra34* -103 (—), *E.rigida/amoena* -106 ( ), *S.myrtina2* -108 (---), *E.racemosa4* -110 (—), *S.inerme12* -113 (-), *K.floribunda34* -115 (—), *S.myrtina4* -116 (—), *S.myrtina3* -117 (—), *S.myrtina1* -142 (-), *K.floribunda2* -145 (---), and *S.inerme34* -154 (—). Clearly black rhinos favour the spizes associated with high fire frequencies since 1955.

Small/medium *D.cinerea*'s and *A.nilotica*'s (<2m) were rated as highly preferred to preferred food items in Umfolozi where grass interference levels were lower. The average axis score in Hluhluwe for these three key preferred food items was +29.75. The average axis score of the other four preferred or slightly preferred food items was -28.25. The remaining 26 highly rejected food items averaged an axis 2 score of -58.0.

#15: If fire had a minimal influence on woody species composition and structure one would have expected the partial fire constrained biplot to reveal very different patterns to those emerge in the DCA (used to generate the 3D spize abundance surfaces in ordination space in chapter 20), and the fire constrained axes (Figure 16.5) would have had lower eigenvalues and possibly not been statistically significant.

#16: Alf J. Wills (pers. comm), plant ecologist based in Hluhluwe from 1981 to 1990, also remarked on the ability of *A.caffra* to withstand repeated severe fires, and B.Brockett (pers. comm.) also believed that this species has been favoured by frequent intense fires in Pilanesberg National Park.

One can speculate, that the ability of *A.caffra* to germinate and establish in areas predisposed to high levels of grass growth and frequent fires, may reflect an ability to accumulate sufficient root reserves during a below average rainfall period to enable emerging trees to withstand subsequent fires and increased grass competition. Wills & Phelan (1983) did not record any mortalities of *A.caffra's* following the 1983 control burns in Hluhluwe. During such below average rainfall periods grass competition will be at its lowest and any emerging plants will be temporarily protected from fire. Avoidance of grass competition, probably explains why the literature consistently has indicated that periods of rapid bush encroachment have occurred during dry periods. Indeed Konstant's work showed that establishing "*Acacia*" seedlings were very susceptible to grass competition. It is noticeable that *A.caffra* is one of the quickest species to flush and grow rapidly after the first spring rains. This may be a strategy to combat grass competition. It remains to be seen whether or not *A.caffra*'s apparent ability to thrive under frequent intense fires may give it a competitive advantage over more fire sensitive "*Acacia*" species.

#17: Following bush clearing, and despite more frequent fires, A.J.Wills commented that *L.javanica* had continued to expand in bush cleared sites in North Hluhluwe. In most of Hitchins' 1969-71 plots that we remeasured *L.javanica* had increased, confirming the expansion of this unpalatable species since 1970. *L.javanica's* ability to tolerate frequent hot fires is shown by its representation in *A.caffra* hillslope communities which experience frequent hot fires. Indeed intermediate *L.javanica* (2-4m) was the spize most associated with overall fire frequencies since 1955 (Figures 16.5). Chapter 7 also showed that in the Hluhluwe study area, *A.caffra* hillslope communities and *L.javanica* dominated lowland communities have been more frequently burnt since 1955 than other communities. *L.javanica* is strongly rejected by black rhinos during most of the year. However, Konstant (*in litt.*) found fire did not stimulate growth of this species as much as the more palatable *H.pauciflorus* and *D.cinerea.* In addition higher fire frequencies occur in areas predisposed to increased grass growth. Those same conditions that favour grass growth may also favour growth of *L.javanica.*

#18: A.J. Wills and L.Wills (pers.comm.) noted that in droughts, baboons (under nutrient stress) noticeably increased barking of medium tall *A.karroo*. These trees in turn were easily killed by subsequent fires. For example, following bush clearing around 1970, a dense almost impenetrable *A.karroo* thicket grew up and developed on the bush cleared area behind the Manzimbovu house on the way to Gontshi. During the drought period in the early 1980s, baboon were observed to strip bark from most of these trees (A.J. Wills and L.Wills pers.comm.). Subsequent fire in these areas then killed the majority of the *A.karroo*'s, opening the area up again, and maintaining those trees that remained in the more preferred shorter size classes (A.J.Wills pers.comm.). Thus the combination of below average rainfall periods, baboons, porcupines and subsequent hot fires may have temporarily maintained or create small medium *A.karroo* habitat rather than promoting the development of mature tall *A.karroo* woodland. This area was subsequently re-cleaned. By 1993, *A.karroo* thicket had regenerated on the area (see Figure 17.2).

#19: *Diospyros* species declined markedly in all areas over the twenty year period, supporting the hypothesis that members of this genus are fire sensitive.

#20: Densities of smaller/medium *M.senegalensis* declined on Hitchins' plots irrespective of clearing frequencies. This suggests that frequent fire may reduce densities of this species. Konstant (1990 *in litt.*) found that in the short term, fires reduced densities of this species, and the preliminary FIRM analyses of the Grid data set indicated that repeated fire reduced densities of this species. However, in 1989, low lying areas in N.E.Hluhluwe still contained many individuals of *M.senegalensis* despite those areas experiencing amongst the highest fire frequencies recorded in Hluhluwe since

1955. A.J.Wills (pers. comm) noted that under a regime of more frequent hot fires, the highly rejected *M.senegalensis* appeared to spread laterally by vegetative suckering underground. Clearly fire alone is insufficient to completely control this unpalatable encroaching species.

#21: It remains to be seen what impact the increase in densities during the 1990s of mixed feeders (and especially impala numbers) in northern Hluhluwe may have on woody plant dynamics (possibly in interaction with fire). The current research by Prof William Bond and colleagues is awaited with interest given the findings of Trollope (1980). However it is noteworthy that the large numbers of mixed feeders in the area a few years prior to the die off (indicated by the very large numbers culled at the time) did not prevent widespread development of *Acacia* thickets and the concomitant build up in black rhino to record densities.

#22: *B.zeyheri* may also have been responding to an increases in canopy cover (and hence suitable seed dispersal (via birds) and germination sites in some areas).

#23: Trollope's (1980) work in the Eastern Cape clearly highlighted the importance of considering the interactions between fire and herbivory. He found that goat browsing and fire together effectively reduced densities of *A.karroo* following a single intense head fire, and that fire alone was far less effective. In subsequent years, the bush density on the burnt plot (without goat browsing) steadily increased despite annual fires (albeit in the form of dwarf coppice bushes), whereas goat browsing and fire prevented any re-establishment of the bush (Trollope 1988). The culling of browsers and mixed feeders in Hluhluwe North in the early 1980s therefore may have been counter productive in terms of controlling bush encroachment. Prof.W. Bond and co-workers (UCT) is currently studying the effect of browsing on *A.karroo* population dynamics in Hluhluwe.

#24: In N.E. Hluhluwe noted that *A.karroo* trees which were damaged in NE Hluhluwe (some bark eaten) by porcupine and baboons (in droughts) appeared to be very susceptible to being killed by subsequent fires (A.J. Wills and L.Wills pers.comm.).

Yeaton (1988) also found that the interactive effect of porcupine damage and frequent burning was a major determinant of woody plant succession at Nylsvley Nature Reserve. Apart from increasing susceptibility to fire, Yeaton (1988) noted that removal of bark also predisposed mature trees to an earlier death by increasing the risk of fungal attack; and that it often took a number of fires to kill basally damaged trees. In this case succession would lead to a closed woodland were it not for regular fires and tree mortality caused by porcupines (Yeaton 1988).

A similar phenomenon was observed on an isolated mature *A.nilotica* tree at Gontshi in N. Hluhluwe. The tree had been partially basally de-barked and was watched over a three year period. The first burn did not kill the tree. However, a subsequent hot fire set the tree on fire at the base at the point where the bark had been removed a few years previously, and the base of the tree burnt and smouldered through until the whole tree fell over.

#25: This interactive effect may be particularly important when one considers the likely future long term impacts of elephants and fire (and also speculate about the possible influence of the lack of elephants and infrequent fires in the past) on Hluhluwe woody dynamics - given that during fieldwork it was noticeable that mature *A.nilotica* trees were one of the spizes which elephants debarked the most in northern Hluhluwe. In the early 1990s elephants also pushed over many tall spindly *A.karroo*. Thus it may be that mature *A.karroo* and *A.nilotica* mortality levels may increase when both elephants (baboons and other browsers) and frequent fires occur together, compared to either elephants or fires operating on their own.

It has been well established that "*Acacias*" do not grow under their own canopies (Smith & Goodman 1986 Whateley & Wills 1996). The removal of mature *A.nilotica's* and *A.karroo's* therefore will also create gaps and more open areas, which if burnt should provide suitable sites for the establishment of favoured small "*Acacias*". Increased mortality of tall *A.nilotica's* may also retard or stop the extensive development of closed canopy *A.nilotica* woodland which is the precursor to the development of *E.racemosa/B.zeyheri* lowland forest. Increased mortality of mature *A.nilotica* and *A.karroo* trees should in turn benefit black rhino.

P.M. Hitchins (pers. comm.) also noted that tall *Cussonia spicata* densities have declined in Hluhluwe . Our observations in Hluhluwe revealed that this decline appeared to be in large measure due to another animal:fire interaction. Damage of basal bark by buffalo bulls and especially more recently by elephant make this species vulnerable to fire. Many trees have been burnt following removal of the protective bark whereas undamaged individuals appear to survive fires. However as tall *C.spicata* trees are not black rhino food, fire:animal induced declines in this spize will not adversely affect black rhino feeding; although some favoured "resting" trees may be removed. Although not really of importance to black rhinos, during fieldwork it was also noticed that elephants regularly debarked *A.robusta* and *S.brachypetala* trees in lower lying areas. The latter species was also noticed selectively debarked by elephants in Botswana's Tuli Block (Bruce Page personal communication).

CHAPTER 17

THE EFFECTS OF MANAGEMENT ACTIONS ON BLACK RHINO HABITAT QUALITY III: SHORT TERM EFFECTS OF BUSH CLEARING

INTRODUCTION

This chapter focuses on the likely short term impacts on black rhino of bush clearing; while the following chapter focuses on the longer term effects of bush clearing. As with previous chapters, this chapter interprets resultant changes in woody spize composition in terms of knowledge of black rhino browse selection patterns.

DID THE EXTENSIVE AND SELECTIVE BUSH-CLEARING IN 1959-60 CATALYSE THE 1961 DIE-OFF OF BLACK RHINO IN NE HLUHLUWE ?

Between 11 July and 27 October 1961, 46 black rhino died in NE Hluhluwe (part of the Grid study area). At the time this area had the highest recorded density of black rhino in Hluhluwe-Umfolozi, and had also recently experienced heavy culling of grazers and extensive bush clearing of *Acacia* scrub. Some authors speculated that bush-clearing probably negatively influenced the rhinos in the area (Thomson 1992). However, at the time there was no clear evidence the die-offs were due to nutritional stress as all the dead animals did not appear in bad condition, pathological examination of samples from five of the rhino that died were inconclusive, and the deaths occurred in all sex and age classes and not predominantly in young and older animals as would be expected if starvation was the primary cause (Hitchins & Anderson 1983).

However, upon closer examination, the evidence indicates the very extensive clearing of *Acacia* scrub in NE Hluhluwe in 1959 and 1960 was probably a causal factor of the 1961 "die-off" of 46 black rhinos in this area. The logic behind this assertion is as follows:

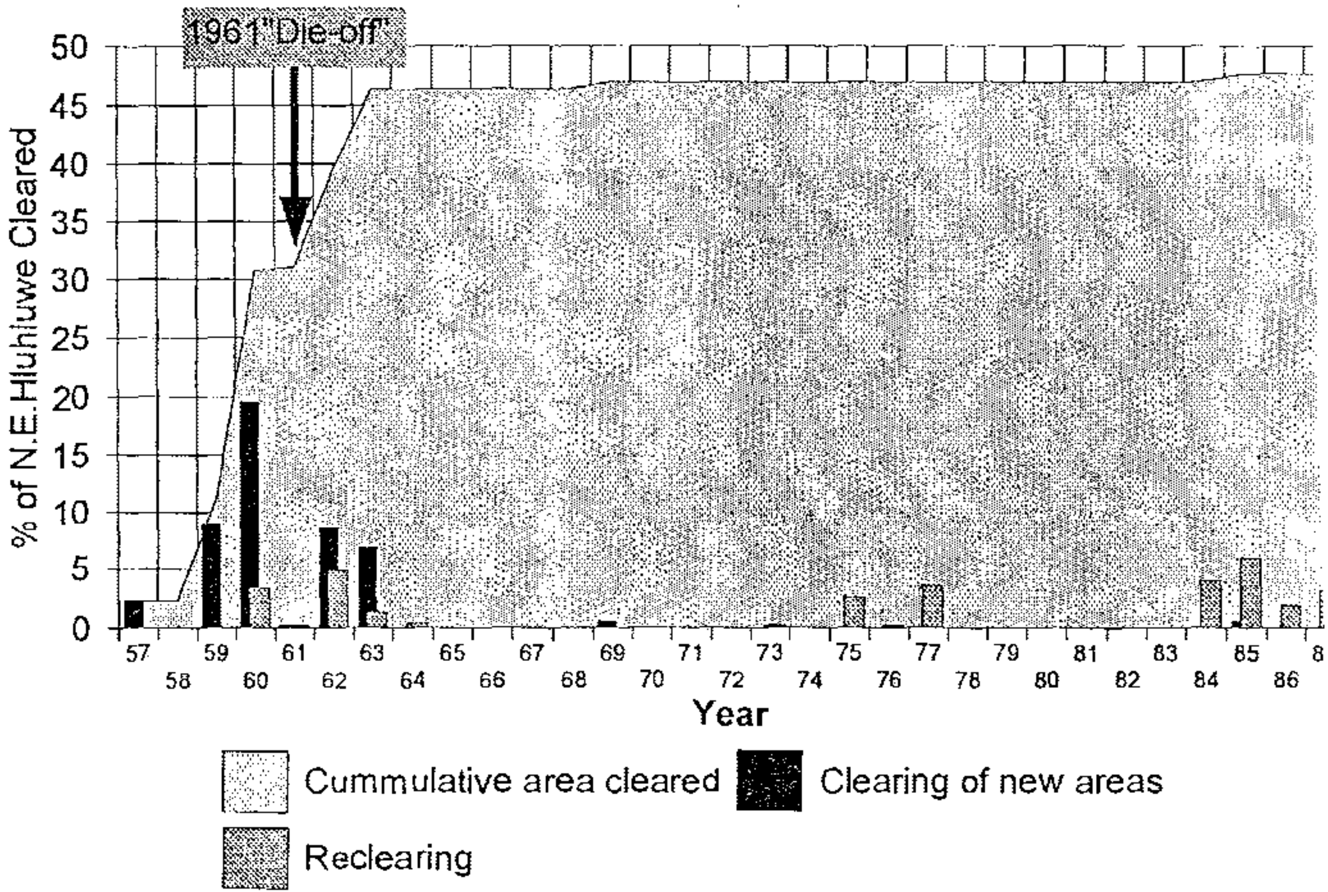
- Just prior to the sudden die-off of 46 black rhino in northern Hluhluwe in 1961 the area held the highest natural density of black rhino ever recorded (1.638 black rhino/km^2 - Table 1.1).

- The development of encroached thicket had been very noticeable since 1948, and historical records and increases in areas of "scrub" on past aerial photographs (King1987) suggested that the high densities of favoured small "*Acacias*" were probably increasing in size and becoming less favoured just prior to the decline. If this was the case, the carrying capacity for black rhino may have peaked or already started to decline around the time of the initial extensive bushclearing in N.E. Hluhluwe. If such an initial decline in carrying capacity took place prior to 1959, this would also not have been obvious to most people[#1]

- Seen against this background, Figure 17.1 shows that the early bush clearing in Hluhluwe Grid study area in the late 1950s early 1960s was very extensive[#2]. **Almost a third (31%) of the Hluhluwe Grid study area was bush cleared at least once from 1957 to 1960, with 29% of the Grid study area being cleared in the two years prior to the 1961 die-off. The most extensive bush clearing in any one year also occurred in 1960 - the year prior to the 1961 die off** - when 19% of the Grid study area was cleared for the first time with a further 3% being recleared (Figure 17.1). **The bush clearing was concentrated in the north eastern part of the Grid study area (where the die-off occurred), and so the proportion of the north eastern area that was cleared was significantly higher than that of the Grid study area as a whole. The initial bush clearing also selectively cleared the *A. karroo / D.cinerea / M.senegalensis* dominated scrub areas (which provided much of the rhino food). Thus probably over half of the north eastern area of Hluhluwe was cleared in a two year period ,and much of what was selectively cleared was rhino food (such as *A.karroo* and *D.cinerea*).**

- **To compound the problem facing black rhino in north east Hluhluwe**, Hluhluwe's first resident ecologist, Roddy Ward (1962 and pers. comm.) reported that a **build up of grass in Hluhluwe went hand in hand with game control measures initiated in 1958**[#3]. Natal Parks Board records show that during the period 1954-64, **the biggest reduction in large grazing/mixed feeder biomass occurred in the area in the two years prior to the die off (1959-1960)**, when a total of 6,136 warthog, 1,762 wildebeest, 1,864 impala, 769 zebra and 729 nyala were removed from Hluhluwe (Brooks & Macdonald 1983). Ward (pers comm) further noted that **it was "*not until the winter of 1960 or better still, that of 1961*" that the build up of grass could be seen clearly.**

Figure 17.1 Proportion of NE Hluhluwe grid study area bush-cleared from 1957 to 1987, showing % of the area newly cleared each year, % of the area with reclearing, and cumulative % of the area that has been cleared at least once.



- Three of the four years, 1957-1960 (including 1960) had above average rainfall, and this will also have contributed to the increased grass growth prior to the 1961 die-off. As northern Hluhluwe is moister than much of the rest of Hluhluwe-Umfolozi Park, it is also more predisposed to the growth of tall grass. Following the widespread bush clearing, tree:grass competition will also have been reduced, further favouring increased grass growth.

- The combination of increased grass growth and the removal of such a high proportion of available palatable browse in an one area in such a short time period, at time when rhino densities in the areas were at record high levels, and habitat quality was probably already declining must have markedly reduced black rhino carrying capacity in the north east in the short term.

- As the surrounding (uncleared) areas of Hluhluwe were also occupied by many other rhinos, dispersal opportunities for animals living in north eastern Hluhluwe were limited.

- In turn, the removal of very extensive areas of *Acacia* food in N.E. Hluhluwe, compounded by increased grass interference is likely to have both reduced dietary quality and forced black rhinos in the area to increase their consumption of unpalatable species with higher levels of secondary plant chemicals (allelochemicals). Evidence for the increased browsing of normally unpalatable species during times of nutritional stress and high black rhino densities come from the very heavy total feeding levels and high levels of offtake of unpalatable species recorded on a transect measured by Bourquin at Zincakeni in 1965 and 1966 (chapter 20), and on Hitchins' plots around 1970 (chapter 10). Although not conclusive, (because of the very limited number of browse samples), on average the "*Acacia*" samples analysed in this project had higher crude protein and phosphorus levels than the unpalatable browse samples suggesting that a diet with more unpalatable species may be poorer nutritionally as well as having elevated levels of secondary plant chemicals. In a detailed study, Owen-Smith's (1994) findings corroborated this, indicating that food quality (as demonstrated by crude protein concentrations in leaves of woody plants) was higher in palatable deciduous spinescent trees ("*Acacias*") compared to unpalatable broadleaved species.

- The detoxification of ingested allelochemicals carries a metabolic cost, as glucose is needed to form glucuronide conjugates and to provide bicarbonates to neutralise excess protons (Foley & McArthur 1994; Illius & Jessop 1995). While animals on a maintenance or above maintenance diet are able to deal with high concentrations of allelochemicals, their ability to deal with these chemicals appears to decline markedly under a sub-maintenance diet when only low concentrations of allelochemicals can be tolerated (Illius & Jessop 1995). In the absence of sufficient energy in the diet, amino acid precursors appear to be broken down to maintain glucose levels increasing nitrogen demand (Illius & Jessop 1995). In simple terms - an animal's tolerance of toxins (eg secondary plant chemicals) will be reduced when under nutritional stress, and to compound matters, in the case of the black rhino, its intake of poorer quality more chemically defended food is likely to increase under conditions of food quality limitation. Potential effects of increased ingestion of secondary plant chemicals under a sub-maintenance diet includes hepatotoxic effects and animals depleting their glucose levels to the extent that there may be insufficient glucose to supply enough energy to nervous tissue (Illius & Jessop 1995)

-Black rhinos have unusually low red cell ATP levels, and any failure to neutralise excess protons (especially if also coupled with reduced protein and phosphorus in the diet) may trigger acute haemolysis, which black rhinos seem to be particularly susceptible to when stressed (Chaplin et al 1986, Du Toit 1987, Paglia 1994, Miller 1994). Indeed acute haemolysis has been a major cause of black rhino deaths in both captivity and wild caught animals (Miller 1994) that have been subjected to nutritional or other stress. Massive haemolytic crises have occurred rapidly in both captive and wild caught animals that otherwise appeared healthy (Paglia 1994). Perhaps because of its sudden onset and rapid progression to death, acute haemolysis has never been documented in the wild (Paglia 1994).

While the above arguments are speculative, it is quite reasonable to hypothesise that the sudden and major decline in carrying capacity in N E Hluhluwe following the very extensive *Acacia* clearing and increased grass growth over a short period (especially 1959-60), will have both reduced dietary quality and increased consumption of normally rejected more heavily chemically defended species. Given the interaction between an animals nutritional status and its ability to detoxify secondary plant chemicals, and the black rhino's

susceptibility to haemolytic crises when stressed, this theoretically could have resulted in otherwise apparently healthy looking black rhino dying rapidly as a result of massive (undetected) haemolytic crises, and appearing to lack energy prior to death. This would be consistent with there being no indication the die-offs were due to starvation at the time (as the dead rhino were not obviously in bad condition).

The observation of three dying animals collapsing on to their forequarters (which carry most of the rhino's weight) when they attempted to charge observers prior to their death (Hitchins and Anderson 1983) is consistent with very sick animals in an energy crisis.

Almost all deaths occurred near water - which is also explainable as sick animals lacking in energy are likely to seek to minimise the energy they need to expend to walk to water. At the time, the animals may also have had to drink more, given their probable increased urea production needed to void the byproducts of secondary plant chemical detoxification. Experienced rhino veterinarian Dr Pete Morkel (pers.comm) concurs with this hypothesis, and notes that very sick animals are often found near water when close to death.

In conclusion, the timing and location of the "die off" (which took place only in the heavily cleared north eastern Hluhluwe area during the nutritional crunch period and not other adjacent uncleared areas) was unlikely to be purely coincidental.

It is also unlikely to be a chance occurrence that the end of the die-off (end October) coincided with the early growing season flush period when highly nutritious "*Acacia*" coppice with high levels of phosphorus is likely to have become available to the animals.

However, the 1961 "die-off" needs to be seen in context of what would have happened had extensive bush clearing not taken place in Hluhluwe North:

As indicated above, given the noticeable bush thickening and increase in "scrub" on the aerial photographs (King 1987), habitat quality for black rhinos was probably already starting to decline by 1961. The continuing low fire frequencies up till 1965 will have meant that in the absence of heavy bush-clearing, succession in existing *Acacia* thickets would have been likely to continue, with a corresponding further decline in habitat quality as tree sizes increased. Given the low fire frequencies at the time, in the longer term, the decline in black rhino numbers in Hluhluwe was probably inevitable without clearing as the *A.nilotica* and *A.karroo* thickets and woodlands would have continued to mature, with a resultant marked decline in black rhino carrying capacity.

Thus, in the longer term the decline in black rhino numbers was probably inevitable, irrespective of whether clearing in the late 1950s and early 60s had taken place or not. It is likely that only frequent fires (and possibly reintroduction of elephant) in the late 1940s and 1950s could have kept the Hluhluwe habitat in its optimal state for black rhinos for longer by maintaining "*Acacias*" in the most preferred small sizes.

SHORT TERM EFFECTS OF BUSH CLEARING ON NICK KING AND TRACY KONSTANT'S EXPERIMENTAL PLOTS

Follow up and additional new clearing and burning treatments were applied to control and cleared study plots on an *A.nilotica* woodland site originally treated and measured by King in 1986 (King 1987, Konstant 1990 *in litt.*). Konstant (1990 *in litt.*) used a replicated factorial design on this site applying two fire treatments (B: Burnt: Plots burnt in 1988 and 1989 [Plots also burnt in 1986], U: Unburnt: Plots protected from fire in 1988 and 1989 [Plots last burnt in 1986]) and four clearing treatments (1: Cleared in 1985, 2:Cleared in 1988, 3:Cleared in both 1985 and 1988, 0:Uncleared control) giving a total of eight different treatments (i.e. B0 B1 B2 B3 U0 U1 U2 and U3). King's (1987) experimentally cleared *A.karroo* and *E.divinorum* woodland plots were also re-measured by Konstant.

The following sections discuss preliminary results to emerge from Konstant's (1990 *in litt.*) measurements on these experimental bush clearing sites.

RESPONSE OF PALATABLE *A.karroo* AND *D.cinerea* ON KING's STUDY SITES TO CHEMICAL TREATMENT AND FIRE

The rapid increase in *A.karroo* densities following clearing and burning suggested a fire dependent seed dormancy mechanism (King 1987). However, four years later densities of this species had returned to pre-clearing levels. Konstant (1990 *in litt*) noted that increased grass competition may have reduced plant vigour making this species more susceptible to the hot fires of 1989 and 1990.

Over a 3-4 year period *D.cinerea* was apparently unaffected by herbicide, stimulated by fire, and vigorous in competition with dense grass swards (Konstant 1990 *in litt.*).

King (1987) also concluded that the removal of canopy cover in bush clearing of *A.karroo* and *D.cinerea* woodland allowed the establishment of large numbers of these species. He also noted that *A.nilotica*, *A.karroo* and *D.cinerea* densities increased following both clearing and a fire. Without a follow up clearing treatment, King (1987) observed that *A.karroo* could regenerate even if it was a dry year.

Figure 17.3 shows a photograph of *A.karroo* regeneration of a recently bush cleared area in Northern Hluhluwe in 1993, while Figure 17.2 shows 1993 photographs of small *Acacia* regeneration on recently bush cleared sites in southern Hluhluwe. In both cases, regrowth following clearing has benefited black rhino in the short term. The burnt small *Acacias* in the foreground of Figure 17.2b have been browsed by black rhino.

A)

Figure 17.2 a) and b). Photographs of small *Acacia* regeneration on recently bush cleared sites in southern Hluhluwe in November 1993. The small *Acacias* in the foreground of 17.2 b) have been burnt and browsed by black rhino.

B)

Figure 17.3. Photograph of small and medium *Acacia karroo* regeneration on a recently bush cleared site in northern Hluhluwe (November 1993).

Figure 17.4. Photograph of good black rhino habitat in rural KwaZulu. Note the availability of many highly preferred small *A.nilotica, A.gerrardii, D.cinerea* and *A.karroo*) and minimal grass interference. The picture was taken in November 1993 from the old Gunjaneni entrance road to southern Hluhluwe. This area experiences heavy cattle grazing, goat browsing, frequent fires and cutting of firewood.

RESPONSE TO REPEATED CLEARING AND BURNING TREATMENTS ON KING'S *A.nilotica* STUDY SITE

Konstant (1990 *in litt.*) concluded that repeated clearing seemed to stimulate the growth of certain fire sensitive species. There was an expansion of shrub growth with the cutting of coppicing plants in the absence of fire. Fire itself had a limited effect on total tree densities on the plots; although it was beneficial to black rhino by killing unpalatable fire sensitive later successional species such as *S.myrtina* and *E.racemosa*.

The unpalatable *R.pentheri* and *D.lyciodes* densities were significantly reduced by repeated clearing and fire (Konstant 1990.). However without burning *R.pentheri* trees had recovered to heights of 2m within 5 years of clearing.

Konstant (1990) also concluded that "*Acacia*" densities were not affected by the disturbance treatments, although the average height of plants was reduced by fire.

Figure 17.4 shows how just outside Hluhluwe, frequent fires, heavy goat browsing, heavy grazing and cutting of firewood have created good black rhino habitat dominated by small and accessible *A.nilotica, D.cinerea,* and *A.karroo* trees.

RESPONSE OF KING's *E.divinorum/E.racemosa* DOMINATED STUDY SITE TO CHEMICAL TREATMENT AND FIRE

The two unpalatable *Euclea* species made up 40% of the pre-clearing density on this site. Other later successional species such as *B.zeyheri, K.floribunda* and *R.pentheri* were also present. Konstant (1990 *in litt.*) concluded that many of the species on this site were unable to sustain high densities with the combined effect of bush clearing and fire. In particular, densities of *K.floribunda* and *M.heterophylla*, and to a lesser extent *B.zeyheri, E.racemosa* and *R.pentheri* declined. The more favoured *A.karroo, Grewia caffra* and *D.cinerea* showed different responses,

starting at relatively high densities on the undisturbed stand, being reduced by bush clearing, but germinating rapidly after the first and subsequent fires to become the most abundant species in the stand by 1990. Favoured *A.robusta* seedlings which had been almost absent, had appeared in large numbers in these areas by 1990.

Thus it appears that the combined effects of bush control in *E.divinorum* dominated areas followed by frequent fires was beneficial to black rhino in the short term by increasing the proportion of this habitat made up of smaller individuals of more favoured "*Acacia*" species. This finding is corroborated by Macdonald's (1981) finding that "*Acacias*" increased on hydrastumped *E.divinorum* areas (see later).

However, before clearing low lying *E.divinorum* areas a number of points need to be considered:

- Scholes (1986) has recommended that heavy machinery should not be used to clear such *Euclea divinorum* areas. According to Scholes these areas often have "a strongly duplex soil (a sandy loam topsoil 200-300mm thick with a sharp transition to a dense clayey (often whitish) subsoil) and are potential sodic sites that should be disturbed as little as possible. Furthermore Scholes states that "*Euclea* species are usually a symptom of underlying potentially or actually deflocculated soils, and are therefore best left alone".

- The main Hluhluwe post-burn survey also revealed that in the Grid study area *E.divinorum* was strongly associated with *E.racemosa* and *R.pentheri* and to a lesser extent with *S.africana* (the latter heavily browsed by black rhino when in more favoured intermediate size classes).

- However, by late 1991, it was noticeable that large numbers of small coppicing *Euclea divinorum* trees were growing up on some previously burnt cleared areas in Sisuze. This indicates that any beneficial effects for black rhino following clearing and burning may be short term and temporary.

- In contrast to clearing of *E.divinorum* at Sisuze, clearing of what was mature *E.divinorum* woodland at the time of the Pilot survey in the Maquanda area of southern Hluhluwe (further from major rivers) appeared to favour the regrowth of *E.divinorum* when it grew back. In this case, cleared *E.divinorum* was not hydrastumped. The Park's current regional ecologist, Dave Balfour has also expressed concern about the regrowth and dominance of *E.divinorum* on some cleared areas of southern Hluhluwe (P.le Roux pers.comm.) speculating that regeneration on these cleared sites may be being influenced by selective browsing of palatable *Acacia* species.

RESPONSES OF UNPALATABLE *M.senegalensis* AND *E.crispa* ON KING's *A.karroo* STUDY SITE TO CHEMICAL TREATMENT AND FIRE

On King and Konstant's *A.karroo* site, treatment of cut trees with the highest concentration of Garlon coincided with a population explosion of the unpalatable *M.senegalensis*. Treatments were not replicated and so this may have been due to differing site conditions. However, this was not the first time that an increase in *M.senegalensis* had been recorded following chemical treatment in Hluhluwe (Vincent 1968). Konstant (1990 *in litt.*) concluded that the effectiveness of the use of Garlon when clearing *A.karroo* woodland is limited.

Konstant (*in litt.*) noticed that unpalatable *M.senegalensis* increased in number on all treatments before burning took place (hot fires in 1988 and 1989). After fire, the densities on all treatments halved, and was composed almost entirely of small plants; and by April 1990 had further decreased with the loss of all plants above 1m except in the control. Konstant (*in litt.*) concluded that while herbicides do not exterminate the unpalatable *M.senegalensis*, it was to some extent fire sensitive (chapter 15). However, this species was still the most abundant species on most treatments. While unpalatable *E.crispa* densities did not increase after clearing, densities were not reduced by a 3% Garlon treatment. Densities of this species decreased to approximately half that on undisturbed stands with repeated fire for all except the control area, where densities remained the same (Konstant 1990 in litt.). She concluded that this species was tolerant of a wide range of disturbances, and this is borne out by its abundance on the frequently bush cleared and burnt lowland black clay areas to the left of the main Memorial gate entrance road to Hluhluwe.

King (1987) also noted that cutting and burning exacerbated coppicing of both *M.senegalensis* and *E.crispa*. Thus the responses of plants on King and Konstant's experimental plots indicate that with the exception of chemical clearing of areas with *M.senegalensis*, bush-clearing was largely beneficial to black rhino in the following 1-3 years when combined with repeated follow up burning. This maintains "*Acacias*" at their favoured size and reduces the number of unpalatable plants.

IAN MACDONALD'S EXPERIMENTAL CLEARING OF *Euclea divinorum*

In the Munywaneni and Sisuze field trials, *E.divinorum* was cleared by hydrastumping. Macdonald (1981) recorded that only four seasons after hydrastumping in these areas, a high density of the favoured *A.nilotica* and other "*Acacias*" had become established in these areas. Macdonald (1981) also recorded that virtually every individual of *A.burkei* and *A.nilotica* showed severe canopy reductions due to browsing. A high proportion of these plants were small. **Thus in the short term hydrastumping of *E.divinorum*, coupled with follow-up burning, appears to have improved habitat quality for black rhinos.**

The importance of frequent burning (see chapters 15 and 16) was again apparent, as Macdonald (1981) noted that biennial fires limited the growth of *Acacias* in this area, therefore keeping them in more favoured size classes for black rhino.

Macdonald (1981) also noted that *A.karroo* invaded the area that was biennially burnt since clearing. This corroborates Konstant's (*in litt.*) observation that the germination of *A.karroo* appeared to be enhanced by burning on cleared plots.

JOHN VINCENT'S CONCLUSIONS ABOUT THE SHORT TERM EFFECTS OF "SCRUB" CONTROL IN ZULULAND

In reviewing the success of early bush clearing operations, Vincent (1968) concluded that "*none of the methods used proved to be more than moderately successful, and several had to be repeated after regrowth had occurred*". Thus confirms that any decline in carrying capacity immediately after bush clearing appears temporary, with small "*Acacias*" regrowing on bush cleared sites.

However, Vincent (1968) also noted that **the use of Tordon 22K was almost 100% effective on *A.karroo*, *A.caffra* and *D.cinerea* (food species)**; whilst on *M.senegalensis* (rejected species) it had little effect as the poison did not appear to penetrate through the thick waxy cuticle of this species. In the short term therefore the use of chemicals during clearing may have given a competitive advantage to less palatable species. Further evidence to support this assertion comes from Konstant's (1990 *in litt*) finding that where the highest concentration of Garlon was applied a population explosion of *M.senegalensis* occurred.

CONCLUSION

With the exception of bush clearing of *E.crispa*, *M.senegalensis*, and possibly mature *E.divinorum* woodland in southern Hluhluwe; provided the extent of the clearances in any one year is limited (unlike 1959-60), growth on bushcleared areas in general favours black rhino in the short term (1-3 years after clearing), despite the immediate and temporary lowering of food availability immediately after clearing. This is especially the case when clearing is combined with fire. However, chapter 18 indicates that any short term beneficial effects of bush clearing are likely to be temporary, and influenced by the degrees of grass interference and subsequent burning regimes.

CHAPTER 17 NOTES

#1: This is because 1) any resultant decline in female reproductive performance in response to poorer nutrition is likely to have gone undetected in the absence of continuous intensive ID-based monitoring in the late 1950s; 2) because adult mortality and overall population density would not have noticeably changed; and 3) because large long lived mammals such as black rhino appear to have the potential to overshoot carrying capacity before declining in numbers (Adcock 1996).

#2: The area cleared during this period was much greater than was cleared over the next two decades, where clearing was concentrated around tourist roads, and up to 1990 almost all clearing was follow-up re-clearing rather than clearing of new areas.

#3: Brooks & Macdonald report that herbivore population control began in earnest in 1954. Over the period 1954-1959 a total of 1,052 zebra, 2,537 wildebeest, 4,670 warthhog, 1,599 impala and 538 nyala were removed from Hluhluwe. From 1960-64 a further 366 zebra, 1,936 wildebeest, 3,124 warthog, 2,108 impala, 295 nyala and 6 black rhino were removed from Hluhluwe. **During the period 1954-64 the heaviest culling was in 1959/60.**

CHAPTER 18

THE EFFECTS OF MANAGEMENT ACTIONS ON BLACK RHINO HABITAT QUALITY IV: LONG TERM EFFECTS OF BUSH CLEARING

INTRODUCTION

BASIC APPROACH

The main part of this chapter presents the results of the polynomially detrended partial canonical correspondence analyses undertaken to study the effects of past bush clearing operations in the Hluhluwe Grid Study area. The aim of these analyses was to determine the variation in the plot woody composition and structure data that is uniquely attributable to the set of bush-clearing variables, taking into account the effects of other physical, environmental and fire covariables (ter Braak and Prentice 1988). The analytical approach adopted was therefore the same as that used to study the effects of fire. In this case, the aim of the analyses was to determine whether the bush clearing variables significantly accounted for any of the residual variation in habitat composition and structure not already accounted for by environmental and fire variables (see chapter 4 for full details of the methods used).

Unfortunately a number of problems with past records and clearing practices limited the potential success of these analyses, and readers should be aware of these problems before reviewing the results. Some of these problems also made interpretation of any changes on Hitchins' plots difficult.

Forty of the transects from Hitchins' 1969-'71 survey of vegetation structure and black rhino feeding were re-measured in 1990. These plots covered the north eastern area of Hluhluwe (which experienced the 1961 die-off and most of the reserve's bush clearing activities had been concentrated in this area prior to 1990). Chapter 10 describes the differences in rhino feeding patterns between 1969-71 and 1989 (Grid survey) and 1990 (Hitchins plots). This chapter also discusses the changes in vegetation on Hitchins' plots over the 20 years period, revealed by Adcock's more detailed analysis of the data with reference to plot location, fire and especially bush clearing treatment (see BR2000 report for more details). The implications of these changes with respect to bush clearing are then interpreted in the light of findings of chapters 6-13 and 20.

Finally the local literature was examined for references to the long term effects of bush clearing.

As before, the implications of any vegetation changes for black rhino were inferred using the knowledge gained about black rhino feeding preferences (chapters 6-13).

PROBLEMS LIMITING THE SUCCESSFUL EVALUATION OF LONGER TERM EFFECTS OF BUSH CLEARING ON BLACK RHINO HABITAT QUALITY

The large number of different bush clearing treatments (species cleared, physical method used, chemicals applied, concentration of chemical solutions, whether diesel was applied, frequency of clearing, etc.), and lack of adequate control sites were highlighted as major problems in chapter 4.

MULTITUDE OF DIFFERENT TREATMENTS

Almost every Grid survey plot in Hluhluwe that had been cleared experienced a different bush clearing history. Similar problems occurred when analysing the data from Hitchins' plots (see Table 3.1). While the large number of different treatments will have contributed to maintaining habitat diversity; the lack of adequate replication makes it virtually impossible to analyse the bush clearing data in detail. The explanatory variables denoting the type of clearing treatment therefore had to be lumped and simplified prior to multivariate analysis. The species cleared were reduced to three classes - *"Acacias"*, *M.senegalensis* and *E.divinorum*. All chemical treatments unfortunately had to be lumped, although a separate dummy variable was included to denote whether diesel had been applied or not. Similarly all physical treatments had to be grouped together. The resulting multivariate analyses therefore examined the effects of frequencies of clearing, time since last clearing and broad type (but not details) of clearing treatment (Table 4.1 lists the bush clearing variables used in the analyses).

FAILURE TO LEAVE ANY UNCLEARED CONTROLS IN SOME LANDSCAPE UNITS

Further problems were caused by the failure to leave uncleared control areas in some areas, which makes it practically very difficult to determine whether habitat composition in an area has been affected by bush clearing or simply is responding to the specific set of environmental conditions and burning treatments in an area.

For example, all of the moist low lying area east of the main entrance road from Memorial gate to the Maphumulo turn off has been cleared at least once. This area is also the most frequently cleared area in Hluhluwe and much of the *M.senegalensis* clearing also took place here. Figure 20.4.shows there is a stark contrast between these cleared flatter lower lying areas and the nearest uncleared areas (controls) which occur higher up on the lower slopes of Magwanxa and Mgodlo. The lack of uncleared control areas in the lower lying sites results in the bush clearing treatments and environmental factors being confounded. One cannot therefore directly compare cleared and uncleared sites, as they occur in different landscape positions with different soil moisture, nutrient levels and microclimates. As a result of this confounding we can expect our constrained ordination axes to be much smaller than they would have been had adequate controls been left. However, fortunately bush clearing histories and environmental conditions were not confounded in all areas.

Ideally one needs to contrast bush clearing treatments within landscape units. By failing to leave adequate controls the potential to learn from past management has been greatly reduced[#1]. Hopefully, Park management can learn a lesson, and ensure that in future adequate control areas will be left and made sacrosanct.

PRE-CLEARING HABITAT COMPOSITION AND STRUCTURE UNKNOWN

Another problem caused by not adopting an adaptive management approach to bush clearing in the past, was that there is no baseline information about habitat conditions in plots prior to bush clearing. While one can study relationships between bush clearing histories and current habitat composition and structure; the current habitat conditions may primarily reflect the special conditions of sites predisposing them to being cleared (or not) in the past. For example, for obvious reasons, past managers will have concentrated on clearing *A.karroo* encroached areas rather than clearing open grassland/parkland areas. In other words bush cleared plots may currently differ from uncleared plots, but this may primarily reflect underlying conditions, rather than the effects of bush clearing per se. If adequate controls had been left in the different landscape units, the problem of not knowing past vegetation composition would not have been as serious.

SCALE OF MAPPING OF BUSH CLEARING

Much of the mapping of bush clearing has been done at a coarse scale using crayons. In a number of cases it was unclear whether plots fell within cleared or uncleared areas because the positions of the exact boundaries of cleared areas were unclear. Fortunately in recent years bush clearing has been mapped at a finer scale.

LONG TERM EFFECTS OF BUSH-CLEARING ON HLUHLUWE HABITAT COMPOSITION AND STRUCTURE: MULTIVARIATE ANALYSES

RUNS UNDERTAKEN

A total of 59 Canonical Correspondence analyses were used to identify the three key fire variables (Fire frequencies 1955-64; 1965-1979 and 1980-88) and 14 key environmental variables which were used as covariables in the bush clearing analyses (see chapters 5, 14 and 16 for details of methods and results).

A total of 24 bush clearing variables were examined in the analyses. The first bush clearing run included all 24 variables, and failed due to numeric overflow caused by extreme collinearity among some of the bush-clearing variables. Just as in chapter 15, it was necessary to undertake a number of runs to select a minimum subset of the "best" bush-clearing variables. (For details of model building and variable selection procedures interested technical readers should refer to chapter 4.) The problem was finding which explanatory variables to select out of the possible 24. Limited explanatory power caused by confounding of treatments and landscape unit and extreme collinearity amongst some variables necessitated 22 Canonical Correspondence bush-clearing analyses[#1] (For more details see the BR2000 report).

RESULTS:

The 21st run finally produced a model where all seven variables had independent effects as shown by small variance inflation factors. The variables selected were:

- Frequency of Bush Clearing *Acacias* from 1957-69 (Fqa)
- Frequency of Bush Clearing *M.senegalensis* since 1957 (Fqm)
- Frequency of Chemical treating of *Acacias* since 1957 (Afc)
- Frequency of Diesel application on *Acacias* since 1957 (Afd)
- Dummy variable for plots that were last cleared of *Acacias* in 1957-1963 (Alc60)
- Variable reflecting time since plots were last cleared of *Maytenus senegalensis* in the 1980s : 0 = not cleared in 1980s ; 1 = last cleared in 1984 ; 2 = 1985 ; 3: 1986 ; 4: 1987, 5: 1988 and 6 : Jan-Mar 1989 (Mlc80)
- Dummy variable for plots that were last chemically treated of *Acacias* in 1957-1960 (Atslc60)

While the explanatory power of the model was very low as evidenced by the small eigenvalues on the three canonical eigenvalues ($\lambda1=0.0478$ $\lambda2=0.0324$ $\lambda3=0.0245$); the Monte-Carlo permutations test showed that the first canonical axis was significant ($p=0.03$). The Species:Environment correlations on the biplot were however reasonable 0.653 (axis1), 0.542 (axis2), and 0.471 (axis3). Significance tests were not carried out on the second and third axes, and so readers should be aware that they may be spurious. However, this seems unlikely, as the resulting spize associations make ecological sense. Figures 18.1 through to 18.3 show the species biplots for all combinations of the three canonical axes derived from this run.

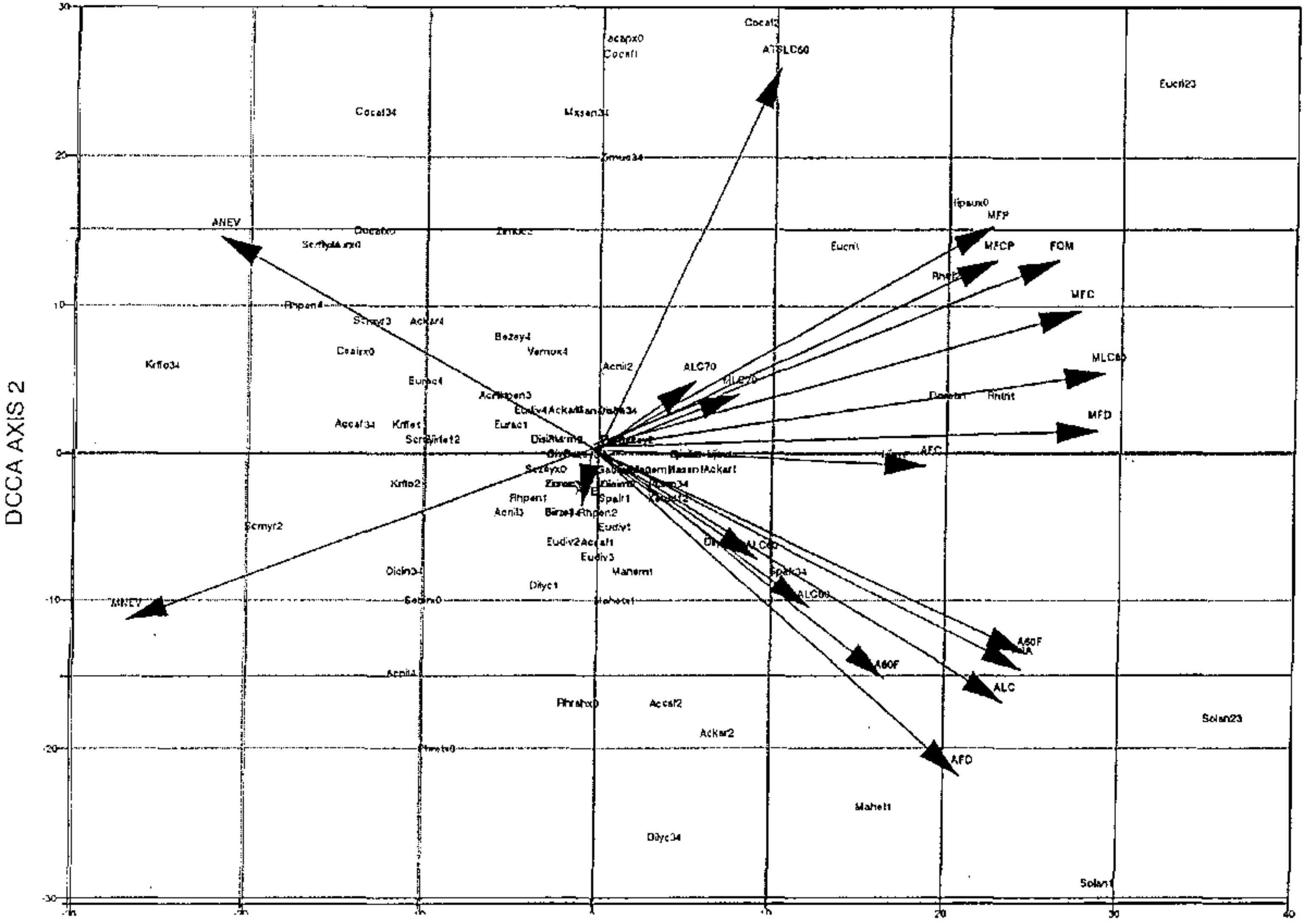
BIPLOT - CANONICAL AXES 1 AND 2

The biplot for axes 1 and 2 (Figure18.1) revealed the following patterns and associations:

o The main axis 1 was a clearing frequency axis; while axis 2 primarily distinguished between recent clearing of *M.senegalensis* and frequent *"Acacia"* clearing (especially between 1957-69 and 1980-89). The biplot also suggested that whether or not the plots had last been chemically cleared of "*Acacias*" in the late 1950s and early 1960s had an independent effect compared to the other "*Acacia*" variables.

o The spizes most associated with recent *M.senegalensis* clearing were generally < 2m tall, with the following species being prevalent *E.crispa*, *H.pauciflorus*, *R.tridentata*, *Solanum* species, *L.javanica* and *D.rotundifolia*. Small medium *C.caffra*, *A.karroo*, *D.lyciodes*, and *A.caffra* were also related to this axis although not to the same extent. The common spize most associated with *M.senegalensis* clearing was *E.crispa* above one metre tall. **However, due to the severe confounding of the bush clearing treatments on the most frequently cleared moist low lying areas in NE Hluhluwe, interpretation of the above spize:*M.senegalensis* clearing relationships is almost impossible.** One cannot conclude whether the high canopy cover of *E.crispa*, *L.javanica*, *R.tridentata*, *H.pauciflorus* and *Solanum* on frequently cleared sites is a result of competitive release following selective clearing (for *M.senegalensis* and "*Acacias*") or alternatively whether this simply reflects the particular physical conditions pre-disposed to the growth of these species and *M.senegalensis* and "*Acacias*".

Figure 18.1. Hluhluwe Spize plot (non forest grid plots) Axes 1 and 2 from Partial Canonical Correspondence Analysis - Bush clearing run 21



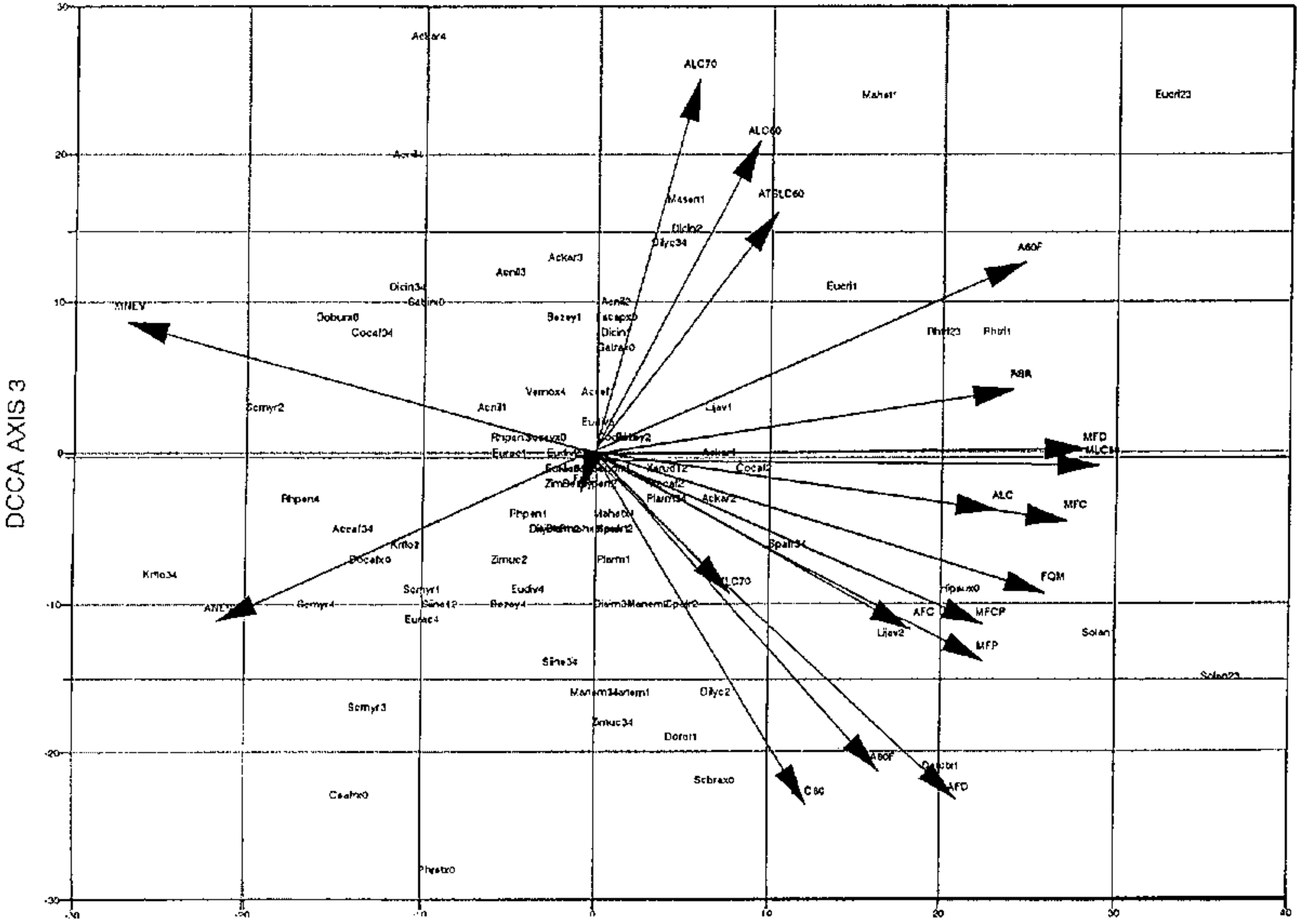
Attempts were made to minimise the latter problem by partialing out a number of key physical parameters prior to the bush clearing analyses. The partialing out of key environmental variables combined with lack of uncleared controls in landscape units in part explains the low eigenvalues recorded in the partial bushclearing-contrained ordination. However, the rainfall and moisture conditions are not known for each plot, and the very frequently cleared area appears to be particularly moist as a result of being frequently kept damp by early morning valley mists. The confounding of treatment and landscape unit may therefore lead to the identification of a particular pattern of spizes within a particular landscape unit, should that landscape unit influence habitat structure and composition in some polynomial function. All the variation in the data due to landscape may therefore not have been removed prior to analysis of bush clearing effects. **This interpretive problem highlights the need to leave adequate uncleared controls in any landscape unit.**

o **Figure 18.1 shows that taller individuals (>4m and sometimes >2m) of *A.nilotica, E.racemosa, B.zeyheri, R.pentheri, C.caffra, D.cinerea, Z.mucronata, D.caffra, C.africana,* and *C.caffra* were most associated with plots never cleared of "*Acacias*". All sizes of *K.floribunda* and *S.myrtina* were also associated with uncleared sites. Many of these spizes are associated with intermediate and late stages of the Whateley-Wills successional model in *A.nilotica* woodland, and are indicators of declines in black rhino carrying capacity.**

o **The height of *A.karroo* and *A.caffra* also appeared to be related to the frequency of clearing of "*Acacias*". Frequent and recent clearing was most associated with high canopy covers of these species between 1 and 2 metres high (favouring balck rhino); whereas the highest canopy covers of tall individuals was associated with plots that had not been cleared since 1957 or were last cleared during 1957-1963. This indicates that frequent clearing of these species appears to have benefited black rhino.**

o Obviously the plots cleared of *M.senegalensis* had significant amounts of this species prior to clearing. The weighted averages for small medium spizes of this species occurred near the origin, suggesting that the recent clearing of this species may have been successful in the short term. However the biplot suggested that **while the tallest *M.senegalensis* spize (>2m) was not associated with frequent clearing, its canopy cover was highest on plots last chemically cleared of "*Acacias*" between 1957 and 1960. This supports the observations of**

Figure 18.2. Hluhluwe Spize plot (non forest grid plots) Axes 1 and 3 from Partial Canonical Correspondence Analysis - Bush clearing run 21



Konstant (1990) and Vincent (1968) that *M.senegalensis* appeared to have a selective advantage when chemicals were applied after bush clearing.

BIPLOT - CANONICAL AXES 1 AND 3

The biplot for axes 1 and 3 (Figure18.2) revealed the following patterns and associations:

○ The biplot arrows indicated that there were differences in plot composition depending on whether the plot been cleared of "*Acacias*" in the previous five years, or had not been cleared of "*Acacias*" for at least 11 and up to 31 years. Higher canopy covers of early and intermediate spizes in the hypothesised Whateley/Wills successional sequence (*A.karroo* >2m, *A.nilotica* >1m, *D.cinerea* all sizes, and small *B.zeyheri* <1m, were negatively associated with recently cleared plots, and positively associated with later cleared or uncleared plots. Of these spizes, the tallest *A.karroo, A.nilotica, D.cinerea,* and *C.caffra* trees were most associated with a longer time since clearing and lower frequencies of clearing compared to the smaller spizes. **The biplot therefore provides further evidence to support the hypothesis that the longer the time since clearing the more advanced the Whateley-Wills pattern of succession.**

The spizes most associated with no "*Acacia*" clearing, and negatively associated with the last "*Acacia*" clearing occurring between 1957 and 1977, were late successional spizes that have come to dominate areas of lowland forest in Hluhluwe (*C.africana, S.myrtina, S.inerme,* and the tallest individuals of *E.racemosa, B.zeyheri, R.pentheri, K.floribunda,* and *E.divinorum*). The tallest *A.caffra* spize was also associated with a lack of clearing.

However, one cannot conclude from these results that lack of clearing per se led to the development of the forest. This is because past clearing has concentrated on areas of "*Acacia*" scrub, and areas with high amounts of *M.senegalensis*. It was only recently (1990s) that developing lowland forest areas were selected as prime areas for clearing. The correlation between forest spizes and lack of clearing is therefore to be expected. Nevertheless the biplot does provide circumstantial evidence to support the Whateley-Wills (1996) successional model.

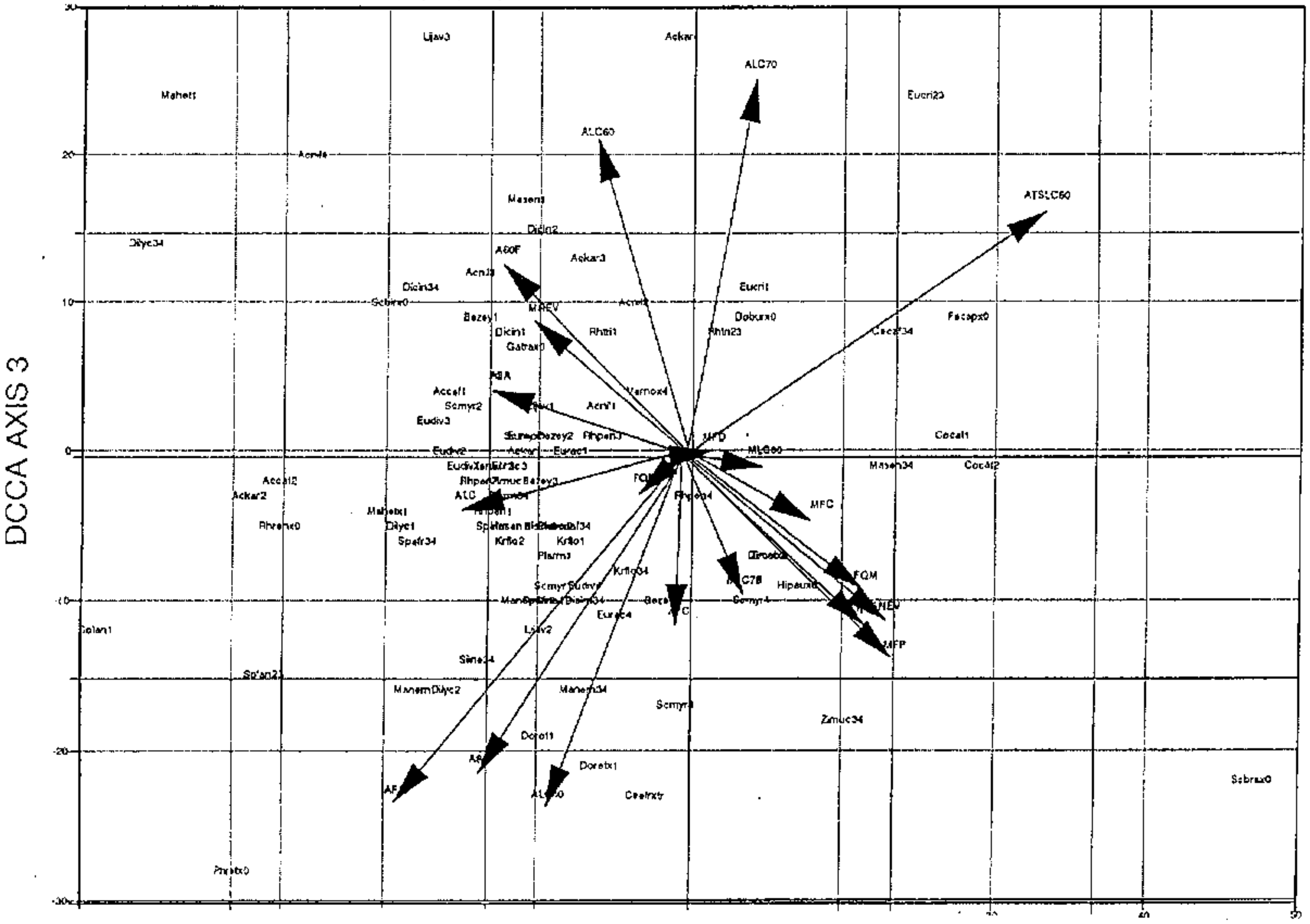


Figure 18.3. Hluhluwe Spize plot (non forest grid plots) Axes 2 and 3 from Partial Canonical Correspondence Analysis - Bush clearing run 21

In particular, the associations of particular spizes indicates that frequent "*Acacia*" bush clearing can prevent the development of closed *A.nilotica/D.cinerea/A.karroo* woodlands, which appear to be the precursor of lowland forest. However the key word here is frequent. Unless clearing is repeated, the data suggest that closed "*Acacia*" thicket or woodland may result in somewhere between 20 and 30 years. If clearing is left long enough, there will be time for evergreen lowland forest to develop. However the introduction of a policy of more frequent burning and the recent re-establishment of elephant may help to slow or prevent these trends.

BIPLOT - CANONICAL AXES 2 AND 3

The biplot for axes 2 and 3 (Figure18.3) revealed the following patterns and associations:

o Tall *A.karroo* (>4m) was associated with areas last cleared in the 1970s, while tall *A.nilotica* (>4m) was most associated with plots last cleared in the late 1950s early 1960s. Both these spizes were negatively related to the dummy variable for plots that had never been cleared of "*Acacias*" since 1957. The ordering of the *A.nilotica* spizes when plots were last cleared in the 1970s was *A.nilotica1, A.nilotica2, A.nilotica3* and finally *A.nilotica4*. This order was reversed in plots last cleared 30 years previously. Although not as marked, the tallest *D.cinerea* spize was more associated with a longer time since clearing. **This suggests that past clearing has probably slowed development of lowland forest patches. It also supports the assertion that unless clearing is repeated, closed "*Acacia*" thicket or woodland may result in somewhere between 20 and 30 years.**

The smaller second and third canonical axes appear to differentiate better between cleared plots; while the main first axis appears to be primarily differentiating between cleared and uncleared plots.

o **The biplot also suggests that canopy covers of taller *E.crispa, C.caffra A.karroo* and *M.senegalensis* were positively associated with plots last chemically treated in 1957-1963.** Just under half of these plots were re-cleared in the 1970s, and none of these plots was subsequently cleared in the 1980s. These species may have been competitively released by chemical clearing; or alternatively the areas receiving this treatment were specially conducive to the growth of these species. All the plots receiving this treatment were contiguous (covering Hidli west of the Manzimbomvu stream and the central Magangeni loop area - see Figure 20.4). Therefore, again, confounding of area and treatment makes interpretation difficult.

o *A.karroo* and *A.caffra* between 1 and 2 metres and *Rhus rehmanniana* were slightly associated with more recent "*Acacia*" clearing. This may simply reflect the fact that clearing only recently occurred in the limited *Rhus rehmanniana* concentration area in N.E.Hluhluwe, and that *A.caffra* and *A.karroo* are common co-dominants with *R.rehmanniana*. Again confounding of treatments and landscape units precludes clear interpretation.

E.DIVINORUM CLEARING

The final (22nd) bush clearing run used the 14 key environmental variables, the three key fire frequency variables and the seven key "*Acacia*" and "*M.senegalensis*" bush clearing variables (identified in run 21) as covariables. The 22nd run tested to see whether the frequency of *E.divinorum* clearing significantly explained any of the residual variation in habitat composition and structure. The eigenvalue was very small (0.0285) and was not significant ($p=0.44$), supporting the earlier conclusion from the biplots of runs 2 and 21 that too few plots were cleared of *E.divinorum* in the Grid study area for this variable to have a major impact on habitat composition and structure in the study area. Only 1.6% of the non-riverine/mature evergreen forest plots were cleared of *E.divinorum* compared to 28% which were cleared of "*Acacias*" and/or *M.senegalensis*.

RE-MEASUREMENT OF HITCHINS' 1969-73 PLOTS IN HLUHLUWE NORTH WITH SPECIAL REFERENCE TO THE LONG TERM EFFECTS OF BUSH-CLEARING

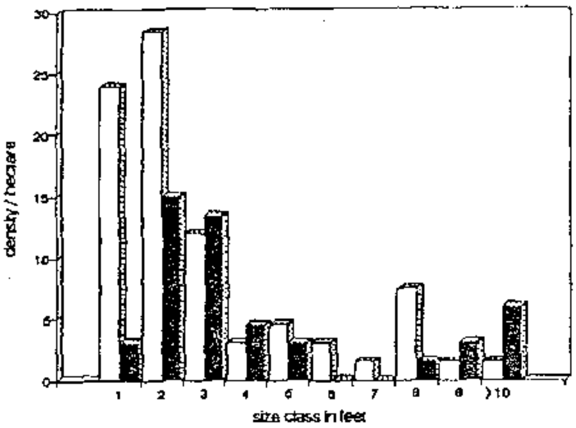
BACKGROUND

This section presents a summary of K. Adcock's examination of subsets of Hitchins' plot data in an attempt to study the effects on habitat dynamics of clearing frequency, time since period of last clearing, *A.karroo* clearing frequency, and *D.cinerea* and *M.senegalensis* clearing. These findings are then interpreted in the light of the findings of chapters 6-13 and 20 (for more details see the BR2000 report).

Unfortunately the multitude of bush-clearing treatments and confounding between initial site composition and treatments (e.g. clearing frequency reflected the initial densities of *A.karroo* and *M.senegalensis*, and thus the potential for bush thickening) meant that virtually each site had its own initial composition and clearing history, followed by its own response over the years. After splitting up the transects into broad treatment types sample sizes became small. As a result of these problems, few clear trends regarding the effects of bush-clearing could be determined from the remeasurement of Hitchins' plots.

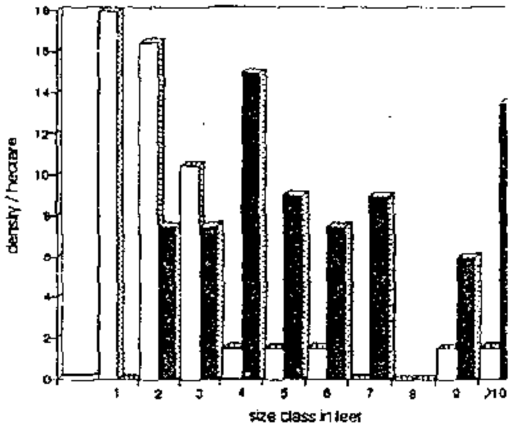
Forty of Hitchins' plots in north-eastern Hluhluwe (Figure 3.7) that were first measured in 1969-71, were remeasured in 1990. Table 3.1 details of the clearing history of the plots. By 1990 seven transects had never been cleared (2 hilltop and 5 well wooded/forest patches); while the other 33 transects experienced various bush clearing treatments from 1958 onwards. Clearing in Hitchins' study area (a sub area of the Grid study area) mainly focussed on removing *A.karroo*, and to a lesser extent *D.cinerea* and *M.senegalensis*. Occasionally all species were cleared. Clearing frequencies varied with some transects being cleared as many as four times before the 1990 survey.

Besides the bush clearing on the transects, fire frequencies over the measurement period were high. Most plots (excluding forest patches) were burnt nine times between 1970 and 1989.



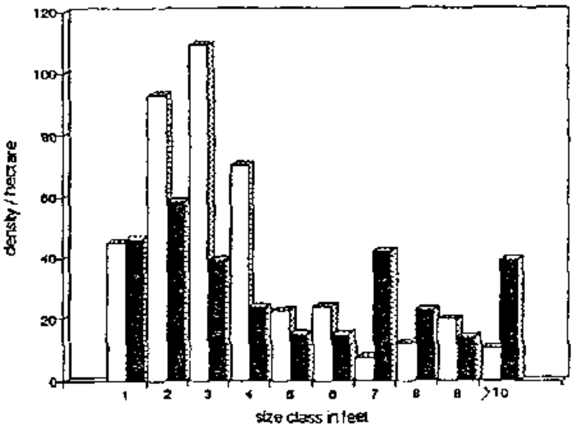
Acacia nilotica

Density change: - 55%



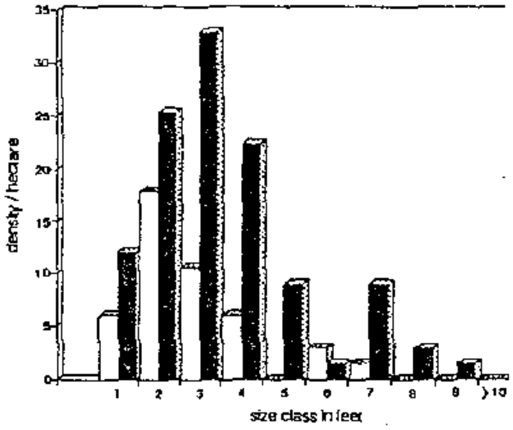
Berkhemia zeyheri

Density change: - 18%



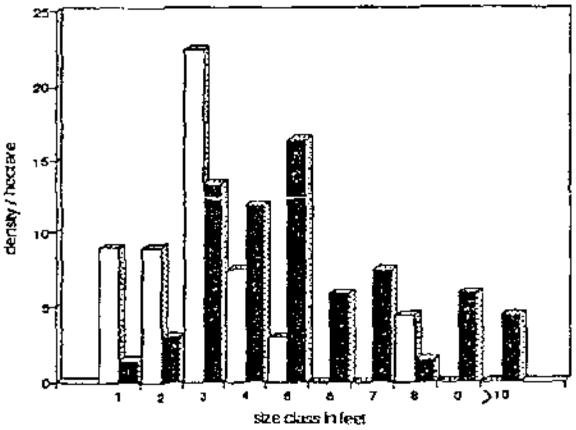
Euclea racemosa

Density change: - 29%



Krausia floribunda

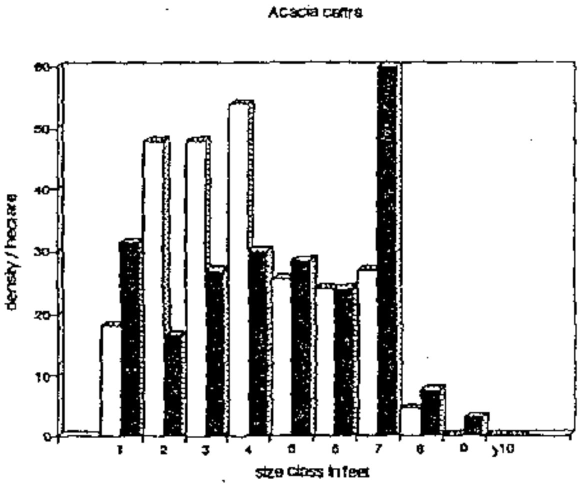
Density change: + 40%



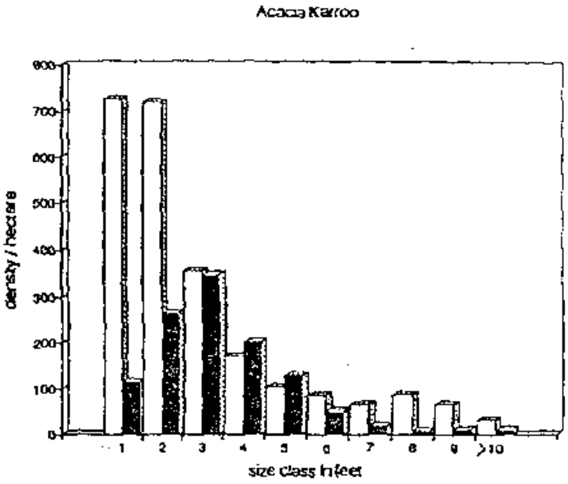
Rhus pentheri

Density change: + 4%

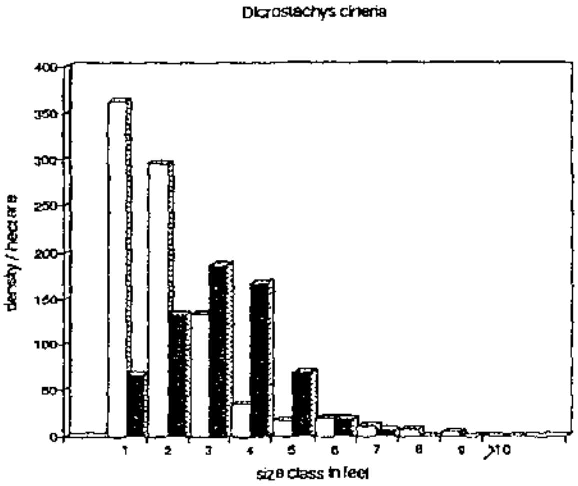
Figure 18.4. Average density/hectare, of all 40 transects, of different size-classes of in 1969-'71 (white) versus 1990 (black): Later successional species



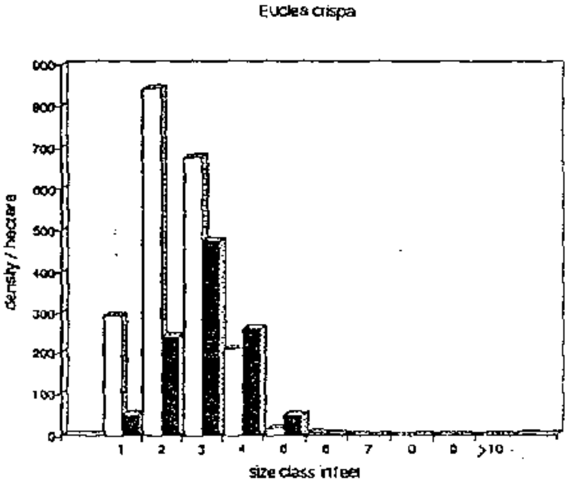
Density change: - 15%



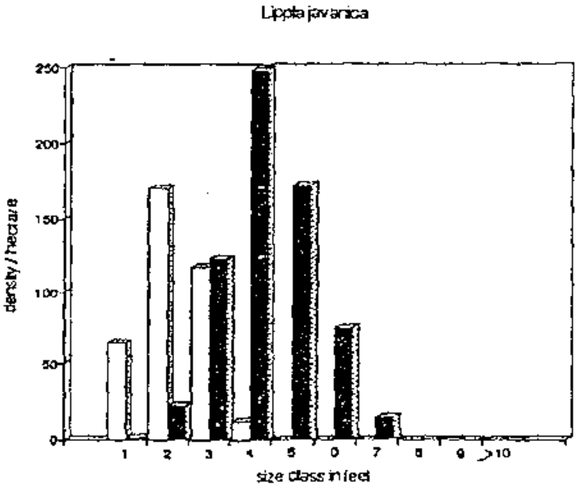
Density change: - 57%



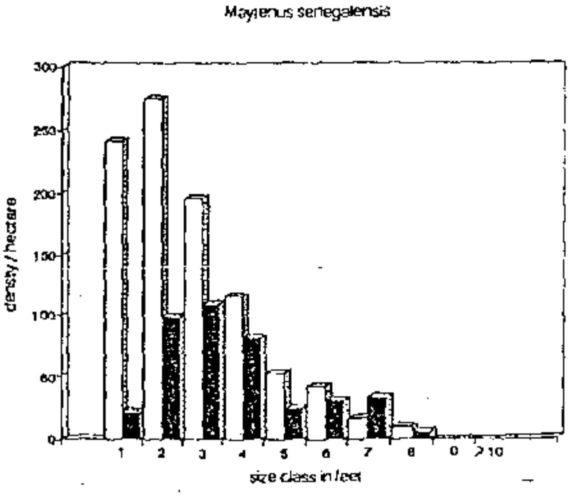
Density change: - 32%



Density change: - 58%



Density change: + 52%



Density change: - 67%

Figure 18.5. Average density/hectare, of all 40 transects, of different size-classes of specie: in 1969-'71 (white) versus 1990 (black): Grassland species.

Diospyros species also declined in density by 76%

CONCLUSIONS ON BUSH CLEARING FROM THE RE-SURVEY OF HITCHINS' PLOTS

As discussed above, the clearing history of the sites was so complicated that few clear trends could emerge. Virtually each site had its own initial composition and clearing history, and followed its own response over the years. After splitting up the transects into broad treatment types sample sizes became small.

As only the beginning (1969-71) and end (1990) states of the vegetation in this study area are known, much of the woody dynamics that must have occurred between these times still remains unclear. For example:- How fast did densities decline? (Immediately after clearing, gradually over the years, or some years later?). Some species may have declined, increased and then declined again between measurements (e.g. *A.karroo* on Hidli vlei, A.J.Wills, pers.comm.).

Despite the problems with analysis, a number a number of trends became apparent.

SPECIES RESPONSES

Figures 18.4 and 18.5 (prepared by K.Adcock) show how average densities of different size classes of *A.nilotica, B.zeyheri, E.racemosa, K.floribunda, R.pentheri, A.caffra, A.karroo, D.cinerea, E.crispa, L.javanica* and *M.senegalensis* have changed on Hitchins' plots from 1969-71 to 1990.

Uncleared and cleared *A.nilotica* (not pure *A.karroo*) woodlands, or more forested sites, followed the Wills-Whateley succession sequence toward forest, losing "grassland" species. A lower fire frequency or intensity here than at other sites may have contributed to woodland site succession. These vegetation changes further reduced black rhino habitat suitability.

Uncleared open sites showed declines in *A.karroo* and *D.cinerea* densities. This was probably a combination of self thinning as trees grew taller, and the frequent fires in these areas.

Subsequent clearing frequency in part reflected the initial densities of *A.karroo* and *M.senegalensis*, and thus the potential for bush thickening may have differed between plots cleared at different frequencies (which together with lack of adequate controls) confounded the study of the impact of clearing frequencies.

D.cinerea clearing appears to have been the least effective, and the most haphazard. Densities of this species declined slightly, irrespective of whether or not it was cleared. However mean tree size did increase over the measurement period. *D.cinerea* densities increased in some areas (e.g. under clearing frequency 4, and sites last cleared '84-'87), possibly as a result of competitive release after heavy *A.karroo* and *M.senegalensis* clearing.

A.caffra was generally only slightly below its former densities (This may be a result of self-thinning, as the plants were slightly taller in 1990). However, in the Ngqungqulu region, where fire frequencies were low, and where some *A.nilotica* woodland occurred, *A.caffra* declined markedly as succession proceeded toward closed woodland/forest. This will have been to the detriment of black rhino.

M.senegalensis also declined irrespective of whether or not it was cleared, although clearing this species did increase the scale of the decline in the short term. However, where there was a long time since initial clearing, and no clearing until recently, it increased in size and density.

IMPLICATIONS FOR BLACK RHINO

The declines in densities of key food spizes, increases in densities of less favoured or rejected spizes, and the increased grass interference in the NE bush cleared area of Hluhluwe, mean that the area's carrying capacity for black rhino probably dropped by more than half since Hitchins first measured the plots.

LONG TERM EFFECTS OF BUSH-CLEARING ON HLUHLUWE HABITAT COMPOSITION AND STRUCTURE: LOCAL LITERATURE

The review of local literature confirmed our findings that while bush clearing may be effective in the short term, it was ineffective in the longer term unless plots were repeatedly cleared in follow up operations. This echoes the conclusion of Scholes (1986) that grassland created by bush clearing will tend back to its woody state unless it is intensively managed by regular burning or re-clearing.

In a review on the longer term effectiveness of bush clearing in Hluhluwe, Wills and Whateley (1983) concluded that digging out of individual *E.divinorum* bushes is the only treatment that "has yielded reasonable success in the medium term". However their long term efficacy is in doubt. Macdonald (1981) speculated that whether or not the newly formed *Acacia* communities on hydrastumped *E.divinorum* areas will eventually be replaced by monospecific stands of *E.divinorum* may depend on whether the current high level of browsing is maintained. Perhaps most importantly, hydrastumping of *E.divinorum* was only successful if trees were "*well pulled*". In addition 30% of the *E.divinorum* trees were too small to be removed by hydrastumper, and in time these trees will undoubtedly mature. Thus sufficient trees remained to recolonise the areas. It would be an interesting exercise to remeasure these plots. However as far as black rhino are concerned the beneficial effects of hydrastumping *E.divinorum* followed by fire appear to be only short term benefits.

E.divinorum also appears to be dominating regrowth on some areas of mature *E.divinorum* woodland that was cleared (not hydrastumped) in south Hluhluwe around the Maquanda area in southern Hluhluwe.

CHAPTER 18 NOTES

#1: Rather than being forced from neccessity to rely more on essentially correletative analysis to study system behaviour, it would be preferable to also be able to undertake medium/longer term experimental research studies in the Park. Unfortunately lack of longer term adaptive management has been a major problem over the years in Hluhluwe-Umfolozi. Apart from Ward's control plots, I personally have had grass population biology transect markers accidentally "tidied up" preventing later remeasurement, while Don Stewart/Orty Bourquin's long term Madlozi and Lubisana plots were also removed without even marking where they had been. Nigel Kemper (pers.comm) had experimental study woody plots accidentally destroyed by managers. Experimental plots in northern Hluhluwe which had experienced a factorial combination of clearing and burning treatments and included control plots (used by Nick King and later Tracey Konstant and Mark Graham) were also later cleared and burnt accidentally by ranger who was unaware of their existence. William Bond (pers.comm.) has also had a student whose fire research experimental design was seriously impacted after being "accidentally burnt" by a cadet ranger. This clearing, tidying up or accidental burning of medium/longer term experimental plots and transects (Hulbert's demonic intrusion!) has been so routine in the Park over the years, that it effectively prevents conservationists from learning long term lessons about savanna dynamics from experimental treatments.

However this will probably not be a practical proposition in future until Park management 1) starts appreciating the critical importance and applied value of such adaptive experimental management and research plots/transects, 2) treats them as inviolate, 3) institutes procedures whereby there can be no excuse that their location (and treatments) was unknown and 4) severely disciplines those staff guilty or responsible for their avoidable destruction. Management also needs to be encouraged to leave more control plots to facilitate future adaptive management. If it was mandatory for every section ranger to have a file detailing "untouchable" plots and transects in his area, and he/she knew they would be in severe disciplinary trouble for their unavoidable damage, then this problem could be reduced to a level which would make longer term experimental adaptive management a realistic option in the Park, and not an over-optimistic unachievable approach.

Part of the problem probably stems from the short terms section ranger's remain at any post (in that they know they probably will not be around to view/remeasure experimental/control adaptive plots they set up 5, 10 or 20 years in future), and also that they personally may not have seen much of applied value to come from such plots. However, if past treatments/control plots were routinely documented with photographs in each Section ranger's plot/transect file, Section rangers could benefit from visiting , looking and learning valuable lessons from control plots/transects initiated by their predecessors. Once the applied value of long term plots starts becoming apparent and being demonstrated to practical field managers, this should be a big incentive to future managers to look after them.

#2: The 22 bush clearing analyses brings the total number of runs in the complete habitat analysis to 81.

#3:Figure 18.2 did not detect a correlation between the frequency of *E.divinorum* clearing and bush clearing in the 1970s - no doubt largely because the number of cleared E.divinorum plots in the Grid study was small.

CHAPTER 19

THE EFFECTS OF MANAGEMENT ACTIONS ON BLACK RHINO HABITAT QUALITY V: GAME INTRODUCTIONS AND REMOVALS

Chapter summary cut from this copy of the dissertation - For a summary please consult either the project summary document or expanded version of the thesis (available on request from the author). For further details consult BR2000 Report.

THE FEEDING ECOLOGY OF THE BLACK RHINOCEROS
(*Diceros bicornis minor*)
IN HLUHLUWE -UMFOLOZI PARK,
WITH SPECIAL REFERENCE TO THE PROBABLE CAUSES OF THE HLUHLUWE POPULATION CRASH

PART IV
PROBABLE AND POSSIBLE CAUSES OF THE HLUHLUWE DECLINE

CHAPTER 20

THE NATURE OF PAST HABITAT CHANGES IN HLUHLUWE AND THEIR IMPACT ON BLACK RHINO

INTRODUCTION

One of the three main objectives of this Thesis was to determine why the black rhino population in Hluhluwe declined; and in particular to evaluate whether habitat changes could have been the major cause of the black rhino decline in Hluhluwe. To meet this objective the probable nature of habitat changes in Northern Hluhluwe in terms of woody plant physiognomy, spize composition and densities needed to be ascertained. The impact of these habitat changes for black rhino could then be inferred given knowledge of black rhino food selection.

The problem was that incomplete and comparatively poor documentation exists on the history and causes of vegetation changes in many of Africa's key wildlife areas over the last century (Dublin 1995), and Hluhluwe-Umfolozi Park is no exception. Much of the information on vegetation dynamics or processes in the park is scattered in a wide variety of sources, and in some cases was never formally recorded. Many earlier vegetation surveys have not been repeated, and their exact locations are unclear.

Given the paucity of long term data and experimental adaptive management treatments, the reconstruction of Hluhluwe vegetation changes and the factors and processes involved, was attempted using a blend of qualitative and quantitative approaches - a similar method to that used by Dublin (1995) in her synthesis of the role of elephants, fire and other factors in the Serengeti-Mara ecosystem.

The patterns and timings of probable vegetation changes in Hluhluwe were determined as far as possible from a number of different sources of information including: analyses of past aerial photographs; photographs of the area taken over the period 1938-93; changes between past vegetation maps in the north-eastern 38% of the Hluhluwe Grid study area (Map study area - see Figure 4.2); comparisons between past vegetation community descriptions and conditions during the 1989 Grid survey; interviews and field visits with selected key staff who worked in the area in the past and knew their woody plants; re-measurement in 1990 of Hitchins' 1969-71 vegetation transects; local literature reviews (including the proceedings of the symposium/workshop on vegetation dynamics in Hluhluwe-Umfolozi held in 1979 - Macdonald *et. al.* 1979); the observed changes in the abundance of selected large herbivore species; multivariate spize-based analyses of a subset of Hluhluwe Grid data; and the use of empirically-derived self-thinning power relationships to estimate the past densities of favoured small *A.nilotica*'s that gave rise to the population of taller trees observed during the 1989 grid survey, contrasting these with observed densities of favoured small *A.nilotica* in 1989.

This chapter summarises the key patterns and timings of probable vegetation changes in Hluhluwe to emerge from the above analyses and review of the evidence (with additional more detailed information being consigned to the chapter notes and appendices).

Some of the evidence simply documents broad scale physiognomic changes, while other information can be used to examine temporal vegetation changes (succession) in more detail within broad landscape/community units (zonation in the vegetation)[#1]. Special emphasis was given to the reported vegetation changes in areas classified as grassland in 1936 (Henkel 1937), which subsequently became encroached with *A.karroo* or *A.nilotica*, as the most striking changes in the vegetation in northern Hluhluwe occurred in these areas. These areas were therefore of particular importance in assessing the impact of habitat changes in northern Hluhluwe for black rhino up to 1990[#2].

The impact on black rhino of the vegetation changes was then inferred using: knowledge of black rhino feeding ecology (and especially spize selection patterns) in Chapters 6-13; the overlay of a 3D plot of black rhino feeding levels (Figure 20.16) over 3D abundance plots of key spizes in the same spize-based ordination space (Figure 20.15 a..k); and an examination of mean offtake levels recorded in 1989 in selected floristic "communities"[#3] representing different seral stages in *A.nilotica* woodland succession.

Conclusions were then drawn as to the likelihood that vegetation changes were the primary cause of the Hluhluwe black rhino decline.

NORTHERN HLUHLUWE VEGETATION MUCH MORE OPEN IN THE 1930s - BUT CONDITIONS CONDUCIVE TO BUSH ENCROACHMENT WERE IN PLACE

In the 1930s, most of Zululand was thornveld which consisted of fairly widely spaced trees with grass in between, and it was seldom that trees formed closed woodland (Bayer 1938). Bayer (1938) hypothesised that fire played an important role in governing woody plant successional patterns, and that it was highly probable that the wide spacing of trees was due mostly to the frequent grass fires in Zululand at that time[#4]. He noted that *"no thorn veld vegetation which is immune from fire exists in Zululand, and it seems quite impossible to provide permanent protection from fire for any portion of this vegetation"* (Bayer 1938).

The earliest accounts of the vegetation of Hluhluwe by Henkel (1937), who produced the first vegetation map of the reserve based on fieldwork in 1936 (see Appendix 20.1), and Bayer (1938), indicated that conditions were very different from today. Hluhluwe was dominated by grassland which made up 49% of the Reserve area (Henkel 1937, Downing 1980). This was reflected in the fauna, as warthog and wildebeest were two of the most abundant species in Hluhluwe in the 1930s (Henkel 1937, Bayer 1938, Bourquin & Hitchins 1979; Brooks & Macdonald 1983)[#5]. Grassland was even more extensive in the north eastern Hluhluwe Map study area, covering 78% of the area in 1936 (Figure 20.1).

Bayer (1938) attributed the development of thorn scrub thickets in Zululand to *"the diminished intensity of grass fires resulting from the destruction of grass cover by cultivation or overgrazing"*. He noticed that these scrub communities were frequent around villages and on *"heavily stocked native land"*; and cites examples at Ulundi, Nongoma and Somkele (villages and towns that are located nearby Hluhluwe-Umfolozi Park). He also concluded that in nearly every case in which thicket development was noted in Zululand savanna, the cause could be attributed to the destruction of the original grass cover (Bayer 1938). Bayer (1938) mentioned *"veld destruction and soil erosion caused by grazing animals"*, likening the effects of the plentiful wildebeest in Hluhluwe to that of high numbers of cattle. Bayer's observations suggest that conditions for subsequent thicket development were in place by the late 1930s[#6].

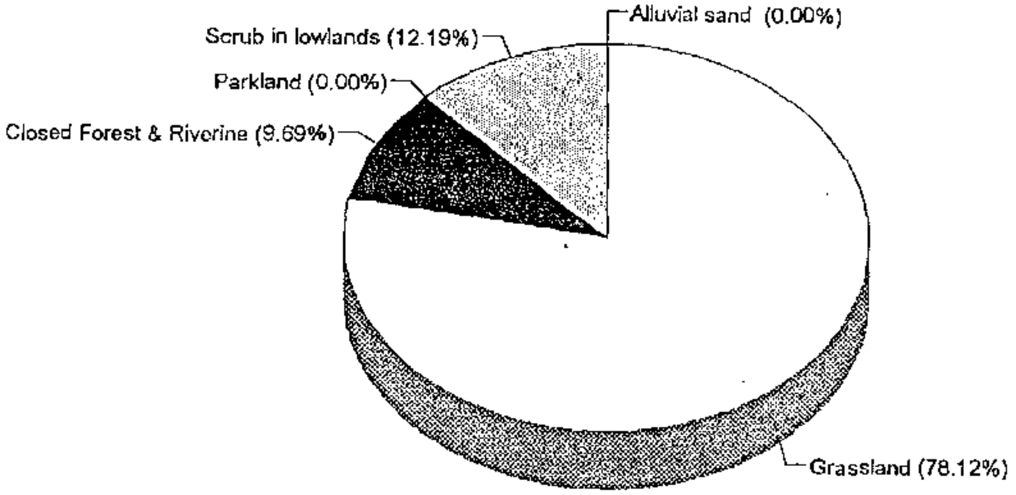


Figure 20.1 Vegetation composition of the Hitchins' map/Grid survey study area in 1937, from Henkel (1937).

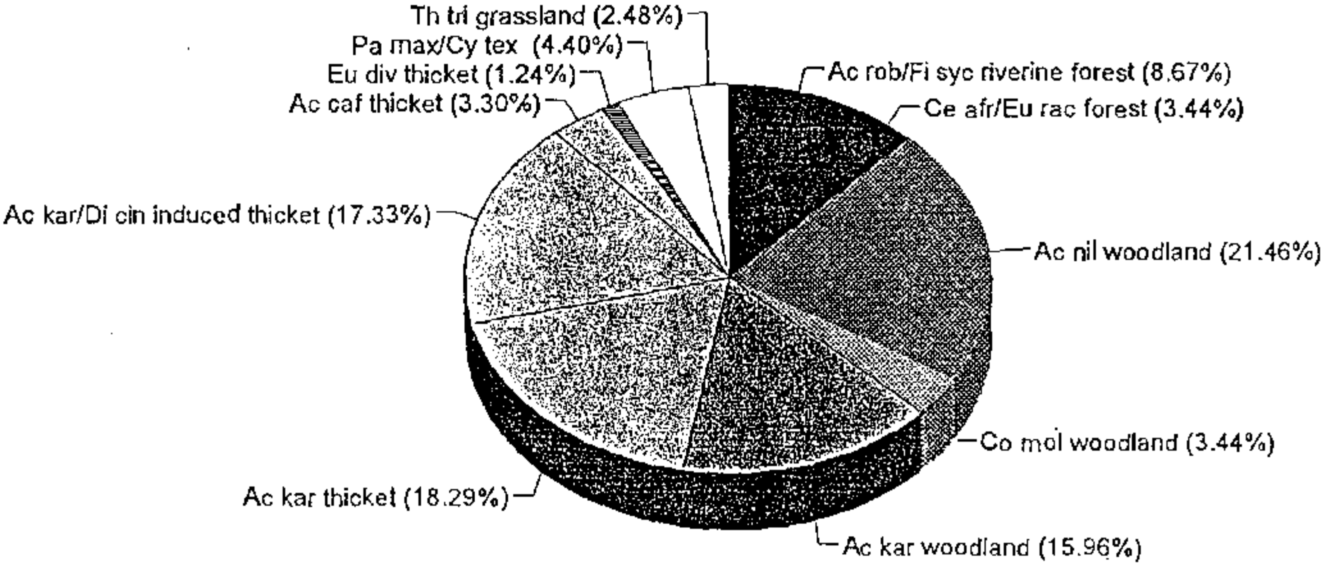


Figure 20.2 Vegetation composition of the Hitchins' map/Grid survey study area in 1975, from Whateley's 1975 map (Whateley and Porter 1983).

Th tri = Themeda triandra , Pa max = Panicum maximum, Cy tex = Cyprus textilis
Eu div = Euclea divinorum, Ac caf = Acacia caffra, Ac rob = Acacia robusta
Fi syc = Ficus Sycamorus, Ce afr = Celtis Africana, Eu rac = Euclea racemosa
Ac kar = Acacia karroo, Di cin = Dicrostachys cinerea, Ac nil = Acacia nilotica
Co mol = Combretum molle

Thus, extensive areas of almost closed *A.nilotica* woodland had not developed in Hluhluwe by 1936; yet there were *A.nilotica* trees and *A.karroo* trees scattered throughout much of the reserve[#7].

In his descriptions of the main vegetation associations in Hluhluwe in 1936, Henkel (1937) recorded that dwarf *A.karroo* and *D.cinerea* shrub association was the most important of the lowland associations and covered a large area. Bayer's photograph of this scrub community in Henkel (1937 - Plate VIIIb) shows excellent black rhino habitat. Indeed, Bayer (1938) noted that *A.karroo* was one of the species most heavily fed on by black rhino in the 1930s. Bayer (1938) also noted that (similar to the findings of this project's surveys) black rhino preferentially fed on medium *S.africana* and on *A.glabrata*[#8].

Experience indicates that most people only generally tend to notice and refer to "thicket" once trees have increased in density and height, canopy cover and browse volumes have increased and lateral visibility has been affected. Given Henkel's survey was a decade prior to the noticeable increase in bush encroachment that took place from the late 1940s, one can speculate that the extensive areas of "grassland" described and mapped by Henkel (1937) may have contained some highly favoured small "*Acacia*'s" (< 1m) which would have also been highly accessible given the high grazing pressure described by Bayer (1938).

Thus by the late 1930s it was likely that habitat conditions for black rhino were reasonable, and that a well distributed seed source for both *A.nilotica* and *A.karroo* existed. This will have facilitated the eventual establishment of large numbers of (animal dispersed) *A.nilotica* and *A.karroo* throughout northern Hluhluwe once conditions became favourable (heavy grazing pressure, below average rainfall period, lack of fire, and possibly DDT spraying[#9] (chapter22)).

Figure 20.3. Picture of Hidli vlei looking accross to the Oncobeni valley and Magwanxa (in Hluhluwe Grid Study area) taken in 1938. (Photo: Mr Roelff Attwell). Following lowering of the water table and drainage line incision , the Hidli vlei area subsequently became encroached with *A.karroo* and has been bush cleared a number of times. Note the more open nature of the vegetation on the background hill slopes in contrast to the thick vegetation seen on the same hillslopes in figure 20.4.

Figure 20.4. 1993 photograph of NE Hluhluwe from Magangeni looking across to Magwanxa. Most of the area in foreground to the foot of the hill has been repeatedly cleared (the photo was taken afer a recent re-clearing). Note how the vegetation on the slopes of Magwanxa has changed from relatively open (figure 20.3) to dense woodland and forest (except for the slopes on the far left of fig. 20.4, which have had various clearing treatments). Also note the abrupt boundary at the foot of Magwanxa between the cleared lowlands and the uncleared slopes This shows the complete lack of bush clearing controls in lower lying areas and the confounding of bush clearing treatments with landscape unit.

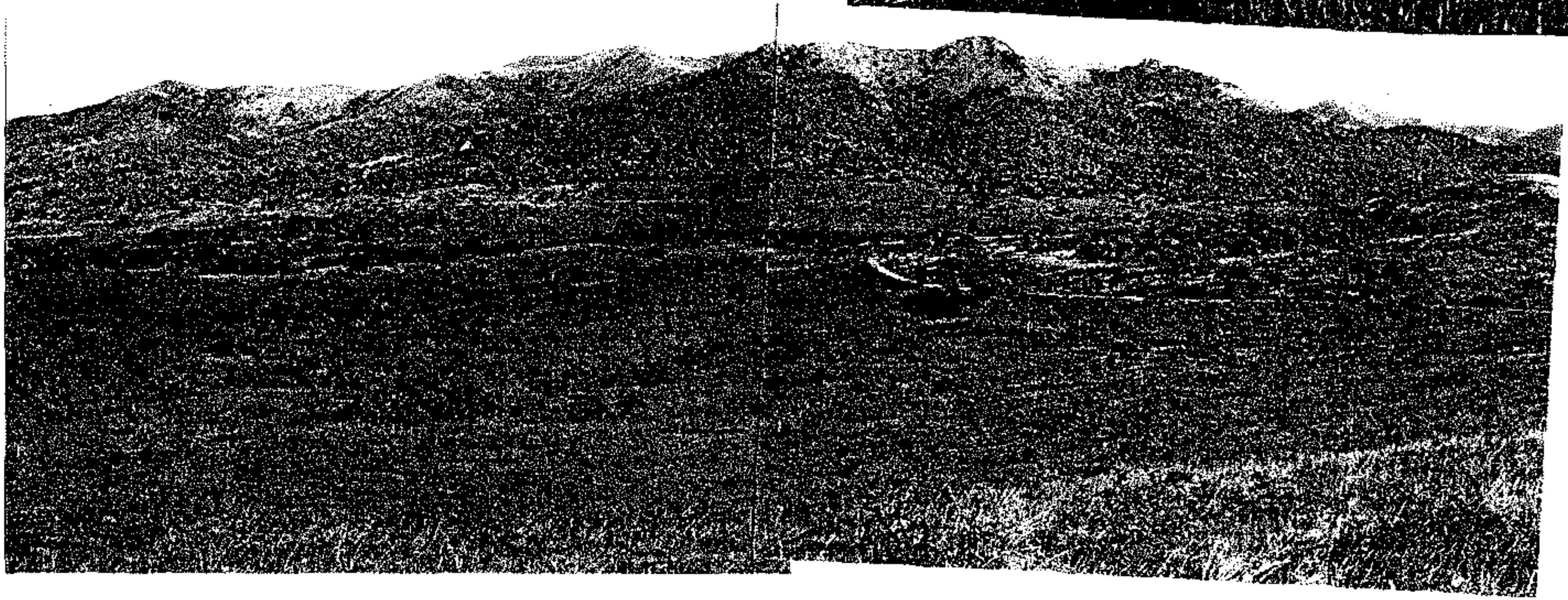


Figure 20.5. Picture looking across to the Mahlungulu Hills (just south of the Hluhluwe Grid study area) taken in 1938. Note the very open vegetation on Mahlungulu. There were only an estimated 18-19 white rhinos in Hluhluwe G.R. at this time. (Photo: Mr Roelf Attwell).

Figure 20.6. Picture of three black rhino in grassland with thicket taken in Hluhluwe in 1938. (Photo: Mr Roelf Attwell)

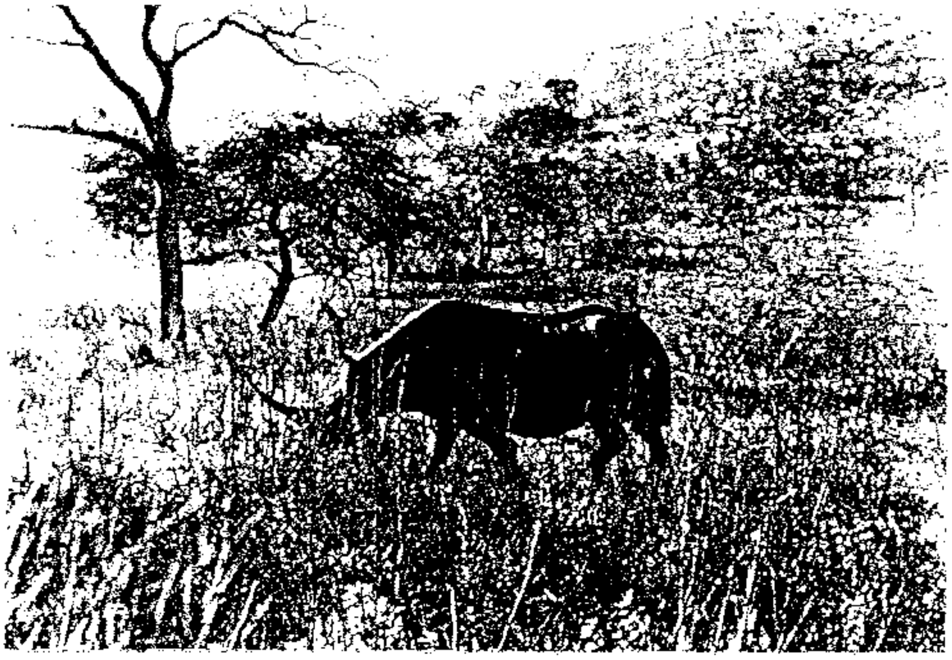


Figure 20.7. Picture of the famous black rhino "Matiala" taken near the Amanzimnyama stream on the Hluhluwe Gird study area in October 1952. Note the developing "*Acacia*" scrub in the background. (Photo: Mr Roelf Attwell).

Figure 20.8. Mating black rhinos in Hluhluwe in November 1954. Note the development of highly favoured small "*Acacia*" scrub in the background. (Photo: Mr Roelf Attwell)

BUSH ENCROACHMENT TAKING PLACE IN HLUHLUWE PRIOR TO 1949

Mr Roelf Attwell kindly allowed me access to a number of his old photographs of Hluhluwe. Figures 20.3, 20.5 and 20.6 were all taken in 1938, and show relatively open woody vegetation. Figure 20.6 shows some black rhinos in a taller grass *Acacia* encroached area. Figure 20.7 was taken by Attwell in October 1942 and shows early stages of bush encroachment providing prime black rhino habitat (a high density of accessible small "*Acacias*").

Attwell (1948) discussed the spread of "*the thorny* A.karroo *and other undesirable plants in the Zululand area*". **The estimated average increase in Hluhluwe black rhino numbers of 4.3% per annum from 1933-1948 is consistent with earlier stages of bush encroachment (so favoured by black rhino) being underway by 1948. Indeed Table 1.1 indicates that by 1948, black rhino densities in Hluhluwe (0.995/km^2) were 82% of maximum levels recorded for Hluhluwe in early 1961 (1.210/km^2), and significantly up from the estimated 0.529/km^2 in 1933.** Attwell (1948) also stated that "*anyone wishing to see black rhino is bound to do so if he visits the Hluhluwe Game Reserve*"

PERIOD OF NOTICEABLE BUSH-ENCROACHMENT : 1949-58

Literature of the 1960s and 1970s which discussed the timing of the onset of widespread bush encroachment in much of Hluhluwe, indicated that **the major period of "*Acacia*" scrub development occurred from 1949-1958** (Bourquin and Hitchins 1979[#10] , Deane 1966 [#11], Vincent 1979 [#12], C.R Ward, J Forest and J.Anderson quoted in minutes of 1979 vegetation dynamics workshop[#13]).

King's (1987) analysis of past aerial photographs also pin-pointed the timing of the biggest increase in what he termed "scrub" (really dense thicket moving towards woodland) between 1954 and 1960[#14]. This indicated that many of the most favoured small encroaching *Acacias* probably became established earlier (coinciding with a dry period with heavy grazing and very few fires). This is consistent with the literature indicating that the obvious rapid encroachment in Hluhluwe took place earlier than 1954. Table 20.1 also indicates that a substantial increase in woody plant cover occurred on aerial photographs of Whateley and Wills' (1996) *A. nilotica* study sites between 1937 and 1954 (Appendix 20.2).

The period 1949-1958 was a time of high grazer numbers and low fire frequencies (in contrast to the 1930s when fires were more common)[#15]. The timing of the encroachment may also have been related to the below average rainfall conditions prevailing in the 1950s (Bourquin & Hitchins 1979), and possibly to the aerial spraying of DDT from 1947-1956 to control tsetse fly[#9] (Bourquin & Hitchins 1979, Macdonald 1979, A.J. Wills pers.comm.). Figure 16.4 shows that only one year (1949) from 1944-56 had significantly above average rainfall, and this was the year when the literature indicated that obvious bush encroachment became noticeable.

The initial period of obvious bush thickening is likely to have favoured black rhino, as medium (1-2m) *Acacias* are still important food sources, and highly favoured small (< 1m) *Acacias* would still have been common. Based on the estimates in Table 1.1, black rhino numbers increased by 8.9% per annum from 1948-50 suggesting that the carrying capacity for black rhino may have increased during this early stage of noticeable bush encroachment. However one should be cautious as this apparently rapid rate of increase could in part be a result of differences in accuracy of the two population estimates and the short (two year) period[#16].

Figure 20.8 was taken by Roelf Attwell in November 1954, and shows early stages of bush encroachment in the background providing prime habitat for black rhino (a high density of accessible small "*Acacias*").

However, from 1954, the noticeable increase in the area of "scrub" on the aerial photographs (King 1987) indicates that a greater proportion of encroaching *Acacias* had grown taller (increasing canopy over). In addition to taller *Acacia* spizes being less preferred, the results of the Pilot study (chapter 6) indicated that if

Acacia thicket becomes very dense, black rhino feeding levels decline. The increase in "scrub" was probably in part a response to the significantly above average rainfall period 1957-60 (three of the four years had significantly above average rainfall), and indicated that **the carrying capacity for black rhinos had probably started to level off or decline in the late 1950s.**

Interestingly, the estimated mean black rhino population growth rate in Hluhluwe between 1950 and 1961 (period of obvious bush encroachment) was only 1.3% per annum - lower than in the 1930s and 1940s[417]. This is consistent with the hypothesis that the prime habitat conditions for black rhino in Hluhluwe probably occurred in late 1940s early to mid 1950s, just before, or during the earlier stages of noticeable bush encroachment, but prior to the marked increase of "scrub" on the aerial photographs.

MAJOR PHYSIOGNOMIC CHANGES IN THE VEGETATION

INCREASE IN WOODY CANOPY COVER AND DECLINE IN GRASSLAND FROM 1937-82

The change from grassland to thicket, closed woodland and lowland forest over much of Hluhluwe indicated by the literature (Ward 1962, Macdonald & Birkenstock 1979, Downing 1980, Bourquin & Hitchins 1979, Watson & Macdonald 1983, King 1987, Whateley & Wills 1987) was confirmed by analyses of aerial photographs taken over the period 1937-1982 (Bourquin & Hitchins 1979, Watson & Macdonald 1983, King 1987 and Whateley & Wills 1996 - see Appendix 20.2 for details) and by quantifying changes between past vegetation maps (Appendix 20.1). Unfortunately no aerial photographs have been taken of the Park since 1982 and the end of this study.

All analyses of the aerial photographs (Appendix 20.2) concluded there had been marked declines in the area of grassland from 1937 with corresponding and significant increases in woody plant cover.

- Kings'(1987) analyses (discussed in more detail in Chapter 16 and Appendix 20.2) revealed that by 1982, thicket/closed woodland (King's "scrub" category) covered 32.2% of Hluhluwe - an area 3.27 times greater than 1937. The area of forest showed a much smaller increase from 12.2 to 16.3% over the same period. Unfortunately there are no recent aerial photographs, but it is likely that the percentage of forest and "scrub" (as classified by King) has increased further since 1982 as many areas classified as "open grassland/parkland by King on the 1982 photograph were bush encroached in 1989, and the main 1989 Post-burn survey revealed that open grassland only accounted for 7.6% of plots in Hluhluwe. - Watson & Macdonald (1983) showed the same trends, with grassland coverage decreasing by over two thirds in three northern Hluhluwe game control blocks from 1937-75, whilst woody plant cover increased despite bush clearing during this period. For example, in one Hluhluwe block, from 1937 to 1975, the percentage of grassland declined from 57% to 12%, while woody plant cover increased from 43% to 88% (Watson & Macdonald 1983)[#18].

- Whateley & Wills' (1996) quantified changes in the canopy cover in their three *A.nilotica* woodland study sites using aerial photos and this showed a similar trend of increasing bush-thickening from 1937-81 (Table 20.1).

Table 20.1 Percentage woody canopy cover values for the Whateley-Wills three study sites (selected in 1985 to represent different seral stages in the development of thicket to *A.nilotica* closed woodland to *E.racemosa/B.zeyheri* lowland forest) on five occasions between 1937 and 1981 (From Whateley and Wills 1996 - see also Appendix 20.8)

1995 seral "age"	Percentage Woody Plant Cover of Woodland				
	1937	1954	1960	1975	1981
Young	5	20	20	70	75
Intermediate	10	40	50	65	80
Old	30	60	75	95	95

The decline in numbers of reedbuck (Deane 1966,Brooks & Macdonald 1983) was a further indicator of the decline of tall open grassland in the reserve.

The vegetation maps of Hluhluwe showed a similar trend of increasing cover and declining area of grassland, (Appendix 20.1) although there was an opening up of the vegetation in the north-east of Hluhluwe in the 1960s up to 1970, when according to Hitchins' maps the vegetation began to thicken up again. The vegetation dynamics workshop also described a thickening up of *A.karroo* areas, although suggesting that this trend occurred later from 1973-74 (Macdonald *et al* 1979).

- Grassland declined from covering 78% of the Map study area in 1936 (based on Henkel's 1937 map) to account for only 32.4% of the Map study area on Hitchins 1960 map, while "dense vigorous scrub" became the dominant vegetation type accounting for 45% of the area.

- Ward's 1961 map reflected the large scale bush clearing that took place in the Map study area, and this coupled with more frequent fires in the late 1960s resulted in grassland increasing to cover 72.3% of the Map study area by 1970 (Hitchins' 1970 map), with "dense vigorous scrub" declining to cover only 5.5% of the area.

- However, by 1973 (Hitchins' 1973 map) the amount of "dense vigorous scrub" had increased to cover 29.3% of the Map study area while grassland declined to 41.4% of the area. Whateley's 1975 map indicated that only 7% of the Map study area was grassland with thicket communities accounting for 40% of the area and woodland (with *A.nilotica* and *A.karroo* being the dominant forms) accounting for a further 41% of the area.

- Areas that were grassland in 1960, largely remained grassland over the period 1960-1973, while the increase in "dense vigorous scrub" on Hitchins' maps from 1970-1973 occurred primarily on areas than had been scrub in 1960 and had subsequently been cleared and frequently burnt (Table 20.2). The increase in scrub in the early 1970s coincided with the start of a period of above average rainfall and reduced fire frequencies.

Table 20.2. Vegetation changes in the Hitchins' map/Grid survey study area from 1960 to 1973. (Based on an analysis of maps from Hitchins 1960, 1970 and 1973).

1960		1970		1973		
Scrub	45.4%	Grsld	41.5%	Scrub	21.0%	Dense vigorous scrub in 1960, open in1970, induced shrubland in wooded grassland in 1973
				Grsld	14.9%	Dense vigorous scrub 1960, open in 1770, grassland in 1973
				A.nil.	3.6%	Dense vigorous scrub in 1960, open 1970, A.nilotica woodland/wooded grassland in 1973
				M.sen.	1.9%	Dense vigorous scrub 1960, open in 1970, and induced Maytenus senegalensis/other spp. woodland in 1973
		Scrub	3.9%	Scrub	3.7%	Dense vigorous scrub 1960 and 1970, and induced shrubland in wooded grassland in 1973
				Grsld	0.1%	Dense vigorous scrub 1960 and 1970, grassland in 1973
Grsld	32.4%	Scrub	1.6%	M.sen.	1.6%	Grassland in 1960, dense vigorous scrub 1970 and induced Maytenus senegalensis/other spp. woodland in 1973
		Grsld	30.8%	Scrub	4.4%	Grassland in 1960 and 1970, induced shrubland in wooded grassland in 1973
				Grsld	26.4%	Grassland in 1960, 1970 and 1973
C.mol	1.9%	C.mol	1.9%	C.mol	1.9%	Combretum molle woodland 1960, 1970 and 1973
Forest	6.0%	Forest	6.0%	Forest	6.0%	Closed mesic forest in 1960, 1970 and 1973
A.nil.	12.0%	A.nil.	12.0%	A.nil.	12.0%	A.nilotica woodland and wooded grassland in 1960, 1970 and 1973
E.rac.	0.3%	E.rac.	0.3%	E.rac.	0.3%	Eulea racemosa woodland in 1960, 1970 and 1973
E.div.	2.0%	E.div.	2.0%	E.div.	2.0%	Euclea divinorum woodland in 1960, 1970 and 1973

Figure 20.9 A time series of photographs from the NPB archives showing how dramatically the southern Hluhluwe vegetation changed in just a 35 year period from open parkland (1949) to a dense *Acacia* thicket (1984). The medium sized *Acacia* in the middle of the 1974 photograph is an *A.nilotica*. Note also how the big trees on the left *(S.birrea)* have provided a nucleation site for the establishment and development of evergreen trees under their canopies

1949

1974
(25 years later)

1984
(35 years later)

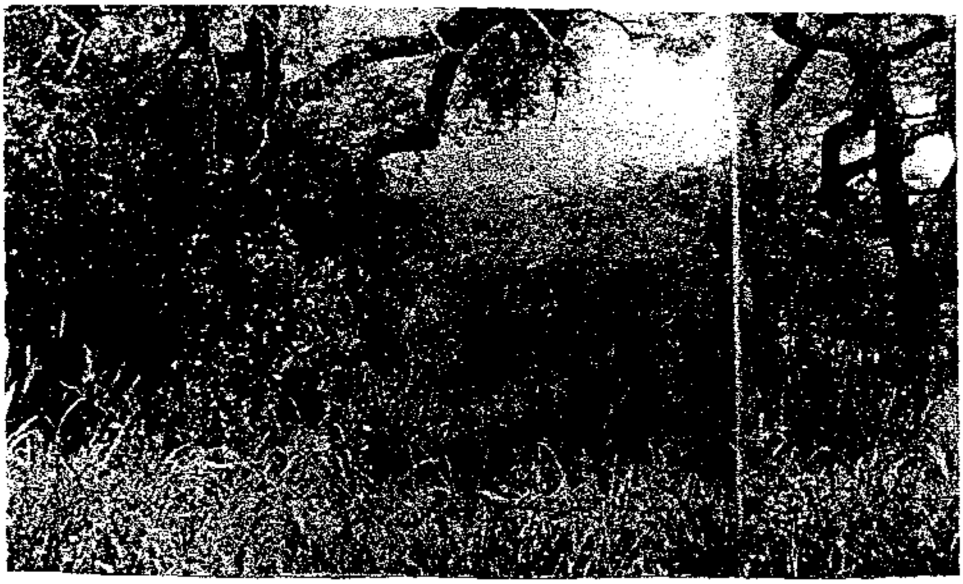


Figure 20.10. Photograph from Magangeni looking towards Ngqungqulu. Photo's taken in May 1949 depict the Ngqungqulu area as open grassland, but by 1954 the area was devoid of grass and was densely covered with encroaching scrub of a maximum height of 1.5m (Bourquin and Hitchins 1979). Whateley's 1975 vegetation map shows the area as *A.karroo* woodland adjacent to the drainage line, *A.karroo* thicket on the slopes and *A.nilotica* woodland on top of the ridge. Staff Sgt. Nqabanefa Ncobo recalled that around 1975, closed canopy woodland vegetation was mainly restricted to the *A.robusta* drainage line in this view from Magagneni, and that the vegetation on the slope had thickened up considerably since then, an observation independently verified by M Brooks and D Densham (pers. comm.). By the 1990's, patches of closed *A.nilotica/A.karroo* woodland and forest had developed on the slopes, with *A.karroo/A.caffra* thicket in between.

Perhaps the most striking evidence of gross physiognomic changes in Hluhluwe is photographic [#19]:

- Figure 20.9 is a time series of photographs from the Natal Parks Board archives showing how dramatically the southern Hluhluwe vegetation has changed in just a 35 year period from open parkland (1949) to what appears to be a dense *Acacia* thicket (1984). Attempts to find this site in 1990 to take a fourth photograph (with only a grid square reference to go by) were unsuccessful[#20]. King's (1987) Thesis has similar sequences of photographs.

- The photograph of north east Hluhluwe in Figure 20.4 was taken in 1993 from the Magangeni road. It shows the Magwanxa hill (on the right hand side) which also is depicted in Attwell's 1938 photograph (Figure 20.3). Note how the vegetation on the slopes of this hill has changed from being relatively open in 1938 to become dense woodland and forest during the 55 year intervening period. Most of the open areas in the foreground of figure 20.4 have been cleared, and been recently re-cleared of *Acacias* (and particularly *A.karroo*), with some areas having been cleared three to four times by 1993 when the photograph was taken.

- Figure 20.10 shows a view of part of Nqungqulu taken from the top of Magangeni in 1993. Hitchins and Bourquin (1979) reported that photographs in 1949 showed that the Nqungqulu area was open grassland but by 1954 the area had become densely covered with encroaching scrub up to a maximum height of 1.5 m. Whateley's 1975 vegetation map shows an area of *A.karroo* woodland adjacent to *A.robusta* forest in the drainage line, with *A.karroo* thicket on the hillslope and *A.nilotica* woodland on the top of the ridge. Staff Sgt. N.Ncobo ret. (pers.comm.) recalled that around 1975 closed canopy woodland was largely restricted to the *A.robusta* drainage line, and that the woody plants on the hillslope have thickened up substantially since then. This observation was corroborated by P.M. Brooks and D. Densham (pers.comm). By the 1990s patches of mature *A.nilotica/A.karroo* woodland had developed on the slopes with *A.karroo/A.caffra* thicket in between.

CYCLICAL THICKENING AND CLEARING OF *A.karroo* DOMINATED AREAS IN NORTHERN HLUHLUWE

A.karroo dominated areas in the lower black clay areas and hillslopes of N.E. of Hluhluwe have been highly dynamic. From being open grassland in the late 1930s (Henkel's 1937 map - Appendix 20.1, Figure 20.13), they became thicket in the 1950s, but were opened up by extensive clearing in the late 1950s early 1960s. Frequent fires from 1965-71 are thought to have kept the habitat open[#21] (Macdonald et al 1979), before these areas once again thickened up in the 1970s (Hitchins' 1970 and 1973 and Whateley's 1975 maps - Table 20.2, Figure 20.14, Appendix 20.1, Macdonald et al 1979).

The evidence as to the timing of the thickening up of *A.karroo* areas in the early 1970s was conflicting. While the analysis of the vegetation maps indicates that substantial thickening occurred between 1970 and 1973 (Appendix 20.1), delegates at 1979 Symposium/Workshop on the vegetation of Hluhluwe-Umfolozi Park (Macdonald et al 1979) noted that the amount of open grassland in northern Hluhluwe increased until about 1974. There is however agreement that a general thickening and maturation of *A.karroo* took place in the 1970s and 1980s[#22].

A.karroo dominated areas in northern Hluhluwe have been the most heavily bush cleared areas in the reserve, with a number of areas having been re-cleared a number of times in the mid 1970s, late 1980s and 1990s (Figure 20.4[#23], Figure 17.2). The effects of bushclearing have only been temporary (chapters 17 and 18, Macdonald *et al* 1979), requiring follow up clearing to maintain open areas such as that shown in the foreground of Figure 20.4 which was cleared shortly before the photograph was taken in 1993. Some areas of *A.karroo* had been cleared three to four times by 1993.

Figures 20.12 and 20.11 show encroaching *A.karroo* thicket and mature woodland, while Figures 17.2 and 17.3 show the early stages of re-establishment of *Acacias* on recently bush-cleared areas.

Figure 20.11. Photograph of mature tall spindly *Acacia karroo* woodland in the Oncobeni valley in 1991. Keryn Adcock is holding a smaller *A.karroo* that has been browsed by a black rhino. Note the high levels of grass interference. Some of the taller *A.karroo*'s in this area were pushed down by elephants enabling rhinos to browsetheir canopies. Vegetation communities growing on moister clayier lowland sites such as this followa different successional pathway to the Whateley-Wills *A.nilotica* woodland succession.

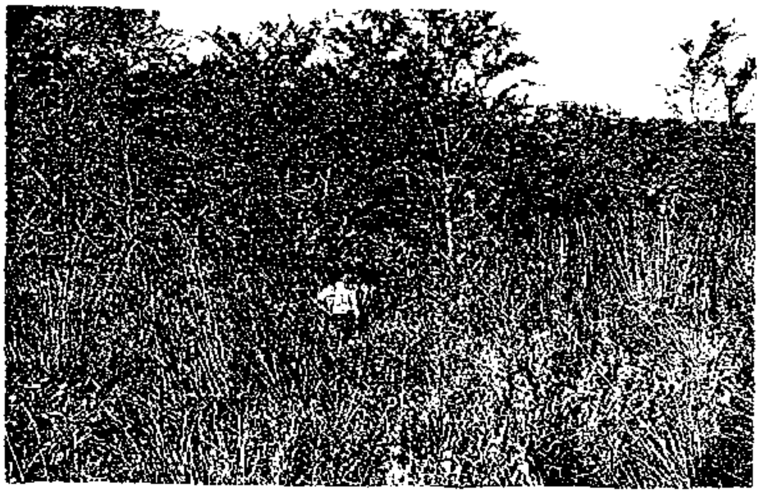


Figure 20.12. Photograph of a radio-horned black rhino in typical *Acacia karroo* dominated scrub in the Corridor area of Hluhluwe-Umfolozi Park. The long term carrying capacity of such habitats will depend upon whether burning is frequent enough to prevent these trees growing to a height where fires will not result in high levels of topkill.

IMPLICATIONS OF HABITAT CHANGES FOR BLACK RHINO

The very extensive clearing of *A.karroo* thicket in north east Hluhluwe in 1959-60, coupled with increased grass growth (following heavy culling and increased rainfall) was implicated as the main cause of the 1961 die-off of 46 black rhino in the area over a four month period (chapter 17).

Given photographs of black rhino in poor condition in 1965 (Appendix 20.4), the high levels of feeding (and especially the high levels of browsing of generally rejected species) on Bourquin's 1965/66 Zincakeni plot and Hitchins' 1969-71 plots, black rhino in north east Hluhluwe were clearly still under nutritional stress in 1970.

The general thickening and maturation of *A.karroo* in the 1970s and 1980s will have reduced habitat quality for black rhino. This was a time of continued black rhino density declines.

The Grid survey and remeasurement of Hitchins plots indicated that carrying capacity for black rhino in north eastern Hluhluwe in 1990 was approximately half that of 1970 (chapter 10). This was corroborated by the observed increase in home range sizes since 1970 (chapter 23).

However, while densities of favoured small *Acacias* declined from 1970-1990 on Hitchins plots (chapter 10), this was possibly due to self thinning as trees grew taller (chapters 10 and 18). Significantly the densities of many associated unpalatable species also decreased on the plots.

Over much of the area repeated bushclearing and fire has in the shorter and longer term benefited black rhino by been preventing extensive areas of mature *A.karroo* woodland developing which would have further reduced carrying capacity, and creating open areas where favoured small *Acacias* can establish and develop. However any benefits from clearing in these areas is only temporary as the A.karroo thicket grows back and matures in the absence of repeated clearing (chapter 18, Macdonald *et al.* 1979).

DEVELOPMENT OF CLOSED CANOPY *A.nilotica* DOMINATED WOODLAND IN 1960s AND 1970s AND SUBSEQUENT SUCCESSION IN THESE WOODLANDS TOWARDS LOWLAND *E.racemosa/B.zeyheri* DOMINATED FOREST

Aerial photographs (Appendix 20.2) and eye witness accounts (Appendix 20.4) indicated that bush encroachment and thickening took place in extensive areas of central and southern Hluhluwe that subsequently became dominated by *A.nilotica* woodland. In 1936, these areas where grassland with small patches of *A.nilotica* parkland (Henkel 1937). By 1961 most of the area centered on Zincakeni (central Grid study area) and en route to Sitezi was still open treeveld on Ward's 1961 map (Appendix 20.1). Bourquin however indicated that sometime between 1965 and 1970 *A.nilotica* had become a dominant species in the Zincakeni area, although a "representative" transect monitored by Bourquin in the area in 1965/66 indicated that *A.niloticas* were on average small (<1m). By 1975, Whateley's Hluhluwe vegetation map indicated that extensive areas of *A.nilotica* woodland had developed in this and other extensive areas of Hluhluwe (Whateley & Porter 1983).This was confirmed by eyewitness accounts (Appendix 20.4).

Whateley's map also revealed that by 1975, thicket communities accounted for almost 40% of the map study area, and woodland had increased to account for a further 41% of the area, with *A.nilotica* woodland (21.5%) being the dominant woodland form. Eye witness accounts of the Zincakeni area indicate that at this time many A.niloticas were still not greater than 2-3m (Appendix 20.4).

However, by the 1989 Grid survey, areas of *A.nilotica* dominated woodland in northern Hluhluwe had changed substantially from the *A.nilotica* woodland community described by Whateley and Porter (Appendix 20.3). In particular, many of the *A.nilotica*'s (that had matured and formed a closed woodland) were starting to or had senesced, and taller growing intermediate and later successional species such as *R.pentheri, B.zeyheri and E.racemosa* had grown up in the woodland to become canopy dominants. By 1989, *E.racemosa* was the biggest contributor to total canopy cover in the Hluhluwe Grid study area. This was in complete contrast to the situation fifty years previously where Bayer (1938) noted evergreen species were uncommon in Hluhluwe, and Henkel

(1937) did not specifically mention *E.racemosa* in his vegetation descriptions of Hluhluwe. The failure of a botanist of Henkel's ability to specifically mention *E.racemosa* is thought to be very significant (Bourquin & Hitchins 1979, A.J. Wills pers.comm), as it indicates the species was not common enough in 1936 to be considered a key species.

Whateley and Wills (1996) described the colonisation of and increasing canopy cover in these areas of closed or semi-closed *A.nilotica* woodland in northern Hluhluwe; and in contrast to Bourquin & Hitchins (1979) advanced an autogenic and disturbance (fire) driven successional model (based on fieldwork undertaken in 1985) to explain the increasing dominance of later successional species like *E.racemosa* and *B.zeyheri* in *A.nilotica* dominated woodland areas [#24]. The nub of the "Whateley-Wills" hypothesis (1996) is that *A.nilotica* (shown as the black trees in Figure 20.13) is the pivotal species in the succession, and reduced fire frequencies under *A.nilotica* canopies played a key role in the successional process leading to the development of lowland forest in Hluhluwe.

Past vegetation descriptions (Appendix 20.3), eye-witness accounts (Appendix 20.4), the partial fire-constrained ordination (chapter 16), 3D spize abundance plots in ordination space (Figure 20.15 - Appendix 20.9), a TWINSPAN floristic analysis of the Hluhluwe data (Appendix 20.5) and an exploratory median method clustering of Grid data[#25] all provided strong corroborative evidence for the Whateley-Wills (1996) hypothesised successional sequence in *A.nilotica* areas, and that *E.racemosa/B.zeyheri* dominated lowland forest development was associated with long term protection from fire.

Figure 20.13 summarises Wills-Whateley's hypothesised successional sequence in *A.nilotica* areas. With minor modifications and additions in the light of the 3D spize abundance plots in ordination space (this chapter) and the partial fire-constrained ordination (chapter 16) it appears that succession in lower lying *A.nilotica* woodland areas throughout northern Hluhluwe has proceeded as follows:

- Fire adapted tree early successional tree species such as *D.cinerea*, *A.karroo*, *A.nilotica* and *M.senegalensis* invade and establish in grasslands and open parkland areas (Figure 20.13a).

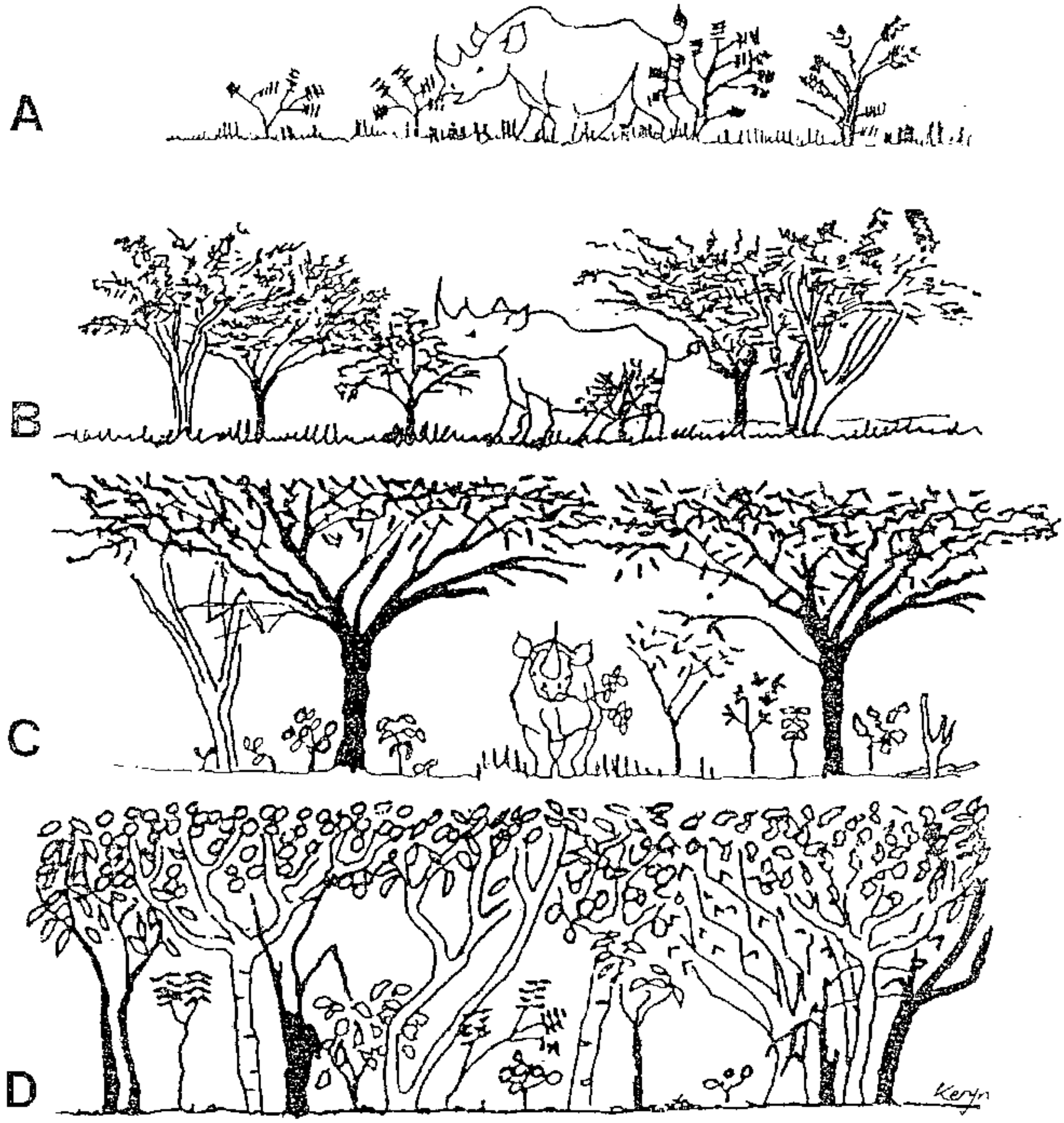


Figure 20.13 Diagrammatic representation of the Whateley-Wills successional model showing development, maturation and senescence of *A.nilotica* woodland and the development of a dry *E.racemosa/B.zeyheri/R.pentheri* lowland forest. C) shows a stage where later successional dominants such as *E.racemosa* and *B.zeyheri* establish under *A.nilotica* canopies. Eventually by stage D), the shorter-lived *A.niloticas* have been overtopped by these species and are senescing and dying.

Figure 20.14

20.14 a) Photograph of *Euclea racemosa / Berchemia zeyheri* dry lowland forest behind Zineakeni dam taken in 1990. The late Norman Deane indicated that in 1954 one could drive around this hill and that wildebeest were caught in the area (minutes of the 1979 Vegetation Dynamics Workshop). The area in the foreground has been bush cleared.

20.14 b) . Mature *A.nilotica* woodland in advanced stages of becoming a *Euclea racemosa / Berchemia zeyheri* dry lowland forest taken near Zineakeni in 1990. Much of this area is currently being bush cleared.

20.14 c) Close up of a mature *A.nilotica* in the middle of the above photograph (note the characteristic dark diamond fissured bark). The grey barked tree to the right of the bole of the *A.nilotica* is a *Berchemia zeyheri* . Whateley & Wills (1996) found that *B.zeyheri* was significantly associated with sites underneath *A.nilotica* canopies close to the bole in earlier stages of colonisation of *A.nilotica* woodland by forest species. *B.zeyheri* has become one of the canopy dominants in the area. Note other broadleaved later successional species under the *A.nilotica* including small establishing individuals of the forest species *Sideroxylon inerme*.

20.14 d) Photograph showing a *Euclea racemosa* sapling establishing next to the bole of an *A.nilotica*. Whateley & Wills (1996) found that this species was significantly associated with sites underneath *A.nilotica* canopies close to the bole in earlier stages of colonisation of *A.nilotica* woodland by forest species.

- If fire frequencies are low, then these trees will grow above effective flame height leading to the formation of thicket vegetation (Figure 20.13b) which eventually develops into closed/semi-closed woodland dominated by *A.nilotica*. *A.karroo* largely dies out but some *D.cinerea* also grows tall.

- The grass layer in more open young *A.nilotica* dominated woodland is relatively uniform, consisting predominantly of tall flammable grass species (eg *Themeda triandra*). At this stage fire still has an even impact in these woodlands.

- As the canopy cover of the *A.nilotica* trees increases, the micro-environment beneath the trees begins to change (light intensity drops, soil moisture content rises and the humus layer builds up). Under these conditions islands of shorter or less flammable grass species develop under the canopies (eg *Dactyloctenium australe & Panicum maximum*). Fire sensitive and more shade tolerant intermediate *(Rhus pentheri* then *B.zeyheri*) and later successional forest species (*E.racemosa, E.divinorum Kraussia.floribunda, Scutia myrtina, Sideroxylon inerme, and Celtis.africana*) are then able to establish in these islands beneath canopies (Figures 20.13c, 20.14c & d).

- As the *A.nilotica* canopies spread, the isolated islands of shorter grass merge. At this stage the protection of forest saplings from fire is complete and later fire sensitive successional species (eg S.myrtina) can germinate, and establish throughout the woodland. [Whateley and Wills (1996) found that species patterns in *old* woodland were not clumped relative to canopies.]

- As the *A.nilotica* trees senesce, saplings of taller growing intermediate and later successional species (*R.pentheri, B.zeyheri, E.racemosa*, and *S.inerme*) grow up through the *A.nilotica* canopy. In time the canopy becomes continuous (Figures 20.13d, 20.14a & b), protection form fire is increased and later successional species can establish and develop throughout the forest. It remains to be seen whether there is sufficient moisture in these areas for *C.africana* to eventually become a canopy dominant in the forest.

The changes in the Zincakeni area over time are consistent with the Whateley-Wills successional sequence.

- Figure 20.14a shows the dense closed woodland/lowland forest *E.racemosa/B.zeyheri* on the Nyakeni hill behind the Zincakeni dam in 1990. The area behind the dam has changed from being open *S.birrea* parkland to short "*Acacia*" thicket to closed/semi-closed *A.nilotica* woodland to dry dominated lowland forest with *E.racemosa* and *B.zeyheri* as canopy dominants (The area in the foreground has been bush cleared.). Figure 20.9b, c and d were also taken near Zincakeni dam in 1990, and show mature *A.nilotica* woodland in advanced stages of becoming a *E.racemosa/B.zeyheri* lowland forest (20.14b) with forest species *B.zeyheri* (20.14c) and *E.racemosa* (20.14d) establishing next to the bole of *A.nilotica*'s. Since 1990 an increasing number of the *A.nilotica*'s have senesced and died in this area indicating this species is relatively short-lived.

Looking at the dense vegetation in figure 20.14, it is hard to believe that in the 1954 it was possible to drive around Nyakeni hill behind the Zincakeni dam (shown in Figure 20.14a), and that wildebeest were caught in the area (The late Norman Deane quoted in the minutes of August 1979 Vegetation Dynamics Workshop, A.J. Wills Pers.com.).

IMPLICATIONS OF HABITAT CHANGES FOR BLACK RHINO

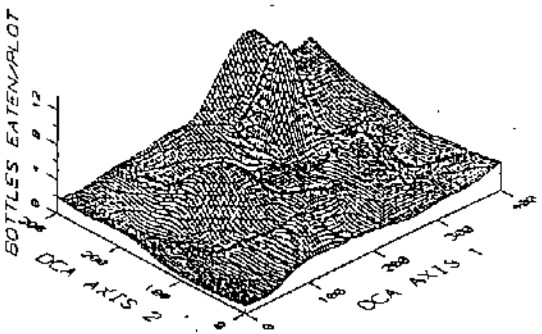
Chapter 6,7 and 9 indicate that the development of closed woodland and later lowland *E.racemosa/B.zeyheri* lowland forest will have significantly reduced black rhino habitat quality and hence carrying capacity. This was corroborated by mean black rhino offtake levels in different seral stages of the Whateley-Wills (1996) successional pathway (defined using a TWINSPAN floristic analysis of Grid data - Appendix 20.6). Mean offtake levels in contiguous groups that had the highest canopy cover of small-intermediate *A. niloticus* was approximately four times greater than that in communities that represented later stages of the hypothesised Whateley-Wills successional sequence. Feeding levels in the most advanced E.racemosa lowland forest grouping was only about 5% of levels recorded for "communities" with small *A.nilotica*.

The 3D cover abundance surfaces of key Whateley-Wills spizes (Figure 20.15a,b,c,d,f,g and h) in ordination space(Appendix 20.5) corroborated the hypothesised Whateley-Wills (1996) successional model, and also supported the existence of vegetation zonation (Figure 20.15 i,j,k). The Whateley-Wills successional trace pattern to emerge has been superimposed as an arrow on Figure 20.16. This shows how levels of black rhino feeding varied over ordination space and in the case of *A.nilotica* areas confirms that the biggest decline in black rhino feeding occurred once the most favoured small/medium (<2m) *A.nilotica* grew taller to develop into closed woodland. Figure 20.16 also indicates that black rhino feeding levels continued to decline (at a reduced rate) as succession proceeded through to *E.racemosa* and *B.zeyheri* dominated lowland forest.

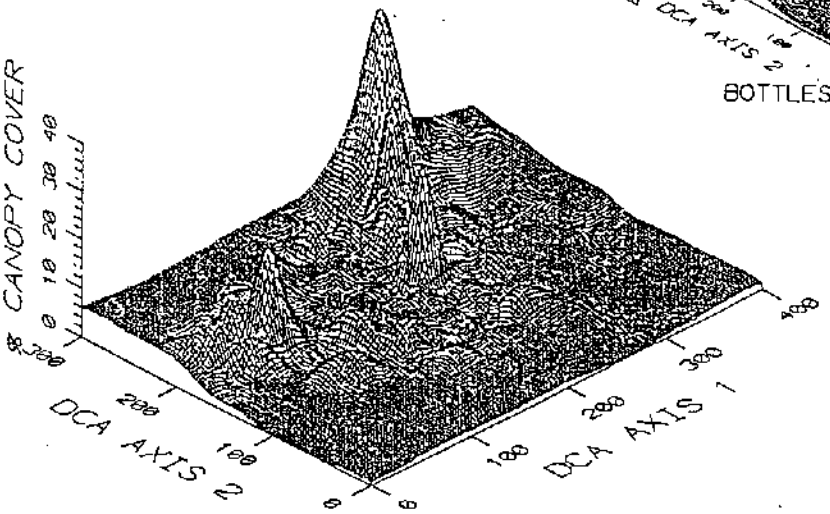
The results of the above multivariate analyses and the Pilot (chapter 6) and Grid surveys (chapter 7) have clearly demonstrated that small *A.nilotica* is one of the most highly favoured spizes by black rhino; but that as this species grows taller it becomes less and less preferred until it eventually becomes highly rejected. By 1990 extensive areas with stands of tall *A.nilotica*'s covered large areas of both the Grid study area and the rest of Southern Hluhluwe. Given the apparently even aged nature of many of the *A.nilotica* closed woodland stands in Hluhluwe (suggesting that a set of conditions probably existed in the past which allowed a whole cohort of seedlings to germinate, establish and mature) it is reasonable to expect a degree of self thinning to have taken place. Using empirically-derived self thinning relationships from the field of plant population biology (White & Harper 1970 ; Harper 1977) it is possible to predict approximate densities of favoured small *A.nilotica*'s that existed in the past, and which gave rise to currently observed densities of taller *A.nilotica*'s. It was estimated that past densities of highly favoured small/medium (<2m) *A.nilotica*'s on the 127 Grid plots containing the species (52.5% of Hluhluwe Grid Study Area), were probably between 2.3 and 5.2 times higher (and may even have been as much as 8 times higher) than the observed 1989 densities (see Appendix 20.7 for details of calculations).This further indicates that habitat quality for black rhinos will have been higher when most of the *A.nilotica* trees became established.

Given the likelihood that there were significantly higher densities of small palatable *Acacias* in the early 1950s, habitat conditions would have been substantially better then than for much of the 1980s. Grazing biomass was high forty years ago with a low proportion of bulk feeders, and this will have further favoured black rhino by

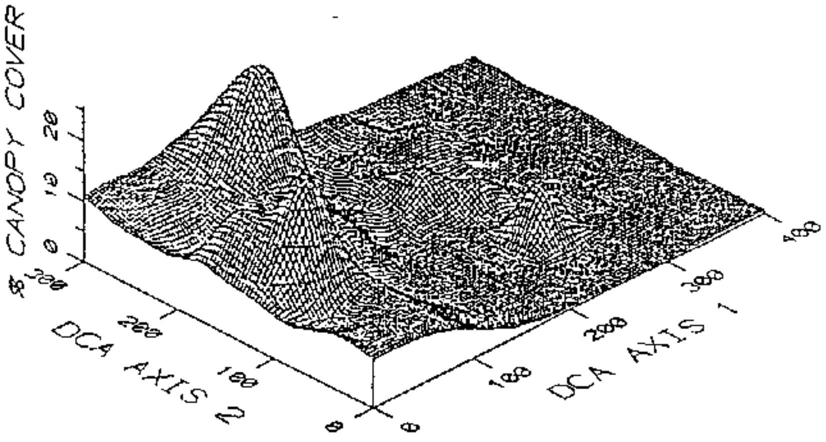
Figure 20.15 A). Canopy cover abundance levels of *Acacia nilotica* spizes as 3D surfaces in spize based ordination space (*based on results of polynomially detrended correspondence analysis of the Hluhluwe grid plots after excluding riverine and true mature evergreen forest plots - note that the Y axis scaling is variable). The small insert is a surface plot of black rhino browsing levels in the same spize-based ordination space.



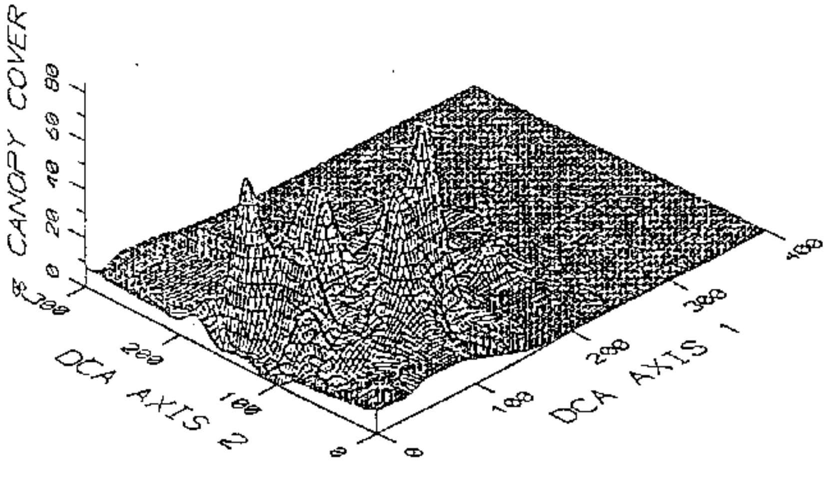
BOTTLES EATEN PER PLOT



Acacia nilotica SIZE 1,2 (<2m) % CANOPY COVER



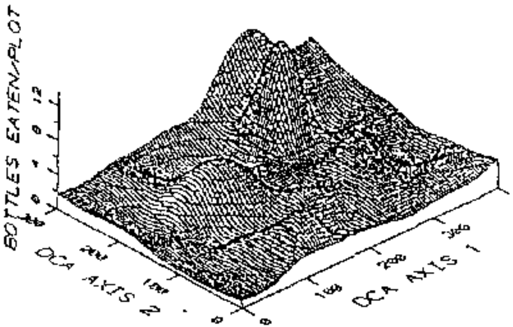
Acacia nilotica SIZE 3 (2-4m) % CANOPY COVER



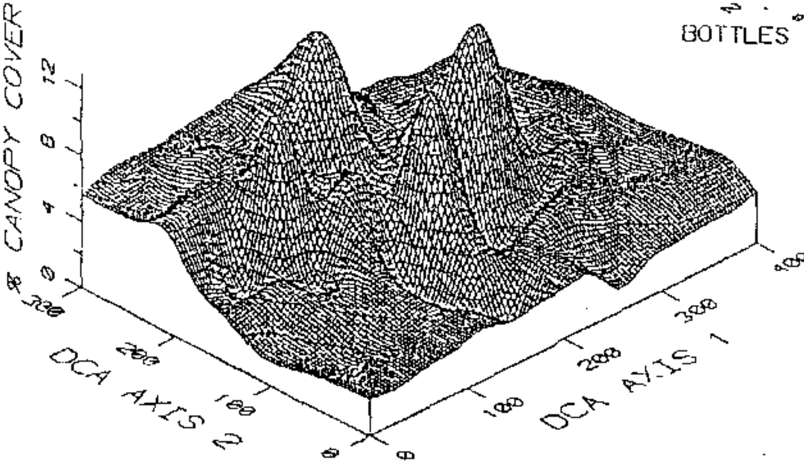
Acacia nilotica SIZE 4 (>4m) % CANOPY COVER

Figure 20.15 B). Canopy cover abundance levels of *Dichrostachys cinerea* spizes as 3D surfaces in spize based ordination space*

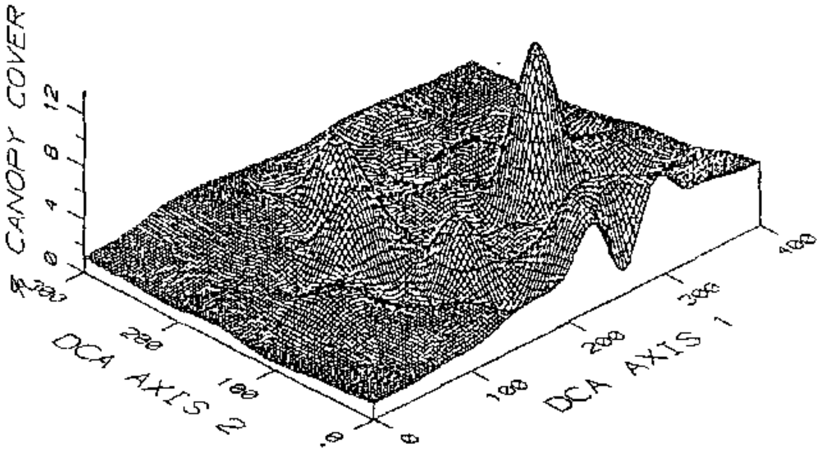
B



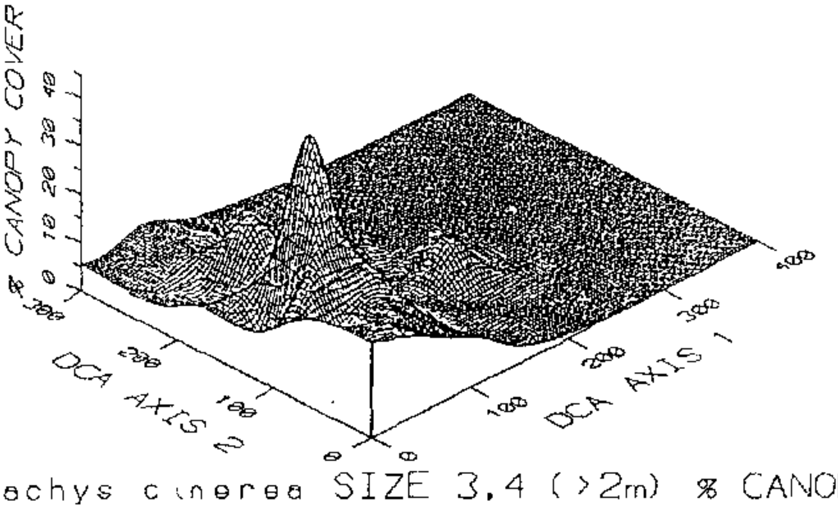
BOTTLES EATEN PER PLOT



Dichrostachys cinerea SIZE 1 (<1m) % CANOPY COVER

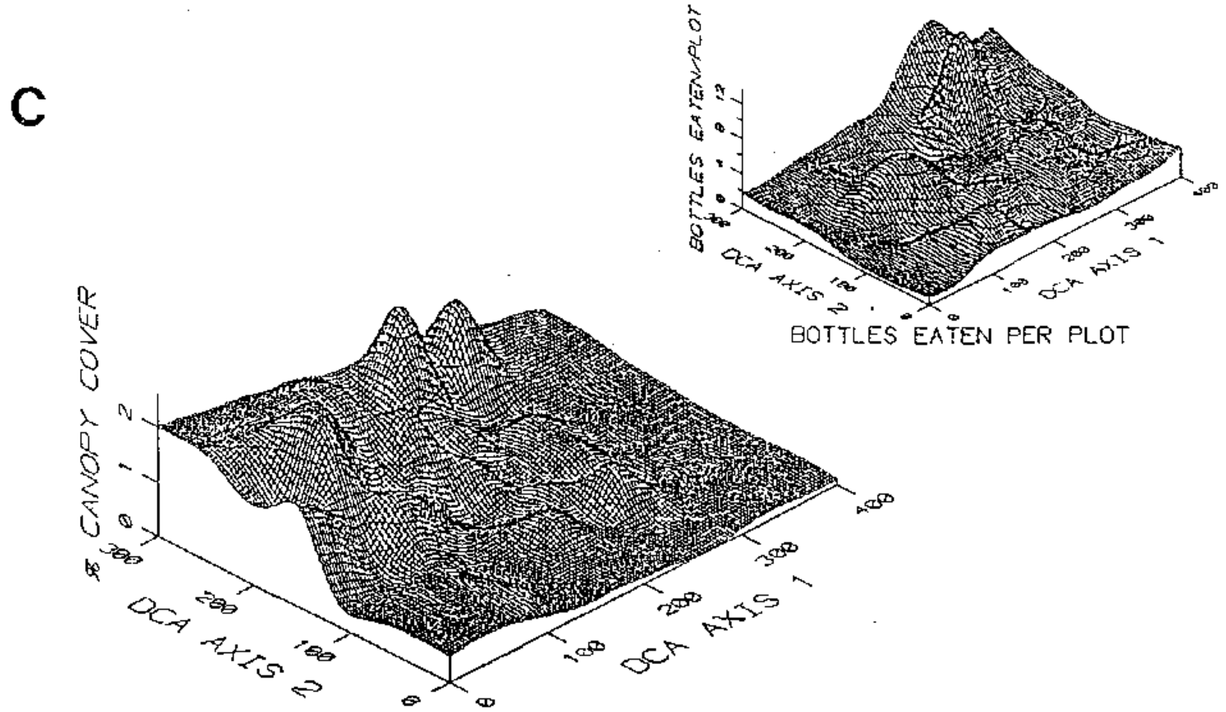


Dichrostachys cinerea SIZE 2 (1-2m) % CANOPY COVER

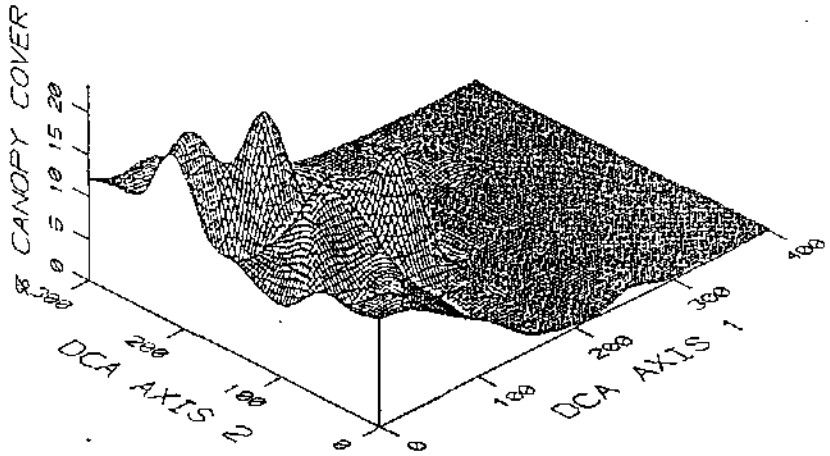


Dichrostachys cinerea SIZE 3,4 (>2m) % CANOPY COVER

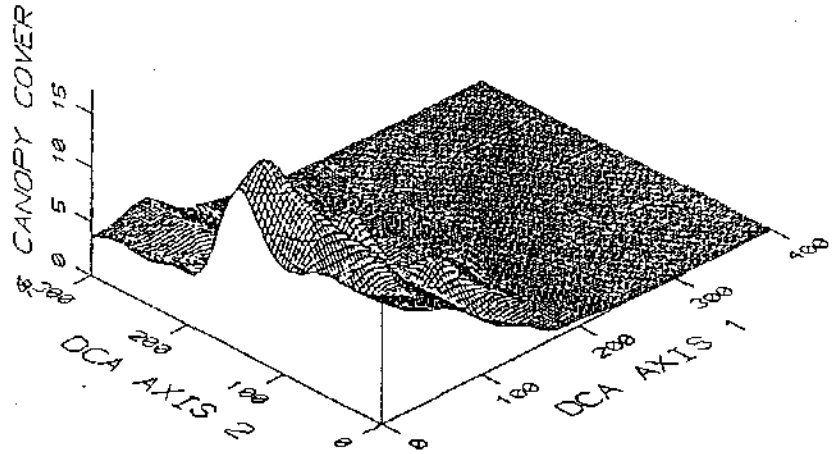
Figure 20.15 C). Canopy cover abundance levels of *Rhus pentheri* spizes as 3D surfaces in spize based ordination space*



Rhus pentheri SIZE 1 (<1m) % CANOPY COVER



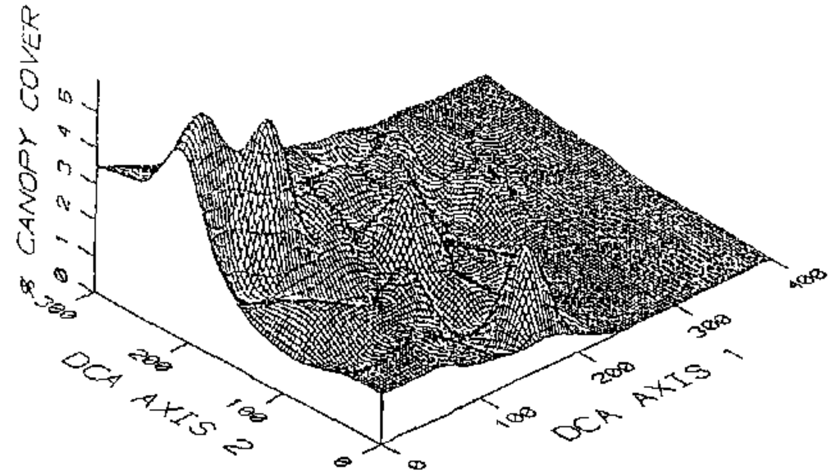
Rhus pentheri SIZE 3 (2-4m) % CANOPY COVER



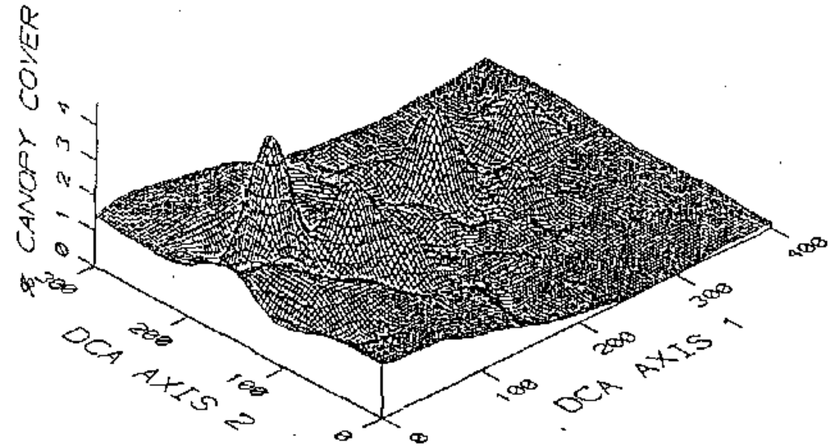
Rhus pentheri SIZE 4 (>4m) % CANOPY COVER

Figure 20.15 D). Canopy cover abundance levels of *Bercehmia zeyheri* spizes as 3D surfaces in spize based ordination space*

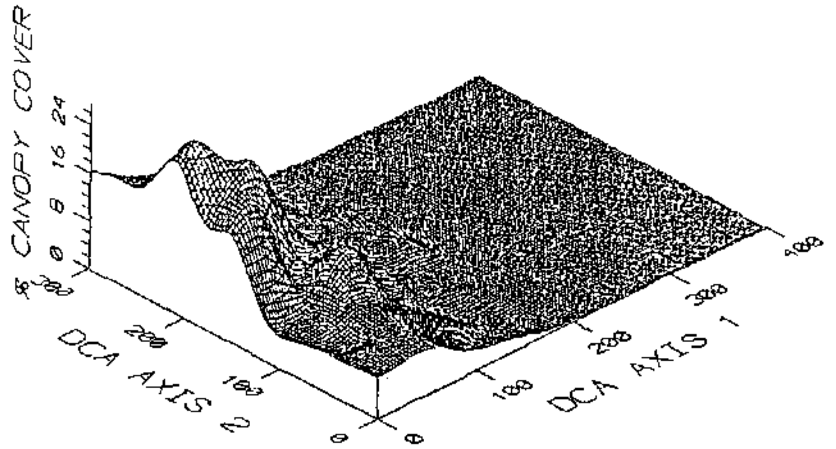
D



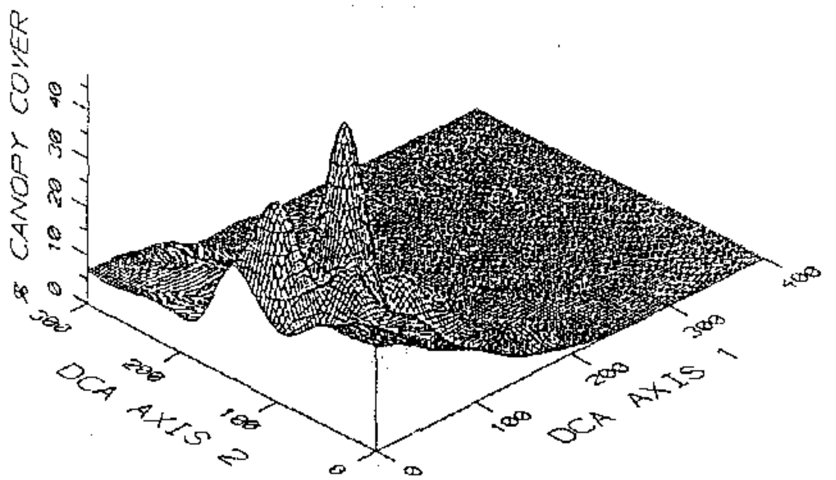
Berchemia zeyheri SIZE1 (<1m) % CANOPY COVER



Berchemia zeyheri SIZE2 (1-2m) % CANOPY COVER

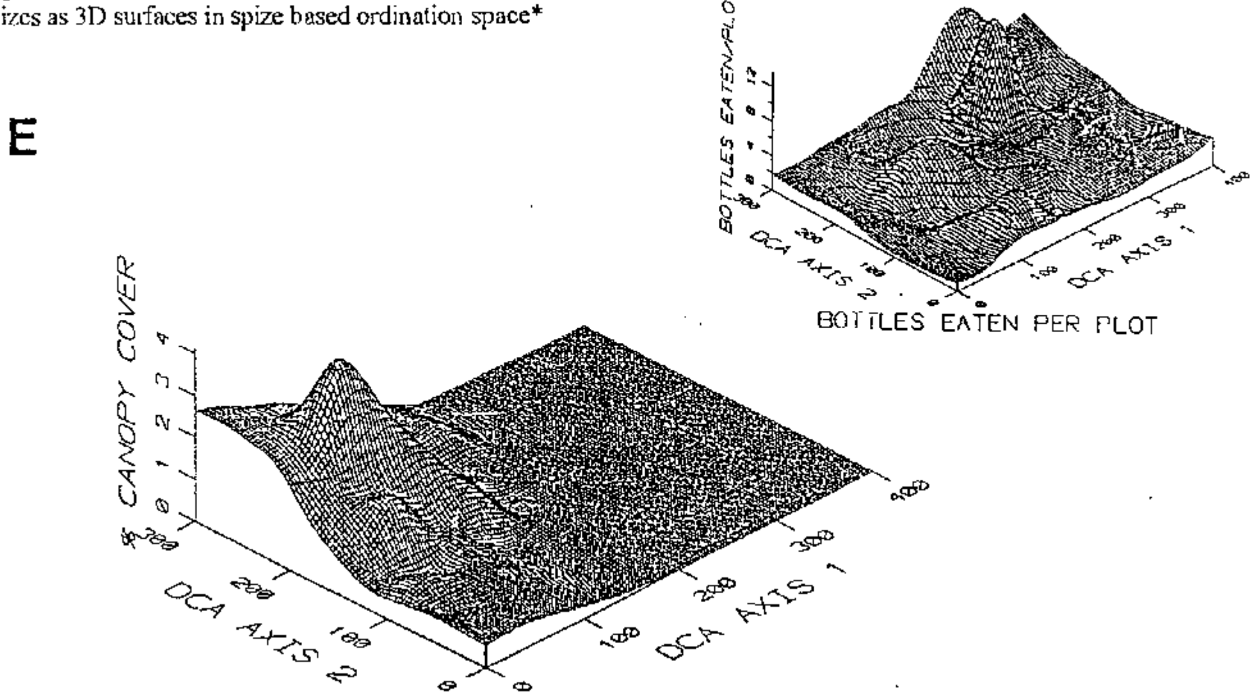


Berchemia zeyheri SIZE3 (2-4m) % CANOPY COVER

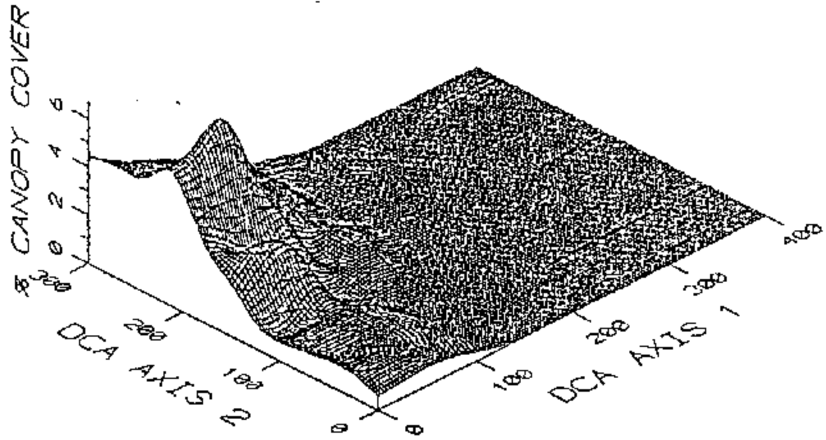


Berchemia zeyheri SIZE4 (>4m) % CANOPY COVER

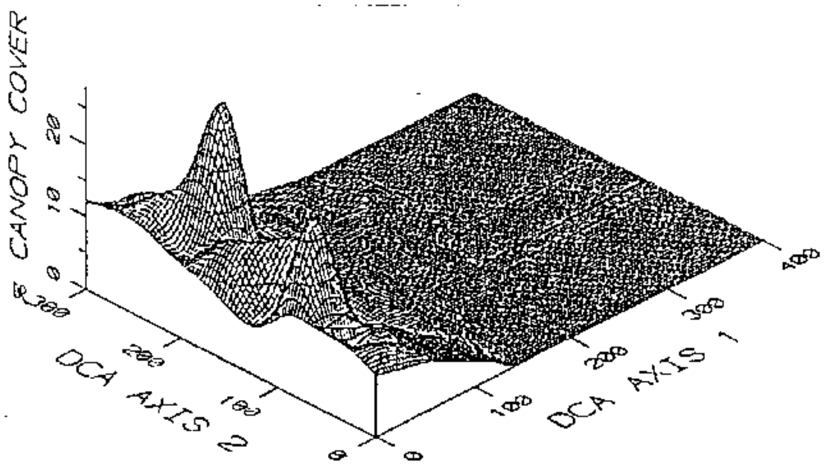
Figure 20.15. E). Canopy cover abundance levels of *Euclea divinorum* spizes as 3D surfaces in spize based ordination space*



Euclea divinorum SIZE 1 (<1m) % CANOPY COVER



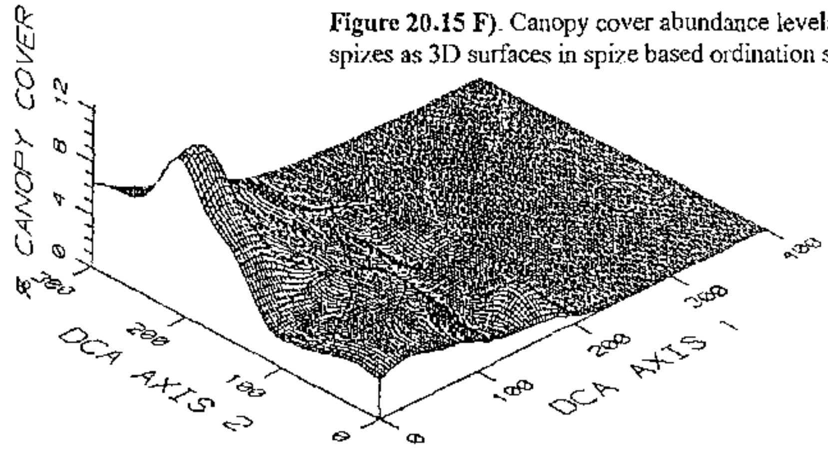
Euclea divinorum SIZE 2 (1-2m) % CANOPY COVER



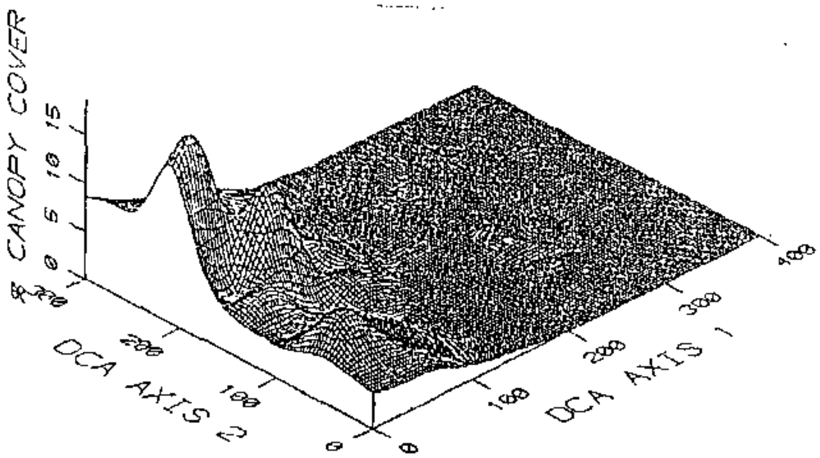
Euclea divinorum SIZE 3,4 (>2m) % CANOPY COVER

F

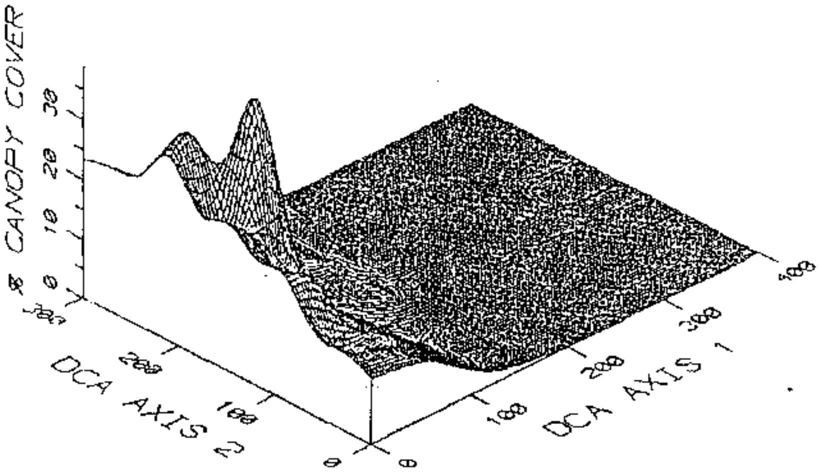
Figure 20.15 F). Canopy cover abundance levels of *Euclea racemosa* spizes as 3D surfaces in spize based ordination space*



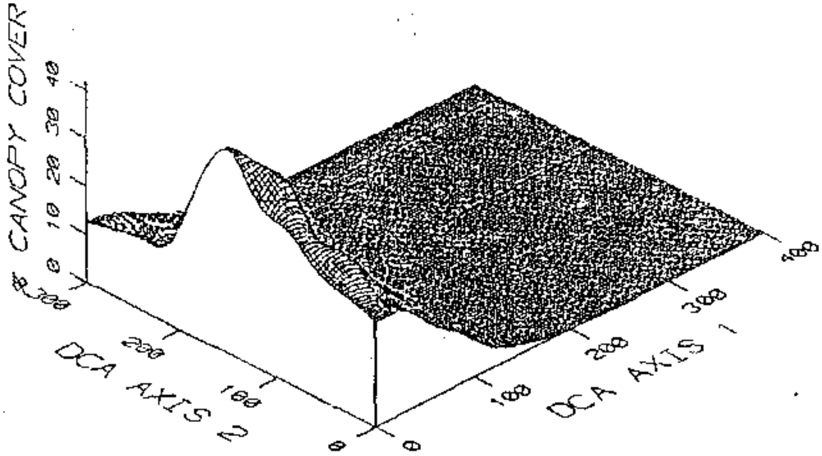
Euclea racemosa SIZE1 (<1m) % CANOPY COVER



Euclea racemosa SIZE2 (1-2m) % CANOPY COVER



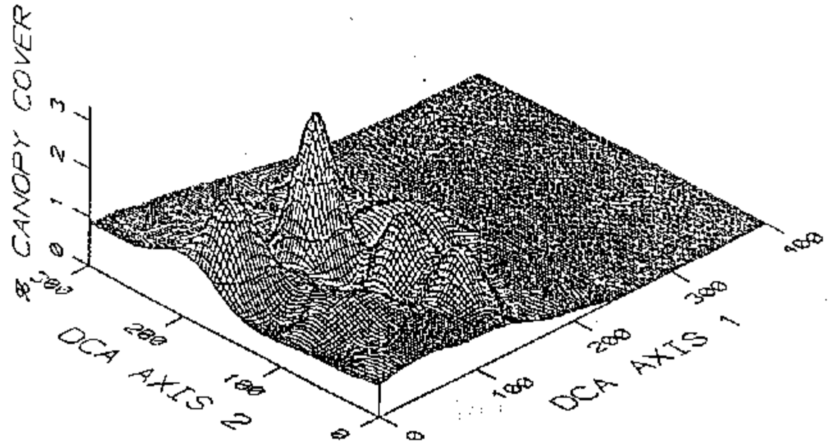
Euclea racemosa SIZE3 (2-4m) % CANOPY COVER



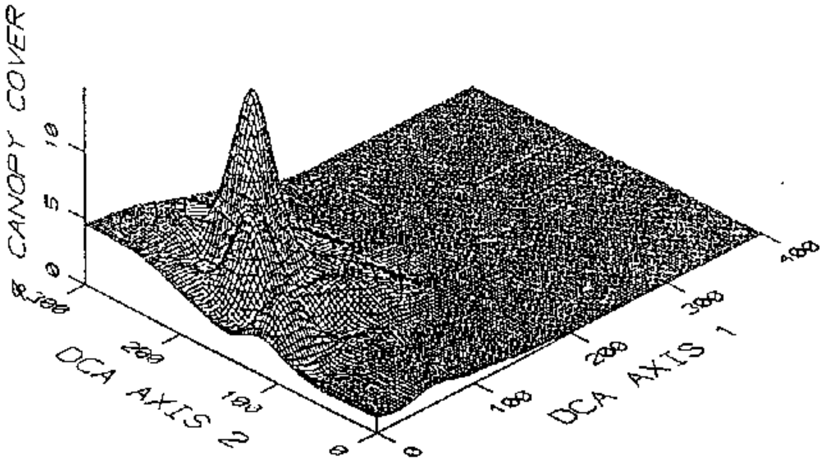
Euclea racemosa SIZE4 (>4) % CANOPY COVER

Figure 20.15. Canopy cover abundance levels of *Sideroxylon inerme* (**G**) and *Scutia myrtina* (**H**) spizes as 3D surfaces in spize based ordination space*

G

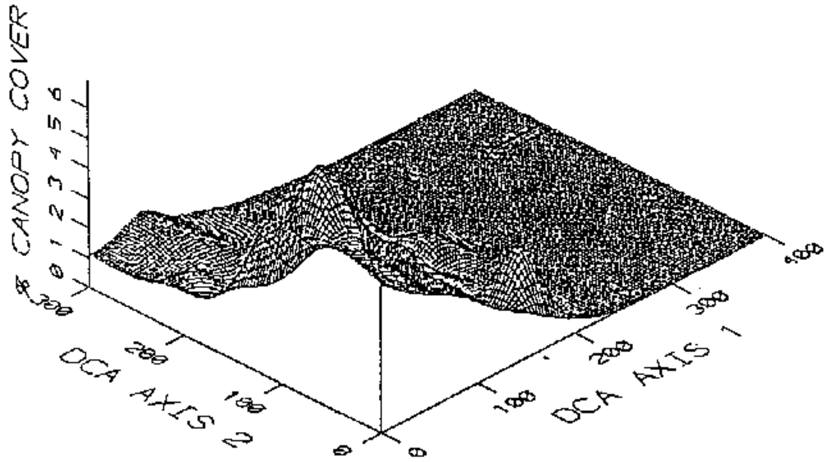


Sideroxylon inerme SIZE 1,2 (<2m) % CANOPY COVER

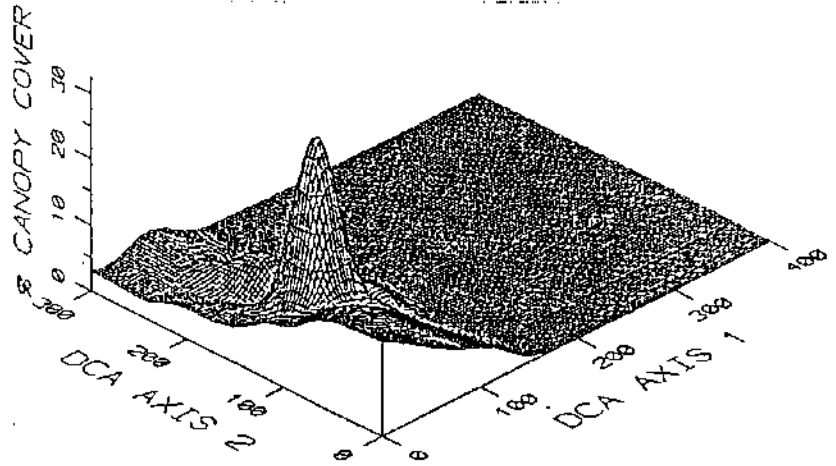


Sideroxylon inerme SIZE 3,4 (>2m) % CANOPY COVER

H

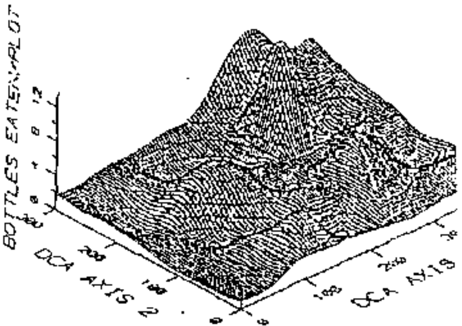


Scutia myrtina SIZE 1,2 (<2m) % CANOPY COVER



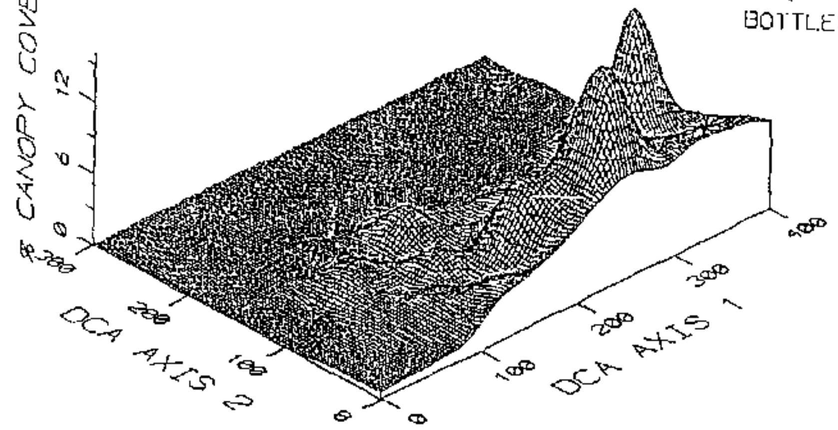
Scutia myrtina SIZE 3,4 (>2m) % CANOPY COVER

Figure 20.15. Canopy cover abundance levels of medium-intermediate 1-4m *Euclea crispa* (**I**); of intermediate-tall (>2m) *Acacia caffra* (**J**); and of *Vernonia subuligera* (**K**), as 3D surfaces in spize based ordination space*



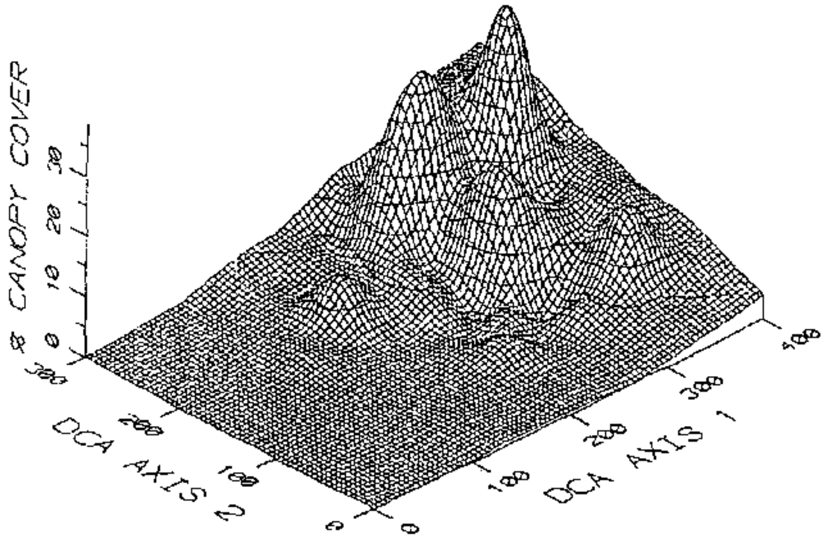
BOTTLES EATEN PER PLOT

I



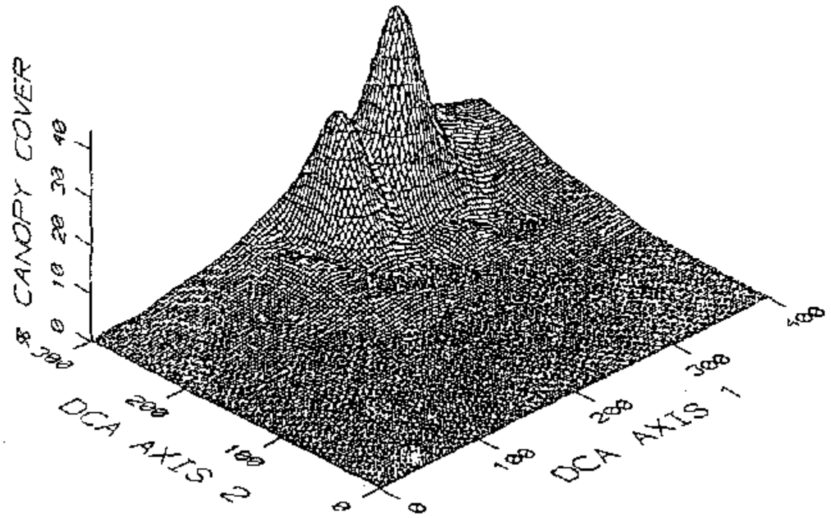
Euclea crispa SIZE 2,3 (1-4m) % CANOPY COVER

J



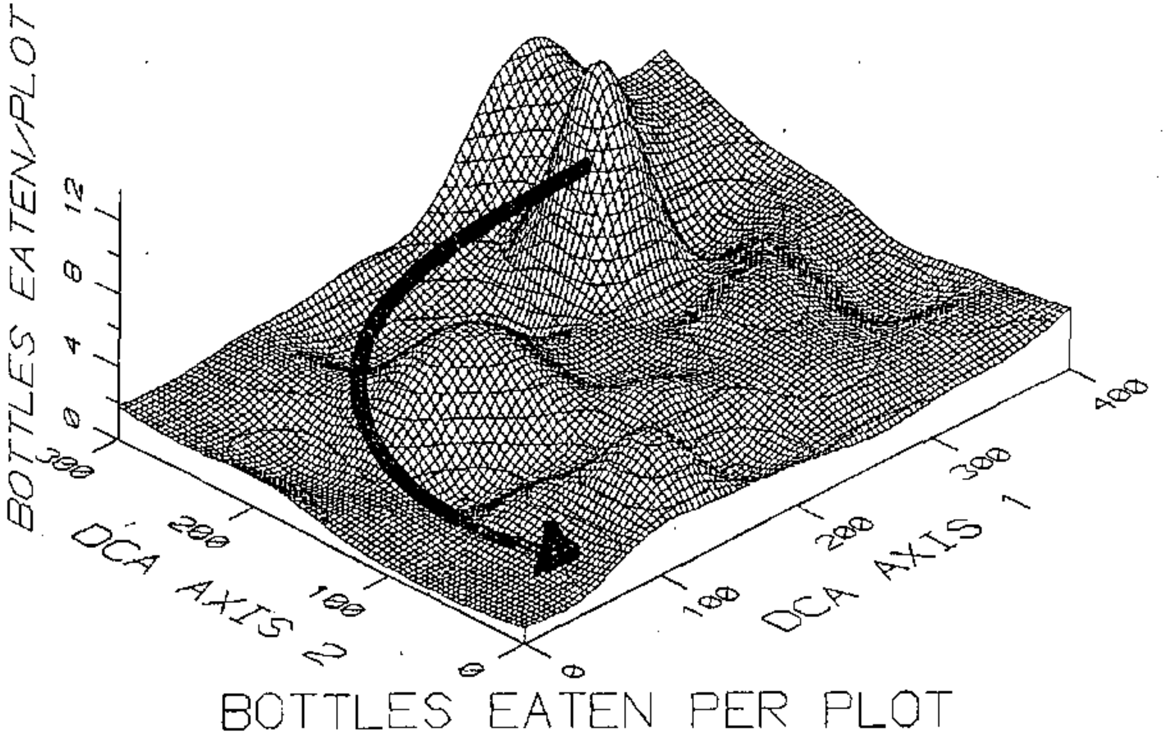
Acacia caffra SIZE 3,4 (>2m) % CANOPY COVER

K



Vernonia subuligera % CANOPY COVER

Figure 20.16. 3 D surface plot of the amount of black rhino feeding (browse bottles eaten per plot) in spize based ordination space.* The arrow shows the successional path from small *Acacia nilotica* through *Acacia nilotica* closed woodland through to a dry lowland forest dominated by *E.racemosa*, *B.zeyheri*, *R.pentheri*, *S.inerme*, *S.myrtina* with some mature *A.nilotica* and *D.cinerea*'s senescing. Note how feeding levels drop dramatically along this pathway ,especially at early stages of succession as *Acacia nilotica's* grow into taller, less preferred spizes.



reducing grass interference on small "*Acacias*". A photograph taken by Roelf Attwell in Hluhluwe in 1956 (Figure 20.8), and shows ideal black rhino habitat with many small *Acacias* visible.

INCREASE IN UNPALATABLE *Eucleas* IN OTHER AREAS

The increase of *E.divinorum* in other areas of Hluhluwe was also discussed by Macdonald (1981) who noted that the *E.divinorum* woodland community "*is spreading through the invasion by* E.divinorum *of senescing closed-canopy* Acacia *woodlands*", and speculated that even if *E.divinorum* was cleared in these areas it would probably return because of selective high browsing pressure. *E.divinorum* also appears to have increased both on eroded bottomland soils near the Hluhluwe river (eg at Sisuze), and in *A.nilotica* woodlands in the drier south of Hluhluwe. Increases in E.divinorum woodland also have reduced black rhino carrying capacity as this species is highly rejected.

Macdonald (1981) observed that the secondary invaders which followed the *Acacia* and *Dichrostachys* thorn scrub stage of encroachment tended to be broadleaved trees, and he listed *E.crispa*, *E.divinorum*, *E.racemosa* and *Maytenus senegalensis* as the main problem species in Hluhluwe. He argued that once *E.divinorum* thicket had formed in the lowlands of the Hluhluwe valley (possibly on areas transformed by Iron Age Man), this species' unpalatability would result in selective browsing pressure, preventing the regeneration of other species, and selectively maintaining *E.divinorum* as an almost monospecific tree community [#26].

PATCHES OF EVERGREEN FOREST PRESENT IN 1930s REMAIN

Bayer (1938) and Henkel (1936) noted that small patches of evergreen forest occurred in lower lying areas in Hluhluwe North[#27]. Small patches of evergreen forest still occur in this area today.

RIVERINE COMMUNITIES IN 1936 APPEARED SIMILAR TO TODAY WITH EXCEPTION OF INCREASE IN *C.odorata*

Bayer (1938) mentioned that *S.africana* formed dense stands along the river banks and was favoured by black rhino. In some localities he noted that these stands may extend 50-100m away from the river itself. He recorded the association of *R.pentheri, P.africanum* and *S.inerme* with this species. He also noted that *A.glabrata* also occurred nearer the river and was favoured by rhino. Based on this description, much of the riverine/alluvial /small drainage line communities appear to have changed little over the last fifty years with the notable exception of the dramatic increase of the alien *Chromolena ordorata* over the last twenty years (and especially since 1990) in these areas. Thus, the drainage line/ alluvial/ riverine areas in Hluhluwe appeared to provide key habitat for black rhino in the late 1930s (Bayer 1938) as in 1989 (Grid survey and Post burn surveys) although the recent increase in *C.odorata* is cause for concern[#2].

CHAPTER 20 NOTES

#1: Soil and physiographic characteristics have a major controlling influence on the spatial distribution of different vegetation communities through their influence on water and nutrient availability as well as microclimate. Smith & Huston (1989) sought to explain the spatial and temporal patterns of plant communities in terms of adaptations of individual species for the use of two resources - available light and water. They proposed that ***succession*** is essentially a ***temporal*** shift in species dominance, primarily in response to autogentic changes in light availability (Smith & Huston 1989), while ***zonation*** of plants is primarily a result of a ***spatial*** shift in species dominance in response to changes in water availability on the dynamics of competition for light. Austin & Smith (1989) and Smith and Huston (1989) further argue that these temporal and spatial patterns arise because of different physiological and morphological adaptations of the different species. The very adaptations that allow a plant to grow well under one set of conditions will prevent it from surviving under some other conditions with the result that different species will hold the competitive advantage in different parts of the water:light resource space. The differential tolerance of different species to disturbance regimes such as fire and browsing also is likely to affect succession in an area. Competition may result in many species having their ecological optimum closer to their physiological limit rather than to the optimum. Different combinations of life history characteristics enable different plant species to succeed under different conditions as there is no such thing as absolute competitive ability, nor any measure (eg growth rate, shade tolerance, seed output or maximum size) that confers competitive ability under all conditions. Early successional species tend to have high seed output and dispersability, greater tolerance to certain stresses (eg grass competition, browsing and or fire), have rapid growth rates as a result of high photosynthetic and respiration rates, but have less efficient photosynthesis at low light; while later successional species tend to be longer-lived, are shade tolerant, have lower transpiration and respiration rates but are more efficient photosynthesisers at low light levels, and tend to grow taller and have more structural strength (Huston & Smith 1987).

As early as the 1930s, Bayer (1938) and Henkel (1937) noted that there appeared to be a spatial zonation of vegetation communities in Hluhluwe reflecting catenal and soil differences. They also noted that a catenal sequence occurred throughout "short *Acacia* veld" of Natal and Zululand; with *A.caffra* and *A.karroo* being associated with upper areas of the catena and moister lower areas; with *A.nilotica* occurring in the intermediate drier parts of valleys (Bayer 1938). These authors also noted that *A.karroo* thicket and woodland was particularly associated with moister clay areas with taller grass. Bayer (1938) however cautioned that this catenal zonation was not always easy to see on steep slopes, and because communities were also influenced by differences in soil conditions.

These observations were corroborated by the environmentally constrained ordination of the Grid survey data (chapter 14) which confirmed the significant influence of soil, altitude and aspect on the zonation of vegetation as hypothesised by Bayer (1938) and Henkel (1937).

Whateley and Hitchins's vegetation maps (see Appendix 20.1) and the 1989 Grid survey also confirmed the spatial zonation of vegetation in northern Hluhluwe.

#2: Since the 1989 Grid survey *C.odarata* appears to have increased markedly in northern Hluhluwe. This observation has also been made the Parks' current Regional Ecologist Mr Dave Balfour (pers.comm) who mentioned this species had increased substantially in many *Acalypha glabrata* areas. Given that *A.glabrata* is an important and favoured black rhino food, and that *C.odorata* may also have smothered other palatable species such as *M.nemorosa*, the increase in *C.odorata* in the 1990s is likely to have negatively affected the carrying capacity for black rhino in these habitats.

#3: While clear spatial zonation of vegetation occurs in response to environmental factors such as soil type, slope, altitude and aspect within a similar landscape unit, many authorities believe that it is more appropriate to examine vegetation in terms of continua or gradients in species and spize composition as opposed to somewhat arbitrary definitions of discrete "communities" (Gaugh 1982). However, on heuristic grounds, it is often useful to examine differences between so-called "communities", even though in practice it may be more appropriate in savanna's to view vegetation in terms of continua in spize composition. "Communities" are discussed in this chapter with a view to contrasting differences between different parts (or seral stages) of a vegetation continuum.

#4: In a discussion on "*deciduous short tree savanna*" Bayer (1938) noted that *"as long as the usual annual grass fires are allowed to pass through, the thorn veld remains open. The effect of fires is to retard succession and to prevent the development of thickets. There is no doubt that in the absence of fire, thornveld would close up to form a closed woodland. It would seem that typical open thornveld does not represent a climatic climax type of vegetation; but is virtually a fire sub-climax. Exactly what the composition of a true climatic climax would be cannot be determined, since no thorn veld vegetation which is immune from fire exists in Zululand,, and it seems quite impossible to provide permanent protection from fire for any portion of this vegetation"*.

By way of contrast to the 1950s and early 1960s, aerial photographs showed that during 1937 at least 34 fires had occurred either partly or totally within the original boundaries of Hluhluwe Game Reserve (Berry & Macdonald 1979). From 1930 onwards the burning policy for Hluhluwe Game Reserve was to instruct game guards to burn any areas that appeared to be rank and to burn along tourist roads to attract game to the roads (Vincent 1979). Funds at the time precluded the burning of firebreaks, so that uncontrolled fires were frequent (H.B. Potter pers.comm. to J.Vincent). The game conservator's report for 1936 reads *"several patches of old dry grass, chiefly on the hills, have been burnt"*. Henkel (1937) also noted that fire was frequent in all but the lowveld areas where the grass cover was too sparse to burn, and he reported that the annual or periodic fires ignited by man *"swept through the reserve"* maintaining *"an equilibrium"*.

The importance of man in setting fires was revealed by Berry & Macdonald's analysis (1979) which indicated that only 9 of 772 fires recorded for Hluhluwe-Umfolozi Park over the period 1955-78 were started by lightening. The authors concluded that given the Park's climatic conditions, the initiation of fire by lightening would not have occurred frequently enough to have maintained open savanna in areas of unimpeded drainage.

#5: While wildebeest were numerous over fifty years ago, it was uncommon to see them in North Hluhluwe in the late 1980s. It is only following the reintroduction of more wildebeest into Hluhluwe North following bush clearing, the reintroduction of elephant, a change to more frequent burning, and ongoing bush clearing in the area, that small herds of wildebeest were more commonly being seen in northern Hluhluwe in the later 1990s. To have so many wildebeest in the reserve in the mid 1930s, Hluhluwe must have been relatively open country at that time. An old South African Railways Post Card from the 1930s shows a herd of wildebeest grazing on an open grassy hillslope.

The high warthog and wildebeest numbers mentioned by Bayer is consistent with the extensive areas of open grassland described by Henkel (1937).

By way of contrast, nyala (which appear to favour intermediate and later stages of succession in closed *A. nilotica* woodlands), have gone from being rare to become the commonest antelope in Hluhluwe (although this has coincided with a dramatic decline in numbers of bushbuck in the reserve).

The decline in numbers of common reedbuck in Hluhluwe (Deane 1966) has also been striking, and is another indicator of the decline of tall open grassland in the reserve over time.

Thus the dramatic changes in numbers of reedbuck, wildebeest and nyala provides additional corroborative evidence that there has been a change from open grassland and open woodland to more closed woodland and forest.

#6 As early as the 1930s Bayer (1933, 1938) identified *A.nilotica, D.cinerea, A.karroo, A.robusta, A.gerrordii, A.caffra, A.tortilis, Phoenix reclinata, M.heterophylla* and *Euclea* species as chief pioneers in the invasion of grassland by trees in Zululand.

Recent work by Prof. William Bond (pers comm) of the University of Cape Town and co-workers also indicates that *A.nilotica* establishment seems to predominantly occur in heavily grazed areas corroborating Bayer's observations.

Bayer (1933) also noted that in Zululand, closed bush (rather than clumped vegetation) was most marked along water courses or around water seepage areas; and that in areas away from drainage lines there was a tendency for the occurrence of thickets of pioneer trees, and especially of *A.nilotica*.

#7: Henkel's *A.nilotica* and *A.karroo* parkland was described as occurring in a limited area of the reserve, although he mentioned it was typical of much parkland throughout Zululand and Natal. The photo of this community in Henkel (1937), and the name parkland, suggests this association was fairly open with a few scattered mature *Acacia* trees. Henkel (1937) also remarked that patches of this association or single trees were found scattered through the scrub association of the lowlands. Henkel (1937) also listed *A.nilotica* and *A.karroo* as occurring in *A.caffra* parkland.

#8: Bayer (1938) also noted that in the 1930s black rhino in Hluhluwe preferentially fed on *S.africana*. He noted that pruning of this species kept it with a stem height of 1.25 - 1.5m tall with much coppice growth which was later browsed. He noted that occasionally the stands of stunted *S.africana* trees may be as much as 0.4 Ha in extent. He noted that along the Hluhluwe river *S.africana* frequently forms closed stands, (and still does - eg south of the Hluhluwe river at Nomagetje), the trees being only 1.25 - 1.85m apart with straight boles. He also recorded that rhinos pushed over individuals of this species. Other food species he noted included *A.glabrata.*.

Attwell (1948) made similar observations to Bayer (1938) about black rhino feeding in Hluhluwe noting that the black rhino "copes with the thorny dwarf form of *A.karroa*, and also numbers the Tambothi tree (*S.africana*) among its favoured food". He also noted that small trees were pushed over and browsed on by black rhino in a number of areas of Hluhluwe.

#9: Although there is no hard evidence, it has been speculated that the aerial spraying of DDT (from 1947-1952) to control tsetse fly might have contributed to increased *Acacia* seed viability (and higher germination rates) by reducing bruccid beetle damage of *Acacia* seeds (Bourquin & Hitchins 1979, Macdonald 1979, A.J. Wills pers.comm.).

However, argument against DDT being a major factor comes from T.M.Smith and S.E.Taylor (unpublished quoted in Smith & Goodman 1986) who concluded that neither seed predation in under canopy environments, or lack of germination appeared to be a factor limiting *Acacia* establishment under canopies. Rather it was the high seedling mortality of "*Acacia*'s" under canopies that was responsible for the *Acacia*'s establishing in open areas. Anderson (1989) has also argued that seed predation is not that important to recruitment of long-lived perennials. Even when insect seed predators destroyed 95% of seeds, Anderson (1989) concluded that these losses did not necessarily have an important impact on population recruitment, because in most years, recruitment appeared to be more limited by a rarity of safe sites and not seed supply. Ernst et al. (1990) also indicated that seed predation by brucchid beetle on *A.nilotica* seed was variable from year to year depending on the quantity of seed produced. In years of good seed production seed survival was higher. (See chapter 22)

#10: Based on photographic evidence and personal communications between them and the late Norman Deane (see also Figure 20. 9a), Bourquin and Hitchins (1979), believed that rapid development of encroachment started in Hluhluwe after 1949, and that the main increase in woody plant densities in grassland took place over a short below-average rainfall period (1950-1958).

#11: Deane (1966) stated that by 1954, "*as a result of overpopulation; grazing conditions had deteriorated throughout the reserve* (Hluhluwe)" and that "*Acacia and other undesirable scrub had invaded at an alarming rate and conditions were rapidly becoming unfavourable for the grazing members of the community.*"

#12: Vincent (1979) also indicated that the major bush encroachment occurred in the 1950s when he postulated that "*the introduction of measures to protect the reserve from frequent fire might be the cause af much of the scrub encraachment which has prevailed since 1950.*"

#13: In reviewing evidence for past vegetation changes in northern Hluhluwe from 1937-1957, the park's first resident ecologist, C.R. (Roddy) Ward (Quoted in the minutes of August 1979 Vegetation Dynamics Workshop Working Group 2 : Past Vegetation Changes - 1937-

1957) also noted there had been a marked increase in *Acacia* scrub and other woody plant species.

The 1979 vegetation dynamics workshop speculatively concluded that the combination of increased grazing pressure, with a series of dry years led to the reduction of grass cover and hence reduced grass: tree competition reducing the impact of fire on woody plants and that this was a major cause of the bush encroachment between 1949 and 1955 (Hitchins & Bourquin 1979, J.Anderson & J.Forest in notes of workshop).

#14: King (1987) indicated that much of what was classified as "scrub" in the Hluhluwe basin (southern-central Hluhluwe to south of Grid study area) was dominated by evergreen species such as *E.divinorum* and was probably closer to forest and scrub. King noted that "scrub" expansion was greatest at low altitudes whereas forest expansion was greatest at higher altitudes (above 300m).

#15 Around the time of major bush encroachment in Hluhluwe, attempts were being made to limit fires. The reserve's first ecologist, C.R. (Roddy) Ward (1957, 1961, pers.comm.) indicated that the policy of indiscriminate "random deliberate" burning in Hluhluwe was halted in 1950. He also noted that for a few years after this, fires were restricted to accidental fires and the influx of fires from the "native reserve" outside Hluhluwe (Ward 1957). Furthermore in 1955, a directive was also issued by Natal Parks Board's head office controlling all burning within the reserve other than the burning of firebreaks. The fire maps at Hluhluwe (see chapter 15) confirm the low incidence and extent of fire during the period of rapid encroachment.

#16: Over such a short period (two years) the effect of estimate inaccuracy will be magnified, while over a longer period this becomes less of a problem.

#17: Data used to estimate population growth rates were taken from Table 1.1 Earlier population estimates (1933, 1937, 1948, 1950) referred to the original boundary of Hluhluwe Game Reserve (160.79 km^2), while the 1961 estimate was for the revised larger Hluhluwe reserve (230.67 km^2). To enable comparison with previous estimates the 46 black rhino from southern Hluhluwe (60.68 km^2) were dropped from the estimate giving a remaining area very similar to the original reserve size. The revised estimate of 233 (279-46) reduces to 220 if scaled on a pro-rata basis to the original reserve size. This translates to an overall increase in numbers of only 30 animals over an 11 year period (reflected in the small increase in densities between 1950 and 1961 in Table 1.1 - 1.182 vs 1.210 black rhino / km^2). Even if one were to take the Hluhluwe population in 1961 as 230 the estimated annual rate of increase from 1950-61 is only 1.8%.

Even if one were to assume that the 1950 figure of 190 was an overestimate, the estimated annual increase from 1948-1961 is 2.5% (2.8% if 1961 estimate = 230). These levels of increase still fall below the estimated average increase of 4.3% from 1933-48.

The earliest estimates in the 1930s are likely to be approximate guesstimates and the apparent greater rate of increase from 1933-37 (7.8% per annum) compared to 1937-48 (3.0% per annum) may be more apparent than real.

#18: According to data presented in Watson and Macdonald (1983) blocks 3, 6 and 8 had average fire return periods over the period 1937-75 of 6.0 years, 6.9 years and 10.2 years respectively; while the results of their study suggested that in order to maintain woody cover at existing levels requires a burning frequency of approximately once every three years. Of the three blocks (3, 6 and 8), the block with the lowest fire frequency (8) had the greatest relative increase in woody plant cover by 1975.

Watson & Macdonald's (1983) analysis indicated that from 1937 to 1960 and from 1960-75 fire frequencies were low to very low in blocks 3,6 and 8 with an average of only 3% (block 6) to 12% (block 8)/ game control block burnt per annum from 1937-1975 and from 12% (block 8) to 24% (block 3) per annum from 1960-1975.

Interestingly, Watson & Macdonald (1983) did not record any decrease in tree of scrub cover despite woody plant removal operations which covered an estimated 17% and 30% of the area during the periods 1957-60 and 1960-69. These apparently conflicting conclusions can be explained, if over the game control block as a whole, increases in scrub and tree canopy cover in uncleared areas cancelled out any temporary declines in scrub density on bush cleared sites. For this reason it was unfortunate that Watson & Macdonald (1983) did not analyse the bush cleared areas separately from uncleared areas. Never the less, despite significant, and in some cases repeated clearing in this block, woody canopy cover still increased by a third between 1937-1975.

#19: While some photographs were very useful, the vast majority of photographs examined were unusable as they tended to depict people and animals rather than the vegetation. In addition the locations of many were unknown or the photographs were undated.

More recently Ian Macdonald had the foresight to start taking fixed point photographs in the early 1980s. Whilst difficult to quantify, these photographs at least provide a record of past vegetation conditions. Unfortunately these photographs were not repeated in the late 1980s early 1990s.

#20: Tony Whateley who took the last photo has emigrated from S.Africa, and all one had to go on was a quarter grid square reference. It may have been that the site was cleared in recent bush clearing operations. However, in future, it is probably worth trying to re-find the site. The grid reference marked on the 1974 photograph was 0282 a/a.

#21:. An annotated map by Dr Orty Bourquin around 1970 indicated that much of the areas cleared around 1960 were either still grassland or were parkland with scattered *Scleocarya birrea* (including most of the bottomlands parallel to main Memorial Gate entrance road - see Figure 20.4). Hitchins' 1960 and 1970 maps (Table 20.2, Appendix 20.1) also show the marked opening up of the vegetation in the area from 1960 to 1970. Hitchins 1970 map (Table 20.2) and measurement of Hitchins' plots confirmed the open nature of the habitat around 1970.

Bourquin (pers.comm.) noted that the opening up of the north-eastern Hluhluwe *A.karroo* areas in the early 1970s was striking and he ascribed the thinning out of the ticket during the 1960s and early 1970s to the more frequent fires at the time (see chapter 16). Although a below average rainfall period, fires were frequent from 1965-71(chapter 16, Figures 16.2 and 16.3). Interestingly, the period 1965-71 was one of only two periods since the 1961 die-off when the underlying trend in black rhino numbers did not decline (chapter 16).

#22: Workshop session 1 Group 3 members Peter Hitchins, John Forrest, Keith Meiklejohn and Jeremy Anderson came to a general agreement after discussing Past Vegetation Changes 1958-1979 that "*Hluhluwe, in particular, the North, had undergone a cycle of this period from scrub invaded grasslands which had opened up and had then reverted to almost their former state*" (Macdonald *et al* 1979). Many of these *A.karroo* dominated areas in N.E. Hluhluwe have been subsequently recleared in the 1980s and 1990s .

#23: Note the abrupt boundary on Figure 20.4 between the cleared lowlands at the foot of the slopes to Magwanxa (where no uncleared controls have been left) and the lack of clearing upslope (except at the Makokhoba slope at the very far left of the picture near Memorial gate) which confounds landscape unit and bush clearing treatments. This significantly reduced the ability of managers to learn from adaptive management (Chapter 18). A.J.Wills (pers.comm.) reports that C.R.Ward left one control plot in this area, but that this plot along with another control he left were unfortunately bush-cleared later by a manager unaware of their existence. This is just one of many instances where experimental plots, marked transects, or exclosures have been accidentally burnt, bush-cleared or "tidied-up" by managers[#43]. This together with a lack of adaptive management (eg failures to leave controls in some bush clearing treatments) has effectively precluded the use of the limited number of long term experimental treatments to study the effects of bush clearing in Hluhluwe.

#24 Whateley and Wills' work in Hluhluwe (Appendix 20.8) built upon the earlier observations in nearby Mkuzi Game Reserve (Smith & Walker 1983; Smith & Goodman 1986, 1987), that sun-loving "*Acacia's*" (*A.nilotica, A.tortilis and D.cinerea*) did not readily establish under their own canopies; whereas deciduous broadleaved or evergreen seedlings were "canopy tolerants" concentrated beneath canopies or independent of established *Acacia's*. These authors hypothesised that these "canopy tolerants" then grow to maturity under the "*Acacia*" canopies, and when the established trees senesce, there is a transition from the microphyllus *Acacia* species to a stand dominated by evergreen and deciduous broadleaf trees (Smith & Walker 1983; Smith & Goodman 1986, 1987; Whateley & Wills 1996). In essence, Bews (1917) and Bayer (1933) postulated this model of succession for moister areas away from drainage lines in Hluhluwe sixty years ago. Whateley and Wills (1996) also hypothesised that as succession proceeded fires were reduced or restricted to open areas between tree canopies favouring the development of later successional species which are more fire sensitive (chapter 16).

The findings of Smith & Goodman (1986, 1987) in nearby drier Mkuzi game reserve were corroborated by the patterns found in Hluhluwe by Whateley & Wills (1996). Smith & Goodman (1986) examined the distribution of species in relation to canopies of *A.nilotica* and *A.tortilis* and found there were two types of species:

- Species whose seedling establishment was associated with under canopy environments.

- Species whose seedling establishment was restricted to open or between canopy environments.

Only two species were studied in the *A.nilotica* community. *A.nilotica* seedlings were almost exclusively found between the canopies but a few individuals occurred at the outer edge of canopies. In contrast *E.divinorum* was found only beneath canopies (Smith & Goodman 1986).

Of the eight species in the *A.tortilis* community, *E.rigida, E.divinorum, Grewia monticola, M.heterophylla* and *Z.mucronata* were associated with under canopy environments; while *A.tortilis, D.cinerea* and *M.senegalensis* were associated with open environments (Smith & Goodman 1986).

Smith and Goodman (1987) and Smith & Walker (1983) proposed a similar model to that of Whateley & Wills (1996) where canopy tolerant species grow to maturity under *Acacia* canopies, and when the established trees senesce, there is a transition of the community from microphyllous *Acacia* species to a stand dominated by evergreen and deciduous broadleaf species. The one exception to this rule appeared to be *M.senegalensis* which Whateley & Wills (1996) classed as a transitional species, but Smith and Goodman (1987) found was associated with more open environments rather than under canopies.

Bayer (1933) postulated that the effect of these pioneers was to *"shade the soil, decrease evaporation rate, and generally to create conditions which favour the development of more hygrophilous types"*. He noted that this change was often accompanied by a change in grass species composition. As a rule he postulated that pioneer woody species were sun-lovers, and as a rule not tall, whereas the taller species which developed under the pioneers eventually overtopped them. He noted that *"the pioneers are not able to endure the shade of these trees and are eventually killed out"* (Bayer 1933, 1938). Bayer (1938) acknowledged that his thorn-veld successional model was the same as that proposed by Bews (1917) for Natal.

Based on an analysis of tree densities between neighbouring *A.nilotica* trees, Whateley and Wills (1996) found that the two species, *D.cinerea* and *A.karroo*, had significantly higher densities in open areas outside *A.nilotica* canopies corroborating Smith & Goodman's (1986) similar finding in nearby Mkuzi Game Reserve (that *Acacia*'s" are sun-loving and do not readily establish under their own canopies); while the *forest* species *C.africana, B.zeyheri, E.racemosa;* and the *transitional R.pentheri* occurred at significantly higher densities under trees in *intermediate A.nilotica* woodland. They also suggested that sites under canopies were better protected from fire and so better establishment sites for more fire sensitive later successional species such as *E.racemosa.*

#25: The exploratory median method clustering (non-standardised Euclidean distance) of a subset of the Hluhluwe Grid plots (after dropping riverine and true Celtis/Harpephyllum evergreen forest plots) provided further confirmatory evidence for the Whateley-Wills (1996) successional model but as these results did not add any further new insight into the vegetation patterns not already revealed by the ordination and TWINSPAN analyses and are therefore not discussed further.

#26 : Macdonald (1981) noted that "under the browsing pressure throughout the *E.divinorum* woodlands in the reserve in the mid 1970s, there was virtually no regeneration of any palatable woody species in this habitat". He speculated that other more palatable woody species would possibly only regenerate on these areas following a considerable reduction of browser numbers.

In a recent visit to Hluhluwe it was noticeable that *E.divinorum* was the dominant species growing up on E.divinorum areas that had been bush cleared in southern Hluhluwe around the Maquanda turn-off lending support to Macdonald's hypothesis.. Numbers of mixed feeders in the area have also increased noticeably over the last 10 years.

27: Bayer (1938) also hypothesised that evergreen sub-tropical forest margin communities were dominated by pioneer species which provided the shade for taller growing later successional species leading to a gradual expansion outwards of forest patches producing a clump type of vegetation described by Bews (1917). Bayer (1938) attributed the more luxuriant vegetation in the lowest parts of the reserve to the regular occurrence of early morning mists.

CHAPTER 21

THE USE OF VORTEX PVA MODELLING TO EXAMINE SOME OTHER POSSIBLE CAUSES OF THE HLUHLUWE DECLINE

CHAPTER SUMMARY

o Previous chapters have examined the possible role of habitat changes (especially those related to fire, bush clearing, culling of grazers and lack of elephant) in the decline of black rhino numbers in Hluhluwe. This chapter is the first of two which investigates other potential causes of the Hluhluwe black rhino population decline.

o The chapter briefly reviews the results of previous Population Viability Analyses (PVA) of black rhino in Kenya (Foose *et al* 1993) and in Hluhluwe-Umfolozi Park (Swart 1994), and then presents the results of heuristic VORTEX PVA modelling (Lacy & Kreeger 1992) of a simulated "Hluhluwe" type population, to investigate the relative importance of possible demographic and other factors in the Hluhluwe decline.

o With the benefit of hindsight, and in the light of growing empirical data on performance and mortality rates of many populations in southern Africa, the conclusions from the Kenyan black rhinoceros PVA workshop (Foose *et al.* 1993) were overly conservative due firstly to the use of a long inter-calving interval of around four years (0.24 births/adult female/year averaged across populations performing well and very poorly); secondly, due to the modelling of very severe catastrophes; and thirdly, because the resultant maximum potential growth rate of modelled Kenyan populations (4.7%) fell well below levels routinely attained in many expanding southern African populations (7%+). Despite this, the results of the Kenyan PVA (Foose *et al* 1993) clearly indicated that demographic stochasticity and inbreeding depression were not likely to be potential causes of the Hluhluwe decline.

o Following Population Persistence Analysis (PPA) PVA modelling of the Hluhluwe-Umfolozi black rhino population, Swart (1996) concluded that although the Hluhluwe-Umfolozi population was large, it remained vulnerable due to demographic fluctuations rather than poaching. Her prediction that the population would become extinct in only 159 years (Swart 1996, Swart & Ferguson 1993) was totally at odds with the results of the Kenyan PVA (Foose *et al* 1993) which indicated that demographic stochasticity could not have caused a decline of the magnitude observed in a Hluhluwe sized population.

On closer examination Swart's conclusion can be discounted, as her PPA modelling of Hluhluwe-Umfolozi park was fatally flawed. Swart preferred to use PPA over other PVA extinction models because only population estimates were needed to estimate a population's persistence time. However, any model is only as good as its input data, and Swart's conclusions were based on the uncritical use of and implicit assumption of the accuracy of dubious rounded population estimates she had obtained for the Park. In particular Swart (1994) unquestioningly interpreted an apparent decline of a hundred animals in just one year from 1985 and 1986 (300-200) as indicating high levels of demographic instability. The rounding off of the 1985 and 1986 estimates she had been given to the nearest hundred did not even rouse suspicion! If she had investigated further, she would found that neither park mortality records nor the intensive black rhino monitoring survey work undertaken by Hitchins in 1985 and 1986 (Hitchins & Brooks 1986, Hitchins 1988) indicated that any major population crash took place in that year, and that my Zucchini-Channing Bayesian Mark Recapture Analysis of Peter Hitchins's 1985 survey data produced a best estimate for 1985 of 241 (and not 300). In focussing solely on population size, Swart's PPA analysis also effectively ignored the key role ecological factors, and in particular habitat changes, can play in influencing black rhino population dynamics.

o In response to the marked decline in carrying capacity in Hluhluwe (Chapter 20) black rhino cows were observed to exhibit both longer inter-calving intervals of 5.25 years and older average age at first calving of 12 years (Hitchins & Anderson 1983). In addition to the poor reproduction, adult mortality levels also increased (♀ 3.5% ♂ 7.3% per annum), with high numbers of adult males being killed fighting (Hitchins & Anderson 1983). All these changes are consistent with a black rhino population under nutritional stress (Bothma 1988).

The question of interest is whether the observed increase in adult mortality, age at first calving and inter-calving interval plus the translocations and other known losses (to poaching, lions and being burnt to death in veld fires) are enough to explain the magnitude of the Hluhluwe decline. If they are, then one can dismiss calf predation as having been a major factor. However, if they are not sufficient to fully explain the decline, then perhaps predation of young calves by spotted hyena may have contributed to the decline. To investigate this question further it was decided to undertake heuristic PVA simulations of a Hluhluwe sized population.

○ Despite identifying a few limitations with its underlying model, it was decided that VORTEX (Lacy *et al* 1995) was still an appropriate tool to undertake heuristic sensitivity analyses to indicate the relative importance of a number of demographic and genetic factors on the population performance of a single Hluhluwe-Umfolozi sized black rhino population. The rest of the chapter presents the results of VORTEX PVA modelling (Lacy *et al* 1995) of a Hluhluwe type population over a 25 year post 1961 die-off period.

○ Parameter values used in the Kenyan PVA were taken as a starting point, and modified on the basis of the most up to date empirical data available. Considerable empirical data was available to guide model parameter setting, with Rhino Management Group of Southern Africa (RMG) annual status reports and syntheses since 1990 being especially useful (Adcock 1995, 1996, 1998). Hitchins (1963), Hitchins and Anderson (1983) and Hitchins and Brooks (1986) also provided much valuable demographic information on the Hluhluwe decline, including observed mortalities in the population. Kenyan PVA parameter values that were modified included age and sex specific mortality rates, inter-calving intervals, sex ratio at birth, and catastrophes.

○ Preliminary VORTEX runs simulated a healthy breeding population, and produced growth rates and sex and final age distributions similar to those observed in rapidly expanding wild populations, giving some confidence in the parameter values used. Modelling confirmed that unless adult mortality was very low (♀ <1% ♂ <1.5% per annum), then long term growth rates of 5.2%-9.4% per annum were possible given inter-calving intervals of 2 - 3.33 yrs and neo-natal mortality rates of 5 - 20%. This concurs with observed growth rates in many increasing populations in southern Africa (Adcock 1988, du Toit 1995), and Owen-Smith's (1988a) conclusion that the maximum sustained rate of population growth for rhinoceroses with a stable age structure is about 9% per annum. Further modelling indicated that simulating the starting sex/age distribution of a Hluhluwe population (based on data in Hitchins 1963) had little effect on the results compared to using a stable starting age structure, and so the latter was used in all subsequent runs.

o A factorial modelling design was then used to investigate the impact of four factors on a simulated Hluhluwe sized population - namely juvenile/adult mortality (2 levels), neonatal mortality (5 levels), inter-calving interval (4 levels) and age at first calving (2 levels) giving a total of 80 different factor combinations (100 replicates per factor combination - total 8,000 runs). Extreme factor levels were set to simulate those recorded for the Hluhluwe population, with the least severe parameter values reflecting a reproductively healthy and rapidly growing population that is not food limited.

For all runs, the initial population was set at 233 (Hluhluwe 1961 post die-off population estimate), and the population was modelled over a 25 year period up till 1986. In reality, the Hluhluwe population declined from an estimated 233 to 87 animals over this period. For the purposes of modelling, the maximum population size was not limited.

A total of 72 animals were "removed" in model runs, with ten males and eight females being taken off on four occasions at five year intervals from year 5 to year 20, to crudely approximate the 52 removals, loss of 7-15 animals to poaching, 2 to veld fires, 1 shot in self-defence, 1 to lion and a further 8 to capture related mortalities over the 25 year period.

The conclusions from the runs were as follows..

- In addition to the removals, an underlying annual population decline of about 2% per annum was required to simulate a decline of the magnitude that occurred in Hluhluwe (233-87 from 1961 post-die off to 1986).

- All four modelled factors significantly affected population performance, but no one factor alone was capable of producing a decline of the magnitude of the observed Hluhluwe decline.

- Mean population size after 25 years averaged 361 across all runs, and varied from 38 (age at first calving =12 years, inter-calving interval = 5.25 years, high adult mortality = ♀ 3.5% ♂ 7.3% per annum and 70% neonatal mortality) to 2,154 (age at first calving = 7 years, inter-calving interval = 2 years, standard adult mortality = ♀ 1% ♂ 1.5% per annum and 5% neonatal mortality).

- The average population size after twenty five years with a healthy calving interval of 2 years was four times greater (680 cf. 174) than for runs with a calving interval of 5.25 years (recorded for Hluhluwe). Increasing inter-calving intervals from 2 years to 3.33 years halved final average population size (680 cf. 331) while the doubling of calving intervals from 2 to 4 years reduced average final population size by 62% to 260.

- Population size was also sensitive to the age at first calving. On average increasing the age at first breeding from 7 years (healthy population) to 12 years (observed in Hluhluwe) reduced average final population size by 38%. With standard levels of adult mortality, inter-calving intervals of 3.33 years and neonatal mortality of 20% the lengthening of inter-calving intervals (7-12 years) reduced average final population size from 721 to 460. However, with short inter-calving intervals of 2 years, and low levels of mortality (standard adult mortality and 5-20% neonatal mortality) lengthening age at first calving approximately halved final population sizes (2,154 - 1,044 with a 5% neonatal mortality; 1,613 - 859 with a 20% neonatal mortality).

- On average increasing adult mortalities from standard levels to the observed very high adult mortality rates observed in the declining Hluhluwe population (♀ 3.5% ♂ 7.3% per annum) plus a slight increase in juvenile mortality reduced average population size after 25 years by 46% from 468 to 254.

- It is appropriate to treat adult mortality and reproductive parameters (age at first calving and calving intervals) as variables which co-vary in response to nutritional stress caused by declining carrying capacity. Healthy reproduction (calving interval = 2 yrs, age at first calving = 7 years), standard mortality levels and removals produced an average final population size of 1,141 - an almost five fold increase in numbers over the 25 year period. However, the increased adult mortality levels (♀ 3.5% ♂ <7.3% per annum) and poor reproductive performance (calving interval = 5.25 yrs, age at first calving = 12 years) observed in Hluhluwe, produced a modelled average final population of 102 (a 91% reduction in numbers). However, given these parameters, final population size was very sensitive to the level of neonatal mortality with average modelled final population size varying from 38 (70% neonatal mortality) to 176 (5% neonatal mortality). Given the observed calving interval of 5.25 years, and assuming that all females conceived (which may not be the case under conditions of nutrient stress),an interpolated neonatal mortality/abortion rate of approximately 53% was required to simulate the scale of the Hluhluwe decline.

- Increases in undetected neonatal mortality or abortions can contribute to overestimation of inter-calving intervals. While there is circumstantial evidence to suggest that spotted hyenas can kill young black rhino calves less than four months old (Chapter 22), one can also expect abortions and neonatal mortalities to increase markedly in a nutritionally stressed population given the higher nutritional requirements of pregnant and lactating cows (Bothma 1988, Nan Schaeffer pers comm). If one follows Hitchins & Anderson (1983), and assumes that all adult females conceived and observed intr-calving intervals in excess of 40 months were because either the neonate did not survive long enough to be recorded or that the female had aborted (i.e. setting the maximum inter-calving interval at 3.33 years), then with poor reproductive parameters (delayed age at first breeding 12 years and 3.33 year inter-calving interval), high observed levels of adult mortality plus simulated removals, an increased interpolated abortion/neonatal mortality rate of approximately 68% was required to simulate the scale of the Hluhluwe decline. Interestingly, Hitchins and Anderson (1983) recorded that 22 out of 32 inter-calving intervals in Hluhluwe were in excess of 40 months, leading them to conclude that the Hluhluwe abortion/neonatal mortality rate may have been in the order of 69% (Hitchins & Anderson 1983). However the setting of a maximum 40 month inter-calving interval by Hitchins and Anderson is arbitrary, and inter-calving intervals longer than this could occur if poor nutrition reduced conception rates.

- As indicated above, one would expect conception rates to decline and/or abortions and neonatal mortalities in Hluhluwe to have increased in response to nutritional stress (Bothma 1988, Nan Schaeffer pers comm). However, even if one assumes a highly improbable worst-case hyena predation scenario where all females conceived, and hyena predation (and not abortions or neonatal deaths due to poor nutrition and other causes) was entirely responsible for a 70% neonatal mortality, this very high level of neonatal mortality was not enough on its own to prevent a reproductively healthy population from increasing.

With modelled removals and age at first calving (7) and inter-calving intervals (2 years) and adult mortality levels set to reflect a healthy population; then despite a 70% neonatal mortality, the simulated Hluhluwe sized population increased on average by 2.84% per annum in non-removal years to reach an average of 368 animals after 25 years (a 58% increase in numbers over 25 years despite removals and very high neonatal mortality).

If the population showed healthy reproduction, then even with the application of the very high observed Hluhluwe adult mortality rates, plus a 70% neonatal mortality the modelled population remained stable in non-removal years (r for non-removal years = 0.0079).

Therefore, one can be confident that calf predation by hyenas could not have been a primary cause of the Hluhluwe decline (see also chapter 22).

- Given the declining carrying capacity and the resulting poor reproduction and high mortality rates, the failure of the Hluhluwe population to grow following the limited removals is to be expected. With the benefit of hindsight and current knowledge it is clear that the South African *D.b.minor* metapopulation would have been significantly bigger today had there been significantly higher removals from Hluhluwe in the late 1950s and 1960s.

- Demographic stochasticity and inbreeding depression were not likely to be potential causes of the Hluhluwe decline (see chapter 22).

o Additional VORTEX modelling indicated that rhino population performance is sensitive to maximum age of breeding (simulated imperfectly in VORTEX by varying the maximum ages of animals). For example, if cows bred up to 35 years compared to 25 years, then this enabled the simulated population to withstand an additional 20% neonatal mortality. One limitation of VORTEX is that modelled reproductive success is the same for all females irrespective of age, yet in captive animals this does not appear to be the case (Norman Owen-Smith pers.comm). More data are still required to quantify the influence of age on reproduction in wild populations and the impact of stocking densities relative to estimated carrying capacities on this (although in the RMG region increasing effort is currently being focussed on monitoring the reproductive performance of individual females). However, if reproductive performance does decline in older animals, and this is further exacerbated by nutritional stress, then reduced abortion/neonatal mortalities would be required to produce a decline of a Hluhluwe magnitude.

○ In conclusion - while some additional neonatal calf predation by spotted hyena in Hluhluwe may have contributed to the decline, the VORTEX modelling indicated that calf predation by hyenas could not have been a primary cause of the Hluhluwe decline. Rather the results of the modelling are consistent with food limitation having been the major cause of the Hluhluwe decline (through negatively affecting reproductive parameters and increasing mortalities), with numbers being further reduced following translocations. Modelling also indicated that inbreeding or demographic stochasticity could be ruled out as potential causes of the Hluhluwe decline.

CHAPTER 22

A REVIEW OF OTHER POSSIBLE CAUSES OF THE HLUHLUWE DECLINE

INTRODUCTION

This chapter reviews other potential causes of the Hluhluwe decline aside from direct mortality and habitat changes as a result of fire, bush clearing, large grazer removals/introductions, and lack of elephants and their re-introdution (already discussed in Chapters 9 and 15-20). It examines the likelihood that population estimation biases, predation (lion and spotted hyena), competition with other browsers and mixed feeders (kudu, elephant, giraffe, bushbuck, impala and nyala), inbreeding, demographic stochasticity, poaching, disease, anaemia, chemical insect control, drought, translocations and inter-specific fighting could have accounted for the decline in estimated numbers of black rhino in Hluhluwe from 1960 to 1987. This chapter also makes reference to the results of chapter 21 which used VORTEX population modelling to examine the possible impact of predation, genetics, demographic stochasticity and past removals on the Hluhluwe population performance.

POPULATION ESTIMATION BIASES

Some animals could have been double counted during the block drive counts (on foot and horseback) in 1961 and 1967 leading to overestimates of population size, although it is more likely that some animals were not seen during these surveys. However, based on the frequency of reported sightings, the high number of animals that died in Hluhluwe North, the greater number of individual animals recognised in Hluhluwe in the early 1970s compared to later estimates, the much higher levels of black rhino feeding recorded by Peter Hitchins around 1970 (compared to levels recorded in this study), and the very much lower population estimate for 1985 based on ID survey data it is clear that a real and major decline occurred in Hluhluwe.

Furthermore the modelling in Chapter 21 indicated that the poor reproductive performance and high mortality observed in Hluhluwe, coupled with known removals and losses to poaching were sufficient to produce a scale of the decline similar to that estimated from the population estimates.

Thus the scale of the decline was not grossly overestimated because of variable undercounting biases in the population estimation methods themselves.

PREDATION

SPOTTED HYENA

Hitchins (1972) hypothesised that the past low black rhino recruitment rate in North Eastern Hluhluwe was most probably due to predation by spotted hyenas on calves (Hitchins 1972). In 1988 and 1986 Hitchins again speculated that the incidence of predation in Hluhluwe may have been "higher than generally thought". Hitchins (1970) believed the low calving rate he recorded for Hluhluwe was probably due to low calf survival. He further argued that out of a range of possible causes (including diseases & parasites, starvation, weather, stress, natural causes, and poaching; there was "*no evidence whatsoever*" to support any other possible cause of high infant mortality in Hluhluwe except spotted hyena predation.

The evidence presented in this Thesis is at odds with this assertion; as it indicates that nutritional stress following the major habitat changes which occurred in Hluhluwe (partly in response to past low fire frequencies and immediately following major clearing in 1959-1960) significantly reduced carrying capacities for black rhino in Hluhluwe (chapter 20), leading to the observed increased adult mortality rates and reduced reproduction (as indicated by increased age at first calving and increased inter-calving intervals). Under conditions of nutritional stress one can also expect conception rates to drop and/or abortions and neonatal mortality to increase significantly (Bothma 1996). Thus because high levels of neonatal mortality (or reduced conception rates) were indicated by the observed longer inter-calving intervals in Hluhluwe, this does not necessarily imply that spotted hyenas were responsible for all or most of this mortality.

VORTEX modelling in chapter 21 indicated that (assuming all adult females conceived) abortions/neonatal mortality levels during the decline may have been as high as 70%. However, it also indicated that on its own (i.e. in a healthily reproducing population with normal adult mortality levels) neonatal mortality of this magnitude could not have caused a population decline. The modelling (chapter 21) indicated that if a population is not food limited and breeding well, and is subjected to a range of normal catastrophes (including some removals), the population will still grow even if neonatal calf mortality in the first year is as high as 70%. Neonatal calf predation alone could therefore not have caused the Hluhluwe decline.

While lack of calves (reflected in observed inter-calving interval) is consistent with the poor nutrition of adults, spotted hyenas may still have killed a proportion of neonatal calves contributing to the scale of the decline. The question is how likely is it that calf predation by spotted hyenas could have been an additional major contributory factor in the Hluhluwe decline, as suggested by Hitchins (1988) and Thomson (1988).

Eye witness accounts of attempted predation by hyaena

To my knowledge, no actual kills of black rhino by spotted hyena have been observed in the wild. Hyenas are active at night, and in thick bush it is impossible to adequately observe and quantify the extent of, and success of hyena predation of rhino calves. Therefore, failure to directly observe calf kills does not mean they could not occur. There is circumstantial evidence in the form of witnessed attacks, torn ears and missing tails indicates that black rhinos are probably vulnerable to predation by spotted hyenas (Goddard 1967a, Kruuk 1972, Hitchins & Anderson 1983, Sillero-Zubiri & Gotelli 1987, 1991, Kunkel 1992).

Hitchins argues that the habit of a black rhino mother running ahead of her calf predisposes it to attack by spotted hyenas (Hitchins 1986). Observations by Kunkel (1991) support this view. However, during observed attacks by spotted hyaena, black rhino cows have invariably been seen to return to defend their calves upon hearing their distress squeals (Goddard 1967b, Sillero-Zubiri & Gotelli 1991).

- Kunkel (1992) observed hyenas attacking a young calf which was lagging behind as its mother ran ahead; although as soon as the cow whirled round and stopped, the calf caught up and was successfully protected by its mother.

- Goddard (1967) witnessed three unsuccessful attempts by spotted hyaena to catch black rhino calves. In all cases they were eventually repulsed by charges from the mother, or the calf itself.

- Kruuk (1972) observed fifteen hyenas attempting to get a month old calf with a broken leg in Ngorongoro. Although its mother protected the injured calf, Kruuk thought the hyenas would probably have killed it in the end had it not been shot for study purposes by another scientist. However, on three of the five occasions Kruuk saw hyenas bothering rhinos he concluded that the hyenas were just "mobbing" the rhino and that "hunger did not seem to be the motivating force behind the hyena's behaviour".

- One yearling calf in the Salient area of the Aberdares was attacked three times by hyenas in 1986, although it survived (Sillero-Zubiri & Gotelli 1991).

- While not witnessing any successful predation attempts, Hitchins nevertheless observed the progressive mutilation of four black rhino calves; two of which subsequently disappeared (Hitchins & Anderson 1983).

Hyaena densities and predation impact

While acknowledging that the impact of hyena predation on the black rhinoceros population was unknown, Hitchins nevertheless speculatively concluded that "it is considered to be fairly high in Hluhluwe, low in the Corridor, and very low in Umfolozi" (Hitchins 1986).

In the absence of any good recent population estimates for spotted hyena, the extent of any current density differentials between Hluhluwe and Umfolozi is unknown. However, work undertaken by Whateley (Whateley and Brooks 1985) in the early 1980s, indicated that densities of hyena's were higher in Hluhluwe, and thus levels of hyena predation may have been higher there.

The recorded density of spotted hyenas in the Salient area of the Aberdares of 1.34/km2 (Sillero-Zubiri & Gotelli 1991) was much higher that the 0.45/km2 and 0.36/km2 recorded for Hluhluwe and Umfolozi respectively (Whateley & Brooks 1985). However despite this, six of the eight black rhino cows which visited the Ark salt lick in the Aberdares National Park, had calves (Sillero-Zubiri & Gotelli 1991). Sillero-Zubiri and Gottelli (1991) further concluded that while hyenas may be a potential factor in infant mortality in the Aberdares, poaching has been the main and probable sole cause for the decline of the Aberdares rhino population.

One fact mitigating against hyenas being major calf predators of black rhino is that the comments below suggest that hyenas were probably common in Hluhluwe in the 1930s, 1940s and 1950s when black rhino numbers were increasing in Hluhluwe (from an estimated 85 in 1933 to 279 in early 1961- Figure 1.1).

- In 1933, Potter (1934) reported that Hyenas were "plentiful".

- The 1962-63, the Natal Parks Board Annual Report mentioned that a "healthy population of hyenas existed" in Hluhluwe; whilst also mentioning that a good number of black rhino calves were produced (Anon 1963).

- Mr Roelf Attwell (pers.comm.) indicated that during his stays at Hluhluwe between 1938-42 he did not find any evidence of hyena predation on black rhino; yet he mentions hyenas were plentiful then. He indicated he would be very circumspect about introducing any large predator control programme with a view to improving population densities of black rhino and speculated that some of the ear disfiguration may be tick related.

- Hyena's were recorded as calling at night in Hluhluwe in 1954 by Steele (1992), although he gave no indication as to whether this was a regular occurrence.

Hyena and lion occur in other areas with black rhino, and this has not stopped populations from breeding up fast (eg Umfolozi and Kruger). Spotted hyenas also occur in many areas of Africa which, prior to poaching, had large numbers of black rhino as well as predators (eg, Zambezi valley). It also seems improbable that the thicker bush in Hluhluwe could have had such an influence on hyena hunting success that it resulted in significantly increased predation in this area compared to other areas.

Scars from hyena predation attempts

In both the Aberdares and Hluhluwe-Umfolozi, a proportion of black rhino have scars or are missing ears and tails (Hitchins & Anderson 1983, Hitchins 1986, Sillero-Zubiri & Gotelli 1987, 1991). About 3.7% of adult animals in Hluhluwe have mutilated ear pinnae, and about 4% have mutilated tails (Hitchins 1990). Of the 38 animals seen in Hluhluwe and the Corridor areas of Hluhluwe-Umfolozi Park with missing ears or a damaged tails, 7 were from the Corridor and 31 came from Hluhluwe (Hitchins 1986). However, on average over the period, the density of rhinos in the Corridor was probably only about a quarter of those in Hluhluwe (Figure 1.1). Thus, the proportion of animals showing signs of hyena attack is similar in the two areas. The Corridor black rhino population did not fall as markedly as Hluhluwe's population, and this suggests that spotted hyena predation is unlikely to be a major causal factor of the decline.

Even if the number of calves taken by hyenas is three times greater than the number of mutilated survivors this still only roughly translates to an extra 20% neonatal mortality. In other African areas, predation has never been suspected of accounting for much more than 10% of neonatal deaths, and in otherwise healthy population, one can expect first year black and white rhino calf mortality to be not more than 10% (Owen-Smith 1988a, Adcock 1994).

RMG mortality data

Available evidence of probable rates of calf predation show levels far below those required if predation was to be a major contributory factor in the decline. Analysis of Rhino Management Group of Southern Africa (RMG) data for South Africa and Namibia over the period April 1989 to December 1996 (Adcock 1998) indicated that only 3 out of 282 reported deaths (or 1.1%) were ascribed to spotted hyena. While recorded mortalities are likely to underestimate hyena predation (because small calf carcasses can be completely scavenged, leaving little evidence to find); if hyena predation was potentially the major factor impacting on black rhino (as hypothesised by Hitchins), one would have expected that more than 3 recorded mortalities in South Africa and Namibia (RMG reporting region) to have been ascribed to hyenas over an 81 month period.

By way of contrast 18.8% (53) of the recorded deaths in the RMG region over the period were caused by fighting, A further 17.4% (49) were caused by poaching, and another 3.6% (10) were related to snare wounds (Adcock 1998). Significantly more animals were also reported as having died as a result of accidents, falls, drowning or being stuck in mud (6.5% or 18).

In summary, available evidence showed that levels of hyena predation were not sufficient to have been a primary cause of the decline, although circumstantial evidence indicates that hyenas might have killed some calves.

LION

Lions cannot be invoked as a cause of the Hluhluwe decline as they only became resident north of the Hluhluwe and Nzimane rivers from 1978 (Whateley & Brooks 1985$^{\#1}$).

GENETICS

It has been hypothesised that in Hluhluwe, genetic problems may have started to surface causing inbreeding depression and reduced population performance. Some authors have ascribed the occasional case of earlessness in black rhinos to genetic causes (Hall-Martin 1986, Goddard 1969). However Hitchins (1986) examined 36 Hluhluwe-Umfolozi animals with missing ears and/or damaged tails; and only one showed what appeared to be a congenital deformity. Hitchins concluded that when one considers this single case in relation of the whole Hluhluwe population over a thirty year period (1955-85) the incidence of a genetic character being responsible for earlessness is rare. Hitchins (1986) further postulated that the vast majority of cases of earlessness in black rhino were due to spotted hyenas and not due to genetic defects. He is probably right, as congenital earlessness has not surfaced to date in any offspring of HUP rhino translocated elsewhere.

A rough rule of thumb in conservation genetics relating to vertebrate species, is that in short term maintenance of a safe level of genetic variability, the maximum rate of inbreeding should be no more than 1 % per generation, and this corresponds to an effective population size of 50[E] du Toit 1987b)[#2]. This translates to the need for any breeding group to be 150 to 200 individuals. At its peak population levels in 1961 the Hluhluwe section of the HUP population was 279, which is above this minimum figure, as is the more recent 1996 Hluhluwe-Umfolozi black rhino population estimate of 416 (Howison *et al* 1997).

While there may have been only between 100 and 135 black rhino in Hluhluwe in 1930, these animals rapidly bred up to reach peak densities thirty years later. Indeed, Gilpin advised a 1987 workshop on population genetics for conservation management that loss of heterozygosity following a bottleneck is likely to be minimised when populations grow at their intrinsic rate of increase. This would apply to the Hluhluwe black rhino.

This argument was strongly supported by the results of a black rhino metapopulation workshop held in Kenya in 1992 (Foose *et al.* 1993[#3]. Although at that time there was no data available on the effects of inbreeding on rhinos, the workshop used 3.12 recessive lethals in the VORTEX population modelling. This figure has been reported for zebra, which was the closest relative to the rhino among the species for which data had been published. This value also represented a level near the median (3.14 recessive lethals) for the 40 mammals species examined (Foose *et al.* 1993). In addition, the workshop considered a worst case scenario, and used a value of lethal equivalents twice as big (6.24). Despite using a long inter-calving interval of 4 years, the workshop concluded that if the inbreeding has no further impact on adult survival or reproduction, and if poaching, disease and drought catastrophes never occur, then even very small populations may be viable. Even with the modelled long inter-calving intervals used in the Kenyan PVA, populations of 30 or more always survived through the 200 year simulations, and populations as small as 10 had a median time to extinction of 161 years (Foose *et al* 1993).

Therefore it appears that any potential loss of heterozygosity in the Hluhluwe population would have been minimal, and it is therefore extremely improbable that genetic factors were responsible for the Hluhluwe decline.

Swart (1994) quantified levels of genetic variation in four black rhino populations (Etosha National Park, Hluhluwe-Umfolozi Park, Mkuzi Game Reserve, and animals being removed from the Zambezi valley in Zimbabwe) concluding that *"the high levels of genetic variation present in the four black rhino populations suggest that they do not experience genetic depletion and that inbreeding does not pose an immediate threat to the survival of the species"*.

Even if it were demonstrated that loss of significant heterozygosity had been the result of inbreeding, this would not necessarily translate directly into a need for genetic management, as different species will show varied responses to similar levels of inbreeding (Ferrar 1987, Van Hensbergen pers.comm. 1987). Meffe and Carroll (1994) caution that strict quantitative rules should generally be avoided, or at least be applied with a great deal of caution. In addition, while heterozygosity is desirable, one should not strive to maintain heterozygosity at all costs, as a degree of homozygosity is acceptable (Ferrar 1987).

While inbreeding has been documented as a real problem in a number of domestic animals, there have been numerous successful population recoveries from a few founders, suggesting that the problem may be less serious in nature. The critical factor is that the total metapopulation should breed up as fast as possible (Gilpin pers.

comm.) and indeed this is precisely what the southern white rhino population has done in only a few generations. From only 20 or so southern white rhino left in Umfolozi in 1895, numbers have built up to over 9,200 worldwide 102 years later (IUCN SSC African Rhinos Specialist Group data). Considering that a few hundred white rhino have also been hunted since 1968, it does not appear that any loss of heterozygosity or inbreeding depression following a bottleneck has negatively impacted this rhinoceros species. Similarly, the Addo black rhino population has bred up from only four founders with apparently no ill effect, and has excellent recruitment rates. The Mkuzi black rhino population also went through a severe bottleneck, being reduced to perhaps only about 15 animals thirty years ago. Despite this, Mkuzi's recruitment has since remained high and Swart's (1994) genetic analysis showed the population still had high levels of heterozygosity. In addition those animals that have been translocated from Hluhluwe-Umfolozi and Mkuzi have invariably bred well in their new homes. If inbreeding had been the problem, this would not have occurred.

Genetic management is an insurance policy against future catastrophes, and therefore falls into the group of theoretical potential problems which are not of the highest priority in the short term, given the current very real problems of low or negative recruitment rates through poaching, overstocking and demographic stochasticity (in small populations).

A further strong argument against inbreeding being responsible for the decline is that the animals in the Umfolozi section of the Park have increased rapidly since the 1960s, as have many animals translocated from Hluhluwe-Umfolozi to set up new populations.

One can conclude that the overwhelming body of theory and practical evidence does not indicate that the Hluhluwe decline could in any way be linked to genetic problems as a result of inbreeding; and we can safely eliminate this hypothesis.

POSSIBLE COMPETITORS

At a 1988 NPB meeting, it was felt that Hluhluwe black rhinos may have suffered from increased competition for food with other browsers, and especially from nyala which increased in numbers tenfold between 1950 and 1972 (Anon 1988).

NYALA

Nyala and black rhino performance may be primarily related to habitat changes, and thus one must be careful not to infer cause and effect simply because the increase in nyala numbers in Hluhluwe was negatively correlated with the decline in black rhino numbers.

Circumstantial evidence suggests that habitat changes may be responsible for the increase in nyala numbers. From driving and walking in Hluhluwe it appeared that nyala particularly favoured areas of intermediate developing closed *Acacia nilotica* woodland progressing to a dry lowland forest dominated by *Euclea racemosa, Berchemia zeyheri* and *Rhus pentheri* (eg. along the road going past Zincakeni dam). With the increased shade, lawns of *Dactyloctenium australe* commonly occurred in these areas, benefiting nyala who eat both leaves and culms of this species in Hluhluwe (Vincent, Hitchins, Bigalke and Bass 1968). The findings of this project (chapters 6,7, 9 and 20) clearly show that such habitat is sub-optimal for black rhino.

Further support for the preference of nyala for closed woodland/closed woodland edges comes from Brian O'Regan's observation (personal communication 1993) that (during his study of browsers in Umfolozi in the early 1980s) sightings of nyala were invariably in the ecotonal zone at the fringe of patches of closed woodland. He further noticed that they ate many small herbs low down in the grass layer. Given their narrow muzzles and smaller size, nyala are therefore able to be more selective for small plants than a black rhinoceros ever could be further reducing potential competition.

Potential competition between nyala and black rhino is immediately reduced by the fact that nyala are mixed feeders. In contrast to black rhino who have been recorded to eat limited amounts of tall grass during periods of nutritional stress, nyala browse most grass when it is fresh and sprouting after the rains (Skinner & Smithers 1990). The recorded proportion of nyala stomach contents made up of grass varied from 30% grass in Hluhluwe nyala stomach contents (Vincent, Hitchins, Bigalke and Bass 1968) and a trace to up to 65% in Mozambique (Tello & van Gelder 1975).

Of the species recorded in nyala rumens in Ndumu Game Reserve by Anderson & Pooley (1977), *Acacia grandicornuta* was the *Acacia* species that contributed most leaves to the nyala diet. It was the only species of "*Acacia*" whose leaves were given an intermediate importance rating. This species was one of the "*Acacias*"that was both unimportant and rejected in the black rhino's diet in Hluhluwe-Umfolozi (this study). While the authors concluded that the estimated contribution of microphyllus species such as "*Acacias*"to the nyala diet was probably under-represented. However, if "*Acacia*"leaves were anything like as important as they are to a black rhino one might have expected that at least some of the "*Acacia*" species to be rated as being intermediately or heavily browsed, although in Mozambique several species of "*Acacia*" were listed as important foods (Tello & van Gelder 1975).

Interestingly, Anderson and Pooley (1977) listed the leaves of three *Euclea* species (*E.divinorum*, *E.natalensis* and *E.racemosa*) as being browsed by nyala from mid winter to spring in Ndumu with *E.divinorum* being rated as intermediate in importance. While black rhino browsing of *Euclea* species (and especially *E.divinorum*) in Hluhluwe also increased immediately after the burns and in the early growing season, these species were usually highly rejected. *Euclea*'s are common in both Hluhluwe and Umfolozi, and so even during crunch periods (late dry season/early growing season) it appears unlikely that black rhino and nyala will compete for this resource.

Nyala are similar to black rhino in that they only browse certain species during winter (Anderson & Pooley 1977, Tello & van Gelder 1975). For example, during winter, nyala in Ndumu browsed the leaves of *Kraussia floribunda* (Anderson & Pooley 1977). While this species has increased in abundance as woody succession has progressed in Hluhluwe to become common, it is highly rejected by black rhino.

Leaves of *Spirostachys africana* were rated as heavily browsed by nyala in Ndumu and as important in Mozambique (Anderson & Pooley 1977; Tello & van Gelder 1975). While this species was the most important woody item in the Hluhluwe-Umfolozi black rhino diet for most of the year, feeding height stratification may be occurring. The most preferred size class of *S. africana* for black rhino recorded in the Pilot study (Chapter 6) was between 1.75 and 2.5 metres tall. The most important *S.africana* spize in both the Hluhluwe and Umfolozi Grid surveys was size class 3 or trees between 2 and 4 metres. Black rhino regularly break down branches of the taller individuals which nyala do not. While *S.africana* size 2's from 1-2 metres tall were also important and generally more preferred that the taller size 3 trees, the Pilot study results indicated that is was the taller individuals within this class that were the most important. Thus although there was some overlap with nyala, the ability of rhino to feed higher acted to reduce possible competition. The similar proportion of *S.africana* in the Hluhluwe and Umfolozi woody plant diets, and the higher preference rating where the species was less abundant (Figure 7.1) did not suggest that *S.africana* dietary intake was being limited by competition from nyala, but rather that there may be a limit to the amount of *S.africana* that can be eaten by black rhino (possibly due to a limit of the amount of toxic secondary plant chemicals that can be ingested).

Another key member of the family *Euphorbiaceae* in the Hluhluwe black rhino diet is *Acalypha glabrata*. Hitchins (1968a) lists nyala in Hluhluwe as also browsing this species. By breaking and pulling branches of this species down however black rhino can access some of this food which is unavailable to nyala.

Nyala in the capture bomas (pens) are known to love browsing cut *Zizyphus mucronata* (Pete Openshaw pers.comm.) and with their fine muzzle are able to deal with the formidable physical defence of this species. Indeed Anderson and Pooley's (1977) study in Ndumu confirmed that for most of the year this species was heavily browsed by nyala. This species was also important in Mozambique (Tello & van Gelder 1975). By way of contrast, *Z.mucronata* was either slightly rejected or intermediate in acceptance by black rhino in Hluhluwe and Umfolozi. It was also not as favoured as other species by Tombi the boma'ed black rhino (chapter 13).

Other species that were recorded as eaten by nyala (Vincent, Hitchins, Bigalke and Bass 1968, Hitchins 1968, Anderson & Pooley 1977, Tello & van Gelder 1975) but were rejected by black rhino in Hluhluwe-Umfolozi included *Carissa bispinosa, Pyrostria hystrix, Combretum species, Ochna natalitia, Rhoicissus tridentata, Gardenia cornuta, Gardenia volkensii, Ozoroa* species, *Lippia javanica, Rhus dentata, Rhus guenzii, Rhus pentheri, Sideroxylon inerme* and *Chaetachme aristata.*

While *Maytenus heterophylla* was heavily browsed by nyala in Ndumu. Once again this species was highly rejected by black rhino in both Hluhluwe and Umfolozi. The only preferred *Maytenus* species in Hluhluwe-Umfolozi favoured by black rhino was *M.nemorosa*; with trees between 2 and 4 metres being most preferred, and so even if nyala favour this species, there is likely to be ecological separation on the grounds of height. Hitchins (1968) recorded nyala as feeding on *M.senegalensis*. This abundant species is highly rejected by black rhino in Hluhluwe-Umfolozi.

Grewias were either slightly or intermediate in importance to the Ndumu nyala diet (Anderson & Pooley 1977). While these species are regularly eaten by black rhino and can be an important dietary item (eg Save Valley Conservancy in the arid Zimbabwe lowveld), in Zululand *Grewias* do not make up more than about 5% of the diet, and were generally slightly rejected or intermediate in acceptance value, appearing to act more as a stop gap filler in the dry season.

Anderson & Pooley found that *Ehretia*'s were important nyala foods in Ndumu, and therefore they could compete with black rhino for this species.

One potential area for competition is in the browsing of forbs. Both nyala and black rhino browse *Solanum panduraeforme, Sida rhombifolia, Hibiscus* species and *Senecio* species (Hitchins 1968, Anderson & Pooley 1977, chapters 6, 7 and 11). However, only *Sida* appears to be a preferred species for black rhino. The development of closed canopy *A.nilotica* woodland going to lowland forest has been detrimental for black rhino in terms of the bulk of their woody diet, yet these same changes favour the growth of many forb species.

Thus while there appears some overlap in the diet between nyala and black rhino, species preferences vary in a number of cases. Nyala also seem to favour different habitats to black rhino, and ecological separation

is increased by the partial vertical separation of feeding between the species. The nyala's habit of browsing fallen leaves during winter (Tello & van Gelder 1975) and grazing more during summer further acts to reduce potential dietary overlap.

One factor which suggests that competition from nyala is not a major factor influencing black rhino performance is that Hluhluwe black rhino performance did not improve following very heavy culling of nyala from 1979 to 83. In the two years 1979-80 alone, 2,952 nyala were removed from Hluhluwe (Brooks & MacDonald 1982).

The increase in numbers of nyala in parts of Umfolozi also has occurred at a time of rapid black rhino population growth. If competition between nyala and black rhino was significant one would not have expected this to occur. It therefore seems most likely that increases of nyala have occurred primarily in response to woody plant succession, and that this species favours later successional stages than black rhino. Brian O'Regan (pers.comm.) shares this view.

Although requiring future research, one possible way high nyala (and impala) densities might negatively impact on black rhino is if heavy shoot browsing makes smaller "*Acacias*" more susceptible to being killed by frequent fires possibly reducing densities of favoured small "*Acacias*" establishing in open areas to the detriment of black rhino[#4]. However, numbers of nyala and impala must have been high in the late 1950s (given estimated numbers in 1964 - Brooks and Macdonald), and this was clearly not enough to prevent the subsequent widespread development of *Acacia* thicket, woodland and lowland forest over extensive areas of north-east Hluhluwe. The removal of 22,481 impala and nyala from Hluhluwe from 1957 to 1981 did not prevent black rhino densities declining substantially during this period (Table 1.1).

IMPALA

Like nyala, impala might negatively impact on black rhino is if heavy shoot browsing makes smaller establishing "*Acacias*" more susceptible to being killed by frequent fires possibly reducing densities of favoured small

"*Acacias*" establishing in open areas to the detriment of black *rhino*[44]. However as indicated above in the section on nyala this hypothesis requires more research.

KUDU

While they seemed to prefer key rhino food "*Acacias*" like *A.tortilis*, *A.nilotica* and *A.karroo* in Umfolozi kudus preferred to feed standing up and usually browse above 2 metres, whilst avoiding the small trees most favoured by the black rhino (Brian O'Regan pers.comm). This conflicts with DuToit's (1990) finding in Kruger that kudu only allocated 33 % of their feeding time to the height range 1.2 to 1.7 metres, and spent more than half of the time feeding below this level.

In Umfolozi kudus like nyala also highly preferred *Zizyphus mucronata* (B.P.O'Regan pers. comm) - a species that ranged from being slightly rejected to intermediate in acceptance for black rhino (chapters 6 and 7).

It appears that kudu and black rhino performance is correlated. Both species have increased dramatically since 1960 in Umfolozi, but until recently have shown marked declines in Hluhluwe. For example, by 1991 the Hluhluwe kudu population was only 36 % of 1972 levels. In the mid to late 1990s however numbers of both black rhino and kudu have increased in Hluhluwe. This apparent positive correlation between numbers of these two species in Umfolozi and Hluhluwe would not have occurred if competition from kudu was a major factor influencing black rhino performance. Kudu can therefore probably be excluded as being a probable factor in the decline of black rhino in Hluhluwe. Experience in a number of southern African reserves indicates that If anything kudu performance and densities indicate how suitable an area is for black rhino.

GIRAFFE

Whilst some Kenyan's perceive giraffe at high densities to be potential competition for black rhinos, up until 1989 giraffe in Hluhluwe never occurred at high densities, and one can safely conclude that giraffe were not responsible for the Hluhluwe black rhino decline[#5].

ELEPHANT

Elephant were only re-introduced to Hluhluwe in 1981, and so elephant competition with black rhino cannot be invoked as a cause of the Hluhluwe black rhino decline.

However, chapter 19 indicated that lack of elephants in the past could have been a contributory factor implicated in the habitat changes that led to the decline[#6].

POACHING

One theory advanced is that poaching was greater than previously thought, especially around the Corridor road (Hitchins & Brooks 1986, Anon 1988). Peter Hitchins believes that at least 15 animals were poached by staff as known individual rhinos were missing in the areas surrounding the game guard camps implicated in the poaching (Hitchins & Brooks 1986, Anon 1988).

Undoubtedly some rhino were poached, but the key question is could undetected poaching have been so high as to have been a major contributor to the Hluhluwe decline? Circumstantial evidence suggests it was not. For example, if poaching had been the major cause of the decline then one would not have expected the Hluhluwe female black rhinos to be older than in Umfolozi when they first calved or to have longer inter-calving intervals.

Experience indicates that white rhinos are easier to hunt partly because they live in more open habitat than black rhinos, with the result than poachers invariably kill more white rhinos than black in parks such as Hluhluwe-

Umfolozi where both rhino species occur. Furthermore, white rhinos are also much more numerous in Hluhluwe-Umfolozi Park. Given that currently about 66 % of detected rhino carcasses in the RMG region are found within one week, and 85 % within a month (Adcock 1998) if poaching of black rhino had been significantly higher than previously thought, a very much larger number of the commoner and more easily hunted white rhino would have been poached, and it is unlikely that this would have gone completely undetected.

DISEASE, POISONING OR ANAEMIA

It has been hypothesised that a disease outbreak, prussic acid poisoning or haemolytic anaemia may have reduced numbers of black rhino.

Browsers such as kudu and giraffe have been known to die of prussic acid poisoning after eating certain wilted browse species such as *A.caffra* and *A.nilotica* (B.Brockett and B.Keffen pers.comm. 1993). In addition deaths from prussic acid poisoning occur evenly across all age and sex classes, and this is what occurred during the 1961 Hluhluwe "die-off". The Hluhluwe rainfall figures were therefore examined for the months prior to and including the die off period to determine the likely chance of a major wilting event occurring and leading to a build up of prussic acid in the foliage. It turned out that there was unlikely to have been a major wilting of browse during this period. This means that **the likelihood of prussic acid poisoning being implicated in the die off seems remote.**

While black rhino have recently been recorded as having died from anthrax in Namibia, this disease has not been recorded in Hluhluwe.

Research undertaken on the blood of Zambezi black rhino in 1986 indicates that black rhino have unusual haemoglobin, making them inherently prone to haemolytic anaemia triggered by a variety of stress factors (du Toit 1987a). This problem has been particularly severe in captive black rhino. One survey in 1986 showed that 40%

of deaths of black rhino in captivity were associated with haemolytic anaemia (Chaplin *et. al.* 1986). Du Toit (1987) speculated on the adaptive advantage the unstable haemoglobin could confer on black rhino, and concluded that it is most likely an adaptation to blood parasites. Du Toit (1987) cited cases of deaths of captured black rhino in Kenya to support his argument that black rhinos generally maintain a delicate balance with their blood parasites. Kenyan animals died from trypanosomiasis and piroplasmosis apparently because physiological stresses of capture, and possible inadequate nutrition in the holding pens reduced the animals' resistance to blood parasites (Clausen 1981 ; McCulloch and Archard 1969).

Du Toit (1987) further suggests that a number of black rhino die offs in the wild that have not been satisfactorily explained may well have been due to reduced resistance to parasitaemia as a consequence of nutritional stress, and/or to forms of excessive oxidant stress on red cells, promoting haemolytic anaemia.

Chapter 17 reviewed the literature detailing the relationship between an animals abilty to process secondary plant chemicals and dietary quality, and concluded that under conditions of declining carrying capacity (such as just prior to the 1961 die-off when very extensive areas of rhino food species were bushcleared and grass growth increased) it is theoretically possible for animals to run into an energy crisis which could have resulted in animals dying quickly as a result of acute haemolysis. However even if acute haemolysis was the proximal cause of death of many of Hluhluwe's black rhino over the years and especially during the 1961 die-off (chapter 17); the probable ultimate causal factor would have still been nutritional stress brought on by declining carrying capacities. **One therefore cannot invoke haemolytic anaemia per se as a major causal factor of the Hluhluwe decline.**

The chemical 245-T was applied to some areas in the early days of bush-clearing in the late 1950s and early 1960s. Depending on the origin of the 245-T used it may have had Dioxin in it at the time of spraying (Sheail 1985). If this was so, this could have negatively affected reproduction of browsers. However the decline in rhino numbers continued long after the spraying of 245-T so it probably was not a key factor in the decline.

CHEMICAL INSECT CONTROL

It is highly improbable that the use of chemicals to control Tsetse flies and Harvester termites in the 1940s and early 1950s contributed to the black rhino decline, as the decline started ten to twenty years later. If anything, the use of chemicals to control insects in the 1940s and early 1950s might have benefited black rhino if this reduced bruchid beetle densities and this contributed to a major pulse in germination of favoured "*Acacia*" species such as *A.nilotica*[#7].

DEMOGRAPHIC STOCHASTICITY

While demographic stochasticity is most likely to have had serious effects in small populations of less than 20, Du Toit (1987) has argued that demographic stochasticity may operate in conjunction with environmental catastrophes to cause the demise of a population of even a 100 or more. Du Toit (1987) speculated that these compounding problems may have had a lot to do with the Hluhluwe black rhino decline. The VORTEX population modelling used at the 1991 Kenyan PVA modelling workshop (Foose *et al* 1993) also clearly demonstrated the potential influence of demographic stochasticity in pushing many smaller populations to extinction. However the Kenyan PVA modelling, and the modelling undertaken in chapter 21 indicated that **the Hluhluwe population was too large for demographic stochasticity to have been a major cause of the decline.**

While demographic stochasticity cannot be invoked as a cause of the major decline in black rhino numbers. However, once numbers had declined to low levels, demographic stochasticity may have impacted on productivity of Hluhluwe north as the area has a preponderance of adult males (Adcock 1998).

DROUGHTS

Figure 16.1 shows that in the late 1960s and early 1980s Hluhluwe-Umfolozi experienced extended periods with generally markedly below average rainfall. Could these droughts have been a contributory factor in the Hluhluwe decline ? On closer examination this does not appear to have been the case.

- The effect of droughts on black rhino is likely to be a function of stocking levels in relation to carrying capacity, and this is demonstrated by the fact that black rhinos can breed well in dry conditions if not overstocked. For example black rhinos survive at low densities in the desert in Kunene region of Namibia, and in what was termed a "record drought", cows with calves in poor condition that were translocated to set up the large Save Valley Conservancy population in the lowveld of Zimbabwe (more arid than Hluhluwe-Umfolozi) survived and successfully reared their calves (Raoul du Toit and Clive Stockil pers.comm.).

- Periods of below average rainfall (droughts) are also common events in semi-arid areas where most black rhino currently survive, and much of the period of black rhino population increase in Hluhluwe coincided with extensive bush encroachment - the initiation of which appears to have been associated with a below average rainfall period coupled with heavy grazing (chapter 20, King 1987).

- Figure 16.4 shows that for the period from 1965-71, rainfall was well below average with the period 1968-70 being especially dry. However Chapter 16 also indicated that despite the fact that the period had seven consecutive years with below average rainfall, fire frequencies increased between 1965 and 1971, and the average fire return period in the Grid study area dropped to 2.8 years, and that, after allowing for translocations, numbers of black rhino remained relatively stable in Hluhluwe over this dry period.

- Hluhluwe is a moist savanna area with an annual rainfall of 850mm in the north and 1,000 mm on its highest hills. Its droughts are therefore likely to be shorter and less severe than in more arid areas. Indeed during the bad drought in 1980, although lower than average, recorded calving intervals were higher in Hluhluwe than in the drier Umfolozi section of the park (Hitchins 1988) which has a lower average rainfall (650-700mm) and where numbers of black rhino were increasing rapidly.

Thus in conclusion the evidence indicates that droughts were not responsible for the Hluhluwe decline.

TRANSLOCATION

Chapter 21 indicated that with healthy reproduction and normal mortality levels, a Hluhluwe type population could be expected to grow rapidly even in years with translocations. Thus, **translocations on their own could not have contributed to the decline**[#8].

FIGHTING

A comparison between the mortality data for Hluhluwe (Hitchins & Anderson 1989) and other areas indicates that adult mortality levels were elevated above normal levels, and this was especially the case for males killed fighting. However, modelling in Chapter 21 indicated that the observed increased adult mortality (due in part to increased fighting) on its own could not account for the Hluhluwe decline.

Increased fighting is also a proximal factor, as the ultimate factor that will have caused increased fighting is the declining carrying capacity of the area (chapter 20) forcing male black rhino to seek to increase the size of their home ranges/territories leading to increased conflict with neighbouring bulls. The declining carrying capacity was evidenced by the major increases in approximate average home range sizes of black rhino in Hluhluwe (chapter 20) from as little as 3 to 5 km^2 in 1962-63 (Hitchins 1969) increasing to around 7.5km^2 by 1971 (Hitchins 1971) to current estimates of around 15 km^2 (Owen-Howison and Keryn Adcock pers.comm, RMG data).

CHAPTER 22 NOTES

#1: Black rhinos can be killed by lions even when adult (Ritchie 1963), although proven cases are rare (Goddard 1967). Their possible future impact on black rhino in the Park can be speculated on from the following evidence of lion predation attempts.

- It appears that a 2 year old black rhino was killed by lions in Umfolozi in 1987 (Elliot 1987). Elliot also noted well defined tooth and claw marks on the dead Umfolozi rhino.

- In the Masai-Mara lions prey on younger black rhino (Holly Dublin pers.comm).

- In Ngorongoro, Grzimek (1964) once found a dead rhino which had apparently been killed by lion, as it neck showed severe injuries from lions claws, and was apparently broken. In this case the lions did not eat any of the rhino.

- In 1995, the same young male lion killed two sub-adult black rhino at Etosha National Park, on separate occasions (Peter Erb, pers. comm., RMG d).

- Between 1950-58 Roelf Attwell (pers comm.) in Luangwa, Zambia, recorded two instances of lion predation on black rhino. He noted that this was exceptional, and that at the time black rhino were plentiful.

- Goddard (1967) watched a lion being killed by a black rhino cow as it tried to kill its calf.

- In Ngorongoro, Kunkel (1992) witnessed a number of encounters between black rhinos and lions. However during most of the "showdowns" that resulted, the lions backed off, although this was not always the case. In one case a young bull looked to be losing a battle with a pride of lions attacking him. However, the rhino managed to hit one of the lions and dislodge the other lions that were holding onto him. The rhino then charged through the lions, who scattered and let him through.

- The National Geographic film "Rhino Wars" shows one young black rhino calf being rescued in Kenya after being severely mauled by lions.

- The reintroduced lions of Phinda Resource Reserve and Pilanesberg National Park have been closely monitored since release by Gus Van Dyk and Luke Hunter. No rhino were killed by lions in the first 2½ years of Hunter's study (Van Dyk pers.comm.).

- In Pilanesberg, a lion was seen attacking an adult white rhino, which easily escaped when the lion did not persevere. An adult female rhino was seen to have been scratched down her side by what could only have been lion claws. She survived, and her calf (c.2 years old) was untouched.

Van Dyk (pers.comm.) has noted that lions don't relish scavenging dead white rhino. In Pilanesberg they just ate a hump and spent a maximum of two days in the vicinity of a dead white rhino. Even after the carcass was split open, not much was eaten. By way of contrast, the same lions spent two weeks scavenging on an elephant carcass (Van Dyk pers comm.). Van Dyk also found one 4-6 month old white rhino calf carcass in Pilanesberg that the lions had fed on. He noticed there was one hole in the calf's neck that a 303 bullet could fit into. While this suggests that lions may have killed the calf; Gus noted that the hole could also have resulted if a lion had simply come across the carcass and tried to move it. In another case, a white rhino cow was killed by a rhinocidal elephant in Pilanesberg, and its yearling calf was seen to keep two big adult male lions at bay for two days until it was caught by Parks Board staff.

- Grzimek (1964) noted that lions apparently play with rhino. He noted that while lions do not often kill black rhino they "*often seem to make butts of them by swatting them on the backside*" and retreating quickly out of reach of the irate rhino (Grzimek 1964). He noted than in one case, the lions lost interest once one black rhino stopped taking notice of further paw slaps on its hindquarters. Luke Hunter has observed similar behaviour at Phinda where a fully grown male lion was seen to swat a fully grown white rhino on the backside (Gus Van Dyk pers.comm.). Mervyn Cowie has also reported lion cubs in Kenya having fun by repeatedly knocking a black rhino on the leg and running away - They only retuned to their mother once the rhino got worked up, squealed like a pig and ran off (Grzimek 1964). In Pilanesberg, Gerhard de Lange reportedly watched a lion running alongside a rhino without making any attempt to touch it, giving the impression this was sport rather than hunting.(Gus Van Dyk pers.comm.).

On the whole it appears predation of rhino by lion is limited; and rhino is not a preferred food. To lions rhinos almost seem to rate higher as toys rather than food!.

Younger rhinos appear the most at risk.

Adcock believes that predation of rhinos by lions is likely to be limited to only the occasional rhino at average lion densities, (Adcock 1993) and should not be a major factor in rhino population dynamics. (Emslie & Adcock 1994).

Even if lions kill the odd rhino, they are major tourist drawcards, and therefore have a major economic value through their contribution to tourism revenue, which in turn can enhance the self sustainability of conservation within parks

#2: An African Rhino workshop held in Cincinnati in 1986 concluded that the minimum long term objective for each black rhino ecotype in the wild is a total population whose genetically effective population size (N_e) is 500. Given estimated Ne/N ratios in the wild of the order of between 0.25 and 0.33, this gives a recommended minimum long term desirable population per ecotype of between 1500 and 2000 (AAZPA 1986, Du Toit 1987b, Ledger 1987).

Walker (1990) has claimed that "*by widely accepted scientific criteria, the (then) 612 animals of the sub-species minor do not represent a genetically viable population.*". However this author strongly disagrees that this assertion is in fact either widely accepted in the scientific community, or correct. Lacy (1992) has argued that minimum viable population sizes (MVP) are likely to be different for different species and acknowledges that we do not know what the MVP is for any species. Franklin's (1980) "magic figure" of an effective population size

(N_e) of 500 was based on the rather rough equations available to geneticists (Du Toit 1987b), and that this figure represents a long term goal. Therefore provided there are sufficient founders and metapopulation numbers breed up to 1500 + there should theoretically be no problem. In the short term, theoretically desirable minimum population sizes are actually considerably less than this . For geneticists dealing with long-lived animals like rhino, 200 years can be considered short term.

The Kenyan PVA modelling (Foose *et al* 1993) however did indicate that inbreeding depression may mean that for smaller populations, the occasional introduction of new blood is desirable. The 1987 Pietermaritzburg "Genetics for Conservation Management" workshop concluded that the genetic variability of small populations could be maintained by the introduction of one "new" animal per generation (Wright 1969, Ledger 1987, Ferrar 1987, Gilpin pers.comm.). The introduction of only two unrelated bears every generation has been found to greatly reduce the loss of genetic variation (Allendorf 1994).

#3: VORTEX modelling at the workshop estimated the percentage loss of initial heterozygosity for different sized populations. Genetic variation was steadily lost in small populations. A loss of 25% representing rather severe inbreeding was reached within 50 years for populations of 10, about 100 years for populations of 20, and about 200 years with a population of 100 (Foose *et al.* 1993). However, this modelling used conservative population growth rates (see chapter 21), and could well have overestimated the genetic threat

Soule (1986) recommended that conservationists strive to keep variation above 90% of its initial value, in order to minimise inbreeding effects and to allow for continued adaptive evolution. That goal could be achieved for 200 years with a population of 100 rhinos (Foose *et al.* 1993). Even with high inbreeding depression (double the lethal equivalents of zebra) it was only the very small populations of 10 that tended to go extinct over a two hundred year period. As soon as the population was greater than 30 the probability of a population going extinct was almost zero (Foose *et al* 1993). Even with modelling high inbreeding, only 5% of initial heterozygosity had been lost after 200 years from a population of 100 (Foose *et al* 1993).

#4: Nyala were virtually absent from Hluhluwe in 1937, by 1964 their numbers (and also impala) had increased greatly (Deane 1965, Bourquin & Hitchins 1979). Based on their observation that *E.racemosa* was rarely eaten by browsers, Bourquin & Hitchins (1979) interpreted the positive correlation between increasing nyala numbers and the apparent increase of *E.racemosa* in forests and woodlands as a direct causal relationship, speculating that the heavy selective browsing of more palatable species by nyala in particular, favoured the growth of the unpalatable *E.racemosa*. However, there is a danger of inferring cause from this correlation, given the possible alternative explanation that vegetation changes, and in particular the development of closed canopy woodland, could simply have favoured increases in population sizes of both nyala and *E.racemosa* (ie that increased nyala browsing was not the primary reason for the increase in *E.racemosa*). Browsing alone cannot be the sole explanation for different spatial distribution of species relative to canopies in intermediate *A.nilotica* woodland recorded by Wills and Whateley (1996), although browsing could have hastened the mortality of light stressed "*Acacia*" seedlings growing under canopies.

The literature and personal observations indicate that browsing in savanna's can have a significant impact on woody vegetation,

- Simulated defoliation only depressed survival and growth of *Acacia senegal* seedlings for the first 38 days after which the number of surviving plants increased (Seif El Din & Obeid 1971)..

- *A.tortilis* in Lake Manyara National Park has only experienced three recruitment episodes during the last century, and these were correlated with population crashes of impala following outbreaks of anthrax, enabling a cohort of seedlings to escape browsing and get away (Prins & Van der Jeugd 1993). This is somewhat in contrast to the major bush encroachment in Hluhluwe from 1949-58 which occurred during a period with high game densities and increasing very high black rhino densities.

- Sheep are suspected of limiting the seedling recruitment of *A.karroo* in the eastern Cape grasslands (Story 1951), and the switch from sheep to mixed sheep/cattle or cattle only has resulted in encroachment of *A.karroo* as cattle do not affect its seedling establishment (Du Toit 1972). The impact of sheep in preventing regeneration of Scots Pine in Scotland is also well known.

- In a fenced exclosure plot in nearby Mkuzi Game Reserve which excluded both grazers and browsers, *A.karroo* has developed and matured inside the plot but not outside where plants present remained small (T. Rushworth and W.Bond pers.comm.). Fires were allowed to pass through the plot. Whether the establishment of *A.karroo* inside this plot is as a result of protection from browsing or because of the taller grass and hotter fires (which may have favoured *A.karroo*) is unknown, although it is thought browsing is the key factor as trees establishing outside the exclosure are not able to grow in height (W.Bond pers comm.).

- Trollope (1983) showed that browsing alone had limited effects on established plants of *A.karroo* but that together browsing and fire reduced survival because browsing maintained coppicing trees in small size classes where they were more susceptible to frequent fires.

- Pellew (1983) showed that giraffe browsing kept Acacia's in smaller size classes which in conjunction with fire led to the demise of these woodlands.

- Belsky (1984) noted that heavy browsing by impala, dikdik, and grant's gazelle can maintain trees <1 m and therefore prolonging the period of susceptibility to fire.

- Dublin (1986) demonstrated that elephant browsing (of a compressed population) was a primary factor in woody seedling mortality in the Mara. Dublin found that frequent fires combined with high elephant numbers were converting and maintaining the Mara system as open grassland. She noted that high elephant density was responsible for removing mature trees at the unsustainable rate of 8% a year. Dependence on browse by elephants in the Mara was also exacerbated by poaching pressure outside the reserve keeping the elephants in the Mara all year rather than letting them follow seasonal migration routes as before (Dublin 1995). Compression of elephants in Tsavo National Park in the past also resulted in opening up of the vegetation (Sheldrake 1973, K. Eltringham pers.comm.). By way of contrast elephant have been heavily poached in the northern part of the Serengeti south of the Kenya-Tanzania border, and following reduction in fuel loads (following the heavy grazing by the large number of wildebeest currently in the Serengeti-Mara ecosystem), fires have been reduced in both frequency and severity, resulting a thickening up of the habitat in the 1970s and 1980s (Sinclair 1995). By way of contrast there was little or no regeneration in the nearby Mara (with its high elephant densities) over the same period.

- A similar pattern to that in the Serengeti-Mara emerges in Garamba National Park in the Demorcratic Republic of Congo. Heavy poaching in the north of the Park has eliminated most of the game and significant numbers of the remaining elephants are concentrated in the south of the Park. With frequent fires the south remains open grassland, while the woody vegetation in the north has thickened up and woodlands have developed (K. Hillman-Smith pers.comm, pers obs.).

- Very high black rhino densities in Solio Ranch in Kenya over a protracted period reduced densities of favoured *Acacia drepanalobium* (Whistling thorn) compared to an adjacent fenced area where rhino had been excluded (T.Oloo pers.comm.).

- Current research by Prof. William Bond of the University of Cape Town (pers.comm.) and co-workers in Hluhluwe, suggests that densities of small *A.karroo* (< 1.5m) may be reduced by heavy shoot browsing by species such as black rhino, kudu and giraffe whereas, this species appears to be tolerant of frequent fires; in contrast to small *A.nilotica*'s which seem better able to tolerate herbivory, but appear more fire sensitive. Bond (pers.comm.) hypothesises that the association of *A.karroo* with taller grass areas may in part be related to the protection from black rhino browsing that tall grass gives (this study) allowing the plants to get to a height where they are less palatable and less susceptible to shoot browsing.

However, during the early period of bush encroachment, while numbers of impala and nyala were low, bushbuck were common. Also while number of nyala and impala must have been high in the late 1950s (given estimated numbers in 1964) this was clearly not enough to prevent the widespread development of *A.karroo* thicket over extensive areas of north-east Hluhluwe.

#5: In Kruger National Park, giraffe fed almost exclusively above 1.7 metres and most commonly above 2.75 metres. At these heights there will be almost no competition with black rhino. While in Kenya it has been shown that giraffe are capable of doing half their feeding at heights of less than 2 metres (Leuthold & Leuthold 1972) this does not appear to be the case in Zululand with giraffe populations at lower densities. If anything higher populations of giraffe in the past would probably have kept "*Acacias*" in lower size classes for longer making them more susceptible to being killed by fire, as appears to have been the case in the Serengeti (Pellew 1982). This would have been beneficial to black rhino by reducing the extent of the development of closed woodlands.

#6: As managers will be concerned about future elephant impacts on black rhinos in Hluhluwe-Umfolozi, potential future competition between elephant and black rhino is discussed briefly here although not strictly relevant to the subject of the thesis. The ring barking and pushing over of tall *A.nilotica* and *A.karroo*'s by elephant is beneficial to black rhinos (Chapter 19). Whilst we noticed the elephants in Hluhluwe also favoured the dense riverine bush, most elephant browsing we saw was above black rhino feeding height. Therefore potential competition for browse between elephants and rhinos at current densities appears very limited largely due to feeding height stratification, and the fact that elephants spend much of their time grazing. On a number of occasions we observed cases where elephants facilitated black rhino feeding by knocking over trees which were subsequently browsed upon by black rhinos.

Any potential negative effects in the short term are more likely to be social, given the enmity the two species show for each other. Already in Hluhluwe black rhino killed a young elephant soon after it was introduced; and recently game guards in Hluhluwe reportedly saw elephants kill a black rhino in a dispute over who had right of way on a game path (T.Morely pers comm.).

#7: The seeds of all "Acacias"are eaten by a variety of insects, and the bruchid beetles are predominant among these predators (Coe & Coe 1987). Some "Acacias"that are primarily animal dispersed (eg *A.nilotica*) have evolved thick coats as a means to avoid damage when being eaten by large herbivores. It appears that passage through the gut of a large herbivore can kill beetle eggs on the outside of seeds and pods. In addition the risk of insect attack is reduced as seeds are transported way from parent trees.

Indeed the importance of insect seed predation is illustrated by Coe & Coe's (1987) conclusion that the dispersion of "*Acacia*" seeds by large herbivores is as important for reducing the attention of beetles, as for simply removing the seeds from the vicinity of the parent plant.

If left out for extended periods some authors have reported very high levels of infestation of *Acacia* seeds by beetles (Coe & Coe 1987). For example Lamprey *et al*. (1974) reported that after one year's storage the attack rate of seeds had risen to 99.6%. It is an advantage for the seeds to be quickly eaten by large herbivores as any beetle eggs on the surface of the seeds or pods will be destroyed. Thus mammalian herbivores play an important role in reducing attack levels of bruchid beetles.

However despite this, the widespread use of insecticides may have temporarily removed the majority of insect seed predators in Hluhluwe. This is likely to have greatly increased the numbers of viable seed produced. With the rising number of game species, animal dispersed seed like *A.nilotica* would also have been widely dispersed. Thus the widespread application of insecticides may have contributed to an episodic recruitment of many "*Acacia*" species. Even those seeds that remained near the parent trees that normally would have a high chance of being attacked would have had a far greater chance of surviving to germinate.

#8 If anything the translocations were beneficial to metapopulation conservation contributing to the setting up of better performing populations elsewhere in South Africa, and reducing densities in Hluhluwe. With the benefit of hindsight and what is now known about black rhino feeding ecology and carrying capacity, it is unfortunate that substantially more animals were not removed from Hluhluwe. Modelling indicates that if they had been around the late 1950s, then South Africa would already have met its black rhino conservation plan goal of breeding up 2,000 *D.b.minor*

CHAPTER 23

CONCLUSIONS ON THE CAUSES OF THE HLUHLUWE DECLINE

CAUSES OF THE HLUHLUWE DECLINE

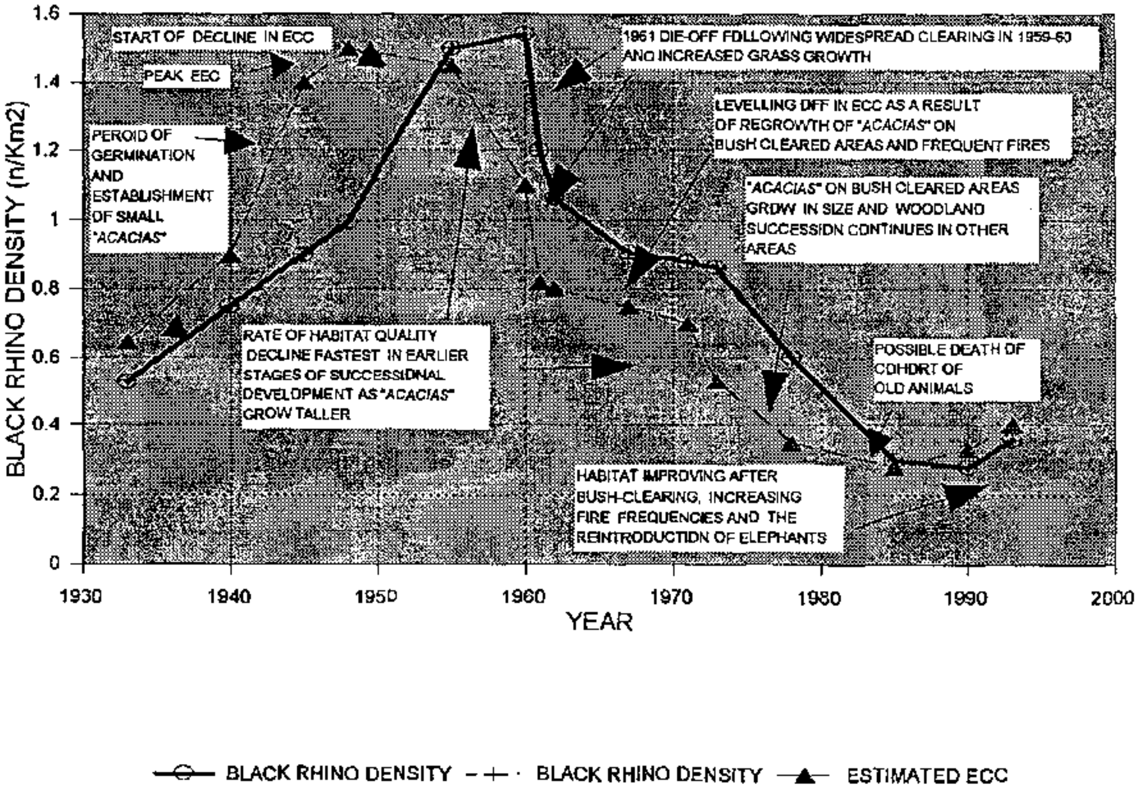
A die-off of 46 black rhino in north-east Hluhluwe over a four month period reduced black rhino densities in north Hluhluwe by 26.0% (177-131) over a four month period (Table 1.1). The rate of decline then slowed over the next decade, and then numbers again fell more rapidly from 1973 to 1991 (Table 1.1). Numbers in northern Hluhluwe bottomed out around 32 (90%CPI 29-35) in 1991 (Source: Adcock *et al.* 1991 - revised estimate calculated using all data 1988-92) representing an 82% decline from peak levels of 177 just prior to the 1961 die off (Table 1.1) and a 75.5% decline from post die-off 1961 levels. The marked declines in black rhino densities have been associated with major negative habitat changes which have reduced black rhino carrying capacity (see below) and coincided with dramatic increases in average home ranges over the same period, from 3-5km^2 in 1962-3 (Hitchins 1969) up to around 7.5km^2 in 1971 (Hitchins 1971) to approximately 15km^2 today (K. Adcock pers.comm. based on unpublished analysis of RMG data from Owen Howison et al 1998).

Based on the evidence presented in this report (chapters 6,7,8and 20) one **must conclude that habitat changes have undoubtedly been the major cause of the Hluhluwe population decline.**

Figure 23.1 shows the hypothesised relationship between black rhino densities and estimated ecological carrying capacity in Hluhluwe over the sixty years 1933-1993, based on a synthesis of the evidence in this thesis. Note that for the whole period from about 1955 until about 1990, the Hluhluwe black rhino population appears to have exceeded hypothesised carrying capacity. Thus population declines were matched by continuing declines in carrying capacity as a result of vegetation changes, and this explains why Caughley's (1986) Partial Compensation Harvesting Model did not hold in Hluhluwe following removals.

The most probable chronological sequence of events is summarised below and in Figure 23.1

FIGURE 23.1: HYPOTHESISED RELATIONSHIP BETWEEN BLACK RHINO DENSITIES AND EEC IN N.HLUHLUWE



1940s AND EARLY 1950s

- The initiation of widespread bush encroachment following heavy grazing temporarily increased black rhino carrying capacity in the 1940s and early 1950s. The high densities of favoured small "*Acacias*" that resulted (especially *A.nilotica*, *A.caffra*, *A.karroo*, and *D.cinerea*) will have temporarily created ideal conditions for black rhinos. Numbers of black rhino bred up to record densities.

LACK OF FIRE IN LATER 1950s AND EARLY 1960s

- Lack of fire in the later 1950s and early 1960s allowed "*Acacia*" scrub to grow beyond the level at which it could be controlled by fire (chapters 15 and 16), and this was reflected in noticeable increases in bush encroachment, and then significant increases in the area of "scrub" on the aerial photographs from 1954-60 (King 1987). As *Acacias* grew taller they became less preferred (chapters 6, 7 and 8) and at later stages of thicket development, physical interference of browse might have contributed to reduced feeding levels (chapter 6).

BY 1960 HLUHLUWE'S CARRYING CAPACITY LIKELY TO HAVE STARTED TO DECLINE

The maturation, and self-thinning of the extensive areas of "*Acacia*" thicket (chapter 20) will have reduced habitat quality for black rhinos by reducing both tree density and palatability of the remaining taller trees and the decline in carrying capacity will have been exacerbated by increased levels of grass interference (chapters 6 and 8) in response to the above average rainfall and heavy removals of grazing herbivores in 1959-60.Thus, by 1960 Hluhluwe's black rhino carrying capacity probably had already declined from peak levels.

Initially this appears to have primarily been reflected in reduced recruitment in the population (reflected in the old age structure recorded for the population by Peter Hitchins in 1963). Thus although peak black rhino densities were recorded in 1961, the evidence suggests that the black rhino population had probably approached or exceeded a declining carrying capacity by 1960, and that peak carrying capacities probably occurred during the earlier, less obvious stages, of *Acacia* encroachment (chapter 20).

1961 DIE OFF IN NORTH EAST HLUHLUWE CATALYSED BY EXTENSIVE CLEARING IN 1959-60

The very extensive bushclearing of black rhino food species in the north-eastern area of Hluhluwe in 1959-1960, at a time of possibly declining carrying capacity, coupled with the increased levels of grass interference will have caused a sudden and abnormally large decline in carrying capacity in the area (chapter 17).

Given limited dispersal opportunities in north eastern Hluhluwe (as neighbouring uncleared areas also had high densities of rhinos), it is hypothesised that the interactive effect of the probable marked decline in dietary quality and increased intake of secondary plant chemicals that would have followed the large scale and sudden drop in carrying capacity in the bushcleared area, could have caused many otherwise apparently healthy looking black rhino to reach a crisis. Their metabolisms would probably have been unable to cope with the high level of conjugation of toxins and neutralisation of acidosis given the combination of their probable lower nutrient intake and increased intake of secondary plant chemicals; and this could have caused rhino to go into an energy crisis (Illius & Jessop 1995) predisposing the animals to die rapidly as a result of massive (undetected) haemolytic crises, which black rhinos are particularly predisposed to under conditions of stress (du Toit 1987, Miller 1994, Paglia 1994).

Indeed, given the exceptionally high density of rhino present at the time it would be very surprising if such a sudden and extensive selective clearing of black rhino food species in north-eastern Hluhluwe in 1959-1960, coupled with increasing levels of grass interference (likely to reduce dietary quality and result in increased consumption of unpalatable plants), was not related to the die-off of 46 animals in the area between the 11 July and 27 October 1961. Noticeably, similar black rhino die-offs did not occur in adjacent uncleared areas. the timing of the end of the die-off also coincided with the early growing season flush period when highly nutritious "*Acacia*" coppice (indicated by the project's limited chemical analyses) will have become available to the animals -

both increasing protein intake and hence significantly increasing the ability of the animals to detoxify secondary plant chemicals (Illius & Jessop 1995) .

IN THE ABSENCE OF BUSH CLEARING A DECLINE IN BLACK RHINO NUMBERS WAS INEVITABLE

Although the extensive bushclearing and culling in 1959-1960 undoubtedly catalysed the 1961 die-off in north eastern Hluhluwe, the decline in black rhino numbers in Hluhluwe was probably inevitable with or without the extensive bushclearing in 1959-60, because given the low fire frequencies at the time, in the absence of clearing (and possibly lack of elephants at the time), *Acacia* woodlands would have continued to develop and mature leading to a continued reduction in black rhino carrying capacity (chapter 20)[#1]

One can speculate that only frequent fires with elephant re-introductions in the late 1940s and 1950s could have kept the Hluhluwe habitat in its optimal state for black rhinos for longer, by maintaining encroaching "*Acacias*" in the most preferred small sizes for longer.

LATER 1960s

The eventual regrowth of small *Acacias* on the extensive bush cleared areas in north eastern Hluhluwe will have in time, benefited the surviving black rhino.

Frequent fires in a below average rainfall period kept bushcleared areas in north Hluhluwe relatively open in the late 1960s, and the underlying decline in rhino numbers appeared to stabilise temporarily (chapter 16).

Nevertheless, in 1970, while there were higher densities of small *Acacias* on Hitchins plots than in 1990 (chapters 10 and 18), the high amount of feeding (especially on normally rejected species) indicated that the still very high density population of black rhinos in northern Hluhluwe was under nutritional stress. The declining carrying capacity since the early 1960s was indicated by increased home ranges in the area (Hitchins 1969, 1971).

CONTINUED BUSH DEVELOPMENT IN THE 1970s AND 1980s

In the early 1970s, fire frequencies once again decreased and rainfall increased, favouring the continued development of large areas of *A.nilotica* closed woodland (eg around Zincakeni - chapters 16 and 20), with maturation of *A.karroo* woodland in some areas (chapter 20) to the detriment of black rhinos (chapter 6,7,20). These successional trends were unchecked due to the lack of elephants until the 1980s, lack of clearing, periods of increased rainfall and reduced fire frequencies. Continued autogenic succession (especially in *A.nilotica* closed woodland) will have further reduced carrying capacity (chapters 7,8 and 20)[#2].

The decline in black rhinos may have been exacerbated by the die off of a cohort of old animals born during the period of peak densities.

IN THE LONGER TERM BUSH CLEARING PROBABLY BENEFICIAL TO BLACK RHINO

With the exception of concentrated very extensive clearing (in 1959-60 in north east Hluhluwe), bushclearing (and later subsequent reclearing) will, in the shorter term, temporarily benefit black rhinos by "turning the clock back on succession", and stimulating regrowth and germination of favoured small *Acacias*. **Given periods of low fire frequencies, and lack of elephants until the 1980s, without bush clearing, the decline in carrying capacity in Hluhluwe in the long term is likely to have been even greater, as maturation of *Acacia* woodland and autogenic succession will have continued unabated.**

INCREASE IN CARRYING CAPACITY IN THE MID-LATE 1990s

The reintroduction of elephant and more grazers, and build up of game numbers following the change to "process-based management" (chapter 19) plus increased bush clearing in the 1990s (including *A.nilotica* closed woodland and *E.racemosa* lowland forest areas) and frequent burning appears to have increased habitat suitability of Hluhluwe for black rhinos. Indeed recent estimates indicate that both black rhino and kudu numbers have started increasing.

However, over the last decade browsing pressure has noticeably increased in northern Hluhluwe (pers.obs), and the future interactive impact of increased numbers of browsers and high fire frequencies remains to be seen.

The noticeable increase in *C.odorata* over the last decade may also reduce carrying capacity in some habitats by smothering food plants such as *A.glabrata* (D. Balfour pers.comm.).

CONCLUSIONS

From the knowledge of black rhino feeding ecology (chapters 6-13 and 20) the known and probable changes in Hluhluwe vegetation composition and structure will have greatly reduced carrying capacity of Hluhluwe for black rhino and were of such a magnitude to have caused the observed decline in rhino numbers.

A number of other factors also indicated that nutritional stress was a key factor in the decline:

- The increase in mortality (especially of males) through fighting in the 1960s (Hitchins & Brooks 1986) was consistent with increased conflict between neighbouring bulls following the observed increases in home range size in response to declining carrying capacity.

-If neonatal calf predation by hyenas was a the major cause of the decline, adult mortality levels should have remained more or less constant. They did not. The Hluhluwe black rhino population instead exhibited all the classic indicators of a nutritionally stressed population (Hitchins & Anderson 1983). The same phenomena have also been demonstrated for elephants under nutritional stress (Laws *et al* 1975);

- The high proportion of unpalatable plants eaten in mid 1960s (Bourquin's Zincakeni plot - chapter 20) and around 1970 (measurement of Hitchins plots - chapter 10)) also indicated that the animals were under severe nutritional stress two decades ago.

VORTEX modelling indicated that either conception rates must have declined or abortion/neonatal mortality must have been high to produce the scale of the observed Hluhluwe decline. While circumstantial evidence collected by Hitchins suggested that hyenas were probably responsible for killing a number of black rhino calves (Hitchins & Anderson 1983; Hitchins 1986), chapters 21 and 22 indicated that hyena predation alone could not have caused the decline. In addition, greatly reduced calf recruitment is to be expected under conditions of nutritional stress.

All the other potential causes of the decline investigated were deemed unimportant or simply were proximal manifestations (eg increased mortality due to fighting) of the ultimate problem caused by high population densities and marked declines in ecological carrying capacity (chapters 21 and chapter 22). The Hluhluwe population has high levels of heterozygosity, (Swart 1994), and its decline could not be linked to demographic stochasticity or inbreeding (chapters 21 and 22). A review of available evidence (chapter 22) indicated that potential browsing competitors nyala, kudu or giraffe were not likely to have caused the decline. Chapter 22 also ruled out droughts, lion predation, disease, prussic-acid poisoning, chemical insect control or haemolytic anaemia as ultimate causes of the decline.

The evidence in Chapters 8,9,15 and 16 indicated that on the whole burning benefitted black rhino in the short-term, by removing grass interference in wet years, maintaining palatable small *Acacias* in their most favoured small spizes for longer, increasing the mortality and hence reducing the establishment of largely unpalatable fire sensitive later successional evergreen species, creating conditions conducive to the early season growth of palatable ground herbs, and increasing palatability of browse immediately following burning (possibly through increasing calcium levels). In the longer-term, Chapters 16 and 20 indicated that it was rather lack of fire in the past (especially from 1955-64) that facilitated the maturation and development of *Acacia* woodlands and subsequent successional changes in *A. nilotica* closed woodlands towards *E.racemosa/B.zeyheri* lowland forest that reduced Hluhluwe's carrying capacity for black rhino. Hitchins' hypotheses that control burning negatively impacts upon black rhino by selectively removing palatable browse plants, and that many more black rhino may have been burnt to death (Anon 1988) were rejected (chapters 9, 15 and 16).

APPLIED RECOMMENDATIONS

Applied recommendations to emerge from both the broader scale and more local reserve specific work of Project Black Rhino 2000 were written up in a document targeted at and distributed to Natal Parks Board management and research staff (copy lodged with Natal Parks Board - optional Appendix) who attended a two day Natal Parks Board BR2000 project recommendations meeting in Hluhluwe-Umfolozi Park in November 1994. Following presentations of the main findings of the project, and a field trip, the workshop then discussed each recommendation in detail. The majority of the recommendations were accepted.

CHAPTER 23 NOTES

#1: This is because favoured spizes will grow into less favoured and eventually rejected taller spizes, and eventually the abundance of generally unpalatable later successional species will increase as autogenic succession proceeds in *Acacia* woodlands. Support for this comes from the fire constrained biplot in chapter 16, the subsequent regrowth and maturation of *Acacia* woodland on bush clearing plots that were not recleared for 20 to 30 years (chapter 18) and the clear relationship between declining black rhino feeding levels and succession in *A.nilotica* areas in transition from grassland to thicket to closed woodland to lowland forest dominated by *E.racemosa* and *B.zeyheri* revealed by chapters 6, 7 and 20.

#2: Once closed *A.nilotica* woodland had developed, intermediate successional species *R.pentheri* and *B.zeyheri* grew taller. Fire would then have rarely penetrated through this woodland allowing more fire sensitive, shade tolerant later successional species such as *E.racemosa, S.inerme*, and *S.myrtina* to establish and mature. Other undercanopy species which increased included *K.floribunda* and *C.caffra*. Eventually taller-growing intermediate and later successional species (*E.racemosa, B.zeyheri, R.pentheri, S.inerme*) matured and overtopped the *A.nilotica* trees to form lowland forest over extensive areas. These successional changes have resulted in significant and major reductions in carrying capacities in these areas (chapter 6, 7 and 20).

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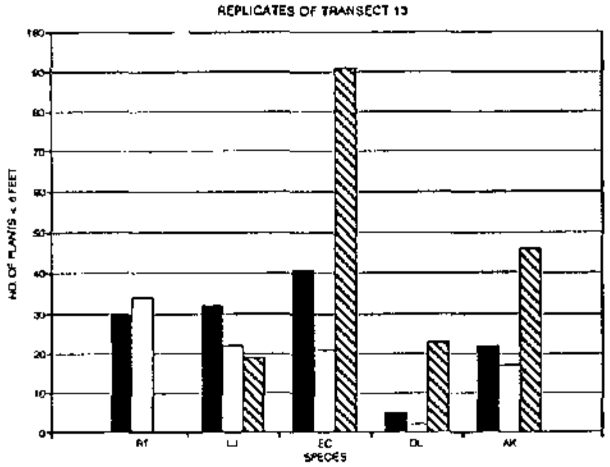
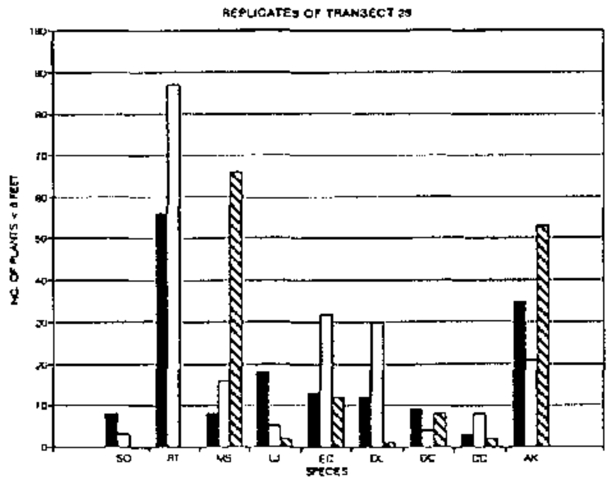
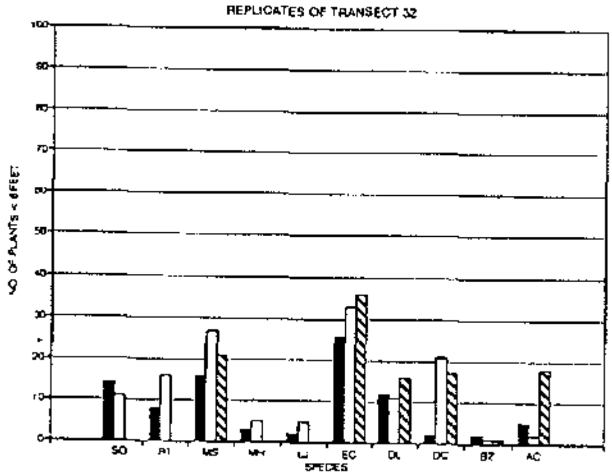
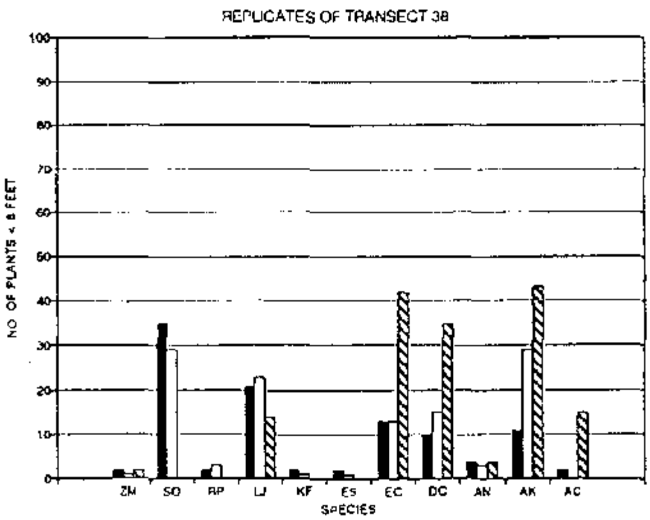
APPENDIX 3.1. Re-measurement of Hitchin's survey, HGR North bush-cleared area.

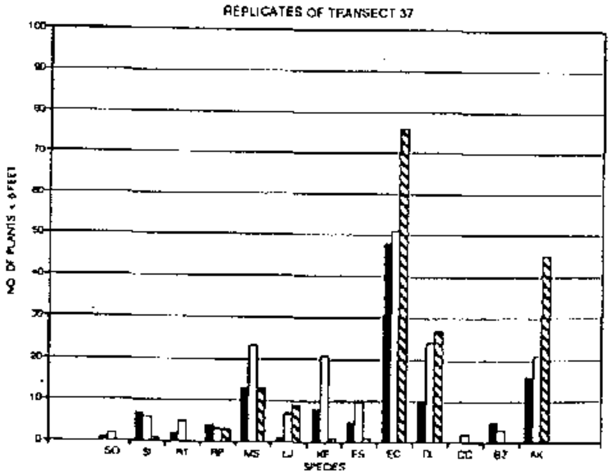
Sample variation due to different positioning of re-measured transects :
The graphs show the densities of plants < 6ft, of the main species, in replicates of the same transects in 1990, versus the those in the transects during Hitchins' time (1969-1973) (WHITE = 1990 replicate 1)
(BLACK = 1990 replicate 2)
(HATCHED = 1969-73 densities)











APPENDIX 3.2. Recent species name changes.

Species	SppName
*dihys	Pyrostria hystrix (Dinocanthium hystrix)
*enspi	Adenopodia schlechteri (Entada spicata)
*eucap	Eugenia natalitia (Eugenia capensis)
*eushi	Euclea racemosa (E.schimperi)
*facap	Zanthoxylum capense (Fagara capensis)
*fison	Ficus glumosa (F.sonderi)
*hibis	Hibiscus/Abutilon spp.
*rhfra	Rhus pyroides (R.fraseri)
*rhmac	Rhus rehmanniana (R.macowannii)
*sccaf	Sclerocarya birrea (S.caffra)
*verno	Vernonia subuligera (V.stipulacea)
*xerud	Coddia rudis (Xeromphis rudis)

APPENDIX 4.1

A LAYMAN'S GUIDE TO SPIZE ORDINATION METHODS; OR HOW TO MAKE SENSE OF BULKY AND COMPLEX HABITAT, ENVIRONMENTAL, MANAGEMENT AND FEEDING DATA

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INTRODUCTION

In the past, woody plant communities have generally been described at a *species* level. However, this approach has its limitations, and it is preferable to instead study vegetation at a *size class* as well as *species* level. This is because different sized individuals of a species represent food sources of differing quantity and quality. In addition, the size structure of a stand of woody vegetation also helps describe its successional status. Functionally a small one metre tall *A.nilotica* bush is very different to a mature flat topped 4m tall *A.nilotica* tree with a dense canopy. For this reason the analyses in this report have focused at a *spize* (SPecies sIZE class) rather than at a *species* level.

This paper looks at the basic principles behind, and output of, a group of multivariate analytical techniques that are collectively known as *ordination* methods. Ordination methods allow us to graphically depict the major variations in habitat composition.

What is perhaps even more important to a conservation manager is the practical implications of how his/her actions are likely to affect habitat composition and structure; and in turn what this all means for key species they may be trying to conserve such as black rhino. New developments in ordination methods allow us to focus on these important conservation concerns. It is not the manager's fault that the output from these methods sometimes has been as clear as mud. The blame lies fairly and squarely with ecologists for not taking the trouble to explain the new methods to their colleagues. This paper aims to correct this situation.

This paper focuses on:

- How we can apply these *ordination* methods to *spize*-based data.
- What the results mean; and in particular how to interpret the graphical output of these methods.
- The kinds of practical problems that can be studied using such methods.

The details of how to do ordinations, and the mathematics behind them, are of no interest to the average reader and are not discussed here. This paper rather concentrates on their value in providing answers to real practical ecological problems and how to interpret their graphical output.

One of the major developments in the analysis of vegetation data in recent years has been the development of so-called ***constrained ordination*** methods. Whilst reducing the complex variations in community composition to a level the human brain can understand, these methods also enable us to directly study how environmental factors and management actions affect habitat species composition (ter Braak 1986, 1987a&b, 1988a&b ter Braak & Prentice 1988).

The application of these ordination methods to spize-based rather than species based data enables us to study habitat structure in addition to species composition; as well as generate hypotheses about probable successional patterns in the vegetation from a single dataset (Austin 1977; Emslie 1991).

The overlaying of contour plots of animal feeding levels onto spize based ordination diagrams further enables us to graphically link feeding levels to community composition and structure. This approach was first used to show how habitat composition and structure influence black rhino browsing levels (Emslie 1993).

One major benefit of these ordination methods is that results of these analyses can be presented in easy to understand pictures.

Spize-based constrained ordination methods therefore offer us a way to get beyond mere vegetation description (of limited use to managers); and start focusing on the factors governing habitat structure, composition and dynamics (very useful to managers). This all sounds marvellous - It is. However, there is a real and quite understandable problem.

Although conservation mangers are increasingly being exposed to *ordination diagrams*; many managers "switch off" as soon as they are presented with such diagrams for one simple reason. Nobody has bothered to take the trouble to explain to them what the hell the diagrams produced by these methods actually represent, or how to interpret them!

While the output from these methods may be easy to understand - it is only easy if you know what to look for. Without any previous training, looking at ordination diagrams must be like trying to read a notice written upside down and back to front. The notice is gobbledegook, until you know that all you need to do is turn it upside down and read its reflection in a mirror. Understanding ordination diagrams involves a similar short "a-Ha" type learning curve. Contrary to popular opinion you do not have to be a "boffin" to understand ordination output.

When the majority of people who could benefit from ordination diagrams can't understand them; and the diagrams contain practically useful information we have a problem. It is not enough for an applied ecologist to produce results that only his/her professional colleagues can understand. He/she must be able to communicate the research findings to a broad spectrum of end users.

It is time that ecologists shared their "secrets" with their conservation colleagues. This represents a Win:Win solution. The results of such work can be of applied value; and ecologists will gain as they can better communicate their research findings. Field conservationists can also gain by being in a position to understand, and apply the new knowledge and insights into system behaviour revealed by the research.

Some conservation managers may still argue that all this technical wizardry is all well and good, but say ..

> "I don't need to know how the research was done or the details of the results;
> I only want to know what the practical implications of the results mean."

One argument against this attitude, is that when you can fully understand the evidence that forms the basis of an argument, you can have much more confidence in the resulting recommendations. You are also more likely to act on them; than if acceptance of recommendations was just a simple matter of faith.

Would you prefer to buy a second hand car on the basis of an AA test report and roadworthy test ?; or just take it on face value from a second hand car salesman that it was the perfect car? I know I would prefer to base my decision on the evidence, unless I had good reason to believe that the salesman was honest and had a reputation of giving fair and unbiased advice. To continue the analogy, you also don't need to be an expert mechanic who knows all about how cars work to be able to tell from an AA report whether the car is a good buy or not.

In just the same way you can get all the benefit from ordination diagrams and yet don't have to know anything about the mathematics and procedures used to build them. The bottom line is that interpreting and understanding the output from spize ordination methods is relatively easy.

In his famous popular book "*A Brief History of Time - From the Big Bang to Black Holes*" Stephen Hawking (1988) says that someone told him that each equation he included in the book would halve his sales. He resolved not to put in any equations, but eventually settled for one : $E=mc^2$!

I have gone one further in this paper - it does not contain any complicated maths or a single equation. I hope the result is intelligible.

I also hope that after reading this paper, you will be able to share the thrill and amazement that ecologists have felt when they realise what these new methods can do.

Above all, after working through the paper you should be able to interpret and understand the graphical output from these ordination methods.

DESCRIBING HABITATS

Habitat species composition and structure is complex, and no two patches of bush are ever exactly alike. While there is pattern in vegetation, the pattern is often messy.

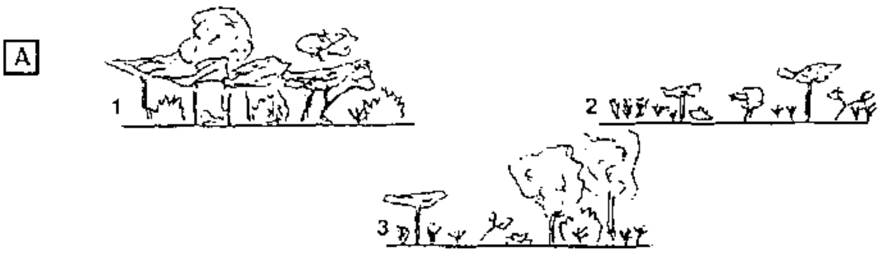
Field experience of a number of workers in bushveld areas has shown it is usually much better and more appropriate to describe habitats according to variation along vegetation composition gradients or continua (instead of trying to pigeonhole plots into neat and discrete habitat types or communities). ***Ordination*** methods form the basis of the identification of the main trends or ***gradients*** in the vegetation.

COLLECTING BASIC HABITAT DATA

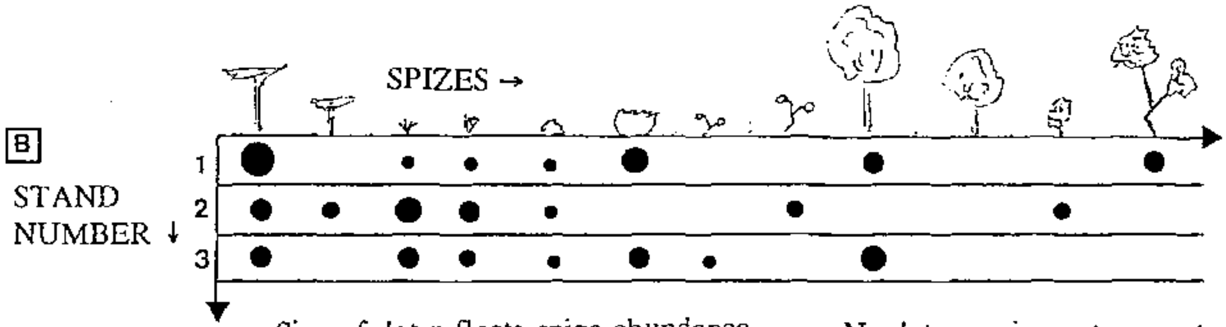
Diagram A shows what the vegetation in three different stands looks like. The stands differ in their make up, with different densities of a range of species and sizes. Ecologists commonly refer to the stands of vegetation that they have measured as ***plots*** or ***transects***.

Diagram B illustrates how habitat structure and composition can be reduced to numbers. Let us suppose, that in the field we have recorded the abundance levels of each spize. The results can be entered into a table. We then end up with a rectangular grid of data with the different spizes along the top, and the different plots down the side. In Diagram B the abundance of each spize is illustrated by the size of the dot. Cells without a dot indicate that particular spize was not present in that particular plot. (Obviously in real life our table would be filled with numbers rather than dots of different sizes).

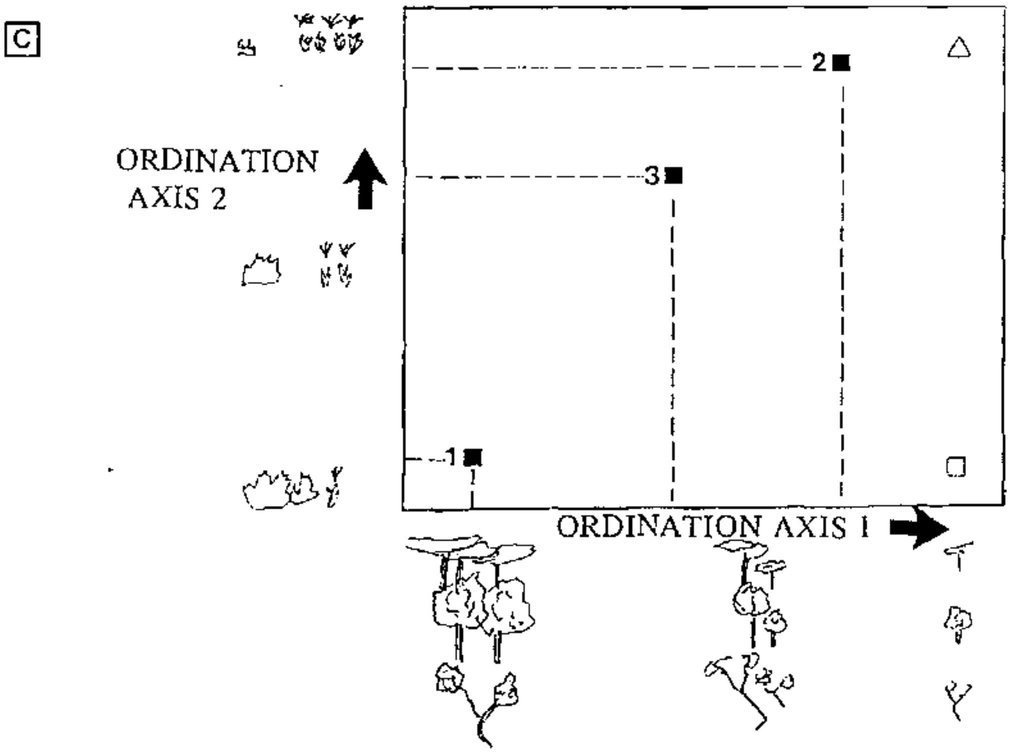
THREE STANDS OF VEGETATION



GRAPHIC REPRESENTATION OF A DATA TABLE



Size of dot reflects spize abundance. No dot = spize not present



BULK AND COMPLEXITY OF VEGETATION DATA

In our example (B), we have a table of 12 spizes (2 size classes of 6 species) by 3 stands. This gives a total of 36 cells in our data table. Although having an identical layout, real world data tables are more complicated that this.

We may record 125 different woody species in our stands. If we further break down our measurements according to four size classes of trees, then we effectively end up describing each stand in terms of the abundance of 500 possible different spizes rather than just 12 as in our example.

In practice one also needs to measure far more than three stands to adequately sample the range of habitat variation. For example, black rhino feeding levels are very variable; and if one is recording the amount of feeding signs in the stands it is necessary to sample a large number of plots. Therefore in practice we are more likely to end up measuring say in the region of 250 plots than only three.

A real life data table with 250 stands and 125 species in 4 size classes may therefore contain 125,000 cells (250 plots by 500 spizes) rather than the 36 in our simplified example. (In reality the number of cells in our raw data table will be less than this, as all species do not usually occur in all four size classes).

In real life, apart from the difficulties of handling and comprehending the sheer amount of data generated by vegetation surveys, the human brain finds it a bit difficult to think in terms of describing vegetation in 500 dimensions!

Fortunately there are mathematical tools that ecologists can use to find and describe the main patterns in the data in a way the human brain can understand (ie 2 to 4 dimensions rather than 500!). One of the main ways to do this is to use ordination methods.

Detrended Correspondence Analysis (DECORANA), Correspondence Analysis, Canonical Correspondence Analysis (CANOCO), Reciprocal Averaging, Factor Analysis and Principal Components Analysis are all examples of ordination methods.

DATA PREPARATION PRIOR TO ORDINATION

It is necessary to pre-process the raw data prior to ordination analysis as such methods are sensitive to rare species or spizes; and are especially sensitive to aberrant sites that are dominated by rare spizes/species. This is not the subject of this paper but is a very necessary step if spize-based ordination methods are to be successfully applied. This process has been automated and RESOURCE software (Emslie 1991) is used to pre-process the raw data. (For further details interested readers should read chapter 5 and/or the notes at the end of the paper)

ORDINATION DIAGRAMS

Ordination methods objectively search for, and describe the main gradient in spize composition in the vegetation. The abundances of the different spizes along this gradient are then quantified. In other words, where a spize occurs along a gradient can be indicated by its score. Spizes and species that commonly occur together (eg. *Spirostachys africana, Plectroniella armata* and *Acacia grandicornuta*) will have similar scores, while spizes from very different communities will have very different scores (e.g. *Acacia caffra* and *Berquaertiodendron natalense*).

Once the species or spize positions along the gradient have been identified, it is then possible to rate each stand according to where it occurs along this gradient. The resultant stand score is a function of its spize composition. Stands dominated by spizes that most commonly occur towards the start of the gradient (i.e. key spizes have low values) will receive a low score. Stands with intermediate scores will tend to be dominated by spizes that have their optima in the middle of the gradient, and so on. Stands with similar spize compositions will get a similar score. Stands that are very different will tend to have very different scores. In ordinations the spize scores are therefore directly linked to the stand scores and visa-versa.

Vegetation doesn't tend to vary along only one gradient. Therefore after building the first gradient, ordination techniques set about examining the remaining variation in the data. A second and subsequent independent gradients are then generated. Vegetation gradients derived using ordination methods are more usually referred to as *axes* by ecologists.

For the sake of this example, we are only going to consider an analysis with only two gradients or axes; although it is possible to build a few more axes if needed.

Spizes and plots can be scored as to where they fit along the second ordination axis in the same way as the were for the first axis.

Each stand (and spize) therefore has a score for each these two axes. We can then plot the position of each stand onto a graph using the first two main ordination axes (ie vegetation gradients) as the X and Y axes. As before, similar stands will occur close to each other, with very different plots being far apart. The only difference is we are dealing with two dimensions instead of one.

The main point to grasp is that we can use ordination methods to objectively reduce the complex data to a level we can understand and visualise (i.e 2+ dimensions rather than 500!). While we lose some information by doing this, we generally more than gain in understanding.

Diagram C shows the positions of our three sites on our derived ordination diagram. The spize pictures on the two axes illustrate the gradients in spize composition along the two axes.

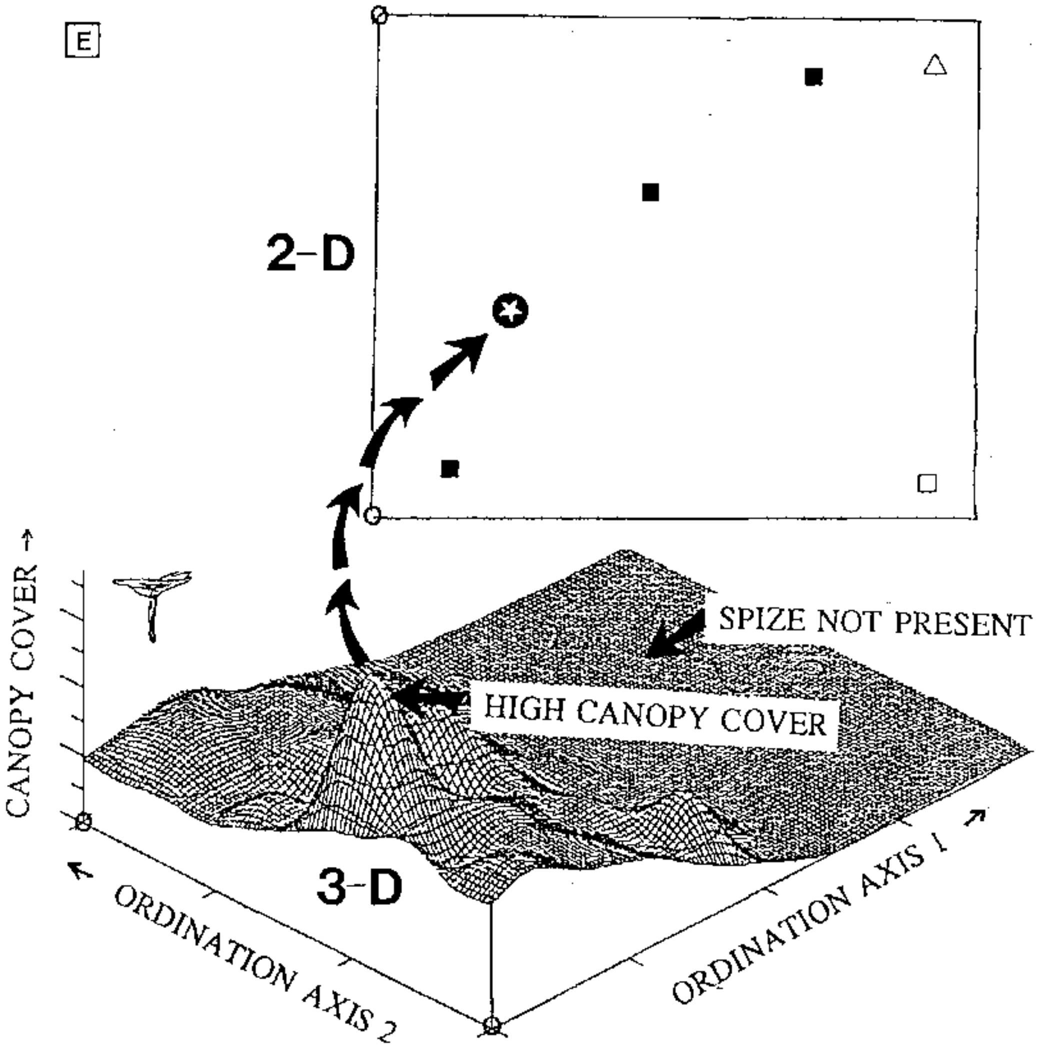
> If we look at the position of plot 1 on Diagram C we can see that it is associated with the tall tree spizes to the far left of the first gradient (X axis) and the big bush spizes at the bottom of the second gradient (Y axis).
>
> We can also see that plot 2 differs more from plot 1 than plot 3 because it is further away on the diagram. This makes sense when we look at the original vegetation plots in Diagram A.
>
> Stand 3 is intermediate in spize composition on both axes.

You should by now see how the ordination has reduced the complicated data to a simple 2D picture where position on the plot indicates spize composition (i.e. species composition and size structure). This also has the advantage that the vegetation is described more appropriately by gradients rather than artificially forcing it into discrete "habitat types" that may not occur in nature.

A further advantage of an ordination plot is that we can estimate the habitat conditions at a site when we know it's axis scores. Let us suppose we have been given the positions of two more plots (the open square and the open triangle on diagram C) on our ordination diagram. From the diagram it is possible to predict the relative spize composition of these two sites (Diagram D). We would expect both plots to be devoid of tall trees, as they both scored high on the first (X) axis. However, the two sites occur at opposite ends of the second (Y) axis. We would therefore expect to find more big bushes in the site shown by the square, and more small scrub in the site shown by the triangle.

We have shown how the position of the sites can be plotted on the ordination diagram (C). In just the same way each spize receives a score on each axis, and so we can also plot the position of spizes on our ordination diagram. Diagram E shows the position of one tall spize associated with low scores on both axes (shown as a circled star). In other words it is most abundant towards the bottom left of our diagram.

The 3D plot in Diagram E shows how the abundance of this particular spize varies throughout the ordination diagram. The position of the spize on the ordination diagram is shown by the circled star. This really reflects its weighted average position on the plot. Generally the spize position on the plot reflects where that spize is most common; and the further away you move from the spize marker on the diagram, the less abundant it will be in the habitat.


E
2-D
3-D
CANOPY COVER →
SPIZE NOT PRESENT
HIGH CANOPY COVER
ORDINATION AXIS 2
ORDINATION AXIS 1

In reality, spizes occur over a range of habitats, but are more common in some than others. Some species also have a wide ecological tolerance and occur in a wide range of communities (eg *Dichrostachys cinerea*) while others may have more restricted distributions (eg. *Harpephyllum caffrum*).

You will notice that the three dimensional picture in Figure E gives much more information about the distribution of the spize throughout the ordination space than simply its averaged position on the 2D diagram. The 3D diagrams give a good indication of the extent of the distribution of different spizes which would be hidden on a simple 2D plot.

Unfortunately to date ecologists have tended to use 2D rather than 3D ordination diagrams. The main reason for this is that none of the standard ordination software packages offers 3D plotting as an option. The creation of 3D plots therefore currently involves additional contour modelling and surface plotting.

RECAP 1

Thus so far we have seen...

How ordination methods can be used to identify and describe the main gradients in vegetation. This enables complex and bulky vegetation data to be reduced to a level the human brain can understand.

That each stand and each spize can be given scores reflecting their overall mean positions along each gradient. These scores can be plotted to produce ordination diagrams.

> *Stands with similar compositions will occur close to each other on the ordination diagrams; while two very dissimilar stands will be far apart on an ordination diagram.*
>
> *Similarly spizes that are commonly associated with each other will also occur close to each other on the diagrams.*
>
> *The spizes most associated with a stand will occur closer to the stand on the ordination diagram, than spizes that generally occur in different habitats.*

The 3D plotting of species abundances over the ordination diagram reveals further information about the relative extent of a species or spize's distribution and ecological tolerance.

USE OF "STATIC" SPIZE ORDINATION TO STUDY SUCCESSION

If we analyse data at a spize level (rather than species level) we can use what is called a "static" ordination approach to generate hypotheses about possible plant succession pathways using a single dataset (Emslie 1991). It is rare that ecologists have the luxury of using a "dynamic" approach to study succession by analysing repeated measurements on the same sites over time.

The assumption behind this "static" approach is that each site represents a sequence in time with the large classes representing the present successional state of the site, and the smaller sizes the possible future composition. By following the path traced by successively larger spizes of key species on ordination diagrams, successional patterns can be detected.

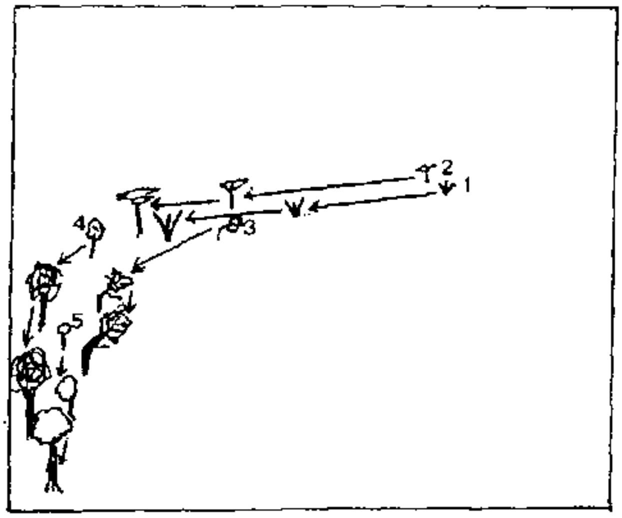
In real data, one will often find that different species come in at different places in the succession with some species eventually dying out to be replaced by other species. Spize ordinations can be very useful in identifying and generating hypotheses about probable successional pathways.

In practice one may find that different successional trends may be taking place in different areas of an ordination diagram. If there are obviously very different processes operating in different landscape units (eg Riverine forest vs. Mistbelt highland forest vs. Woody succession in more open areas) it is generally worth analysing a subset of stands you are interested in (rather than using all the data you collected). In this way the analysis can focus on the subject of interest.

A successional pathway is illustrated by Diagram F. By "joining the dots" we can trace the maturation of the five species shown on the ordination diagram from near the middle to the bottom left. Note how these pathways do not have to be in the form of a straight line. In this simplified case the two species 1 and 2 have matured and grown tall together. Species 3 appears to be intermediate in the succession while Species 4 only appears later when Species 1 and 2 are tall. Species E only seems to develop when species 3 and 4 have grown tall.

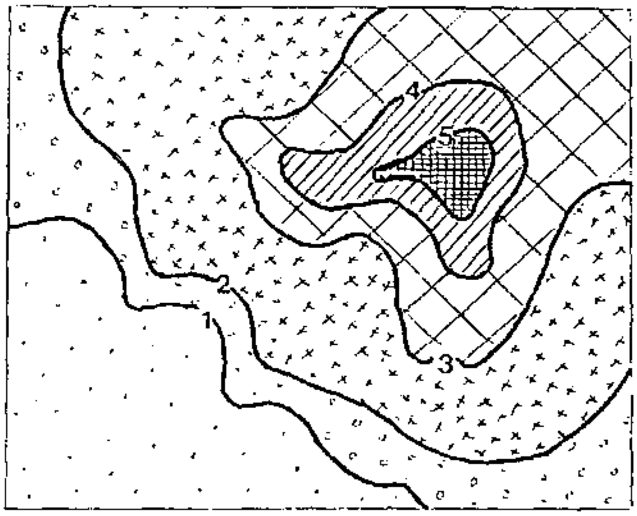
This ordination suggests that species 1 and 2 may change conditions which facilitate the development of later successional species. This hypothesis could be investigated further on the ground.

F



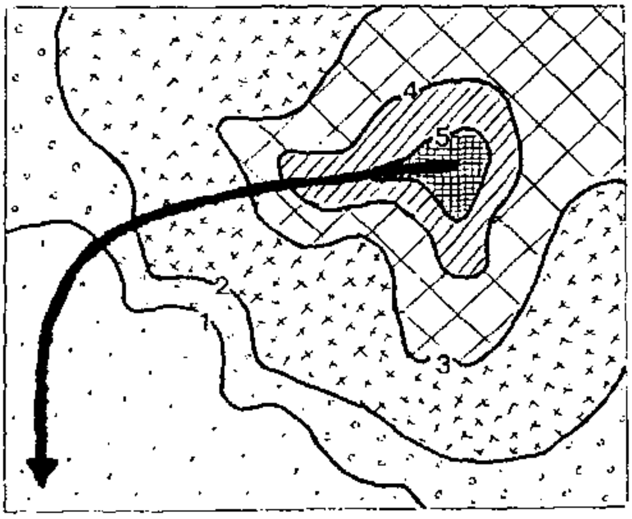
STATIC ORDINATION APPROACH TO THE STUDY OF SUCCESSION

G



CONTOUR MAP OF BLACK RHINO BROWSE OFFTAKE LEVELS

H



SUPERIMPOSITION OF SUCCESSIONAL PATHWAY ON FEEDING MAP

RELATING HABITAT COMPOSITION AND STRUCTURE TO BLACK RHINO FEEDING

If we have also quantified the amount of black rhino feeding sign in each vegetation plot, we can build a contour map showing how black rhino feeding levels vary through ordination space (Diagram G).

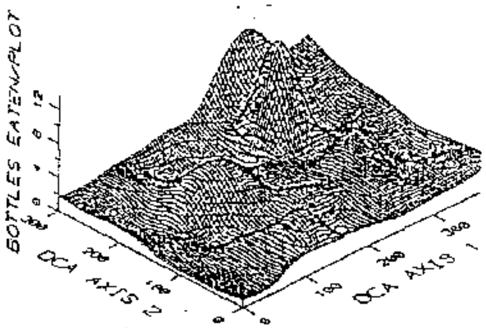
The principle in drawing such a rhino feeding map is the same as drawing a topographical contour, rainfall or air pressure map. In the latter cases we use altitude, rainfall and air pressure readings taken at a number of known locations (recorded as X and Y coordinates on the ground) to make our contour and 3D topographical maps. In the case of rhino feeding levels we have made our measurements at known places in the more abstract vegetation (ie ordination) space, as well as at known locations on the ground (ie. in physical space).

To make the feeding map we simply use vegetation axis 1 and 2 scores to denote the "location" of each stand instead of physical X and Y co-ordinates. We are just dealing with "location" in a more abstract space rather than physical location on the ground. However the principle is the same - we have simply mapped changes in abundance of a variable Z (rhino feeding levels) over a space demarcated by axes X and Y (ordination axis 1 and 2 scores).

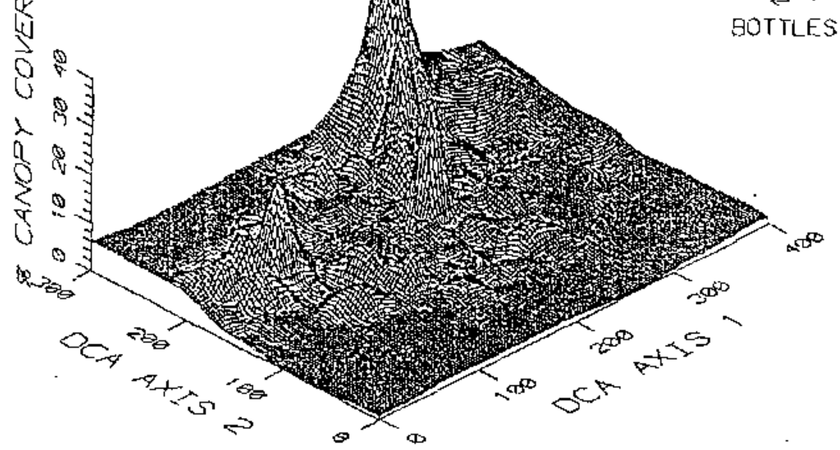
We can then superimpose such a feeding contour map (G) onto the spize ordination picture (F). Our example (H) shows that black rhino feeding levels decline markedly as the vegetation matures from stands dominated by small individuals of species 1 and 2 to stands dominated by species 3,4 and 5. In other words we can link habitat composition and structure to something else (eg black rhino feeding levels) by overlaying a map onto our ordination diagram. In practical terms, if a manager in our imaginary reserve could prevent the vegetation from maturing, and maintain a high abundance of small sizes of species 1 and 2 he/she could prevent black rhino habitat quality from declining. (The actual building of contour maps is a technical issue and will not be discussed here).

A real world example is shown overleaf. The three main surface plots show how the relative abundance (in this case canopy cover) of different sizes of *Acacia nilotica* varies over ordination space in the northern Hluhluwe area of Hluhluwe-Umfolozi Park. The smaller diagram (top right) shows how black rhino offtake levels varied throughout the same ordination space (in this case a 3D surface rather than a 2D contour plot). It is clear that the growth of smaller *A.nilotica*'s (<2m) to become taller trees results in a reduction in black rhino habitat quality.

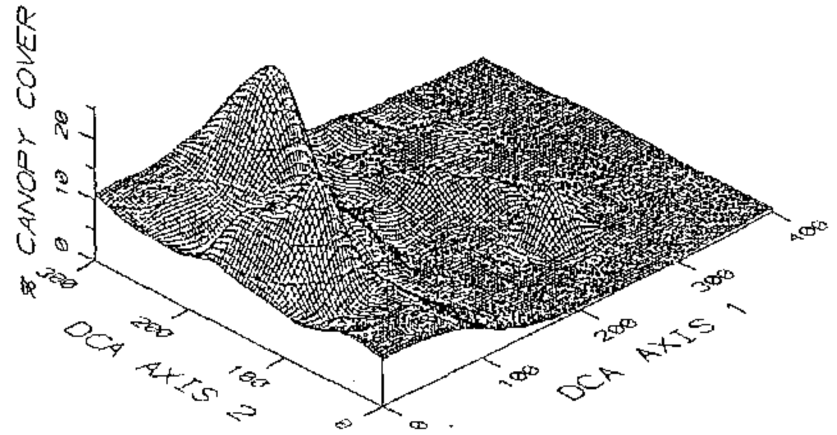
A REAL WORLD EXAMPLE : 3-D PLOTS SHOWING HOW THE ABUNDANCE OF DIFFERENT SIZES OF *Acacia nilotica* VARIES OVER ORDINATION SPACE IN HLUHLUWE GAME RESERVE; AND HOW BLACK RHINO FEEDING LEVELS VARY THROUGHOUT THE SAME ORDINATION SPACE (Top Right). The abundance measure used in this case was % Canopy Cover. Riverine and evergreen mistbelt forest plots were dropped prior to analysis. A "Bottle" is a measure of browse volume. DCA refers to polynomially Detrended Correspondence Analysis.



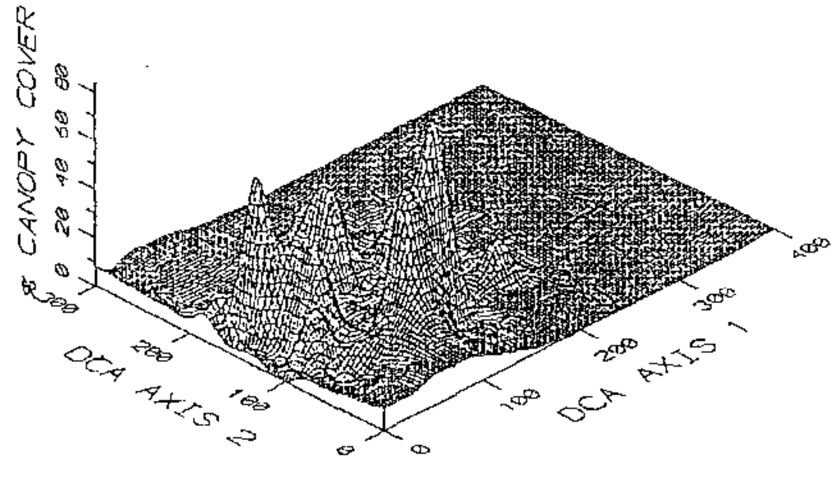
BOTTLES EATEN PER PLOT



Acacia nilotica SIZE 1,2 (<2m) % CANOPY COVER



Acacia nilotica SIZE 3 (2-4m) % CANOPY COVER



Acacia nilotica SIZE 4 (>4m) % CANOPY COVER

RECAP 2

We have further seen that spize based ordination plots can be used to identify and hypothesise about possible successional pathways.

The superimposition of feeding maps onto spize based ordination diagrams also enables one to determine how feeding levels are related to habitat structure and composition, as well as to possible successional pathways.

IDENTIFICATION OF THE FACTORS GOVERNING HABITAT COMPOSITION STRUCTURE AND DYNAMICS

So far we have seen how we can describe habitat in 2 (or 3) dimensional pictures, as well as identifying what different habitats mean to black rhino by overlaying a contour map of feeding levels. From a management point of view the next question may be ...

> "Well that's all very well but what factors cause habitat to be X rather than Y ? In other words what are the effects of my management actions (eg burning, bush clearing, stocking rates, fire policy etc.) on the habitat ? It is not much use knowing which habitat is best for species X, if I don't know how management actions affect habitat species composition and structure."

Fortunately Cajo ter Braak has developed tools to help ecologists answer these important practical questions. His program CANOCO (ter Braak 1988b) is used to undertake these analyses. What does CANOCO do ? ; and perhaps more importantly - How can one interpret and use the results to answer the practical questions above?

The family of techniques he has developed are ***constrained ordination*** methods; with the most common form being ***canonical correspondence analysis***. Constrained ordination axes are usually referred to as ***canonical*** (ie. joint vegetation :environment) axes.

Before we can study how environmental factors and management actions influence community composition we first need to make up an explanatory variable data table (just as we did for the vegetation data). Our raw vegetation data consisted of a big table of spize abundances over a whole set of transects. Our environmental or management data takes a similar form to our vegetation data table (B).

Instead of listing spizes as column headings along the top of the data table (as in B) we can list the various variables describing the basic physical characteristics of each site (e.g. altitude, slope, aspect, soil type etc.) and management histories (eg fire frequencies at different times, time since last fire, time since last chemically bush cleared of "*Acacia's*" etc.) as column headings. Each plot (rows) can then be rated for each explanatory variable to produce an environmental/management data table.

In the past, ecologists were reduced to describing vegetation patterns using ordination methods. Then, as a subsequent and separate exercise, they *indirectly* studied how these vegetation patterns were related to a set of explanatory variables.

Constrained ordination analyses have the advantage that they analyse both data sets together. The final vegetation ordination pattern produced is *constrained* by the explanatory variables. In other words, the analysis relates community composition *directly* to known variation in the environment and/or management treatments that we are interested in.

The key point to grasp is that constrained ordination methods reveal the patterns in the vegetation that are best explained by a given set of explanatory variables, rather than just the overall pattern in vegetation. In effect this means that different sets of explanatory variables can produce different ordinations.

A constrained ordination shows not only the pattern of community variation related to the set of explanatory variables (as in standard ordination); but also the distributions of spizes in relation to the various environmental/management variables.

The degree of dispersion of spize abundances along an environmental variable provides a measure of how well that particular variable (eg soil moisture) explains the spize data. What the constrained ordination analysis is effectively doing is finding the linear combinations of explanatory variables which maximally separates all the spizes. The results of such analyses are often illustrated using a special form of ordination diagram called a ***biplot***. On biplots, the spizes and plots are shown as before - but with the explanatory variables being shown as arrows. Diagram I is an example of such a biplot. The two boxes above the biplot symbolise the two vegetation (A,B,C..) and explanatory (1,2,3..) datasets which together are used to produce the biplot.

In a biplot, the spize and plot points jointly represent the dominant patterns in community composition in so far as these can be explained by the environmental/management variables. The spize points and the explanatory variable arrows jointly reflect the spize distributions along each of the environmental variables. A biplot is therefore a joint picture of both spize and explanatory variables in a single ordination diagram. This allows us to infer the relationship of the different spizes to the different explanatory variables.

Each arrow representing an environmental/management variable determines a direction or "axis" in the ordination plot. The species points can then be projected perpendicularly onto each explanatory variable axis (the arrow can be extended through to the other side of the origin). This has been done for explanatory variable 1 in diagram I. The real beauty of biplots is that the order of the projected points on the arrow approximately corresponds to the ranking of the "***weighted averages***" of the spizes with respect to that explanatory variable. The "weighted average" of a spize basically indicates the "centre of gravity" of that spizes' distribution along an environmental gradient.

This has been illustrated for some of the spizes in Diagram J which represents a cross section through the plot along the line of the arrow for variable 1. To avoid clutter only some of the spizes shown on diagram I have been shown on Diagram J.

Let us suppose that arrow 1 on Diagram I represents fire frequencies over the previous fifty years. Diagram J therefore shows how the abundances of the different spizes vary over the fire frequency gradient. One can see that spizes J and C have a much wider range of distribution (greater realised niche) than spize G. We also can see how spizes M and A are only found at the extremes of the gradient. From the biplot we can conclude that spizes A,B and C are most associated with high fire frequencies while species K,L and M are most associated with the lowest fire frequencies.

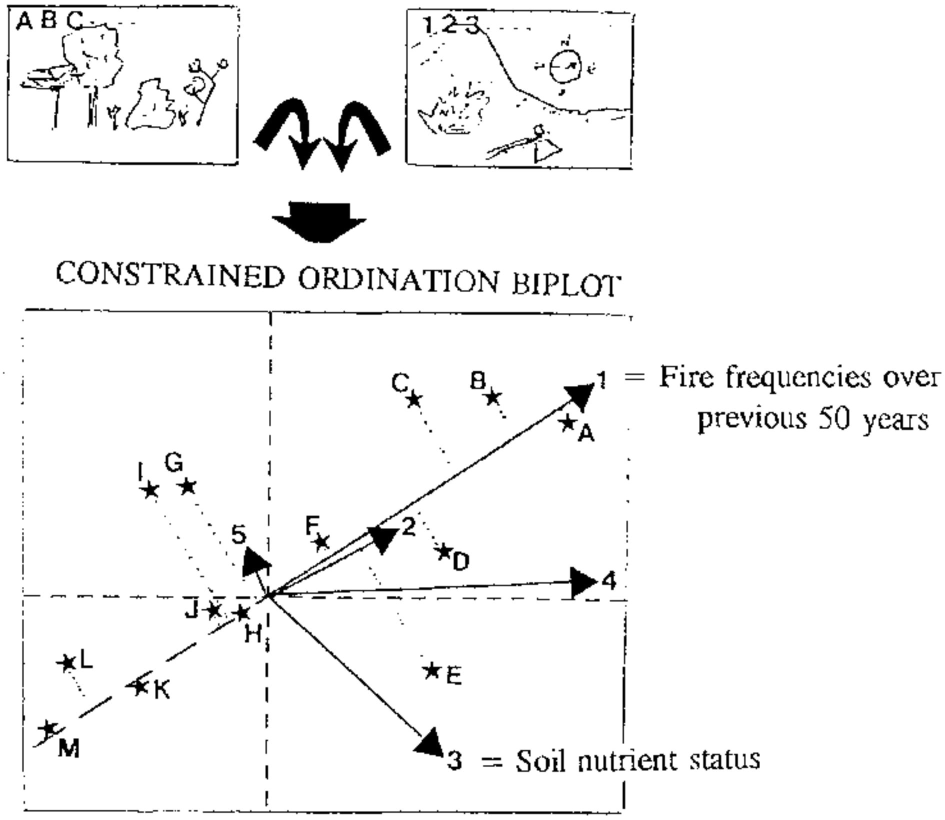
An important feature of biplots is that the angles between arrows indicate whether the explanatory variables work in similar ways or not. Narrow angles indicate the variables have the same effect. The corollary is that biplot arrows at right angles to each other have independent effects. For example the biplot arrows in diagram I for variables 1 and 2 show these variables operate in the same way. By way of contrast, the arrow for variable 3 (soil nutrient status) is almost at right angles to the arrows 1 and 2. This indicates that the influence of soil nutrient status is independent of fire frequencies. For example when projected onto arrow 3, the spizes C, F, J and M are similarly placed along variable 3 at intermediate soil nutrient status levels. Yet we can see that these same spizes are affected very differently by fire with M being fire sensitive and C fire tolerant.

Spizes F and J are either intermediate in tolerance or alternatively are unaffected by fire. Unfortunately the only way to decide which is the case, is to plot out abundance along the axis as done in diagram J. If a spize is unaffected we can expect it to occur all along the axis; whereas if it truly favours an intermediate position we can expect its abundance to peak in the middle.

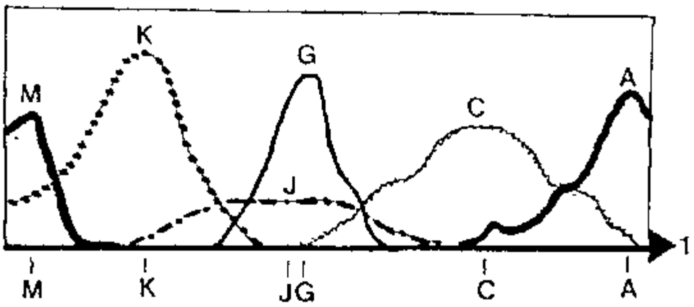
Indeed, the most important current practical shortcoming of ordination plots and biplots is that spizes that are unrelated to the ordination axes tend to be placed in the centre of the ordination diagram and are not distinguished automatically from spizes that have true optima there. Three D plots of species abundance levels in ordination space (see Diagram E) are useful in this regard.

DATA

I



J



PLOT OF SPIZE DISTRIBUTIONS ALONG FIRE FREQUENCY (VARIABLE 1) AXIS
N.B. To avoid clutter only some of the spizes in Diagram I have been shown.

Another useful feature of biplots is that the length of the arrows indicates the importance of the different variables in influencing community composition. In our example (Diagram I) variables 2 and 5 have short arrows meaning they are not very important compared to the other three variables. Variables with very short arrows are often dropped to produce a more parsimonious model.

The biplot also shows that variable 4 is important, and is most strongly associated with the first axis.

We can conclude that Variable 1 has the biggest influence on community composition as it has the longest arrow. Variables 3 and 4 also have long arrows; and are therefore also key determinants of habitat composition. We also can conclude that the effect of variable 3 on habitat composition is independent of the effect of variable 1 because the biplot arrows are almost at right angles to each other.

It is also possible (using CANOCO's Non-Parametric Monte-Carlo Permutations test) to determine whether the derived species:environment relationships shown in the biplots are likely to be real, and were not just spuriously generated by chance (ie whether a derived canonical axis or axes are statistically significant).

OTHER OUTPUT - EIGENVALUES AND INTER-SET CORRELATIONS

The methods also supply useful output to help interpret the results. A number called an *eigenvalue* (shown by the symbol λ) measures the strength of the relationship for each canonical axis. The higher the eigenvalue the more important the ordination axis.

However, even an ordination diagram that explains a small percentage of the total variation in community composition (ie has a small eigenvalue) may be quite informative.

For example, gross changes in vegetation may be primarily related to the physical environment (reflected by the biggest eigenvalues) ; yet management actions may still have important secondary influences on community composition. In most cases we are generally much more interested in the latter.

The *inter-set correlations* provided as part of the output are very useful as they give both the sign and relative importance of different explanatory variables for each of the ordination axes. The bigger the inter-set correlations the bigger the influence of the variable on the axis. High positive and High negative inter-set correlations therefore represent key explanatory variables at opposite ends of a constrained ordination axis.

RECAP 3

Constrained ordinations allow us to directly study how vegetation patterns are influenced by a set of explanatory variables.

The results of constrained ordination are usually presented graphically as biplots. In a biplot the spize and plot points jointly represent the dominant patterns in community composition in so far as these can be explained by the environmental/management variables. A simple spize-based biplot can show complex relationships between a given set of explanatory variables and vegetation composition and structure.

> *The length of biplot arrows show which environmental variables out of a set have the biggest influence on habitat composition and structure, and which ones have little influence. The longer the arrow the more important.*
>
> *The angle between biplot arrows indicates the degree to which particular variables have similar effects. The same angle = similar effects; while angles at right angles have independent effects. In this way superfluous variables that duplicate other variables, or those that have little explanatory power can be dropped.*
>
> *The ordering of perpendicularly projected spizes onto a biplot arrow indicates the approximate order of the different spizes along that particular explanatory variable.*
>
> *The constrained ordination techniques produce statistics that enable one to determine 1) whether the derived biplot is real and not a spurious artefact of chance with no biological meaning; and 2) the relative strength of the relationships between the explanatory variables and the vegetation data.*

PARTIAL CONSTRAINED ORDINATION

The analyses can be further extended in a practically very useful manner. In a ***partial constrained ordination*** the influence of a set of explanatory variables (called ***covariables***) is removed from the data prior to analysis. Analysis then proceeds as before, with the difference that the focus of study is whether the remaining explanatory variables account for any variation in community composition not already accounted for by the covariables.

The lower the eigenvalues, and the shorter the arrows compared to a normal run (without covariables), the more we can conclude that the variation in an explanatory variable is already being explained by the covariables.

Partial constrained ordination is practically very useful as it allows us to answer questions like:

> Is the correlation of community composition with fire simply because particular combinations of physical conditions favour increased grass growth (i.e. greater fuel build-up) and hence such areas are predisposed to being burnt more frequently; rather than fire per se having a significant influence on habitat composition in its own right ?

To solve this "*chicken and egg*" type problem we might enter a whole set of physical variables relating to soil moisture status, microclimate, soil structure and nutrient status (eg altitude, aspect, slope, soil type, underling geology, and soil texture) as covariables; and use a set of fire variables as our explanatory variables. We can then test to see whether the fire variables significantly account for some of the remaining variation in habitat composition on their own. If they do not, we can conclude that burning treatments did not add anything more that could not already be "explained" by the environmental covariables.

Partial analyses also allow us to uncover more subtle yet still important spize/environment/management relationships. For real world examples of the use of partial constrained ordination interested readers should refer to chapters 16 and 18.

The recent development of partial constrained ordination methods have given the adaptive manager a powerful tool. For example, suppose one is testing the effects of bush clearing on some plots. Let us assume that four sites were chosen for an adaptive management experiment; and that in each site, some of the area was cleared and some of the area left uncleared as a control (ie a randomised block sampling design). Let us also suppose that researchers measured habitat composition and structure in cleared and control transects in each site before clearing; and then remeasured them again sometime later.

Within each site, differences between transects almost certainly existed prior to clearing; reflecting both within and between site differences in soil nutrient and moisture status, and past management history. In other words, growth after clearing may partly be a function of both the plot characteristics and prior differences in community composition on the transects. From an applied point of view we are not interested in this. What we want to know is: what was the effect of the clearing treatment? Was it effective?.

Fortunately using partial constrained ordination methods we can now remove any variation due to plot differences in community composition prior to treatment using covariables. Our analyses can then concentrate on determining the effects of our management treatment.

CONCLUSIONS

By superimposing a contour plot of say black rhino feeding onto a constrained (or partial constrained) ordination plot we therefore can summarise a huge amount of complicated detail in only one picture.

The use of constrained and partially constrained ordination biplots enables us to directly study the nature and strengths of relationships between habitat species composition and structure, and the particular explanatory variables we are interested in. A statistical test is available to determine whether the patterns produced by analyses are real or are likely to be spurious.

These ordination methods allow us to make sense of huge and complex vegetation, environmental and management data sets. Furthermore interpretation of the results is made easier as we can show the results as a picture. The use of 3D plots of the distribution of spizes in ordination space further adds to understanding.

It is the author's hope that this paper has enabled non-specialists to interpret and understand the result of spize based ordinations; as well as showing their potential practical conservation value.

ACKNOWLEDGEMENTS:

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Thanks must go to Cajo ter Braak for writing so clearly on the subject of constrained ordination methods.

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NOTES:

PRE-PROCESSING OF DATA USING RESOURCE TO DEAL WITH PROBLEMS OF RARE SPIZES/SPECIES AND ABERRANT STANDS IN ORDINATION

Rare species and spizes can greatly reduce the success of any ordination analyses. This is because rare species/spizes and especially aberrant sites come to dominate the derived ordination axes. It is therefore necessary to identify drop such rare spizes/species and/or stands prior to analysis. A tailor made program RESOURCE has been written by the author (Emslie 1991) to prepare the spize data prior to analysis, and prevent these problems affecting the success of the analysis by identifying rare spizes/species and aberrant sites.

When there is insufficient data to analyse data for each size class of a species separately it is necessary to amalgamate size classes to form composite spizes prior to ordination.

For example, there are only few *Acacia caffra* trees in Hluhluwe that are over 4m high (size 4). Those that are, are just over 4m tall. Basically size 3 and size 4 *A.caffra*'s functionally represent the same thing - tall *A.caffra*. If we were to simply drop data for the spize *A.caffra4* from analysis, we would be throwing away useful information. It therefore makes better sense to make a new composite spize for tall *A.caffra* by amalgamating size classes 3 and four to form a new spize - *A.caffra34*.

In other cases there may only be enough data to describe a less common species at a species level. However just knowing that a species is present still gives us some useful information about a stand (eg. whether or not the forest species *Celtis africana* and *Scutia myrtina* are present in a patch of *Acacia nilotica* dominated woodland).

In more extreme cases all records of rare species should be dropped from the analysis when there is not enough data. It is particularly important to identify and drop any aberrant sites prior to ordination.

The determination of which composite spizes to use in analysis, and which stands should be excluded from analysis because they are aberrant is undertaken using RESOURCE software (Emslie 1991).

In our example with 500 possible different spizes we probably will end up analysing data on around about 110 key spizes and composite spizes. Maybe around 4% of the 250 stands will be flagged as aberrant. Therefore instead of analysing a data table with 125,000 cells; in reality after the raw data have been processed by RESOURCE we would be more likely to end up analysing a data table with just over 26,000 cells (240 stands by 110 common spizes/composite spizes).

As can be imagined the identification of which spizes/composite spizes should be used; and the generation of the new composite spizes from the raw data is a complicated and time consuming business. In the case of a species that has data for all four size classes, there are 8 possible size class combinations to consider, ranging from treating each spize separately through various composite spize combinations to treating the data at a species level. RESOURCE software (Emslie 1991) was written to specifically to automate this process. Doing the task manually is not a practical proposition.

For example, in a real world example from Hluhluwe Game Reserve, 124 different species were recorded in the raw data set of 242 plots. Four size classes were used, and a total of 337 different spizes were recorded. There were a total of 4651 unique plot/spize records in the raw data set. After RESOURCE processing, a total of 109 different spize/composite spize combinations of 47 of the more common species were included in the final dataset. The other 77 species were flagged as rare. A total of 4072 spize combination records were selected out of a possible 15,404 records. Apart from dropping rare species and amalgamating rare spizes; RESOURCE recommended that data from 11 aberrant plots (4.5%) should be excluded from any subsequent ordination analyses.

EXPLANATORY VARIABLE AXES

The linear combinations of explanatory variables used in constrained ordination can be used to produce explanatory variable axes. Just as with the vegetation data we can condense a large number of explanatory variables into just a few environmental or management axes.

PASSIVE VARIABLES OR SPIZES

Ecologists may sometimes refer to *passive* spizes or variables. This does not really need to be of any concern to field conservationists.

There are technical reason why sometimes one needs to exclude some rare spizes and some highly correlated explanatory variables when undertaking constrained ordinations. However, it still is possible to include these spizes and explanatory variables in the final constrained ordination plot. Variables (and spizes) that not used directly to build the ordination axes, but that are still shown on the ordination diagram are called *passive*.

APPENDIX 4.2

MAIN VEGETATION/BROWSING DATABASE (HM) Files = *Hgrid89* n=4651 records

Records in HM contain summary data for each of the 4651 unique spize:plot combination records in the North Eastern and Central Hluhluwe Game Reserve 1989 Grid Study Area.

NAME	VARIABLE DESCRIPTION
RecNum	Record Number (1 to 4651)
Plot	Plot name (Alphanumeric 001 - 242)
Species	5 digit acronym for species name. Genus (2) + Species (3)
Size	Size Class (1: < 1m ; 2: 1m-1.99m ; 3: 2m - 3.99m ; 4: ≥4m)
Spize	Concatenation *Species* + *Size* (6 digit acronym)
N/Plot	Number of individuals per Plot (= 300m^2)
DENxx	Tree density (n/ $^{1}/_{242}$Ha)
X/B/T	The mean number of bottles per individual tree
TB/Plot	Total Bottles in the plot within reach of black rhino (Available). Foliage on spindly individuals which could be pushed over was classed as available.
TBxx	Total Bottles/ $^{1}/_{242}$Ha within reach of black rhino (Available). Foliage on spindly individuals which could be pushed over was classed as available.
FB/Plot	Free Bottles/Plot not hidden by grass (TB/Plot-HB/Plot).
FBxx	Free Bottles/ $^{1}/_{242}$Ha not hidden by grass.
HB/Plot	Bottles hidden by grass / plot (on trees ≤ 2m).
HBxx	Bottles hidden by grass / $^{1}/_{242}$Ha (on trees ≤ 2m).
G.Interf	Grass Intereference - Mean estimated percentage browse hidden by grass per *Spize* (for trees ≤2m)
GRASS2	Grass Interference Class Values (1 : <50% Grass Interference of Available Bottles ; 2: ≥50% ;
GRASS3	Grass Interference Class Values (1 : <33% Grass Interference of Available Bottles ; 2: ≥33% <67% ; 3 : ≥67%)
GRASS4	Grass Interference Class Values (1 : <25% Grass Interference of Available Bottles ; 2: ≥25% <50% ; 3 : ≥50% <75% ; 4 : ≥75)
GRASS5	Grass Interference Class Values (1 : <20% Grass Interference of Available Bottles ; 2: ≥20% <40% ; 3 : ≥40% <60% ; 4 : ≥60% <80% ; 5 : ≥80%)

BBQ	Braun-Blanquet Score with minor classes lumped in class 1 (1: ≤5% Canopy Cover ; 2: 5-25% ; 3: 25-50% ; 4: 50-75% and 5: >75%)
Cover	BBQ score % cover value (class range mid points)
NnoEAT	The number of individual trees and bushes with signs of *both* "old" (grey) and "new" (light) browsing by black rhino.
NnEAT	The number of individuals with signs of *only* "new" (light) browsing by black rhino.
NoEAT	The number of individuals with signs of *only* "old" (grey) browsing by black rhino.
Nold	The number of individuals with signs of "old" (grey) browsing by black rhino.
Nnew	The number of individuals with signs of "new" (light) browsing by black rhino.
Nall	The number of individual trees and bushes with signs of browsing by black rhino.
BnEAT	The total number of "new" bottles eaten in the plot per spize
BoEAT	The total number of "old" bottles eaten in the plot per spize
BallEAT	The total number of "new" and "old" bottles eaten in the plot per spize.
Ballxx	The total number of "new" and "old" bottles eaten per spize per $^1/_{242}$ hectare.
Nallxx	The number of individual trees and bushes with signs of browsing by black rhino $^1/_{242}$ hectare.
BOxx	The total number of "old" bottles eaten per spize per $^1/_{242}$ hectare.
BNxx	The total number of "new" bottles eaten per spize per $^1/_{242}$ hectare.
Visclass	Acronym describing assessment of habitat/physiognomic type based on eyeballing data.
Fcode	Fuzy coded dummy variable for forest type (1 = forest/riverine forest 0.5= forest margin 0 = other).

MAIN EXPLANATORY/BROWSING DATABASE (HP) File = *Hplotdat* n=242 records

Records contain summary data for each of the 242 different plots. The records can be sub-divided into broad data categories.

PLOT NAMES & NUMBERS

NAME	VARIABLE DESCRIPTION
Plotnum	Plot number (Numeric 1 - 242)
Plot	Plot name (Alphanumeric 001 - 242)

PLOT LOCATION

NAME	VARIABLE DESCRIPTION
Xcoor	X Coordinate from Grid used for mapping (1 unit = distance between grids = 450m)
Ycoor	Y Coordinate from Grid used for mapping (1 unit = distance between grids = 450m)
Mapn	Orthophoto Map Number
Dist2DL	Shortest Distance (m) to nearest Drainage Line (measured on Orthophoto's)
Dist2Wat	Distance (m) of Plot from Semi-Permanent to Permanent Water (measured on Orthophoto's)
Log2dl	Log of the Shortest Distance (m) to nearest Drainage Line (measured on Orthophoto's) + 1
Logd2w	Log of the Distance (m) of Plot from Semi-Permanent to Permanent Water (measured on Orthophoto's) + 1

PLOT ALTITUDE, SLOPE AND ASPECT

NAME	VARIABLE DESCRIPTION
Altitude	Altitude (m) taken from Orthophotos
AltGtRiv	Plot altitude above 80m - the lowest altitude recorded along Hluhluwe River in the study area (taken from Orthophorto's).
Logagtr	Log of Plot altitude above 80m + 1 - the lowest altitude recorded along Hluhluwe River in the study area (taken from Orthophorto's).
North	Fuzzy Coding of Dummy Variable for North facing slopes (Slope ≥ 1) : North = 1 North-East and North-West = 0.5
East	Fuzzy Coding of Dummy Variable for East facing slopes (Slope ≥ 1) : East = 1 North-East and South-East = 0.5
South	Fuzzy Coding of Dummy Variable for South facing slopes (Slope ≥ 1) : South = 1 South-East and South-West = 0.5
West	Fuzzy Coding of Dummy Variable for West facing slopes (Slope ≥ 1) : West = 1 North-West and South-West = 0.5

Seasp	Fuzzy Coding of Dummy Variable for South East facing slopes (Slope ≥ 1) : South-East = 1 South and East = 0.5
Nwasp	Fuzzy Coding of Dummy Variable for North West facing slopes (Slope ≥ 1) : North-West = 1 North and West = 0.5
Swasp	Fuzzy Coding of Dummy Variable for South West facing slopes (Slope ≥ 1) : South-West = 1 South and West = 0.5
Neasp	Fuzzy Coding of Dummy Variable for North East facing slopes (Slope ≥ 1) : North-East = 1 North and East = 0.5
Se2nw	Fuzzy Coding of Dummy Variable for South East facing slopes (Slope ≥ 1) : South-East = 1 South and East = 0.5 ####
Sw2ne	Fuzzy Coding of Dummy Variable for South West facing slopes (Slope ≥ 1) : South-West = 1 South and West = 0.5 ####
Se2sa	Fuzzy Coding of Dummy Variable for South East to South facing slopes (Slope ≥ 1) : South-East to South = 1 ####
Slope	A categorised variable (0: Flat ; 1: Gentle >5mm between 5m contours next to plot on orthophoto measured at the angle of the main slope (ie not along transect) ; 2: Medium >2mm but <5mm ; and 3 : Steep <2mm)
Altslp	Interaction variable Altitude * Slope

UNDERLYING GEOLOGY (From Geological Succession (Pre-Cretaceous) Map - Sheet 2832 AA - Fuzzy Coded Dummy Variables)

Dolerite	Dolerite sills and dykes
LowBeauf	Emakwezini Formation Lower Beaufort Series - Sandstone, Sale & Coal
LoMiEcca	Lower Ecca Series - Pietermaritzburg Shales & thin Sandstones; and Middle Ecca - Vryheid Sandstones & Shales
UpprEcca	Upper Ecca Series - Volksrust Shales & thin Sandstones
Breccia	Breccia dykes
ClarStor	Clarens Formation Stormberg Series Argillaceous Sandstones
UppBeauf	Nyoka Formation Upper Beaufort Series Mudstones, Shales & Sandstones
Basalt	Letaba Formation Stormberg Series Amydaloidal Basalt Lavas
Igneous	Igneous rocks
Sedmntry	Sedimentary rocks
Sed_Brec	Sedimentary rocks excluding Breccia dykes
Ecca	Ecca Series
Beaufort	Beaufort series

SOIL (Dummy variables for soil types and estimates of soil texture and depth based on data in Barrow 1986 and MacVicar & DeVilliers 1977)

FreeDRYB	Dummy variable for Soil Type - Freely drained red and yellow brown soils (Hutton & Shortlands forms)
DupAlluv	Dummy variable for Soil Type - Duplex and Alluvial soils (Valsrivier, Oakleaf and Dundee forms)
Blkclay	Dummy variable for Soil Type - Black Clay Soils (Bonheim, Inhoek, Mayo, Milkwood & Rensburg forms)
Lithosol	Dummy variable for Soil Type - Lithosols (Glenrosa & Mispah forms)
RegicSnd	Dummy variable for Soil Type - Regic sands (Fernwood type)
Hutton1	Dummy variable for Soil Form Hutton - Series Msinga & Shorrocks
Hutton2	Dummy variable for Soil Form Hutton - Series Doveton, Makatini, Vimy & Marikana (probably moderately low nutrient status)
Shortlnd	Dummy variable for Soil Form Shortlands - Series Glendale, Richmond, Shortlands (possible moisture stress)
Valsrivr	Dummy variable for Soil Form Valsrivier - Series Arniston & Lindley
Oakleaf	Dummy variable for Soil Form Oakleaf - Series Levubu, Okavango, Jozini, Limpopo, Koedoesvlei & Mutale
Dundee	Dummy variable for Soil Form Dundee - Series Dundee
Bonhm1	Dummy variable for Soil Form Bonheim - Stanger Series
Bonhm2	Dummy variable for Soil Form Bonheim - Series Glengazi & Bonheim (possible moisture stress)
Inhoek	Dummy variable for Soil Form Inhoek - Series Coniston & Drydale
MayoMilk	Dummy variable for Soil Form Mayo Series Msinsini & Soil Form Milkwood Series Milkwood (shallow & possible moisture stress)
Rensburg	Dummy variable for Soil Form Rensburg - Series Phoenix & Rensburg
Glenrosa	Dummy variable for Soil Form Glenrosa - Series Williamson & Trevanian
Mispah	Dummy variable for Soil Form Mispah - Series Mispah
CLAYpc	Estimated % Clay (based on available literature)
SANDpc	Estimated % Sand (based on available literature)
SILTpc	Estimated % Silt (based on available literature)
Bdepth	Score from 1 to 3 reflecting depth of B horizon (based on data in Barrow 1986)

Deep	Fuzzy Dummy variable for Deep Soils
Shallow	Fuzzy Dummy variable for Shallow Soils
SAND	Fuzzy Dummy varaible for sandy soil
S-loam	Fuzzy Dummy variable for Sandy Loam soil (based on available literature)
Sc-loam	Fuzzy Dummy variable for Sandy-Clay-Loam soil (based on available literature)
S-Clay	Fuzzy Dummy variable for Sandy-Clay soil (based on available literature)
C-loam	Fuzzy Dummy variable for Clay-Loam soil (based on available literature)
CLAY	Fuzzy Dummy variable for Clay soil (based on available literature)
Hut1shrt	Fuzzy Dummy variable for Hutton 1 and Shortlands (see Barrow)
Inhkrens	Fuzzy Dummy Variable for Soil Forms Inhoek and Rensburg
Fdr2	Fuzzy Dummy Variable for Hutton 2 Free draining red soils
Logclay	Log of Estimated % Clay+1 (based on available literature)
Logsand	Log of Estimated % Sand+1 (based on available literature)
Logsilt	Log of Estimated % Silt+1 (based on available literature)
Blkclay1	Dummy variable for Soil Type - Black Clay Soils (Bonheim, Inhoek, Mayo, Milkwood & Rensburg forms) ####
Blkclay2	Dummy variable for Soil Type - Black Clay Soils (Bonheim, Inhoek, Mayo, Milkwood & Rensburg forms) ####
Hutton	Fuzzy Dummy variable for Hutton soils

BLACK RHINO BROWSING AND SIGN IN PLOT

NOnEAT	The number of individual trees and bushes per plot with signs of both "old" (grey) and "new" (light) browsing by black rhino.
NnwEAT	The number of individuals per plot with signs of only "new" (light) browsing by black rhino.
OnEAT	The number of individuals per plot with signs of only "old" (grey) browsing by black rhino.
Bn/p	The total number of "new" bottles eaten per plot
Bo/p	The total number of "old" bottles eaten per plot
Ba/p	The total number of "new" and "old" bottles eaten per plot
Nn/p	The number of individual trees and bushes per plot with signs of "old" (grey) browsing by black rhino.

Nn/p	The number of individuals per plot with signs of "new" (light) browsing by black rhino.
Na/p	The number of individuals per plot with signs of browsing by black rhino.
Bnxx	The total number of "new" bottles eaten per $^{1}/_{242}$ hectare
Boxx	The total number of "old" bottles eaten per $^{1}/_{242}$ hectare
Baxx	The total number of "new" and "old" bottles eaten per $^{1}/_{242}$ hectare
Noxx	The number of individual trees and bushes per $^{1}/_{242}$ hectare with signs of "old" (grey) browsing by black rhino.
Nnxx	The number of individuals per $^{1}/_{242}$ hectare with signs of "new" (light) browsing by black rhino.
Naxx	The number of individuals per $^{1}/_{242}$ hectare with signs of browsing by black rhino.

BLACK RHINO BROWSING AND SIGN IN AREA SURROUNDING PLOT

Grdbr	An assessment of the amount of black rhino feeding seen per $\approx$ 225m walking to and $\approx$ 225m from plot (0 : No signs of browsing ; 1 : 0.5 to $<$4 bottles eaten ; 2 : 4 to $\leq$ 10 bottles ; 3 : 10 to $\leq$ 20 bottles and 4 : $\geq$ 20 bottles) This variable provides an index of the feeding in the area surrounding each plot.
Dung	The number of different dung piles seen per $\approx$ 225m walking to and $\approx$ 225m from plot. Two different age lots of dung on a dung pile were counted as 2 not 1. Given problems of differential visibility this gave a very approximate index of black rhino use of the area surrounding each plot.

FIRE HISTORY

Ff55t59	Fire Frequencies per plot for the period 1955 to 1959 - obtained after extracting data from the individual annual NPB burn maps. (Plots which fell on a burn boundary or were listed as a Patchy burn were counted as 0.5)
Ff60t64	Fire Frequencies for the period 1960 to 1964 using methods outlined above.
Ff55t64	Fire Frequencies for the period 1955 to 1964 using methods outlined above.
Ff65t71	Fire Frequencies for the period 1965 to 1971 using methods outlined above.
Ff72t79	Fire Frequencies for the period 1972 to 1979 using methods outlined above.
Ff65t79	Fire Frequencies for the period 1965 to 1979 using methods outlined above.
Ff55t79	Fire Frequencies for the period 1955 to 1979 using methods outlined above.
Ff80t88	Fire Frequencies for the period 1980 to 1988 using methods outlined above.
Ff55t88	Fire Frequencies for the period 1955 to 1988 using methods outlined above.

Fire88	Dummy Variable for Fire the year before measurement. (Plots which fell on a burn boundary or were listed as a Patchy burn were counted as 0.5)

BUSH CLEARING HISTORY (Based on data extracted from NPB bush clearing maps. Plots which were situated on clearing boundaries scored as 0.5)

Fqa	Frequency of Bush Clearing *Acacia*'s since 1957
Fqm	Frequency of Bush Clearing *Maytenus senegalensis* since 1957
Fqe	Frequency of Bush Clearing *Euclea divinorum* since 1957
Afc	Frequency of Chemical treating of *Acacia*'s since 1957
Afp	Frequency of Physical removal of *Acacia*'s since 1957
Afcp	Frequency of Combined Physical & Chemical treatment of *Acacia*'s since 1957
Afd	Frequency of Diesel application on *Acacia*'s since 1957
A60f	Frequency of Bush Clearing *Acacia*'s from 1957-69
A70f	Frequency of Bush Clearing *Acacia*'s from 1970-79
A80f	Frequency of Bush Clearing *Acacia*'s from 1980-Feb 89
Anev	Dummy variable for plot's that have never had bush clearing of *Acacia*'s
Alc60	Dummy variable for plots that were last cleared of *Acacia*'s in 1957-1963
Alc70	Dummy variable for plots that were last cleared of *Acacia*'s in the mid 1970's (1973-77)
Alc80	Variable reflecting time since plots were last cleared of *Acacia*'s in the 1980's (0 = not cleared in 1980's ; 1 = last cleared in 1984 ; 2 = 1985 ; 3: 1986 ; 4: 1987 and 5: 1988)
Alc	Variable reflecting time since plots were last cleared of *Acacia*'s (0 = since 1957 plot has never been bush-cleared ; 1 = last cleared during 1957-1963 ; 2 = last cleared 1973-1977 ; 3: last cleared 1985-March 1989)
Mnev	Dummy variable for plot's that have never had bush clearing of *Maytenus senegalensis*
Mlc70	Dummy variable for plots that were last cleared of *Maytenus senegalensis* in the mid 1970's (1973-77)
Mlc80	Variable reflecting time since plots were last cleared of *Maytenus sengalensis* in the 1980's (0 = not cleared in 1980's ; 1 = last cleared in 1984 ; 2 = 1985 ; 3: 1986 ; 4: 1987, 5: 1988 and 6 : Jan-Mar 1989)
Mfc	Frequency of Chemical treating of *Maytenus senegalensis* since 1957
Mfp	Frequency of Physical removal of *Maytenus senegalensis* since 1957

Mfcp	Frequency of Combined Physical & Chemical treatment of *Maytenus senegalensis* since 1957
Mfd	Frequency of Diesel application on *Maytenus senegalensis* since 1957
Atslc60	Dummy variable for plots that were last chemically treated of *Acacia*'s in the the late 1950'2 and early 1960's (1957-1960)
Atslc80	Variable reflecting time since plots were last chemically cleared of *Acacia*'s in the 1980's (0 = not cleared in 1980's ; 1 = last cleared in 1984 ; 2 = 1985 ; 3: 1986 ; 4: 1987 and 5: 1988)

GRASS INTERFERENCE

GrassHt	Modal plot grass height (cm)
GHtClass4	Modal plot grass height (cm) expressed as a categorical variable with a 50cm class interval.
GHtClass6	Modal plot grass height (cm) expressed as a categorical variable with a 33cm class interval.
GHtClass8	Modal plot grass height (cm) expressed as a categorical variable with a 25cm class interval.
HB12	Total number of bottles on trees <2m hidden by grass (Bottles/Ha)
HB1	Total number of bottles on trees <1m (Size 1) hidden by grass (Bottles/Ha)
HB2	Total number of bottles on trees <2m but >1m (Size 2) hidden by grass (Bottles/Ha)
GrassInt	Mean % Grass Interference (Total HB/Plot expressed as a % of the total TB/Plot on trees <2m).
Gint1	Mean % Grass Interference on trees <1m
Gint2	Mean % Grass Interference on trees 1-2m
Gint12	Mean % Grass Interference on trees <2m
G1c2	Size 1 (<1m) Mean Grass Interference Class Values (1 : <50% Grass Interference of Available Bottles ; 2: ≥50%
G1c3	Size 1 (<1m) Mean Grass Interference Class Values (1 : <33% Grass Interference of Available Bottles ; 2: ≥33% <67% ; 3 : ≥67%)
G1c4	Size 1 (<1m) Mean Grass Interference Class Values (1 : <25% Grass Interference of Available Bottles ; 2: ≥25% <50% ; 3 : ≥50% <75% ; 4 : ≥75)
G1c5	Size 1 (<1m) Mean Grass Interference Class Values (1 : <20% Grass Interference of Available Bottles ; 2: ≥20% <40% ; 3 : ≥40% <60% ; 4 : ≥60% <80% ; 5 : ≥80%)
G12c2	Size 12 (<2m) Mean Grass Interference Class Values (1 : <50% Grass Interference of Available Bottles ; 2: ≥50%
G12c3	Size 12 (<2m) Mean Grass Interference Class Values (1 : <33% Grass

	Interference of Available Bottles ; 2: ≥33% <67% ; 3 : ≥67%)
G12c4	Size 12 (<2m) Mean Grass Interference Class Values (1 : <25% Grass Interference of Available Bottles ; 2: ≥25% <50% ; 3 : ≥50% <75% ; 4 : ≥75)
G12c5	Size 12 (<2m) Mean Grass Interference Class Values (1 : <20% Grass Interference of Available Bottles ; 2: ≥20% <40% ; 3 : ≥40% <60% ; 4 : ≥60% <80% ; 5 : ≥80%)
G2c2	Size 2 (1-2m) Mean Grass Interference Class Values (1 : <50% Grass Interference of Available Bottles ; 2: ≥50%
G2c3	Size 2 (1-2m) Mean Grass Interference Class Values (1 : <33% Grass Interference of Available Bottles ; 2: ≥33% <67% ; 3 : ≥67%)
G2c4	Size 2 (1-2m) Mean Grass Interference Class Values (1 : <25% Grass Interference of Available Bottles ; 2: ≥25% <50% ; 3 : ≥50% <75% ; 4 : ≥75)
G2c5	Size 2 (1-2m) Mean Grass Interference Class Values (1 : <20% Grass Interference of Available Bottles ; 2: ≥20% <40% ; 3 : ≥40% <60% ; 4 : ≥60% <80% ; 5 : ≥80%)

PLOT PHYSIOGNOMY

DEN1	Total density of trees (n/Ha) of size class 1 (<1m)
DEN2	Total density of trees (n/Tree) of size class 2 (1-2m)
DEN3	Total density of trees (n/Tree) of size class 3 (2-4m)
DEN4	Total density of trees (n/Trees) of size class 4 (>4m)
DEN	Total tree density of trees in plot (n/Ha)

PLOT BROWSE BOTTLE DENSITIES

TB1	Total Browse Bottles available on Size 1 trees (<1m) expressed in Bottles/Ha
TB2	Total Browse Bottles available on Size 2 trees (1-2m) expressed in Bottles/Ha
TB3	Total Browse Bottles available on Size 3 trees (2-4m) expressed in Bottles/Ha
TB4	Total Browse Bottles available on Size 4 trees (>4m) expressed in Bottles/Ha
TB1234	Total Browse Bottles available on all trees expressed in Bottles/Ha
FB1	Free Browse Bottles (ie. not hidden by grass) available on Size 1 trees (<1m) expressed in Bottles/Ha
FB2	Free Browse Bottles available on Size 2 trees (1-2m) expressed in

	Bottles/Ha
FB1234	Free Browse Bottles available on all trees expressed in Bottles/Ha

MAIN VEGETATION/BROWSING DATABASE (UM) File = Ugrid89 n=2354 records

Records in UM contain summary data for each of the 2354 unique spize:plot combination records in the North Western Umfolozi Game Reserve 1989 Grid Study Area.

NAME	VARIABLE DESCRIPTION
RecNum	Record Number (1 to 2354)
Plot	Plot name (Alphanumeric 001 - 242)
Species	5 digit acronym for species name. Genus (2) + Species (3)
Size	Size Class (1: $<$ 1m ; 2: 1m-1.99m ; 3: 2m - 3.99m ; 4: $\geq$ 4m)
Spize	Concatenation *Species* + *Size* (6 digit acronym)
N/Plot	Number of individuals per Plot ($\approx$ 300m^2)
DENxx	Tree density (n/ $^{1}/_{187}$hectare)
X/B/T	The mean number of bottles per individual tree
TB/Plot	Total Bottles in the plot within reach of black rhino (Available). Foliage on spindly individuals which could be pushed over was classed as available.
TBxx	Total Bottles/ $^{1}/_{187}$Ha within reach of black rhino (Available). Foliage on spindly individuals which could be pushed over was classed as available.
FB/Plot	Free Bottles/Plot not hidden by grass (TB/Plot-HB/Plot).
FBxx	Free Bottles/ $^{1}/_{187}$Ha not hidden by grass.
HB/Plot	Bottles hidden by grass / plot (on trees $\leq$ 2m).
HBxx	Bottles hidden by grass / $^{1}/_{187}$Ha (on trees $\leq$ 2m).
G.Interf	Grass Intereference - Mean estimated percentage browse hidden by grass per *Spize* (for trees $\leq$ 2m)
GRASS2	Grass Interference Class Values (1 : $<$50% Grass Interference of Available Bottles ; 2: $\geq$50%
GRASS3	Grass Interference Class Values (1 : $<$33% Grass Interference of Available Bottles ; 2: $\geq$33% $<$67% ; 3 : $\geq$67%)
GRASS4	Grass Interference Class Values (1 : $<$25% Grass Interference of Available Bottles ; 2: $\geq$25% $<$50% ; 3 : $\geq$50% $<$75% ; 4 : $\geq$75)
GRASS5	Grass Interference Class Values (1 : $<$20% Grass Interference of Available Bottles ; 2: $\geq$20% $<$40% ; 3 : $\geq$40% $<$60% ; 4 : $\geq$60% $<$80% ; 5 : $\geq$80%)
BBQ	Braun-Blanquet Score with minor classes lumped in class 1 (1: $\leq$5% Canopy Cover ; 2: 5-25% ; 3: 25-50% ; 4: 50-75% and 5: $>$75%)

Cover	BBQ score % cover value (class range mid points)
NnoEAT	The number of individual trees and bushes with signs of *both* "old" (grey) and "new" (light) browsing by black rhino.
NnEAT	The number of individuals with signs of *only* "new" (light) browsing by black rhino.
NoEAT	The number of individuals with signs of *only* "old" (grey) browsing by black rhino.
Nold	The number of individuals with signs of "old" (grey) browsing by black rhino.
Nnew	The number of individuals with signs of "new" (light) browsing by black rhino.
Nall	The number of individual trees and bushes with signs of browsing by black rhino.
BnEAT	The total number of "new" bottles eaten in the plot per spize
BoEAT	The total number of "old" bottles eaten in the plot per spize
BallEAT	The total number of "new" and "old" bottles eaten in the plot per spize.
Ballxx	The total number of "new" and "old" bottles eaten per spize per $^{1}/_{187}$hectare.
Nallxx	The number of individual trees and bushes with signs of browsing by black rhino per $^{1}/_{187}$ hectare.
BOxx	The total number of "old" bottles eaten per spize per $^{1}/_{187}$hectare.
BNxx	The total number of "new" bottles eaten per spize per $^{1}/_{187}$hectare.

MAIN EXPLANATORY/BROWSING DATABASE (UP) File = *Uplotdat* n=187 records

Records contain summary data for each of the 187 different plots in the NW Umfolozi Grid Survey Study Area. The records can be sub-divided into broad data categories.

NAME	VARIABLE DESCRIPTION
PLOT NAMES & NUMBERS	
UOrignum	Original Plot Number (Numeric 1 - 187)
Plotnum	Plot number (Numeric 301 - 487)
Plot	Plot name (Alphanumeric 301 - 487)
PLOT LOCATION	
Xcoor	X Coordinate from Grid used for mapping (1 unit = distance between grids = 500m)
Ycoor	Y Coordinate from Grid used for mapping (1 unit = distance between grids = 500m)
PLOT ALTITUDE, SLOPE AND ASPECT	
Altitude	Altitude (m) taken from Orthophotos
AltGtRiv	Plot altitude above the lowest altitude recorded along Black Umfolozi River in the study area (taken from Orthophorto's).
North	Fuzzy Coding of Dummy Variable for North facing slopes (Slope ≥ 1) : North = 1 North-East and North-West = 0.5
East	Fuzzy Coding of Dummy Variable for East facing slopes (Slope ≥ 1) : East = 1 North-East and South-East = 0.5
South	Fuzzy Coding of Dummy Variable for South facing slopes (Slope ≥ 1) : South = 1 South-East and South-West = 0.5
West	Fuzzy Coding of Dummy Variable for West facing slopes (Slope ≥ 1) : West = 1 North-West and South-West = 0.5
Slope	A categorised variable (0: Flat ; 1: Gentle >5mm between 5m contours next to plot on orthophoto measured at the angle of the main slope (ie not along transect) ; 2: Medium >2mm but <5mm ; and 3 : Steep <2mm)
BLACK RHINO BROWSING AND SIGN IN PLOT	
NOnEAT	The number of individual trees and bushes per plot with signs of both "old" (grey) and "new" (light) browsing by black rhino.

NowEAT	The number of individuals per plot with signs of only "new" (light) browsing by black rhino.
OnEAT	The number of individuals per plot with signs of only "old" (grey) browsing by black rhino.
NBot	The total number of "new" bottles eaten per plot
OBot	The total number of "old" bottles eaten per plot
NOBot	The total number of "new" and "old" bottles eaten per plot
OLDn	The number of individual trees and bushes per plot with signs of "old" (grey) browsing by black rhino.
NEWn	The number of individuals per plot with signs of "new" (light) browsing by black rhino.
ALLn	The number of individuals per plot with signs of browsing by black rhino.

FIRE HISTORY

Ff55t64	Fire Frequencies for the period 1955 to 1964 - Data extracted from NPB burn maps.
Ff65t71	Fire Frequencies for the period 1965 to 1971 using methods outlined above.
Ff72t79	Fire Frequencies for the period 1972 to 1979 using methods outlined above.
Ff80t88	Fire Frequencies for the period 1980 to 1988 using methods outlined above.
Fire88	Dummy Variable for Fire the year before measurement. (Plots which fell on a burn boundary or were listed as a Patchy burn were counted as 0.5)
Ff55t88	Fire Frequencies for the period 1955 to 1988 using methods outlined above.

GRASS INTERFERENCE

GrassHt	Modal plot grass height (cm)
HB12	Total number of bottles on trees <2m hidden by grass (Bottles/Ha)
HB1	Total number of bottles on trees < 1m (Size 1) hidden by grass (Bottles/Ha)
HB2	Total number of bottles on trees <2m but > 1m (Size 2) hidden by grass (Bottles/Ha)
GrassInt	Mean % Grass Interference (Total HB/Plot expressed as a % of the total TB/Plot on trees <2m).
GINT1	Mean % Grass Interference on trees < 1m
GINT2	Mean % Grass Interference on trees 1-2m

G1c2	Size 1 (<1m) Mean Grass Interference Class Values (1 : <50% Grass Interference of Available Bottles ; 2: ≥50%
G1c3	Size 1 (<1m) Mean Grass Interference Class Values (1 : <33% Grass Interference of Available Bottles ; 2: ≥33% <67% ; 3 : ≥67%)
G1c4	Size 1 (<1m) Mean Grass Interference Class Values (1 : <25% Grass Interference of Available Bottles ; 2: ≥25% <50% ; 3 : ≥50% <75% ; 4 : ≥75)
G1c5	Size 1 (<1m) Mean Grass Interference Class Values (1 : <20% Grass Interference of Available Bottles ; 2: ≥20% <40% ; 3 : ≥40% <60% ; 4 : ≥60% <80% ; 5 : ≥80%)
G12c2	Size 12 (<2m) Mean Grass Interference Class Values (1 : <50% Grass Interference of Available Bottles ; 2: ≥50%
G12c3	Size 12 (<2m) Mean Grass Interference Class Values (1 : <33% Grass Interference of Available Bottles ; 2: ≥33% <67% ; 3 : ≥67%)
G12c4	Size 12 (<2m) Mean Grass Interference Class Values (1 : <25% Grass Interference of Available Bottles ; 2: ≥25% <50% ; 3 : ≥50% <75% ; 4 : ≥75)
G12c5	Size 12 (<2m) Mean Grass Interference Class Values (1 : <20% Grass Interference of Available Bottles ; 2: ≥20% <40% ; 3 : ≥40% <60% ; 4 : ≥60% <80% ; 5 : ≥80%)
G2c2	Size 2 (1-2m) Mean Grass Interference Class Values (1 : <50% Grass Interference of Available Bottles ; 2: ≥50%
G2c3	Size 2 (1-2m) Mean Grass Interference Class Values (1 : <33% Grass Interference of Available Bottles ; 2: ≥33% <67% ; 3 : ≥67%)
G2c4	Size 2 (1-2m) Mean Grass Interference Class Values (1 : <25% Grass Interference of Available Bottles ; 2: ≥25% <50% ; 3 : ≥50% <75% ; 4 : ≥75)
G2c5	Size 2 (1-2m) Mean Grass Interference Class Values (1 : <20% Grass Interference of Available Bottles ; 2: ≥20% <40% ; 3 : ≥40% <60% ; 4 : ≥60% <80% ; 5 : ≥80%)

PLOT PHYSIOGNOMY

DEN1	Total density of trees (n/Ha) of size class 1 (<1m)
DEN2	Total density of trees (n/Ha) of size class 2 (1-2m)
DEN3	Total density of trees (n/Ha) of size class 3 (2-4m)
DEN4	Total density of trees (n/Ha) of size class 4 (>4m)
TOTDEN	Total tree density of trees in plot (n/Ha)
DEN1xx	Total density of trees (n per $^{1}/_{157}$ hectare) of size class 1 (<1m)
DEN2xx	Total density of trees (n per $^{1}/_{157}$ hectare) of size class 2 (1-2m)
DEN3xx	Total density of trees (n per $^{1}/_{157}$ hectare) of size class 3 (2-4m)

DEN4xx	Total density of trees (n per $^{1}/_{187}$ hectare) of size class 4 (>4m)
TOTDENxx	Total tree density of trees in plot (n/per $^{1}/_{187}$ hectare)

PLOT BROWSE BOTTLE DENSITIES

TB1	Total Browse Bottles available on Size 1 trees (<1m) expressed in Bottles/Ha
TB2	Total Browse Bottles available on Size 2 trees (1-2m) expressed in Bottles/Ha
TB3	Total Browse Bottles available on Size 3 trees (2-4m) expressed in Bottles/Ha
TB4	Total Browse Bottles available on Size 4 trees (>4m) expressed in Bottles/Ha
TB1234	Total Browse Bottles available on all trees expressed in Bottles/Ha
FB1	Free Browse Bottles (ie. not hidden by grass) available on Size 1 trees (<1m) expressed in Bottles/Ha
FB2	Free Browse Bottles available on Size 2 trees (1-2m) expressed in Bottles/Ha
FB1234	Free Browse Bottles available on all trees expressed in Bottles/Ha
TB1xx	Total Browse Bottles available on Size 1 trees (<1m) expressed in Bottles per $^{1}/_{187}$ hectare
TB2xx	Total Browse Bottles available on Size 2 trees (1-2m) expressed in Bottles per $^{1}/_{187}$ hectare
TB3xx	Total Browse Bottles available on Size 3 trees (2-4m) expressed in Bottles per $^{1}/_{187}$ hectare
TB4xx	Total Browse Bottles available on Size 4 trees (>4m) expressed in Bottles per $^{1}/_{187}$ hectare
TB1234xx	Total Browse Bottles available on all trees expressed in Bottles per $^{1}/_{187}$ hectare
FB1xx	Free Browse Bottles (ie. not hidden by grass) available on Size 1 trees (<1m) expressed in Bottles per $^{1}/_{187}$ hectare
FB2xx	Free Browse Bottles available on Size 2 trees (1-2m) expressed in Bottles per $^{1}/_{187}$ hectare
FB1234xx	Free Browse Bottles available on all trees expressed in Bottles per $^{1}/_{187}$ hectare

MAIN POOLED VEGETATION/BROWSING DATABASE (UM) File = Jntgrid89 n=7005 records

Records contain summary data for each of the 7005 unique spize:plot:reserve combination records in both Grid study areas. The pooled variables are not listed here as their names are self-explanatory, and the same as those in the files above.

MAIN JOINT EXPLANATORY/BROWSING DATABASE File = Jntpltdt n=429 records

Records contain summary data for each of the 429 different plots in both Grid Study Areas. The pooled variables are not listed here as their names are self-explanatory, and the same as those in the files above.

APPENDIX 5.1 : AN EXAMPLE OF A RESOURCE OUTPUT FILE

An example RESOURCE output file follows. The file was generated during a resource level analysis of Braun-Blanquet abundance data for woody plants in Hluhluwe Game Reserve in 1989. Data were collected on 124 species in 242 plots. Data were collected separately for four size classes 1: SMALL (Less than 1 metre high) 2: MEDIUM (From 1 to 2 metres high) 3: INTERMEDIATE (From 2 to 4 metres high) 4: TALL (Greater than 4 metres high). Data on the volume of total browse volume/spize/plot were available as were measures of the browse volume hidden by grass/spize/plot.

To help understand the output, a summary of the salient features of the report precedes the actual output file:

The original data set contained 4651 records (unique spize/plot combinations). The species summary data set contained 2893 records (unique species/plot combinations).

The combination weight was selected, and critical Drop and Passive weights were set at 0.25 and 0.4 respectively. 24 species were not down weighted, and a total of 47 had down weights greater than the critical passive weight. RESOURCE temporarily dropped 304 records of 77 species with down weights less than 0.4.

The 47 non passive species were then subdivided into a possible 419 different spizes generating a data set with 15404 possible spize records. RESOURCE then selected 4072 spize records and dropped the remaining 11332.

Potential resource records and the temporarily dropped species summary data were then added back to the 4072 spize records, to give a resource database with 6748 records. 185 records of 66 rare species were then dropped from this data set, as their down weights were all less than the critical drop value. RESOURCE then examined remaining 6563 possible resource records and selected 4191 of them for inclusion in the final output data set. A total of 130 different resources were included in the final resource output database.

The Aberrant Index 1 (calculated using all original data) was selected and critical drop and passive values were set at 40% and 60% respectively. In this case the option NOT to drop aberrant sites from the data set was selected. Two plots (218 and 222) were identified as deviant, with site weights almost a quarter of the maximum possible site weight (26.21% and 27.43%). Note that their numbers (PlotNum column) remained the same as their names (Plot column) - This would not have been the case had the two deviant plots been dropped. A further six plots, had an aberrant indices less than 60% (but all six were above 50%).

To summarise the output 66 of the original 124 species were dropped from the final output data set as they were classed as rare (eg. acburx2 = *Acacia burkea* all sizes lumped - the suffix x2 means there were no size class 2 acbur's in the data set). RESOURCE recommended that a further nine species should be made passive in subsequent analyses.

The 130 resources which were included in the final output data set occurred a hierarchy of resolutions from a broad species level through to a fine resource level. From a broad to fine level the categories, examples of each category of resource included are :

1) Less common species which RESOURCE recommends should be made passive in subsequent analyses (eg acgerx0 = *Acacia gerrardii*) 2) Species for which there are sufficient data to be actively included in subsequent analyses, but not enough data to subdivide further on the basis of size class (eg facapx0 = *Fagara capensis*). 3) Lumped spizes where data have been pooled for different size classes, but there are insufficient data to subdivide the data into their original size classes (eg accaf34 = *Acacia caffra* greater than 2 metres high - In Hluhluwe there are only a few *Acacia caffra*'s over 4 metres, and then only just. Therefore the size grouping in this case makes ecological sense. 4) Individual spizes (eg accaf1 = Small *Acacia caffra*'s less than 1 metre high - *Acacia caffra* areas generally have tall grass and this explains why RESOURCE concluded there was not enough data to subdivide either of the smaller accaf's further according to grass interference). 5) Individual resources (eg acnil1H = Small *Acacia nilotica*'s (less than 1 metre high) with high grass interference (more than half the available browse hidden by grass). In this case, the weights indicate that both small *Acacia nilotica* and *Acacia karoo* less than 1 metre high occurred more commonly occurred with high rather than low grass interference.

```
Comments
-----------------------------------------------------------------
Braun-Blanquet values (1-5) extracted from table rawdat

4651 original records

242 different plots in raw data-set

2893 different species summary records in data-set
124 different species in data set

Weight selected = Combination Weight

Species.....Downweight
acbur         .05
accaf         1
acger         .317
acgla         .776
acgra         .019
ackar         1
acnil         1
acrob         1
acsch         .014
acson         .196
almar         .002
aspar         .098
aztet         .005
beluc         .028
benat         .014
bezey         1
caaet         .374
caine         .776
canth         .002
casep         .014
caspp         .014
cator         .155
catra         .002
ceafr         .948
chari         .374
clani         .098
clpul         .287
cocaf         1
cogre         .009
cohar         .014
comol         .517
crcap         .002
crodo         .174
crsyl         .07
cucap         .014
cuspp         .005
daarm         .098
daobo         .575
dicin         1
dilyc         1
diosp         .103
disim         1
diwhy         .002
```

Comments	
dobur	.431
docaf	.603
dorot	1
enspi	.259
erema	.006
errig	.69
eucri	1
eudiv	1
eugna	.031
eunat	.431
eushi	1
facap	.805
fison	.002
fispp	.014
fisur	.009
fisyc	.002
forb	.005
gatra	.546
geran	.012
gomph	.002
grcaf	.025
grflv	.006
grocc	.261
hacaf	.005
henat	.546
hibis	.287
hipau	.776
indig	.019
krflo	1
lijav	1
lyciu	.006
macon	.047
madis	.019
mahet	.862
manem	1
masen	1
medid	.039
mocaf	.202
ocnat	.025
orbac	.003
ortri	.006
ozeng	.002
pacap	.016
pagol	.12
peafr	.093
phret	.805
plarm	1
pscap	.002
rhchi	.546
rhgue	.006
rhmac	.891
rhpen	1
rhrho	.002
rhspp	.112
rhtom	.019
rhtri	1

```
Comments
------------------------------------------------------------
scbir          .718
scbra          .776
scmyr          1
scsp           .002
sczey          .805
seses          .019
siine          1
solan          1
spafr          .747
stinn          .002
stmad          .003
tacam          .008
teger          .006
tenat          .003
thacu          .019
trgla          .005
trori          .062
tuflo          .002
unkno          .186
verno          .948
vihav          .003
vimar          .002
xerud          .862
xicaf          .224
zimuc          1

Critical drop weight set at .25
Critical passive weight set at .4

304 records of 77 species temporarily dropped

419 spizes in non-passive spize data set
47 non-passive species in spize data set
4072 spize combination records for the non-passive
species selected out of a possible 15404 records

Resource processing option selected
6748 potential resource records examined

185 records of 66 resources will be dropped

After dropping rare resource records.....
4191 resource records in final data-set
with a total of 130 different resources

Plot  FullDownWt Aberrant I1       DownWt     Aberrant I2
001     16.565     69.02%          16.545     78.79%
002      10.92     68.25%          10.679        89%
003     16.199     95.29%          16.199     95.29%
004     13.192     87.95%          13.192     87.95%
005     13.788     65.66%          13.788     65.66%
006      6.167      88.1%           6.167      88.1%
007      3.603     90.06%           3.603     90.06%
008     13.522     84.51%          13.522     84.51%
009     13.923     99.45%          13.923     99.45%
010     14.487     96.58%          14.487     96.58%
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Comments
----------------------------------------------------------------------------
011      6.179    88.28%         6.179    88.28%
012     12.259    76.62%        11.929    85.21%
013     15.872    88.18%        15.872    88.18%
014     23.326    83.31%        23.269    86.18%
015     17.333    86.67%        17.333    86.67%
016     23.947    88.69%        23.919       92%
017     10.609    88.41%        10.609    88.41%
018     16.936    89.14%        16.936    89.14%
019     19.691    72.93%        19.417     80.9%
020      4.276    85.51%         4.276    85.51%
021      9.237    92.37%         9.237    92.37%
022     17.782    93.59%        17.782    93.59%
023     25.102    86.56%        24.813     91.9%
024     22.505    75.02%        21.891    95.18%
025     13.096    87.31%        13.096    87.31%
026     20.763    94.38%        20.763    94.38%
027      6.212    88.74%         6.212    88.74%
028     19.103    95.51%        19.103    95.51%
029     11.686    89.89%        11.686    89.89%
030      9.333    93.33%         9.333    93.33%
031     14.942    93.39%        14.942    93.39%
032     21.795    94.76%        21.795    94.76%
033     32.414    83.11%        31.872    91.06%
034     15.481    57.34%        14.359    65.27%
035     27.534    80.98%        27.442    83.16%
036     17.372    91.43%        17.372    91.43%
037     37.769    87.84%        37.769    87.84%
038      5.962    99.36%         5.962    99.36%
039     30.549    92.57%        30.481    95.25%
040      13.66    97.57%         13.66    97.57%
041     14.378    89.86%        14.378    89.86%
042     10.782    89.85%        10.782    89.85%
043     11.292    62.73%        10.923    68.27%
044     20.486    75.87%         20.25       81%
045     12.897    85.98%        12.897    85.98%
046     16.297    85.77%        16.269    90.38%
047     18.404    92.02%        18.404    92.02%
048     12.705     84.7%        12.705     84.7%
049     33.578    90.75%        33.532    93.14%
050      16.34    77.81%         16.34    77.81%
051     13.115    87.44%        13.115    87.44%
052      9.111    75.92%         9.083    82.58%
053      8.978    81.61%         8.833    88.33%
054      5.205    86.75%         5.205    86.75%
055     39.562    76.08%        39.244    87.21%
056     22.188    85.34%        22.044    88.18%
057     10.244    64.02%        10.244    64.02%
058     14.724    86.61%        14.667    91.67%
059     15.214    80.08%        15.214    80.08%
060      9.647     87.7%         9.647     87.7%
061     17.449    91.84%        17.449    91.84%
062     30.626    92.81%        30.462    95.19%
063     18.147    86.42%        18.147    86.42%
064     18.814    94.07%        18.814    94.07%
065     36.606    91.51%        36.462    93.49%
066     36.444    93.45%        36.423    95.85%
```

Comments

067	32.814	96.51%	32.814	96.51%
068	5.302	75.75%	5	100%
069	33.635	98.93%	33.635	98.93%
070	41.288	91.75%	41.288	91.75%
071	19.346	87.94%	19.346	87.94%
072	40.833	97.22%	40.833	97.22%
073	50.006	96.17%	50.006	96.17%
074	27.697	95.51%	27.468	98.1%
075	17.167	95.37%	17.167	95.37%
076	37.229	84.61%	37	86.05%
077	15.956	66.48%	15.654	71.15%
078	39.372	93.74%	39.372	93.74%
079	47.838	90.26%	47.769	91.86%
080	41.178	87.61%	41.141	89.44%
081	50.016	94.37%	49.878	97.8%
082	34.583	93.47%	34.583	93.47%
083	35.303	76.75%	35.294	78.43%
084	28.564	98.5%	28.564	98.5%
085	37.473	81.46%	36.923	87.91%
086	37.283	86.7%	37.212	90.76%
087	41.147	89.45%	41.147	89.45%
088	22.447	74.82%	22.154	85.21%
089	29.083	83.1%	29.083	83.1%
090	21.423	93.14%	21.423	93.14%
091	37.65	89.64%	37.641	91.81%
092	49.864	92.34%	49.864	92.34%
093	8.868	88.68%	8.868	88.68%
094	16.462	96.83%	16.462	96.83%
095	24.226	86.52%	24.135	92.83%
096	13.661	62.09%	12.518	78.24%
097	23.263	89.47%	23.263	89.47%
098	20.218	91.9%	20.218	91.9%
099	8.681	78.92%	8.66	86.6%
100	34.887	87.22%	34.885	89.45%
101	38.572	80.36%	38.256	88.97%
102	43.009	84.33%	43	86%
103	33.167	97.55%	33.167	97.55%
104	46.455	92.91%	46.455	92.91%
105	42.256	89.91%	42.256	89.91%
106	7.917	87.96%	7.917	87.96%
107	29.282	88.73%	29.282	88.73%
108	17.121	74.44%	17.112	81.48%
109	19.008	86.4%	18.699	93.49%
110	12.731	97.93%	12.731	97.93%
111	18.538	88.28%	18.538	88.28%
112	15.571	86.5%	15.571	86.5%
113	20.661	79.47%	20.496	81.99%
114	20.147	91.58%	20.147	91.58%
115	17.808	65.96%	17.609	73.37%
116	24.933	75.56%	24.878	82.93%
117	29.996	81.07%	29.923	83.12%
118	30.724	76.81%	30.724	76.81%
119	29.306	73.26%	28.821	80.06%
120	20.801	90.44%	20.801	90.44%
121	48.621	83.83%	48.538	88.25%
122	42.994	91.48%	42.994	91.48%

Comments

123	28.558	83.99%	28.558	83.99%
124	40.336	89.64%	40.071	95.41%
125	37.208	75.93%	37.006	86.06%
126	41.543	79.89%	41.314	81.01%
127	13.875	92.5%	13.875	92.5%
128	46.25	94.39%	46.25	94.39%
129	20.167	91.67%	20.167	91.67%
130	21.381	82.23%	21.381	82.23%
131	17.68	84.19%	17.667	88.33%
132	15.21	80.05%	15.045	83.58%
133	43.021	91.53%	42.929	93.32%
134	34.471	93.17%	34.295	95.26%
135	16.137	89.65%	16.135	94.91%
136	23.31	86.33%	23.282	93.13%
137	7.699	96.23%	7.699	96.23%
138	23.89	70.27%	23.647	76.28%
139	19.003	67.87%	18.827	69.73%
140	15.455	85.86%	15.455	85.86%
141	21.968	95.51%	21.968	95.51%
142	18.167	90.83%	18.167	90.83%
143	15.587	51.96%	14.903	70.97%
144	1.865	93.27%	1.865	93.27%
145	16.718	87.99%	16.718	87.99%
146	54.511	87.92%	54.282	88.99%
147	54.128	94.96%	54.128	94.96%
148	23.346	93.38%	23.346	93.38%
149	29.334	75.21%	28.878	84.94%
150	13.872	86.7%	13.872	86.7%
151	7.418	74.18%	7.397	82.19%
152	26.359	90.89%	26.359	90.89%
153	38.378	95.95%	38.378	95.95%
154	29.442	89.22%	29.442	89.22%
155	16.854	76.61%	16.571	87.21%
156	39.941	76.81%	39.897	79.79%
157	35.522	86.64%	35.522	86.64%
158	33.138	80.82%	32.994	82.48%
159	34.417	90.57%	34.417	90.57%
160	30.109	91.24%	30.109	91.24%
161	35.118	92.42%	35.109	94.89%
162	33.19	87.34%	33.154	89.6%
163	39.056	86.79%	39.019	88.68%
164	32.628	90.63%	32.628	90.63%
165	26.968	84.27%	26.968	84.27%
166	28.333	94.44%	28.333	94.44%
167	17.009	60.75%	16.231	81.15%
168	12.601	78.75%	12.436	82.91%
169	20.846	83.38%	20.846	83.38%
170	16.736	72.77%	16.462	78.39%
171	17.1	90%	16.949	94.16%
172	17.234	82.06%	16.904	93.91%
173	18.797	93.99%	18.795	98.92%
174	29.363	83.89%	29.051	90.79%
175	15.814	60.82%	15.141	79.69%
176	8.943	59.62%	8.865	88.65%
177	12.917	99.36%	12.917	99.36%
178	27.905	68.06%	27.637	76.77%

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Comments
-------------------------------------------------------------
179     18.701    89.05%        18.701    89.05%
180     17.224    78.29%        17.038    85.19%
181     25.783    88.91%        25.554    91.26%
182      54.31    90.52%        54.045    93.18%
183     24.198    67.22%        24.141    77.87%
184     39.462    83.96%        39.368    87.48%
185     40.131    91.21%        39.987    92.99%
186     18.635    98.08%        18.635    98.08%
187     32.304    89.73%        32.301    92.29%
188     20.699    94.09%        20.699    94.09%
189     24.061    89.11%        23.917    91.99%
190     20.513    93.24%        20.513    93.24%
191     12.212    87.23%        12.212    87.23%
192     11.295    80.68%        11.295    80.68%
193     14.032    73.85%        14.032    73.85%
194     14.321     68.2%         14.07    74.05%
195     11.724    90.19%        11.724    90.19%
196     11.462    88.17%        11.462    88.17%
197     14.205     94.7%        14.205     94.7%
198      2.848    56.96%         2.821    70.51%
199     11.865    91.27%        11.865    91.27%
200     10.537    61.98%         10.48    74.86%
201      8.368    83.68%         8.368    83.68%
202      6.994    99.91%         6.994    99.91%
203      6.264     78.3%         6.236    89.09%
204     10.289     68.6%         10.06    71.86%
205     14.853    92.83%        14.853    92.83%
206     32.518    83.38%        31.955    96.83%
207     40.446    89.88%        40.301    91.59%
208       6.74    84.25%         6.731    96.15%
209     18.442    83.83%        18.442    83.83%
210     12.045    92.65%        12.045    92.65%
211     13.109    93.64%        13.109    93.64%
212     16.455    91.42%        16.455    91.42%
213     11.159    85.84%        11.157    92.97%
214     10.005    90.96%        10.005    90.96%
215      9.807    89.15%         9.807    89.15%
216     18.314    91.57%        18.314    91.57%
217     17.555    67.52%        17.246    74.98%
218      4.979    26.21%         4.895    48.95%
219     13.016    59.16%        12.768    75.11%
220     10.563    52.81%        10.038    77.22%
221      2.564    85.47%         2.564    85.47%
222      7.953    27.43%         6.474    46.25%
223       9.25    84.09%          9.25    84.09%
224     14.814    87.14%        14.814    87.14%
225      12.66    97.39%         12.66    97.39%
226     26.038    86.79%        26.038    86.79%
227      4.932     82.2%         4.929    98.59%
228     16.564    82.82%        16.564    82.82%
229     24.071    92.58%        24.071    92.58%
230     17.006     77.3%        17.006     77.3%
231     22.333    89.33%        22.333    89.33%
232     11.327    94.39%        11.327    94.39%
233     17.006    94.48%        17.006    94.48%
234      17.66     88.3%         17.66     88.3%
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Comments
-----------------------------------------------------------------
235      13.429     95.92%           13.429     95.92%
236       6.939     86.73%            6.929     98.99%
237      25.958     92.71%           25.958     92.71%
238      16.712      98.3%           16.712      98.3%
239      20.324     84.68%           20.276     92.16%
240      27.564     95.05%           27.564     95.05%
241       6.243     62.43%            6.131     87.59%
242      15.801     87.78%           15.744     92.61%

RESOURCES INCLUDED
Resource         Weight      ResourceNum
accaf1            .962          1
accaf2               1          2
accaf34              1          3
acgerx0           .385          4
acgla1            .641          5
acgla2            .737          6
acgla34           .449          7
ackar1H              1          8
ackar1L           .897          9
ackar2H           .545         10
ackar2L              1         11
ackar3               1         12
ackar4            .865         13
acnil1H              1         14
acnil1L           .641         15
acnil2               1         16
acnil3               1         17
acnil4               1         18
acrob1            .929         19
acrob23           .513         20
acrob4            .545         21
bezey1H           .962         22
bezey1L              1         23
bezey2               1         24
bezey3               1         25
bezey4               1         26
caaetx0           .417         27
cainex0           .865         28
ceafrx0              1         29
charix0           .417         30
clpulx4           .321         31
cocaf1               1         32
cocaf2               1         33
cocaf34           .994         34
comolx0           .577         35
crodox0           .256         36
daoboxD           .641         37
dicin1H              1         38
dicin1L              1         39
dicin2               1         40
dicin34              1         41
dilyc1H           .801         42
dilyc1L           .929         43
dilyc2               1         44
dilyc34           .897         45
```

APPENDIX 20.2

QUANTIFICATION OF VEGETATION CHANGES ON AERIAL PHOTOGRAPHS

BOURQUIN & HITCHINS' ANALYSIS

Aerial photographs for 1936, and 1961 and 1969 were used to map apparent differences in the vegetation. Although not quantified, a visual comparison between the aerial photographs of 1936 and 1969 showed an increase in the area covered by woody plant communities (Bourquin & Hitchins 1979) and confirms the difference between the vegetation maps of Henkel and those of Hitchins.

KINGS'S ANALYSIS

Kings'(1987) analysis of the 1937, 1954, 1960, 1975 and 1982 aerial photographs (discussed in more detail in chapter 16) documents how woody plant canopy cover in Hluhluwe increased greatly since 1937 with the area of forest and especially "scrub" more than doubling from 1937-82 (increasing from 22.0% to 48.5%).

By 1982, thicket/closed woodland (King's "scrub" category) covered 32.2% of Hluhluwe - an area 3.27 times greater than in 1937, with the area of forest increasing by 33% from 1937-82.

According to King (1987) the area of forest and "scrub" vegetation in Hluhluwe increased from 22% in 1937 to 25.6% in 1954 to 34.5% in 1960 to 42.4% in 1975 and to 48.5% in 1982.

The biggest increase in King's "scrub" category occurred between 1954 and 1960 indicating that most of small encroaching *Acacias* probably became established earlier (coinciding with a period with very few fires). This is corroborated by the literature (see earlier) which indicated that the obvious rapid encroachment in Hluhluwe took place from 1949.

Whateley produced a vegetation map for Hluhluwe dated 1975. Details of the fieldwork and community descriptions plus simplified maps are presented in Whateley and Porter (1983). The different landscape units were identified on aerial photographs using a stereoscope. According to the authors, field work was extensive, with large areas being traversed on foot in order to fix boundaries of the various plant communities. A total of 166 PCQ transects were also undertaken within what the authors termed "representative" examples of each community. Fieldwork and the compilation of the Hluhluwe and northern Corridor section of this map was completed in 1975. The Hluhluwe section of the map was in part based on the 1969 aerial photographs of the area (Whateley & Porter 1979).

Figure 20.14 presents the proportional area of the Map study area made up by Whateley and Porter's different vegetation communities.

- In contrast to 1937 when 75% of the Map study area was classified by Henkel as grassland, Whateley's 1975 map indicates that only 7% of the Map study area was grassland.

- In 1975 thicket communities (light grey) accounted for almost 40% of the Map study area with *A.karroo* and *D.cinerea* being the dominant species.

- In 1975, woodland accounted for a further 41% of the area with *A.nilotica* woodland (21.5%) and *A.karroo* woodland (16.0%) being the dominant forms.

maps) suggests 1) that either the extent of woodland and forest did not change over the period (unlikely) or 2) that the maps most accurately reflect changes in scrub and grassland; and in particular 3) that little confidence should be placed in the apparent lack of change in the woodland areas on these maps.

Table 20.2 quantifies the changes in vegetation revealed by the analysis of the 1960, 1970 and 1973 maps, and focuses on the areas of scrub and grassland in 1960 where most of the changes took place.

- While grassland covered just over three-quarters of the Map study area in 1937, by 1960 it accounted for only about a third of the area.

- "Dense vigorous scrub" was the most common vegetation type by 1960 accounting for about 45% of the area, although much of this area was subsequently bushcleared.

- Between 1960 and 1970 there were major vegetation changes in the Map study area with grassland increasing from 32.4% to cover 72.3% of the area in 1970, with the amount of "dense vigorous scrub" declining to cover only 5.5%.

- By 1973, the amount of scrub was once again increasing to cover 29.3%, with an additional 3.6% of *M.senegalensis* and other species woodland. Between 1970-1973 the area of grassland correspondingly decreased from 72.3% to 41.4% of the Map study area.

The analyses of these maps confirm the conclusions at the 1979 vegetation dynamics workshop (Macdonald *et al* 1979) that following initial clearing in the *A.karroo* areas and game control, the areas opened up to thicken up again in the mid 1970s.

WHATELEY'S 1975 MAP

symbols (grassland) or marked as scattered pockets of "Open Treeveld - former savannah" reflecting the intensive clearing operations in these areas just prior to the map being drawn.

Despite some of the detail in Ward's 1961 vegetation map of Hluhluwe being lost during printing (especially the location of thicket communities), it was not possible to quantify the proportional contribution of different vegetation types on this map. However it was possible to discern that much of the areas that later became dominated by *A.nilotica* woodland was marked as "Open Treeveld" on Ward's map.

Dr Orty Bourquin (pers.comm.) showed me his annotated copy of Ward's map on which he had colour shaded the dominant woody species (sometime from the mid 1960s to 1970). Stands of *A.karroo* (size not specified) were present in some areas (Ngqungulu valley, foot of Gontshi hill, part of Hidli vlei and parts of Manzimbomvu valley).

HITCHINS' 1960, 1970 and 1973 MAPS

Three maps were found which covered the same area, and based on the handwriting on them, it is clear they were drawn up by Peter Hitchins. The existence of these maps was also referred to in Bourquin and Hitchins (1979). The 1960 map was based on aerial photographs (Job442 Strip 8) while the 1970 map was derived from aerial photographs (Job 608 - 1969 Strips 11 and 12) plus fieldwork. The 1973 map has a key covering all vegetation types and also showed the location of Hitchins' vegetation belt transects. Based on comments in Bourquin (1969) and Bourquin and Hitchins (1979) it appears Hitchins did most of the fieldwork, and that the maps may have been jointly produced by Hitchins and Bourquin.

The area covered by the other vegetation types in the Map study area (with the exception of *Acacia nilotica* woodland which increased in extent from 12.0% to 15.6% from 1970-73) somewhat surprisingly remained exactly the same on all three maps (Table 20.2). This, and the fact a further professionally reproduced map appended to Bourquin and Hitchins' 1979 paper (presented at the Vegetation dynamics workshop) only showed changes in the extent and distribution of dense vigorous scrub from 1960 and 1970 (taken directly from the 1960 and 1970 included *E.racemosa/B.zeyheri* lowland forest, *A.nilotica* woodland, *A.caffra* hillslope parkland/thicket, *A.robusta* riverine, and *E.divinorum* woodland, *S.africana* thicket, *S.africana* woodland, *A.glabrata* thicket).

HENKEL'S 1937 MAP

The first vegetation map covering the original area of Hluhluwe Game Reserve was produced by Henkel (1937) based on fieldwork in 1936. Downing (1980) planimetered this map and estimated that in 1937 grassland covered 49% of the area, lowland scrub 28%, forest 12%, alluvial sand communities 6% and riverine forest 5%.

Figure 20.13 gives the breakdown of vegetation types on Henkel's map in the Map study area indicating that the Map study area was more open than the rest of Hluhluwe as grassland covered 78% of the Map study area in 1936. This can be contrasted with Figure 20.14 which shows that by 1975, grassland had declined to cover only about 7% of the Map study area.

WARD'S 1961 MAP

C.R. (Roddy) Ward's map was dated 1961, and entitled "Sketch Map of Hluhluwe Game Reserve and Environs" and was based on 1:50,000 sheets, aerial photographs (jobs 332 and 442) and field work. It was drawn up in the year of the black rhino die-off, and soon after much of the extensive initial *A.karroo* bush clearing in the north-east of Hluhluwe.

Unfortunately much of the detail was lost in the reproduction of Ward's original 1961 map ,and it is not easy to distinguish between a number of his vegetation categories. In particular, it was not easy to distinguish between the"drier more open communities" named "Semi-deciduous forest patches through dense bush" and "Scrub communities". However it was possible to distinguish categories "Coastal Evergreen Close Forest" and "Open Treeveld (former savannah)". Areas with no symbols were presumed to be grassland. Most of Magangeni, Ngqungulu, Hidli, and bottomlands parallel to main Memorial Gate entrance road appeared to be mainly without

APPENDIX 20.1

QUANTIFICATION OF AREA COVERED BY DIFFERENT VEGETATION TYPES IN PAST MAPS OF A STUDY AREA IN THE NORTH EAST OF THE HLUHLUWE GRID STUDY

METHODS

Vegetation changes on five available maps from 1937-1975 were quantified using a "dot-grid" analysis (Norton-Griffiths 1979, Lamprey 1985, Dublin 1991). Transparent sheets with dots in a regular pattern were overlain onto the vegetation maps. To quantify the proportional contribution of different vegetation types within each map, the numbers of dots falling within each vegetation type were counted within the Map study area (Figure 4.2) crossing out each dot counted with a marker pen to prevent double counting. Although not as accurate as a planimeter or GIS approach (A planimeter was not readily available, and all maps had not been digitised) this simple method was fast and adequate to reveal the gross trends that had occurred in the periods between maps.

MAP STUDY AREA

Some of the past vegetation maps only covered a limited area of north east Hluhluwe, while others covered the whole reserve. To facilitate comparison, a Map study area (Figure 4.2) was chosen and the results refer to this area, and not necessarily to the whole area of each original vegetation map. The Map study area was defined as the 84% (1,850 ha) of the area covered by the 1960, 1970 and 1973 vegetation maps drawn up by Hitchins that overlapped that of the Grid study area. The Map study area covers the north-eastern 38% of the bigger Hluhluwe Grid Study area (4,900ha).

The vegetation communities occurring in the Map study area were not representative of the vegetation throughout the whole larger northern Hluhluwe Grid study area. Most of the *A.karroo* dominated hillslope and lower-lying black clay areas that have been bush-cleared fall within the Map study area, and this section of Hluhluwe was also the area where many black rhinos died during the 1961 die-off. Other communities that are under-represented

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Comments
-------------------------------------------------------------
229     92.58        229
230      77.3        230
231     89.33        231
232     94.39        232
233     94.48        233
234      88.3        234
235     95.92        235
236     86.73        236
237     92.71        237
238      98.3        238
239     84.68        239
240     95.05        240
241     62.43        241
242     87.78        242

SUGGESTED RESOURCES TO MAKE PASSIVE
Resource      Number       Weight
   acgerx0         4        .385
   clpulx4        31        .321
   crodox0        36        .256
   enspix0        54        .288
   groccx4        71        .385
   hibisx4        73        .321
   mocafx4        93        .298
   unknox3       123        .275
   xicafx4       126         .33

4191 records in Final table
```

Comments

167	60.75	167
168	78.75	168
169	83.38	169
170	72.77	170
171	90	171
172	82.06	172
173	93.99	173
174	83.89	174
175	60.82	175
177	99.36	177
178	68.06	178
179	89.05	179
180	78.29	180
181	88.91	181
182	90.52	182
183	67.22	183
184	83.96	184
185	91.21	185
186	98.08	186
187	89.73	187
188	94.09	188
189	89.11	189
190	93.24	190
191	87.23	191
192	80.68	192
193	73.85	193
194	68.2	194
195	90.19	195
196	88.17	196
197	94.7	197
199	91.27	199
200	61.98	200
201	83.68	201
202	99.91	202
203	78.3	203
204	68.6	204
205	92.83	205
206	83.38	206
207	89.88	207
208	84.25	208
209	83.83	209
210	92.65	210
211	93.64	211
212	91.42	212
213	85.84	213
214	90.96	214
215	89.15	215
216	91.57	216
217	67.52	217
221	85.47	221
223	84.09	223
224	87.14	224
225	97.39	225
226	86.79	226
227	82.2	227
228	82.82	228

Comments

110	97.93	110
111	88.28	111
112	86.5	112
113	79.47	113
114	91.58	114
115	65.96	115
116	75.56	116
117	81.07	117
118	76.81	118
119	73.26	119
120	90.44	120
121	83.83	121
122	91.48	122
123	83.99	123
124	89.64	124
125	75.93	125
126	79.89	126
127	92.5	127
128	94.39	128
129	91.67	129
130	82.23	130
131	84.19	131
132	80.05	132
133	91.53	133
134	93.17	134
135	89.65	135
136	86.33	136
137	96.23	137
138	70.27	138
139	67.87	139
140	85.86	140
141	95.51	141
142	90.83	142
144	93.27	144
145	87.99	145
146	87.92	146
147	94.96	147
148	93.38	148
149	75.21	149
150	86.7	150
151	74.18	151
152	90.89	152
153	95.95	153
154	89.22	154
155	76.61	155
156	76.81	156
157	86.64	157
158	80.82	158
159	90.57	159
160	91.24	160
161	92.42	161
162	87.34	162
163	86.79	163
164	90.63	164
165	84.27	165
166	94.44	166

```
Comments
------------------------------------------------------------

055      76.08        55
056      85.34        56
057      64.02        57
058      86.61        58
059      80.08        59
060       87.7        60
061      91.84        61
062      92.81        62
063      86.42        63
064      94.07        64
065      91.51        65
066      93.45        66
067      96.51        67
068      75.75        68
069      98.93        69
070      91.75        70
071      87.94        71
072      97.22        72
073      96.17        73
074      95.51        74
075      95.37        75
076      84.61        76
077      66.48        77
078      93.74        78
079      90.26        79
080      87.61        80
081      94.37        81
082      93.47        82
083      76.75        83
084       98.5        84
085      81.46        85
086       86.7        86
087      89.45        87
088      74.82        88
089       83.1        89
090      93.14        90
091      89.64        91
092      92.34        92
093      88.68        93
094      96.83        94
095      86.52        95
096      62.09        96
097      89.47        97
098       91.9        98
099      78.92        99
100      87.22       100
101      80.36       101
102      84.33       102
103      97.55       103
104      92.91       104
105      89.91       105
106      87.96       106
107      88.73       107
108      74.44       108
109       86.4       109
```

```
Comments
-----------------------------------------------------------

NON-ABERRANT PLOTS
Plot     Weight     Plotnum
001      69.02         1
002      68.25         2
003      95.29         3
004      87.95         4
005      65.66         5
006       88.1         6
007      90.06         7
008      84.51         8
009      99.45         9
010      96.58        10
011      88.28        11
012      76.62        12
013      88.18        13
014      83.31        14
015      86.67        15
016      88.69        16
017      88.41        17
018      89.14        18
019      72.93        19
020      85.51        20
021      92.37        21
022      93.59        22
023      86.56        23
024      75.02        24
025      87.31        25
026      94.38        26
027      88.74        27
028      95.51        28
029      89.89        29
030      93.33        30
031      93.39        31
032      94.76        32
033      83.11        33
035      80.98        35
036      91.43        36
037      87.84        37
038      99.36        38
039      92.57        39
040      97.57        40
041      89.86        41
042      89.85        42
043      62.73        43
044      75.87        44
045      85.98        45
046      85.77        46
047      92.02        47
048       84.7        48
049      90.75        49
050      77.81        50
051      87.44        51
052      75.92        52
053      81.61        53
054      86.75        54
```

```
Comments
------------------------------------------------------------
erema13        .009
eugna12        .046
fison2         .002
fispp2         .021
fisur2         .014
fisyc2         .002
forb 12        .007
geran2         .018
gomph2         .002
grcaf12        .037
grflv1         .009
hacaf4         .007
indig12        .027
lyciu1         .009
macon13        .069
madis34        .027
medid1         .057
ocnat12        .037
orbac12        .005
ortri1         .009
ozeng1         .002
pacap14        .023
pagolx4        .176
peafrx0        .137
pscap3         .002
rhgue14        .009
rhrho1         .002
rhspp12        .165
rhtom34        .027
scsp 3         .002
seses12        .027
stinn1         .002
stmad12        .005
tacamx0        .011
teger4         .009
tenat4         .005
thacux3        .027
trgla24        .007
trorix1        .092
tuflo1         .002
vihav4         .005
vimar2         .002

All data used to calculate aberrant plot index
Critical Aberrant Index Values..
To drop plots ... < 40%
To list passive plots ... < 60%
Aberrant plots were NOT dropped from final data set

SUGGESTED PLOTS TO DROP
Plot    Weight    PlotNum
218     26.21       218
222     27.43       222

SUGGESTED PLOTS TO MAKE PASSIVE
Plot    Weight    Plotnum
034     57.34        34
143     51.96       143
176     59.62       176
198     56.96       198
219     59.16       219
220     52.81       220
```

```
    Comments
    ---------------------------------------------------------------
    rhpen2           1        102
    rhpen3           1        103
    rhpen4         .994       104
    rhtri1H        .962       105
    rhtri1L        .962       106
    rhtri23          1        107
    scbirx0        .801       108
    scbrax0        .865       109
    scmyr1           1        110
    scmyr2         .962       111
    scmyr3         .865       112
    scmyr4         .545       113
    sczeyx4        .897       114
    siine12          1        115
    siine34        .737       116
    solan1H        .449       117
    solan1L        .801       118
    solan23        .929       119
    spafr1         .641       120
    spafr2         .481       121
    spafr34        .577       122
    unknox3        .275       123
    vernox4          1        124
    xerud12        .962       125
    xicafx4         .33       126
    zimuc1H        .513       127
    zimuc1L        .545       128
    zimuc2         .769       129
    zimuc34        .833       130

    RESOURCES DROPPED
    Resource        Weight
    acburx2        .073
    acgrax4        .027
    acsch12        .021
    acsonx4        .224
    almar3         .002
    asparx4        .144
    aztetx4        .007
    belucx4        .041
    benat13        .021
    canth1         .002
    casep12        .021
    casppx4        .021
    catorx3        .229
    catra3         .002
    clanix4        .144
    cogre13        .014
    cohar1         .021
    crcap2         .002
    crsylx4        .103
    cucap1         .021
    cuspp4         .007
    daarmx0        .144
    diospx0        .151
    diwhy1         .002
```

```
Comments
--------------------------------------------------------------------
disim1            1        46
disim2            1        47
disim34        .609        48
doburx4        .481        49
docafx0        .673        50
dorot1H        .513        51
dorot1L        .545        52
dorotx1        .865        53
enspix0        .288        54
errigx4        .769        55
eucri1H           1        56
eucri1L        .929        57
eucri23           1        58
eudiv1            1        59
eudiv2            1        60
eudiv3            1        61
eudiv4         .673        62
eunatx4        .481        63
eushi1H        .609        64
eushi1L           1        65
eushi2            1        66
eushi3            1        67
eushi4            1        68
facapx0        .897        69
gatrax0        .609        70
groccx4        .385        71
henatx0        .609        72
hibisx4        .321        73
hipaux0        .865        74
krflo1H        .545        75
krflo1L           1        76
krflo2            1        77
krflo34           1        78
lijav1H        .929        79
lijav1L        .417        80
lijav2H        .769        81
lijav2L           1        82
lijav3         .481        83
mahet1         .577        84
mahetx1        .577        85
manem1            1        86
manem2         .769        87
manem34        .994        88
masen1H        .641        89
masen1L        .962        90
masen2            1        91
masen34           1        92
mocafx4        .298        93
phretx4        .897        94
plarm1         .897        95
plarm2         .641        96
plarm34        .673        97
rhchix0        .609        98
rhmacx4        .994        99
rhpen1H        .673       100
rhpen1L           1       101
```

The marked decline in open-parkland in Hluhluwe North between 1937 and 1982 can be seen by examining the map in Figure 7 and Plate 3 of King's (1987) thesis. Unfortunately there are no recent aerial photographs, but it is likely that the percentage of forest and "scrub" (as classified by King) has increased further since 1982 as many areas classified as "open grassland/ parkland by King on the 1982 photograph were bush encroached in 1989, and the main post-burn survey revealed that open grassland only accounted for 7.6% of plots in Hluhluwe North in 1989.

WATSON & MACDONALD'S ANALYSIS

Watson & Macdonald (1983) analysed the 1937, 1960 and 1975 aerial photographs in four game control blocks in Hluhluwe and one in Umfolozi. Two of these blocks (3,6) and part of a third block (8) fell within the Hluhluwe Grid study area. Their analyses of these three blocks showed the same trends with grassland coverage decreasing by over two thirds over the period 1937-75 in north-eastern Hluhluwe, whilst woody plant cover increased despite bush clearing during this period.

The percentage grassland in the three blocks (3,6 and 8) declined from 37%, 40% and 57% in 1937 to 19%, 12% and 12% respectively by 1975. Over the same period total woody plant cover increased from 63%, 60%, and 43% to 80%, 88% and 88%. The authors ascribed the relatively lower increase in canopy cover in block 3 to the extensive woody plant removal operations in this area.

Given the net increases in shrub cover over all four Hluhluwe blocks, the author's speculatively concluded that the frequency of burns that had been applied, appeared to be too low for the effective long term arrestment of the woody components.

WHATELEY & WILLS' ANALYSIS OF THEIR STUDY PLOTS

Whateley & Wills (1996) used aerial photos from 1937-81 to quantify the canopy cover in their three *A.nilotica* woodland study sites (selected to representative three different aged seral stages in the succession from *Acacia* thicket to *A. nilotica* closed woodland through to *E. racemosa/B. zeyheri* lowland forest). The results presented in Table 20.1 show a similar trend of increasing bush-thickening over time.

> Canopy cover of the "young" *A.nilotica* woodland in Greece dramatically from 20% to 70% from 1960 to 1975 reaching 75% by 1981.
>
> Canopy cover in the "intermediate" age *A.nilotica* woodland increased from 10% to 40% from 1937 to 1954, have this steadily increased to reach 80% by 1981
>
> Canopy cover in the "old" *A. nilotica* closed woodland in transition to *E. racemosa/B. zeyheri* lowland forest was 30% in 1937 rising to 60% in 1954, and reaching 95% as early as 1975.

APPENDIX 20.3

COMPARISON OF CURRENT VEGETATION WITH WHATELEY & PORTER'S COMMUNITY DESCRIPTIONS

The last vegetation map made of the whole of Hluhluwe-Umfolozi was drawn up by Whateley & Porter (1979, 1983), although the Hluhluwe part of the map (discussed above) was completed by Whateley in 1975. As *A.nilotica* and *A.karroo* dominated areas are of particular interest in terms of assessing the impact of habitat dynamics in northern Hluhluwe on black rhino (see chapter 20 introduction) this appendix gives descriptions of these communities by Whateley & Porter (1979, 1983).

DESCRIPTION OF *A.nilotica* WOODLAND

It is noteworthy that Whateley & Porter (1979, 1983) did not describe a *E.racemosa/B.zeyheri* dominated lowland forest community. This provides confirmatory evidence for the hypothesis that current extensive areas of lowland forest in northern Hluhluwe developed over the last two decades. However, based on data in Whateley & Porter (1983) stands of taller *A.nilotica* woodland had clearly developed by 1975.

Further evidence of the earlier successional state of *A.nilotica* woodland in the Corridor and Hluhluwe during this period comes from Whateley & Porter's (1979) descriptions of their *A.nilotica* woodland community.

- Canopy cover in 1975 varied between 50% and 80%. Whateley & Porter (1979) also referred to an average canopy height of 4.1m and described the community as having flat-topped trees (ie mature *A.nilotica*'s).

- *A.nilotica* was the most frequent and numerous and dominant woody species in this community having a percentage frequency in the upper stratum (>2m) of 60.9% and 25.4%

in the lower stratum (0.3-2m)

- Commonly associated taller spizes (>2m) included *A.karroo* (9.3%), *D.cinerea* (9.3%), *R.pentheri* (3.1%) and *M.senegalensis* (2.1%). Taller *A.caffra* occurred at a frequency of 1.4%.

- Taller later successional species *E.racemosa*, *E.divinorum*, and *B.zeyheri* only occurred at lower frequencies of only 1.6%, 2.3% and <0.2% respectively.

Of the smaller trees (0.3-2m), *D.cinera* was as common as smaller *A.nilotica* (25.3%). Frequencies for smaller (0.3-2m) spizes of "woodland" and "transitional" species identified by Whateley & Wills (1996) were: *A.karroo* (9.1%), *A.caffra* (5.1%), *R.pentheri* (2.9%) and *M.senegalensis* (6.4%).

Smaller (0.3-2m) later successional species occurred at low frequencies or were not recorded: *E.racemosa* (2.3%), *E.divinorum* (1.8%), *B.zeyheri* (2.2%), *M.heterophylla* (4.3%), *E.natalensis* (2.3%) *K.floribunda* (2.3%), *H.pauciflorus* (not recorded), *C.caffra* (0.5%), *Ehretia rigida* (<0.2%), *S.inerme* (<0.2%), *C.africana* (not recorded), *S.zeyheri* (not recorded), and *S.myrtina* (not recorded).

The authors recorded that a moderately tall, often dense sward of tufted perennial grasses dominated the herbaceous layer of *A.nilotica* woodland. *T.triandra* was the dominant grass in the open, with *P.maximum* commonly occurring under canopies. They also recorded *D.australe* as dominating the grass layer where the canopies became more continuous. This pattern was corroborated by Whateley & Wills (1996).

During fieldwork (this study) it was noticeable that the odd tall mature *Sclerocarya birrea* tree occurred in late successional "*Whateley-Wills*" *A.nilotica* woodland in transition to *E.racemosa/B.zeyheri* dominated lowland forest bearing testament to the area being open *S.birrea* parkland in the past.

DESCRIPTION OF *A.karroo/D.cinerea* THICKET

Whateley & Porter (1983) also described an *A.karroo-D.cinerea* thicket community which especially occurred throughout the Corridor and much of northern Hluhluwe (Whateley & Porter 1983). This community was found at all altitudes, commonly occurred on steeply undulating hillsides, and was often associated with a tall to very tall grass sward. The authors speculated that the structure and density of this thicket was mainly determined by the frequency and intensity of the fires which readily penetrated this community (Whateley & Porter 1979). Areas of thicket were the most frequently burnt in the reserve, particularly during above average rainfall periods. The height of the woody plants in this community varied from grass height to 4m. As many as 5,840 per hectare were recorded.

From Whateley & Porter's (1983) descriptions it appears there was considerable overlap in species between the *A.nilotica* woodland and *A.karroo/D.cinerea* thicket communities in 1975, although the forest species were less frequent in the thicket and A.karroo was the most numerous species.

- The most frequently recorded taller spizes (>2m) were *A.karroo* (44.2%), *A. nilotica* (19.1%) *D.cinerea* (17.0), *M.senegalensis* (6.6%), *A.caffra* (2.0%) *S.birrea* (2.0%). Taller spizes of key transitional and forest species were also uncommon with only *R.pentheri* (1.3%) and *C.caffra* (1.1%) occurring at a frequency > 1%. Taller *E.racemosa, E.divinorum* and *B.zeyheri* were recorded but at very low frequencies (<0.2%).

- The most frequently recorded smaller spizes (0.3-2m) were *A.karroo* (31.0%), *A.nilotica* (10.3%) *D.cinerea* (23.5), and *M.senegalensis* (7.2%), were the dominant species in this community. Smaller spizes of key transitional and forest species were relatively uncommon although many species present in later successional *E.racemosa/B.zeyheri* dominated lowland forest did occur: *R.pentheri* (1.4%) *E.rigida* (3.0%) *S.zeyheri* (0.4%) *K.floribunda* (0.2%), *D.dichrophylla* (2.7%), *C.africana* (0.2%) *F.capensis* (0.3%) and *C. caffra* (<0.2%).

The authors noted that widely spaced, emergent, often grouped trees of *S.birrea* trees were often a characteristic feature of *A.nilotica* woodland. It was therefore interesting to note that the frequencies of occurrence of *S.birrea* trees was almost identical in both the *A.nilotica* woodland and *A.karroo/D.cinerea* thicket communities.

Whateley and Porter (1979) also noted that in Northern Hluhluwe a successional trend has occurred where the *A.karroo/D.cinerea* thicket has changed in time towards the *A.karroo* woodland community.

From ground knowledge obtained during fieldwork, and looking at the 1975 Hluhluwe map some areas marked as *A.karroo* thicket and *A.karroo/D.cinerea* by Whateley & Porter has changed to become taller *A.karroo* woodland by 1989.

APPENDIX 20.4

INTERVIEWS AND FIELD OUTINGS

Memory is fickle, and most people interviewed could not remember much detail about vegetation changes as their interest was primarily in the animals and birds. Most just could remember that particular areas "had thickened up", but could not give specific details of the vegetation changes. However there were a few individuals who knew their woody plant species well, and whose testimony was useful.

THE LATE STAFF SERGEANT NQABANEFA NCOBO

Just before he retired from the field in 1990, a field trip was undertaken with the late Staff Sergeant N.Ncobo to discuss vegetation changes he had noticed since 1975 (when he came to work at Hluhluwe). A NPB research technical assistant acted as a translator during the field trip with S.Sgt Ncobo. During the field trip every attempt was made to avoid using loaded questions.

S.Sgt.Ncobo made the following points (my comments indented):

o In the past the slopes of Qolwane didn't have the large amounts of *A.nilotica* present today.

o The Zincakeni area (Figure 20.9) was one of the first places to thicken up. In 1975 most *A.nilotica* trees in the area were smaller (<2m); and often had *D.cinerea* growing above. He remembered being able to see black rhinos' heads and shoulders above a lot of the vegetation.

> The vast majority of *A.nilotica* trees in this area have matured and in many cases these trees have now been overtopped by taller later successional species such as *B.zeyheri* and *see E.racemosa*. Tall *D.cinerea* trees were still present in these areas in 1989.

○ *E.racemosa* has greatly increased in extent since 1975.

> This corroborated the conclusion of Bourquin & Hitchins (1979), and the 1989 Grid survey which recorded this species as having the highest canopy cover in northern Hluhluwe.

○ Most of the *A.karroo* that were tall in 1990 were ≤ 2m in the late1970s . For example, he remembered the tall *A.karroo* woodland that occurred near Memorial Gate in 1990 as being ≈ 2m tall (these trees have subsequently been cut down in bush clearing operations). In 1975 he remarked that there were many black rhino on Hidli, where there was much short *A.karroo*.

> This corroborates the data from the remeasurement of Hitchins' plots, reports in the Vegetation dynamics workshop and the analysis of Hitchins' 1973 and Whateley's 1975 maps (see above) which indicated that the area of thicket was increasing compared to 1970.

○ He remembered that there was not much *A.karroo* on the road past King and Konstant's experimental plots en route to Sitezi, and that this area used to be dominated by mainly small *A.nilotica*'s and *D.cinerea*.

> *A.nilotica* closed woodland / *E.racemosa-B.zeyheri* lowland forest subsequently developed in this area, although some of this has recently been bush cleared.

○ When looking at the Nqunqulu area as seen from the top of Magangeni (see Figure 20. 10) he remembered that around 1975, the thick bush was mainly restricted to the drainage lines.

○ Outside the Grid Study Area, he remembered the area of seemingly even aged semi-closed *A.nilotica* woodland seen at Seme (en route to Nquemeni outpost) as short "*Acacia's*".

> *A.nilotica* closed or almost closed woodland subsequently developed in this area. On walks in closed *A.nilotica* dominated woodland near the Seme road in 1997 and 1998 I noticed many individuals of later successional species such as *E.racemosa*, *E.divinorum*, *B.zeyheri* and

S.inerme growing up. It was noticeable that many of these later successional species occurred near the bole of the *A.nilotica*'s as hypothesised in the Whateley-Wills (1996) successional model. Although the walks were undertaken when the trees were not in leaf, many of the *A.nilotica*'s appeared to be senescing.

THE LATE DUMISANE NGOBESE

Before his death, I went on a field trip with Dumisane Ngobese to discuss vegetation changes that he had noticed in Hluhluwe. Dumisane knew his plant species well, having at an earlier stage of his career worked for the Parks Board's Research section in Hluhluwe as a Technical Assistant .

Dumisane pointed out many areas of Hluhluwe which he had remembered thickening up. His observations agreed with those of S.Sgt.Ncobo. He confirmed that *A.nilotica* was one of the key species to grow up and that *E.racemosa* had become much more dominant. He also remembered that areas of shorter *A.karroo* had grown up to form mature *A.karroo* woodlands in some areas of North Eastern Hluhluwe.

Dumisane Ngobese took me to visit an old retired game guard (who had worked with Peter Hitchins in the past), and had since retired to live at his homestead near the boundary of Hluhluwe. As we looked over into the South Eastern part of Hluhluwe reserve, both men pointed to an area which had extensive areas of almost closed *A.nilotica* woodland, and remarked how they remembered the same area being open in the past.

DR ORTY BOURQUIN

Dr Orty (Ortwin) Bourquin worked for Natal Parks Board's Research section in Hluhluwe from 1965 till 1970.

In referring to a map showing the changes in "dense vigorous scrub" between 1960 and 1970 (directly based on the Hitchins' 1960 and 1970 maps described above), Bourquin noted how striking the changes in the woody vegetation from thicket to grassland had been during the 1960s, and that he believed this change was a result of the higher fire frequencies following the early extensive bush-clearing.

He indicated that the category "grassland" on the map did not mean that there were no woody plants, but rather referred to whether trees or grass dominated the canopy cover. In areas classified as grassland, woody plants were short, and grass rather than trees dominated the canopy cover. For areas to be classified as dense vigorous thicket, the scrub would have grown taller above grass height and visually been very obvious. He also noted that it was really only during the measurement of vegetation plots in the area that he became aware just how many small "*Acacia*'s" and other woody plants were hidden in the grass layer in grassland areas. This observation concurs with my interpretation of Kings' "scrub" category, and indicates that the highest densities of favoured small "*Acacia's*" probably occurs just prior to obvious bush encroachment (when trees grow tall enough to noticeably affect lateral visibility).

Bourquin also showed me three black and white photographs of black rhinos he had taken in northern Hluhluwe during the winter of 1965. Although the pictures were taken four years after the 1961 die-off, the population of black rhinos in the area was still very dense. The first picture was that of a black rhino taken at the base of Makhokoba (NE of Grid Study Area) in August 1965. The photograph shows very open parkland with isolated *S.birrea* trees but with many small (< 1m) woody plants that look like "*Acacia*'s" that have been burnt but appear heavily browsed. The black rhino in the picture is not in good condition, although it does have a big front horn suggesting it is an older animal. Bourquin had another photograph of another older very long horned female with calf in the Manzimbovu area taken in 1965. This animal is also not in good condition. In the third picture one of two black rhino in a photograph taken at Hidli in the late dry season the same year (September 1965) is also in poor condition. Whilst these three rhino photographs of Bourquin's are not conclusive proof that the rhinos were under nutritional stress in the winter of 1965, they do suggest that this was quite possibly the case. Corroborative evidence to support the latter view comes from the measurement of Bourquin's 1965/66 Zincakeni plot and the subsequent measurement of Hitchins' plots in 1969-70 which both showed that an extraordinarily high proportion of woody plants were being browsed including a very high proportion of normally rejected unpalatable species. Bourquin also remarked on the large number of black rhino in Northern Hluhluwe during the period.

MR RODDY WARD

The Park's first ecologist, C.R. (Roddy) Ward (pers.comm.) mentioned that by 1960, the combination of extensive bush-clearing and culling of grazers was having a noticeable effect, and had significantly increased the extent of grassland in north eastern Hluhluwe. He noted that the increase in grass following the heavy culling and the increased rainfall became especially noticeable just prior to the 1961 die-off of black rhino in the area (see chapter 17).

MR DOUG PHEASANT

Doug Pheasant put in the first lighting plant at Hilltop and remembered the time when the sight of a white rhino in Hluhluwe caused a major stir. I went for a drive with him around the Hluhluwe study area. He particularly remembered that the top part of the Isavivaneni road area being much more open with smaller trees. Bourquin's 1966 Isivivaneni transect also indicates that the area was more open in the past.

RUSTENBURG WILDLIFE SOCIETY BRANCH MEETING

At the end of a talk I gave to the Rustenburg branch meeting of the Wildlife Society in 1993 a member of the audience said how amazed he was at the extent of the development of closed woodland/forest in Hluhluwe following a recent visit there. His previous last visit had been in the mid 1970s which he remembered as more bushed than when he first visited the reserve in the late 1950s. He remembered many areas as having been open during this period.

APPENDIX 20.5

THREE DIMENSIONAL SURFACE PLOTS OF CANOPY COVER OF SELECTED SPIZES IN ORDINATION SPACE

RESOURCE processed Grid survey spize data (after excluding plots with riverine and true evergreen forest patches) were subjected to heuristic multivariate descriptive analysis using a detrended correspondence analysis. Three dimensional (3D) interpolated surface plots were then produced for a number of key spizes (using the plot axes scores from the spize ordination to give eastings and northings for each plot) enabling a static ordination approach to be used to generate and examine hypotheses about probable zonation and successional pathways in Hluhluwe woody vegetation (See Appendix 4.1).

The results were also examined to see if they supported the proposed successional Whateley-Wills sequence in *A.nilotica* woodlands, and they did. The similarity of the relationships between key spizes in the hypothesised succession between the DCA (used to derive the 3D spize cover-abundance surface plots) and the partial fire constrained ordination (chapter 16) emphasises the key role fire (or rather lack of fire) has had in the development of lowland forest areas in Hluhluwe.

As measures of black rhino feeding were obtained for each plot, it was also possible to produce an approximate (inverse distance squared) interpolated 3D surface of black rhino feeding levels (using the plot axes scores from the spize ordination to give eastings and northings for each plot). The interpolated feeding surface plot (Figure 20.16) can therefore be directly compared to the abundance surfaces of key spizes (and hence "communities" and different seral stages) revealed by the spize-based ordination (Figure 20.15 a..k) and gives an indication of the relative impact vegetation succession could have had on black rhino carrying capacity.

SPIZE BASED STATIC ORDINATION SURFACE PLOTS

The assumption behind this "static" approach to studying succession (Austin 1977) is that each site represents a sequence in time; with the larger size classes representing the present successional state of the site, and the smaller size classes the possible future composition (Enright 1982, Emslie 1991d). By following the paths traced by the centroids of successively larger spizes of key species on ordination diagrams, successional patterns can be detected (Emslie & Adcock 1990a, Emslie 1991d). Figure 20.15 a..h improves upon this approach, by following changes in three dimensional abundance surfaces for successively larger key spizes and these contain much more information about a spize's abundance than simple 2D centroid points in ordination space (See Chapter 4 and Appendix 4.1 for more details of the techniques used).

The distribution of rhino feeding (average browse bottles eaten per plot) over ordination space was also plotted as an interpolated 3D surface (Figure 20.16 and included as small inserts top right of Figure 20.15). By mentally superimposing this diagram onto the 3D spize surface plots it is possible to determine the extent to which successional trends may have been detrimental to rhino.

The Whateley-Wills successional sequence closely follows the arrow superimposed onto Figure 20.16.

Figure 20.15 a shows canopy cover abundance levels of *A.nilotica* spizes as 3D surfaces in spize based ordination space. *A.nilotica* was one of the most ubiquitous species in the grid study area occurring on 127/242 plots.

> Figure 20.15 A clearly shows that the different spizes of *A.nilotica* predominantly occur at different locations in ordination space. This considerable separation is consistent with A.nilotica being a pivotal species in woody plant autogenic succession as hypothesised by "Whateley-Wills" (1996).
>
> Peak abundance of small/medium *A.nilotica*'s (less than 2m) occurs at between 200 and 300 on Axis 1 and less than about 150 on Axis 2.

Peak abundance for intermediate sized (2-4m high) *A.nilotica* occurs between about 50 and 100 on Axis 1 and again at less than about 150 on Axis 2. This represents a sideways shift of about -200 on Axis 1. However although peak levels of Size 3 *A.nilotica*'s occur at a similar position on Axis 2, the spize has become abundant along the whole of Axis 2 as long as the Axis 1 score is less than about 125.

Mature Size 4 *A.nilotica* trees (>4m) also occur predominantly at low Axis 1 scores, although peak abundance levels have shifted downwards from the upper half of Axis 2 to the lower half of Axis 2. The fact that smaller *A.nilotica* trees are not associated with these mature trees corroborates Whateley and Wills's (1996) finding that *A.nilotica* did not establish and survive under its own canopy. Canopy cover levels of mature A.nilotica trees are also greater presumably as their flat topped canopies have spread laterally.

These three *A.nilotica* surfaces suggest a succession trace that has progressed in an almost right angled curve starting high on Axis 2 and medium-high on Axis 1, moving leftwards along Axis 1, before turning and then moving down Axis 2 (see arrow superimposed on Figure 20.16).

By contrasting the small insert (top right) with the three *A.nilotica* surfaces one can see that "communities" with smaller *A.nilotica*'s had high amounts of black rhino feeding, but that as the species matures habitat quality declines markedly. Habitat quality declines fastest as trees grow above 2m.

The fact that *A.nilotica*'s distribution does not extend throughout the whole ordination space indicates that while the "Whateley-Wills" model may hold for sites with *A.nilotica* it does not occur in all areas in the Grid survey study area. This is consistent with the spatial zonation of different vegetation communities.

Figure 20.15 B shows canopy cover abundance levels of *D.cinerea* spizes as 3D surfaces in spize based ordination space.

D.cinerea clearly has a wide ecological tolerance as shown by the distribution of small (<1m) individuals throughout ordination space. Indeed this species was the most ubiquitous of any species in the grid survey occurring in 174/242 grid plots.

Peak levels of small *D.cinerea* occur towards the middle of Axis 1 and upper two thirds of Axis 2. By way of contrast tall *D.cinerea* are associated with tall mature *A.nilotica* although canopy cover levels are lower.

Peak levels of medium (1-2m) high *D.cinerea* occurred on sites with little or no *A.nilotica* and this spize was had a similar abundance surface to medium-intermediate *E.crispa* (Figure 20.7 I). This part of ordination space reflects the *A.karroo, D.lyciodes, M.senegalensis, D.cinerea, E.crispa* dominated community on the heavy low lying black soils in north-eastern Hluhluwe.

Figure 20.15 C shows the canopy cover abundance levels of *R.pentheri* spizes as 3D surfaces in spize based ordination space. This species was the second most ubiquitous species in the grid study area occurring in 142/242 plots.

This species follows a similar course in ordination space to *A.nilotica* although it appears to come in a little later in succession as indicated by the association of high amounts of small (<1m) high *R.pentheri* in areas with most intermediate *A.nilotica* 2-4m high.

Figure 20.15 D shows how canopy cover abundance levels of *B.zeyheri* spizes varies in spize based ordination space. This species was the third most ubiquitous species in the grid study area occurring on 132/242 plots.

This species shows a similar "curved" successional pattern to *R.pentheri* and *A.nilotica* although it is clearly a later successional species than either *R.pentheri* and *A.nilotica*.

E: Canopy cover abundance levels of *E.divinorum* spizes as 3D surfaces in spize based ordination space.

This species was associated with

F: Canopy cover abundance levels of *E.racemosa* spizes as 3D surfaces in spize based ordination space.

This species was clearly a later successional species than either *R.pentheri* and *A.nilotica* only coming in low on Axis one and mature trees predominating at low axis 2 scores.

G: Canopy cover abundance levels of *S.inerme* spizes as 3D surfaces in spize based ordination space.

This species was also clearly a later successional species than either *R.pentheri* and *A.nilotica* coming in low on Axis one and mature trees predominating at low axis 2 scores.

H: Canopy cover abundance levels of *S.myrtina* spizes as 3D surfaces in spize based ordination space.

This fire sensitive species was also clearly a later successional species than either *R.pentheri* and *A.nilotica* coming in low on Axis one and mature trees predominating at low axis 2 scores.

The following three species 3D plots were included to show the existence of spatial vegetation zonation.

I: Canopy cover abundance levels of medium/intermediate *E.crispa* spize as a 3D surface in spize based ordination space.

This species is associated with another system (and not the *A.nilotica* system). In this case E.crispa is associated with lower lying *A.karroo* dominated areas on black clay soils, small medium D.cinerea (see 20.15b), *H.pauciflorus*, *D.lyciodes* and *M.senegalensis*.

J: Canopy cover abundance levels of intermediate tall *A.caffra* spize as a 3D surface in spize based ordination space and **K**: Canopy cover abundance levels of *V.subuligera* spize as a 3D surface in spize based ordination space.

> These 3D plots confirm these two species are associated with another system. In this case - frequently burnt tall grass hillslope habitat dominated by *A.caffra* and *V.subiligera with L.javanica, and some A.nilotica and A.karroo.*

Figure 20.16 shows a 3D plot of black rhino feeding levels - and shows the major decline in carrying capacity following succession from open areas through *A.nilotica* woodland to lowland *E.racemosa* lowland forest. Appendix 20.5 confirms this with later successional stages of E.racemosa lowland forest having as little as 5% of feeding levels in earlier seral stages. The drop in carrying capacity as succession progresses in *A.nilotica* areas is also consistent with individual spize selection and rejection patterns (chapters 6 and 7).

As a heuristic tool, the static approach proved to be a valuable tool for examining possible spatial zonation and temporal succession using 3D abundance plots of key spizes in ordination space (using RESOURCE processed data). The superimposition of the feeding surface onto these plots also enabled the implication of habitat changes and differences for black rhino to be determined.

APPENDIX 20.6

TWINSPAN FLORISTIC ANALYSIS OF HLUHLUWE GRID DATA

Strong confirmatory evidence for the Whateley-Wills hypothesis model comes from an examination of the output from the preliminary spize based TWINSPAN analysis discussed in chapter 7 (Table 7.23). This analysis corroborated the earlier conclusion that black rhino suitability declined as *A.nilotica* dominated closed woodland changed into *E.racemosa, B.zeyheri, R.pentheri* dominated lowland forest. **Mean offtake levels by black rhino in mature *E.racemosa* dominated lowland forest were only about half those in transitional lowland forest developing from *A.nilotica* closed woodland.**

A further TWINSPAN analysis was undertaken using the same data set used to produce the cover abundance surface plots in ordination space (ie Grid survey cover abundance data set after excluding riverine and true mature evergreen forest plots).

The first major division in the TWINSPAN dendrogram differentiated between forest/closed woodland communities and more open associations (Division 1: λ=0.51) and provided strong corroborative evidence to support the "Whateley-Wills" model.

Firstly **the pivotal role of *A.nilotica* in development of forest in Hluhluwe** as postulated by Whateley & Wills (1996) **was indicated by the analysis. Small *A.nilotica*1's (<1m) were 1.5 times more likely to occur on the open side of the divide; yet tall mature *A.nilotica*4's (>4m) were 4.5 times more likely to occur on the forest side of the divide.**

Secondly, **all sizes of *E.racemosa, B.zeyheri* and *R.pentheri* occurred on the forest side of the divide. Furthermore as tree size of these species increased so did the likelihood of the plot being allocated to the forest side of the divide** (Table 20.2). Figure 20.2 also indicates that *E.racemosa* is a later successional species than the other two species confirming the results of the static ordination. Indeed all four *E.racemosa* spizes together with *K.floribunda*1 were the five indicators listed for the forest side of the main divide.

In all cases the spizes of these three species listed in Table 20.2 were more frequently found on the forest side of the divide. For example, small (<1m) *E.racemosa* was 12.7 times more likely to occur in plots on the closed woodland/forest side of the first main TWINSPAN divide than on the more open woodland/short thicket/grassland side of the divide. Table 20.2 also shows that as each of the three species increases in size it is more likely to be classified on the forest side than the more open side of the main divide.

Thirdly, small *A.karroo*1 (<1m) and *L.javanica*2 (1-2m) were key indicators listed on the open side of the main divide. Medium *A.karroo*2's (1-2m) were also 4.0 times more frequent on the open side of the divide.

Fourthly, an examination of the mean percentage canopy cover scores for key spizes for each of the 18 "communities" produced by the TWINSPAN analysis of the Braun Blanquet Cover Abundance data corroborated the successional trends shown in the 3D surface plots of spizes in ordination space (Appendix 20.5, Figure 20.15). A few of the most salient points to emerge are discussed below...

> Contiguous TWINSPAN groupings 3,8,9,10,11,14,15 & 17 had the **highest canopy covers of small-intermediate *A.niloticas***; and the weighted average black rhino feeding offtake in these "communities" with smaller *A.niloticas* (n=68 plots) **was 281 bottles/Ha** (new & old).
>
> **Contiguous groupings 1,2 and 4 that had high canopy covers of taller *E.racemosa, S.myrtina, B.zeyheri, R.pentheri, D.cinerea* and *A.nilotica. K.floribunda* .** The weighted average **black rhino feeding offtake in these "communities", which represent late stages of the hypothesised "Whateley-Wills" successional sequence (n=35 plots), was only 71 bottles/Ha (new & old) which represents only a quarter of the feeding levels in "communities" with small *A.nilotica*'s.**
>
> TWINSPAN Grouping 1 represented the **most advanced form** of "Whateley-Wills" succession. The combined canopy cover percentage points of the tallest spizes of *E.racemosa, E.divinorum, S.myrtina, C.caffra, K.floribunda, C.pulchella, B.zeyheri,* and *R.pentheri* in this "community" was 101%. The tallest spizes of earlier successional *A.nilotica, D.cinerea* and to a lesser extent *A.karroo* contributed a further 33%. The combined canopy cover of medium-tall (2-4m) *E.racemosa, B.zeyheri*, and *R.pentheri*

in this "community" accounted for a further 32%. The medium-tall spizes (2-4m) of earlier successional *A.nilotica*, and to a lesser extent *A.karroo* and *M.senegalensis* contributed a further 14%. **Mean black rhino feeding levels in this lowland forest *E.racemosa* dominated "community" was only 14 bottles/Ha (old & new). This is only 5% of mean levels recorded for "communities" with small *A.nilotica*'s.**

The results of the TWINSPAN analysis clearly corroborates Appendix 20.5 and Figures 20.15 and 20.16 which show that the development of lowland forest communities over much of Hluhluwe has resulted in a major lowering of Hluhluwe's carrying capacity for black rhino.

APPENDIX 20.7

USE OF SELF-THINNING POWER LAWS TO ESTIMATE APPROXIMATE PAST DENSITIES OF SMALL A.nilotica

A particularly important study of self thinning was made by Yoda et al (1963) who found that when the log of mean plant weight (ie of survivors) was plotted against the log of density of survivors the values of successive harvests were found to lie around a slope of around -1.5 (Harper 1977). A slope of -1.5 implies that while the numbers of individuals present in the population is decreasing, the weight of the population as a whole increases. The rate of growth of individuals more than compensates (and is probably responsible for) the fall in numbers. This self-thinning relationship has been written as.. $Log_{Weight} = C\, x\, Log_{Density}{}^{-3/2}$, and is otherwise known as the 3/2 power law.

The 3/2 power law has been mainly tested mainly with annual plants, but there is evidence it holds true for forest trees as well. The empirically derived thinning tables derived by foresters to optimise timber production conform rather well (Harper 1977). In Forestry the log of mean timber volume per tree is usually plotted against the log of survivor densities. There is again a striking relationship, but with gradients that are considerably steeper than expected under Yoda's self thinning law (gradients ranging from -1.72 to -1.82). The use of timber volume rather than mean weight/individual may be enough to steepen the regression slope. Slopes of -1.48 to -1.62 have been empirically derived for yield:density relationships of long lived stands of oak (*Quercus robur*) and beech (*Fagus sylvaticus* ;White & Harper 1970).

In mature *A.nilotica* closed woodland plots measured during the Hluhluwe Grid survey, 74.9% of individuals were >2m tall; with a total density of 246/Ha. *A.nilotica* trees over 4m tall occurred at a density of 125 trees/Ha. However as most size class 3 trees (2-4m) were near 4m tall the density of taller *A.nilotica*'s was equivalent to around 200 trees/Ha.

If one takes the empirically derived mean slope of -1.77 rather than -1.5, and assumes that if the weight of a tall *A.nilotica* is 100 units and the weight of a small *A.nilotica* is 2 units then using the self thinning power law one would estimate that the past density of small *A.niloticas* (<1m) would be 1,823/Ha (2,714/Ha using a slope of -1.5). This density is 8.0 times the 1989 densities of smaller (<2m) *A.nilotica* recorded in the 127 Grid plots containing *A.nilotica* (11.9 times > using a slope of -1.5).

In the 127 Grid plots containing *A.nilotica* the mean percentage cover points/tree was 11.82 for tall (>4m) *A.nilotica*'s and 0.707 for small (<1m) *A.nilotica* trees. The number of canopy cover points per tree was 14.6 times greater for taller size 34 (>2m and most >3.25m) compared to smaller size 12 (<2m and most < 1m)) *A.niloticas*. If we use this empirically derived relationship between canopy cover % points/tree and tree size in the power law and use Yoda's 3/2 power law this returns a lower predicted past density of smaller (<2m) *A.nilotica*'s of 1,193/Ha. This density is 5.2 times the 1989 densities of smaller (<2m) *A.nilotica* recorded in the 127 Grid survey plots which contained *A.nilotica*.

Depending on the slope of the power law used, the number of smaller (<2m) *A.nilotica* trees to die (as a result of self-thinning) to produce each taller (>3.25m odd) *A.nilotica* tree ranged from an estimated 4.2 to 10.9 trees. In the 127 Grid plots (just over half of the Hluhluwe Grid study area) containing *A.nilotica* the current density of taller (>2m and most >3.25m) *A.nilotica*'s was 101/Ha. This translates to a predicted average past density of smaller *A.nilotica*'s (<2m) prior to self thinning of roughly 525-1200/Ha (in the 127 plots). These densities are between 2.3 to 5.2 times higher than the 1989 densities of 175/Ha small(<1m) and 54/Ha medium (1-2m) *A.nilotica*'s on the 127 Grid plots (= 52.5% of Hluhluwe Study Area) containing the species. Given that forty years ago grazing biomass was high with a low proportion of bulk feeders this will have further favoured black rhino by reducing grass interference.

An analysis of the size class structure of *A.nilotica* trees in Hluhluwe and Umfolozi highlights the markedly more mature age structure in Hluhluwe. The average contribution of each *A.nilotica* tree to total canopy cover in Hluhluwe is 2.18 times higher in Hluhluwe. Medium-tall to tall (>2m) *A.nilotica*'s make up 30.6% of all *A.nilotica* individuals in Hluhluwe compared to only 10.6% in Umfolozi. The density of tall *A.nilotica* individuals (>4m) was 15.4 times greater in the Hluhluwe compared to Umfolozi study area. Furthermore, mean total canopy cover of *A.nilotica* in the Hluhluwe Grid study area was 7.25 times greater than in the Umfolozi Grid study area (9.28% vs 1.28%). While 85% of *A.nilotica* canopy cover was made up of trees >2 m in Hluhluwe the corresponding figure for Umfolozi was only 28%.