SADC REGIONAL PROGRAMME FOR RHINO CONSERVATION

RMG BLACK RHINO CARRYING CAPACITY MODEL
Version 1.0

USER GUIDE
(*Evaluation Draft*)

Keryn Adcock

Improving and standardizing methods of Black Rhino Carrying Capacity Assessment
Semester 3 task 4.2-2.1

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ABOUT the SADC Regional Programme for Rhino Conservation:

The Programme is funded by the Italian Ministry of Foreign Affairs, Directorate General for Development Cooperation (Project AID 5064).

The Programme is contracted to CESVI and implemented through a regional consortium which comprises:
- The Secretariat of the Southern Africa Development Community (SADC)
- IUCN-ROSA (The World Conservation Union - Regional Office for Southern Africa)
- The IUCN African Rhino Specialist Group
- WWF-SARPO - (World Wide Fund for Nature - Southern Africa Regional Programme Office)
- CESVI (Cooperazione e Sviluppo)

The ***Programme goal*** is to contribute to maintain viable and well distributed metapopulations of Southern African rhino taxa as flagship species for biodiversity conservation within the SADC region.

The ***Programme objective*** is to implement a pragmatic regional rhino strategy within the SADC region following the acquisition of sound information on, firstly, the constraints and opportunities for rhino conservation within each range state and secondly, the constraints and opportunities for rhino metapopulation management at the regional level.

DISCLAIMER

The information, opinions and materials presented herewith do not necessarily reflect the official views of any of the organisations involved, including the Italian Ministry of Foreign Affairs, SADC, CESVI, IUCN-ROSA, WWF-SARPO, AfRSG or governments of SADC member countries.

CONTACT DETAILS FOR THE PROGRAMME:

Dr. Rob Brett
SADC Regional Rhino Programme Coordinator
IUCN-ROSA
6 Lanark Road Belgravia PO Box 745 Harare, Zimbabwe
Tel: 263-4-728266 Fax: 263-4-720738
Email: robb@iucnrosa.org.zw

SADC Secretariat
Directorate of Food, Agriculture and Natural Resources
P O Box 0095 Gaborone Botswana

CESVI Zimbabwe Office
9 Northwood Rise, Mt Pleasant, Harare, Zimbabwe
TEL/ FAX: 263-4-882243, 884492, 850898
EMAIL: cesvi@africaonline.co.zw

Ministero degli Affari Esteri
Direzione Generale per la Cooperazione allo Sviluppo,
Unità Tecnica Centrale
Viale Contarini (angolo Viale Farnesina)
00194 ROMA ITALY

PROGRAMME WEB SITE: We invite you to vist our web site : www.rhino-sadc.org

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SECTION 1 - WHAT IS THIS MODEL?

- This model is a set of multiple-regression coefficients from 4 regression equations, which combine to produce a predicted ecological carrying capacity estimate for a black rhino area.

- The regression variables and coefficients were developed from 15 “baseline” black rhino areas (12 in South Africa, 2 in Namibia), by examining these and alternative variable relationships to prior “expert” estimates of black rhino carrying capacity (the dependent variable in the regression equations).

- The model regression coefficients are for variables representing
    - average annual rainfall
    - rainfall concentration (monthly spread)
    - coldness or frost incidence
    - soil fertility
    - available standing browse biomass
    - browse suitability or quality.

- For users to predict a carrying capacity for a new or other rhino area, input values of the variables for that area need to be determined by the user and calculated according to procedures documented in this manual and the spreadsheet software.

This model must only be used for black rhino carrying capacity determination by workers with the appropriate ecological and preferably black rhino background, approved by the relevant rhino conservation and management authorities in the SADC country or region concerned.

Users can move directly to section 3 - section 5 to read about procedures for using this model. However, it is strongly advised that users first read through section 2 and the accompanying appendices, to understand the reasoning behind the procedures used in this model.

Please note that additional work on this model for black rhino carrying capacity assessment is planned:
This aims to:

- improve model “calibration” by updating variable values using better information from recently completed research from several baseline areas,
- explore improvements in model construction using Structural Equation Modelling, and
- Improve the index of browse availability.
- Also, Zimbabwean and Kenyan rhino conservation authorities have also expressed interest in developing the model to include their rhino areas.

WHAT THIS MODEL DOES AND DOES NOT DO

It DOES....

It does capture to a great extent the current knowledge and understanding of the author and many other experienced people on the broad-scale determinants and levels of black rhino carrying capacity in different habitats in South Africa and Namibia.

It also provides a framework and approach by which further improvements in understanding and prediction can be developed.

It does produce a *ballpark* prediction of the ecological carrying capacity and dominant male carrying capacity of an area; given its current conditions;

It does provide indications of *some* of the *potential* promoting and limiting influences on black rhino population performance in an area.

It does NOT....

It does not claim to be the last word in black rhino carrying capacity and performance issues, but merely a start.

It does not produce absolute predictions of black rhino carrying capacities for new or existing rhino areas in SA or Namibia, without error or potential bias.

As with any regression model, it does not allow users to extrapolate outside the range of the model. The model may not produce reasonable carrying capacity predictions for areas or circumstances where habitat conditions fall outside of the range of those covered by the 15 areas. This would exclude infertile areas with c.600-1000mm rainfall (eg, Miombo areas), medium to highly fertile areas with a double rainfall season (eg, in east Africa), lowveld mopane areas, and winter rainfall and Karoo biomes, among others.

And most importantly....

Note that the black rhino carrying capacity in an area is not fixed.

It can and does change as habitat conditions change. Firstly, carrying capacity alters with year-to-year fluctuations in annual rainfall total and monthly distribution, although much of this (bar harsh droughts and floods), will be accounted for in the model prediction.

Specifically, standing available browse, browse suitability (and condition) and climate may change over the medium and longer term. (E.g. with burning regime, vegetation succession, impacts of black rhino and other browsers on vegetation, global warming (dare we say)). Thus routine re-assessment of carrying capacity over time is needed to optimise black rhino management.

List of 15 “Baseline” areas used to develop the RMG black rhino carrying capacity model v.1.

ADD	Addo Elephant National Park (Elephant Camp)
AUG	Augrabies Falls National Park (North Section)
AVS	Andries-Vosloo section of the Great Fish River Reserve Complex
ESH	Eastern Shores - Tewati Wilderness section
HLU	Hluhluwe section of Hluhluwe-Umfolozi Park
ITA	Ithala (Itala) Game Reserve
K-W	Kunene West - General
LAP	Lapalala Nature Reserve - (Rhino section)
MKU	uMkhuze - (Mkuze) - excluding the controlled hunting area
NDU	Ndumo Game Reserve
PIL	Pilanesberg National Park
UMF	Umfolozi section of the Hluhluwe-Umfolozi Park
VAA	Vaalbos National Park
WEE	Weenen Nature Reserve
WPP	Waterberg Plateau Park

Disclaimer

This model emanates from research undertaken by Keryn Adcock in her capacity as consultant to the Rhino Management Group, funded primarily by her company Wild Solutions, with partial funding contributed by WWF (SA), and information and field assistance provided by each black rhino conservation agency involved. The **SADC Regional Programme for Rhino Conservation** production of this model version, software and supporting documents (see below).

The contents of this work do not necessarily reflect the views or policies of any sponsor, rhino conservation agency or employee thereof. This model and its predictions are to be used entirely at the risk of the user / using organization. Keryn Adcock, Wild Solutions, the Rhino Management Group, WWF and the SADC Regional Rhino Conservation Programme, make no warranty, expressed or implied, and will bear no legal liability or responsibility for the accuracy, completeness or usefulness of any information in this model, nor for any consequences arising out of the use of this software, or the predictions it produces.

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Save the Rhino Trust

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AUTHORSHIP and OWNERSHIP of DATA

This model software, the compiled calibration data values*, variables and coefficients, and the software and user manual, were researched, designed, developed and produced by **Keryn Adcock (Wild Solutions)**. No part of the model software data (including original or derived variable values* or model coefficients) and manual contents may be used for any other purpose than black rhino carrying capacity /productivity assessment in the SADC region, without prior written consent from Keryn Adcock.
(*excluding annual rainfalls and minimum July temperatures.)

All the raw data from which the variables were developed, belongs to the relevant **conservation organization; or to the relevant individuals** in the case of unpublished reports or theses and published papers. (Authors of raw data are documented as much as possible in the section below and in the model spreadsheet support information itself (eg. File *BrCCSupport*).

CONTRIBUTORS

GENERAL IDEAS ON BROWSER ECOLOGY

Prof. Norman Owen-Smith, Univ. Witwatersrand, Johannesburg
Raoul Du Toit, WWF SARPO, Zimbabwe
Dr Richard Emslie, IUCN SSC African Rhino Specialist Group
Blythe Loutit, Save the Rhino Trust, Namibia
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Dr Rob Brett, SADC rhino programme
(Others - see references)

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Keryn Adcock, Wild Solutions, through the RMG black rhino Status Report Summaries 1989 to 1998 and this project
Raoul Du Toit, WWF Rhino programme officer, Zimbabwe
Dr Richard Emslie, IUCN SSC African Rhino Specialist Group
Dr Peter Goodman, KwaZulu-Natal Wildlife
Dr Mike Knight, National Parks Board of South Africa

AGRO-CLIMATIC DATA

Prof. RE Schulz, and Ms M Maheraj, Dept Agricultural Engineering, Univ. Natal. Pietermaritzburg

DEVELOPING SOIL FERTILITY RATINGS

Dr Jeff Hughes, University of Natal, Pietermaritzburg
(Others - see references)

DEVELOPING GEOLOGICAL FERTILITY RATINGS

Prof. Mike Watkeys, University of Natal, Durban
(Others - see references)

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South African Rhino Areas

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Clive and Connita Walker, Lapalala
Clive Ravenhill, Lapalala
Keryn Adcock, Wild Solutions

Pilanesberg National Park
Gus Van Dyk, North West Parks and Tourism Board
George Phiri, North West Parks and Tourism Board
Bruce Brockett, North West Parks and Tourism Board
Hans Hansen
Hanna Lindemann
Michele Hofmeyr

Ithala Game Reserve
Ian Rushworth, KwaZulu-Natal Wildlife
Trevor Wolf, KwaZulu-Natal Wildlife
Donovan Kotze, University of Natal, Pietermaritzburg

Weenen Nature Reserve
Neil Langley, KwaZulu-Natal Wildlife
Athol Marchant, KwaZulu-Natal Wildlife
Ian Rushworth, KwaZulu-Natal Wildlife
Tim O'Connor, University of Natal, Pietermaritzburg / Univ. of the Witwatersrand
Lorene Breebaart, University of Natal, Pietermaritzburg

Hluhluwe-Umfolozi Park
Owen Howison, KwaZulu-Natal Wildlife
Richard Emslie, IUCN SSC African Rhino Specialist Group
Keryn Adcock, Wild Solutions
A Whateley and RN Porter

uMkhuzi Game Reserve
Craig Mulquweeny, KwaZulu-Natal Wildlife
Peter Goodman, KwaZulu-Natal Wildlife
A Huggins

Ndumo Game Reserve
Wayne Matthews, KwaZulu-Natal Wildlife
Ferdie Myburgh, KwaZulu-Natal Wildlife
Cathrine Hannekom, KwaZulu-Natal Wildlife
Else Pooley
Ken L Tinley

Eastern Shores, (Lake St Lucia Greater Wetland Area)
Dirk Rossouw, KwaZulu-Natal Wildlife
Andy Blackmore, KwaZulu-Natal Wildlife
J Beytenbach

Great Fish River Reserve
Brad Fike and staff, Eastern Cape Nature Conservation
Peter Lent, Fort Hare University
Tony Palmer, Agricultural Research Institute

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Mike Knight, National Parks Board of South Africa
Guy Castley, National Parks Board of South Africa
Kenneth G Buk, University of Copenhagen
H Bezuidenhout, National Parks Board of South Africa

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Mike Knight, National Parks Board of South Africa
Guy Castley, National Parks Board of South Africa
Kenneth G Buk, University of Copenhagen
H Bezuidenhout, National Parks Board of South Africa

Addo Elephant National Park
Mike Knight, National Parks Board of South Africa
Guy Castley, National Parks Board of South Africa
Wain Erlank, National Parks Board of South Africa
Hall-Martin AJ, T Erasmus & BP Bothma
Penzhorn BL, PJ Robbertse & MC Olivier
CF Johnson
Prof. Shone University of Port Elisabeth

Namibian black rhino areas

Kunene West,
Mike Hearn, Save the Rhino Trust
Blythe Loutit, Save the Rhino Trust
Rudi Loutit, Namibian Ministry of Environment and Tourism
HO Reuter, Save the Rhino Trust
PJ Viljoen

Waterberg Platteau National Park, **Namibia**
Peter Erb, Namibian Ministry of Environment and Tourism
Werner Killian, Namibian Ministry of Environment and Tourism
HO Reuter, Save the Rhino Trust
Prof Jankowitz, Univ. of Namibia, Windhoek

SECTION 2 - BACKGROUND TO THE MODEL Version 1.0

2.1 WHY WORRY ABOUT BLACK RHINO CARRYING CAPACITY AND PRODUCTIVITY?

Each country that holds remaining stocks of the endangered black rhino has a National Conservation Plan for this species. In each plan, a major goal is to increase overall rhino numbers as fast as possible, to minimise loss of remaining genetic diversity and to provide a buffer against potential poaching losses. To achieve rapid growth of the national herd, the rhino and the habitats in which they live must be managed so that rhino breeding performance is maximised, death rates are minimised, and the rhino food resource base is not compromised, wherever possible.

Monitoring and managing black rhino numbers relative to the carrying capacity of the habitat (i.e. at around 75% of carrying capacity) is one important potential way of promoting rhino productivity, and preventing *density-dependent* declines in rhino breeding performances and increases in mortalities. Introductions of rhino into new areas can be planned at well below carrying capacity to minimise social stresses and losses during the settling down period and promote maximum opportunities for population growth.

75% of ecological carrying capacity is the *approximate* highest density at which population productivity is unaffected by density-dependent feedback. Productivity curves for large mammals are skewed towards carrying capacity, and are not near ½ of carrying capacity as with smaller mammals. This is due to their typically high adult survivorship, long gestation periods and relatively old ages at first calving, which limit the range over which life-history parameters can change in response to changing density or food supply. (see McCullough 1992 for a summary large herbivore population dynamics).

The concept of *ecological carrying capacity* as used in this work, is probably most closely defined as “the maximum number of animals of a given (rhino) population supportable by the resources of a specified area” (i.e. *sensu* Caughley 1976, McCullough 1992).

Density dependent effects on black rhino population parameters should share similarities with those reported for other large mammal species such as white rhino, moose, red deer, bovids and equids (e.g. Clutten-Brock and Albon (1989), McCullough (1992), Owen-Smith (1988), Owen-Smith (1990), Freeland, & Choquenot.(1990)). These include delayed ages at first calving, delayed time to next conception after giving birth (longer inter-calving intervals), lowered infant, calf and subadult survival, lowered survival of old animals, overall slow or declining population growth rates. Potential evidence of many of these effects have been found among those southern African black rhino populations which have been at high densities relative to their habitat conditions (eg. Hitchins and Anderson (1983), RMG status report information, Adcock 1995 ...2000).

The impact of male rhino territoriality and “social” interactions between rhino are also density dependent and can affect population dynamics. In smaller (<c.600km^2) areas, there is a limit to the number of dominant, adult male black rhino that can be carried. (Adcock 1993, Adcock, Hansen and Lindemann 1998, RMG status report summaries : Adcock 1995, ‘96, ‘98, ‘2000). The author also hypothesises that the numbers of subordinate and subadult males that are tolerated within a dominant male range, are also to some extent limited, to only a handful (4-7 as a ballpark figure - this aspect needs further research).

Several additional issues and hypotheses are also relevant to black rhino population dynamics and productivity, but are not the subject of debate in this model version. These are described in more detail in Appendix 4, and include:

- The overshooting of carrying capacity.
  Rhino densities may overshoot carrying capacity due to birth-lag effects, especially under conditions which allow fast initial population growth.
- Population responses in highly fluctuating environments.
  In areas with a high degree of annual variation in browse production (eg, high variation in annual rainfall), rhino densities may never attain the “average” carrying capacity density, but can reach densities which are high enough to inflict long-term damage on vital browse resources during times of low browse supply (eg. drought).
- Competition and the impacts of other browsing game on black rhino carrying capacities.
  The browsing of other game species can reduce food supply to black rhino, and contribute to inducing vegetation changes which affect black rhino carrying capacity.

- The existence of Key resources

  In most habitats, black rhino can only obtain a diet of adequate quality (at least during critical times of the year) by selecting certain food plants or parts. Not all apparently available vegetation is suitable browse for black rhino.
- Possible lack of population productivity in low-nutrient environments

  Low-nutrient environments may only supply a near-maintenance diet to rhino, allowing little capacity for good calf production.
- Susceptibility to over-browsing in high-quality habitats

  Areas dominated by highly palatable browse promote rapid population growth and the tendency to overshoot carrying capacity. Such plant resources may not always have some resistance to browse pressure (e.g. structural defences or regrowth ability), and can become severely depleted, causing carrying capacity to drop.

2.2 A THEORETICAL BASIS FOR DETERMINING BLACK RHINO CARRYING CAPACITY: BROAD-SCALE DETERMINANTS OF AFRICAN BROWSER CARRYING CAPACITY

In general, large mammalian herbivore biomass increases with increasing annual rainfall on fertile and infertile soils, but increases less rapidly on infertile soils, and may even decline at annual rainfalls over 700mm. (Bell 1982 and East 1984). These fundamental relationships between primary and secondary production provide a starting point for assessing black rhino carrying capacities.

2.2.1 RAINFALL

The role of total annual rainfall (precipitation)
The exact role of annual rainfall amount in causing differences in woody browse production between sites has not been well studied. For grasses, there is a well-documented, linear, positive relationship between annual rainfall and grass production across areas. Within arid areas, the general positive relationship between total annual rainfall and total woody plant production have been shown. Specifically, ligneous production is highly dependent on rainfall (Le Houerou HN 1980). However, on a year-to year rainfall basis, Rutherford (1984) found evidence that woody production in a dystrophic, broad leafed savanna (c.630mm annual rainfall) was unaffected by rainfall in the current or previous year, except in drought years, and thus may be buffered by its links to soil moisture reserves.

How rainfall controls primary production
Woody plants initiate growth in response to temperature and day-length changes in late winter/spring, but only if residual soil moisture is sufficient (probably at rooting depths below those of grasses) (e.g, see Dekker and Smit 1996, Scholes and Walker 1993). Nutrient supply rate probably controls the *rate* of growth once growth has been initiated (as in grasses - Scholes 1990, Scholes and Walker 1993), and soil water availability probably controls the *length* of the growth period.

Growth rates
A plant’s production rate is constrained by its nitrogen metabolism; and nitrogen uptake to supply this is controlled by the soil’s nitrogen mineralization rate which is in turn controlled by water availability (and temperature, the size of the nitrogen pool and soil phosphorus (P) availability). P mineralization is also dependent on the presence of available moisture in the soils. (Scholes and Walker 1993) [e.g. In central Mali, on a transect of the rangelands between 200 and 1000 mm annual rainfall, the average P yield of the above ground herbaceous biomass on 35 sites increased significantly in relation to rainfall / water availability (Kessler and Breman 1991)].

Leaching of minerals
Under high rainfalls (over c. 700–900mm), and depending on the soil characteristics, prolonged leaching of basic cations (Ca, Mg, K and Na) can result in declines in these minerals and increased soil acidity. With increasing rainfall in east Africa, maximum soil fertility was found to occur at approximately 750 mm of annual rainfall. This phenomenon was related to a maximum base saturation of the soils in this region, due to an optimal relation between organic matter buildup by the vegetation and mineral losses due to leaching (Scott 1961). (Note that east African soils are *generally* more fertile than those in southern Africa).

The role of rainfall concentration (spread across months of the year)
The link between plant production and the amount of time essential processes are active, suggests that not only is the absolute *amount* of annual rainfall relevant in browse production and thus black rhino carrying capacity, but also the spread of rainfall through the year (i.e, is it concentrated in a few months or spread over most months of the year?) In this vein, Owen-Smith (1990, 1993 Property Assessment workshop, 1994, 1997) emphasized the importance of the length of dry versus wet seasons in potential seasonal food supply changes for browsers.

Summary
Thus annual rainfall affects browse production by affecting
- the amount of time during which plants are actively growing;
- the amount of time during- and extent to- which N and P are being mineralized in soils and these and other nutrients can be assimilated; and
- the quantities of leachable nutrients in soils needed for plant growth.

Rainfall-effect modifiers

Rainfall's effect on water availability and essential growth process becomes modified by

- soil texture, which affects plant-available water. (High clay soils tend to induce aridity under lower rainfalls, while sandy soils can store plant available moisture);
- soil depth: shallow soils cannot hold large volumes of water, while very deep, well drained soils may carry moisture beyond the rooting zone;
- soil water-logging (were lack of oxygen can prevent or inhibit woody plant survival or growth), and
- topography: by creating run-off versus run-on sites, this affects water availability and nutrient distributions. (Highly rocky terrain also has this effect, as in Augrabies Falls NP).

From personal observations, the author suggests that in east-African ecosystems, soil texture and resulting soil-water availability differences result in a possibly important dichotomy in effects on black rhino carrying capacity: The contrast occurs in semi-arid areas of <c. 600mm annual rainfall. In areas dominated by highly fertile volcanic, black cotton / turf soils, greater aridity and reduced carrying capacity results from induced xeric soil conditions in dry periods (e.g. parts of Lewa); while those areas on more sandy, basement-complex-derived soils of the right depth , have better reserves of plant-available moisture that allows a steadier production of browse (parts of Ol Jogi).

2.2.2 SOIL / GEOLOGICAL FERTILITY

Substrate "fertility" can influence black rhino carrying capacity in three ways:
1) by increasing the amount of annual primary production of browse;
2) by influencing plant species composition and through this dietary quality (nutrient content, digestibility and secondary plant chemical content),
3) by providing (through the available browse or soil licks) adequate supplies of potentially limiting mineral nutrients to black rhino.

Influence of substrate fertility on browse plant productivity

It is hard to distinguish in the literature between differences in rhino-relevant-browse productivity with different soil type (e.g, from Le Houerou 1980, Scholes and Walker 1993, Schultz 1997, Walter and Breckle 1984). Most reports record standing biomass or primary productivity for whole vegetation communities, but this information has little relevance to black rhino due to differences in plant densities and vertical structure between areas, which are seldom described.

However, we know that increasing soil fertility increases browse production (why else do we fertilize our crops?) Prins and van de Jeugd (1992) found that individual shrubs of the same species under the same rainfall grew significantly faster on fertile volcanic soils compared to infertile soils derived from Basement Complex gneiss. On average, the shrubs grew 1.56 times faster in height and 1.49 times faster in stem diameter, resulting in a c.50% greater amount of browse production on fertile soils. Differences in elephant density also occurred between these two areas - with more on fertile soils.

Phosphorus is important soil-derived mineral promoting soil fertility. P Levels are affected by innate soil mineral composition, and accumulation / cycling (e.g. in humus) versus leaching. Primary productivity in semi-arid areas is constrained by the rate of uptake of P and N, which is controlled by water availability as described above and temperature (see later). P availability can influence the rate at which microbial decomposers mineralise nitrogen, and can also directly influencing plant growth.

General soil fertility can also determine the soil microbial biomass. Lower microbial biomasses are found in less-fertile soils (Reuss and NcNaughton 1987), and thus lower rates of nutrient recycling occur on less fertile soils.

Soil / geology also provides the rest of the range of essential plant nutrients. Deficiencies in one or more essential macro or trace element can severely slow plant growth, but can also affect mineralisation in soils: e.g. cobalt is required by rhizobia for N fixation (Judson and McFarlane 1998).

Evidence that soil or rock mineral patterns are reflected in plant nutrient content?

Evidence is inconsistent on direct relationships between apparent substrate mineral contents and vegetation mineral composition, especially with respect to individual minerals and individual plant species. Data for browse material is also (as always) more sparse than that for grasses.

Jumba et. al. (1996) found that neither bedrock type nor soil mineral concentrations had detectable relationships with the macro-and micro-nutrient mineral content of herbage within species. Only herbage sulphur and copper showed some relationship to soil and geology. Global studies involving wheat and maize showed similar results (Silanpaa 1982). Du Toit et. al (1990) found that leaf N and P levels in *A.tortilis* and *A.nilotica* at two sites did not reflect differences in soil "available" levels of these nutrients. Bailey and Scholes (1997) found that two woody species (*Acacia tortilis* and *Carissa bispinosa*) growing on sodic soils with elevated levels of Na, K, Ca and Mg, did not reflect these higher levels of nutrient concentration in their foliage, compared to the same species growing on adjacent, lower-nutrient soils. However, grass species specific to the sodic soils did have higher levels of these minerals than non-sodic species.

Van Der Merwe and Perold (1967) did find differences in trace element contents of grasses that reflected the geology (and general soil fertility) of 4 different sites.

Reasons for lack of clear patterns in plant-soil mineral correlations may be that soil-extraction methods do not always seem to provide adequate measures of plant-available soil minerals (Jumba et al 1996).

Another important reason is that plant mineral composition is plant species-dependent to a significant extent (eg. Ernst and Tolsma 1989, Dougall and Glover ###, Adcock unpublished data).

In summary...
Soil / geology determine plant species composition to a significant extent; and it is these different species which display differences in mineral content. **Thus substrate fertility and plant species composition indices are well-correlated** (and would partially substitute for each other in a carrying capacity model).

Mineral provision to black rhino by the substrate

Geological type and soils are known to determine broad-scale patterns of mineral abundance which may affect herbivores. For example, Grant et. al. (1996) found significant differences in Ca, P, I and Mn in animal tissue between areas of different geology in Namibia. Spatial distribution and movement patterns of herbivores have also been found to correspond to forage mineral compositions related to geology and soils (NcNaughton 1990, and McNaughton and Georgiadis 1986). Maskall and Thornton (1996) examined mineral profiles in several Kenyan wildlife areas and discussed possible implications for wildlife. Adcock (1998) found that you could discriminate between black rhino areas based on a mineral analysis of their black rhino dung. Rhino horn can also be "fingerprinted" based on its mineral composition profile (Emslie et. al. 2000). However, there is not yet a comprehensive synthesis of information on the exact source and effects of mineral deficiencies, excesses or imbalances in black rhino habitats. Neither is the mineral nutrition of black rhino well-understood.

The opportunity to eat vegetation and perhaps eat soils from a range of different gross geological and soil morphological origins may well be important in determining black rhino health and productivity. Small scale variations in soil fertility/mineral composition are made use of by black rhino as licks or to feed on. Heightened fertility or mineral contents may also occur in the following sites:

- Under large trees
- On / around termitaria
- At lower catenal sites
- On old kraal sites

Quantifying mineral distributions and measuring their impact on rhino productivity and relative carrying capacity at the cross-continental level remains very difficult. (A summary of potentially relevant mineral issues is in preparation).

Influence of soil fertility on browse quality:

The dichotomy in ecological system structure and functioning between fertile and infertile soils is a major feature of African savannas (eg. Scholes 1990). It has been observed that even when the standing biomass of vegetation is similar on fertile and infertile soiled areas of similar rainfall, the biomass of large herbivores is much greater (Bell 1982, East 1984) and therefore the proportion of primary production converted to herbivore biomass much higher, in fertile than in infertile areas (Scholes and Walker 1993). **Food quality is thus a key constraint on secondary production (and thus black rhino production)**.

Bell proposed that food quality is usefully indicated by the ratio of plant metabolic (M) constituents (cell cytoplasm containing proteins, several minerals and soluble carbohydrates) to structural carbohydrate (C) constituents (cell walls / fibre: cellulose, hemicellulose and lignin - plus cell-wall-bound secondary chemicals - see below). Bell also proposed that this M:C ratio is influenced by soil nutrient availability. Food quality is determined by these ratios because higher fibre proportions decrease food digestibility.

Higher soil fertility leads to higher proportions of metabolic (M) constituents with respect to fibre (C). However, high water availability is proposed as increasing C content at the expense of M. Fertile, lower rainfall areas are thus indicated as having a greater utilizable proportion of annual plant production than infertile, high rainfall areas. Adcock unpublished data (in prep), found differences in plant and black rhino dung fibre (C) content between more arid and higher rainfall areas that potentially support this theory.

Food quality is not only decreased by higher fibre contents. Certain secondary plant chemicals which interfere with digestion and /or are toxic to mammalian herbivores, also decrease food quality. Indeed, the fibre component and tannin / phenolic components of plants are intimately linked in location and origin (Reed 1986). These secondary chemicals also interfere with plant fibre, fibre-bound nitrogen, and available protein and digestibility analyses (Mould and Robbins 1981, Reed 1986).

Janzen (1974) first put forward evidence for soil fertility effects on plant secondary chemical profiles within plant communities, and suggested links to animal numbers. Increasing biomass (and carrying capacity) of colombine primates across 5 sites was found to be closely correlated with increasing protein/Acid Detergent Fibre ratios (similar to Bell's M/C ratio) in the vegetation (Waterman et. al. 1988). Low protein:ADF ratios and high levels of secondary chemicals were also linked to lower soil fertilities in some of the sites.

Cooper and Owen-Smith (1985), Owen-Smith and Cooper (1987), Bryant el. al. (1989) and Owen-Smith (1993) have shown evidence for links between soil nutrient status, plant palatability and secondary plant chemicals. Jachman (1987, 1989) also found evidence for this link in the context of elephant ecology in the Miombo woodlands of Kasungu NP, Malawi.

High levels of carbon-based constituents (fibre, secondary plant chemicals) relative to N and P content in plant litter also adversely affect ecosystem productivity by slowing decomposition rates and thus mineralization rates and uptake by plants (Enriquez et. al. 1993). Appendix 2 gives some background information on possible effects of fibre and secondary chemicals in rhino nutrition.

2.2.3 TEMPERATURE AND FROST

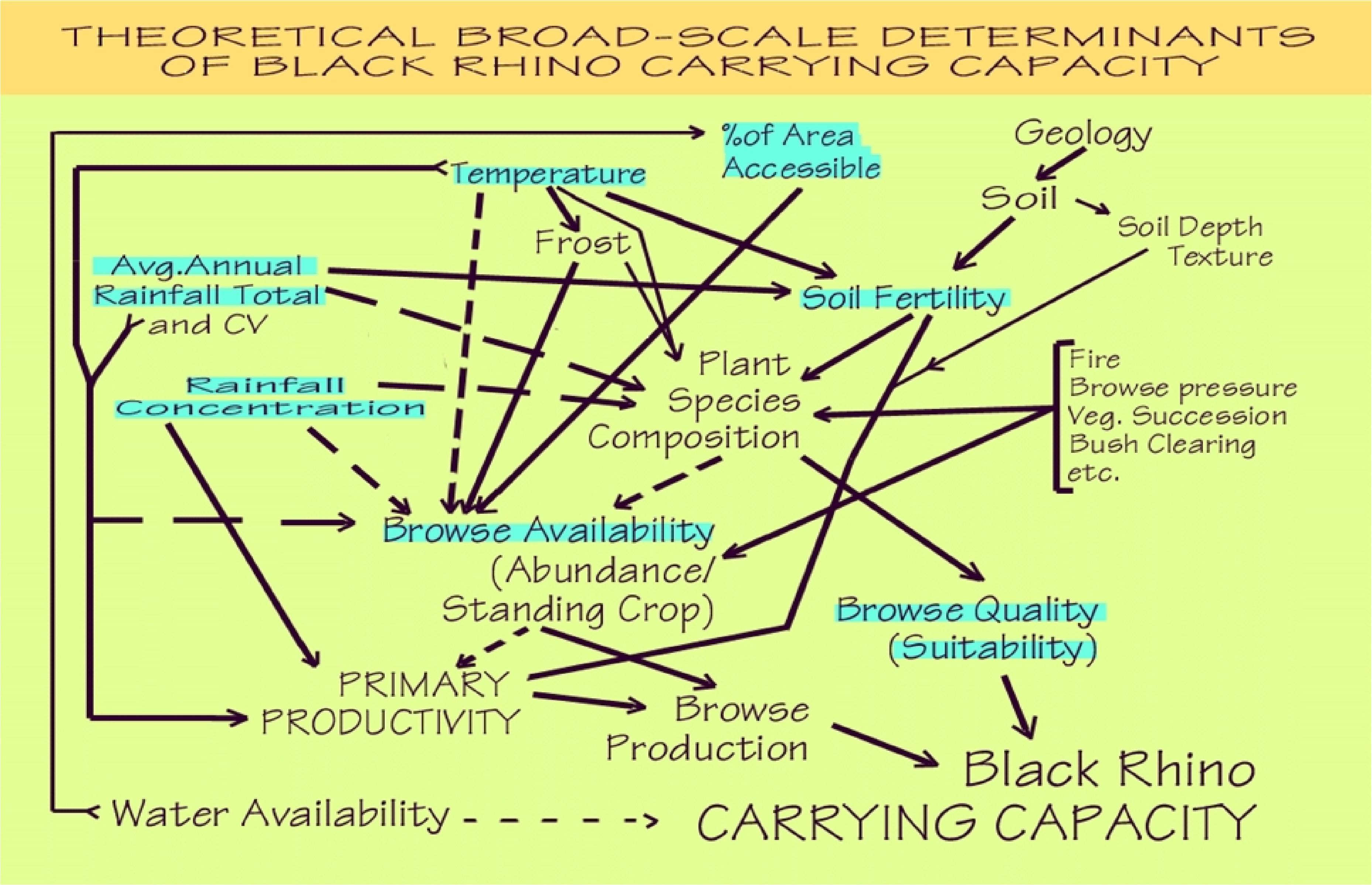
Several workers have observed how frost events have the particular effect of suddenly reducing browser food availability and/or quality. However, more specific information has not been found regarding frost effects on browse. Joubert and Ellof (1971) noticed frost effects in Etosha, and remarked how rhino tended to seek unfrosted branches - e.g. those protected by the grass sward.

Temperature along with moisture availability and soil fertility also has a part to play in affecting plant palatability. (To recap - plant palatability is affected by (among other things) the balance between the extent of carbon and nitrogen assimilation. More carbon (C) assimilation leads to greater formation of plant structural material and carbon-based secondary chemicals, while more nitrogen assimilation leads to more plant metabolic (M) constituents, and possibly nitrogen-based secondary chemicals). Ellery et. al. (1995) proposed the following mechanisms by which temperature had its effects:

(After Ellery et. al. ...) In plants, carbon assimilation begins at lower temperatures, and has a lower temperature optimum of 25-28^{o}C than nitrogen assimilation, which is optimal at 35-40^{o}C. Similarly, N assimilation continues in soils too dry to permit plant stomatal opening. In wet soils, nitrogen is lost by leaching and de-nitrification, but carbon assimilation continues even in soils which are nearly saturated. As a result, cool, wet conditions favour carbon assimilation, while hot dry conditions favour nitrogen assimilation. The climatically-controlled balance between carbon and nutrient assimilation is altered by the size of the nutrient pool in the soil. In the presence of a large nutrient pool, enough will mineralise even under cool conditions to balance the carbon assimilation. These interactions are proposed as determining the occurrence of *"sourveld"* (cooler, moister areas, or those with parent material that gives rise to sandy, low-nutrient soils) versus *"sweetveld"* (warmer, dryer areas, or those where the parent material produces soils with a high content of high-activity clays, which allow the accumulation of organic nitrogen).

In southern Africa, there is a degree of correlation between average temperatures and geological type / fertility. Ancient, infertile basement complex geologies tend to be inland at high altitudes, with lower average temperatures, while younger, more fertile geologies (e.g. rift or incised valleys) occur at lower altitudes where the climate is warmer.

Figure 2.2.1 A summary of the relationships between the factors discussed above, factors measured and incorporated into the model (discussed below), and black rhino carrying capacity.



2.3 DESIGNING POSSIBLE VARIABLES FOR A CARRYING CAPACITY MODEL

The 1993 Black Rhino Property Assessment workshop participants highlighted a range of factors likely to influence black rhino carrying capacity, including those described in section 2.2.

When this project began, an attempt was made to get an assessment of most of these in the 15 baseline areas. However because some were so difficult to quantify, or assess because of the author's and residents staffs' own time/funding limitations in rhino areas, some variables were abandoned - namely:

- an index of the condition / size/ number of termitaria and "nutrient hot-spot" bush clumps,
- details on the size and state of riverine / drainage line vegetation - this aspect was more generally accounted for by having such vegetation as its own type in vegetation maps;
- an index of apparent browse pressure on the vegetation (e.g. - hedging, plant breakages etc);
- fire regime and impact: fire frequency is anyway highly positively correlated with total annual rainfall at the cross-continent scale. Field measures of fire impact on browse where to difficult to obtain and interpret.

Some other factors were measured, but were not included specifically as variables on their own in the carrying capacity model: e.g.

- Proportion of the area that is inaccessible - although this is significantly correlated with prior carrying capacity estimates, inaccessibility was accounted for in the browse availability and suitability indeces (see later).
- Altitude - this was very highly correlated with minimum July temperature.
- Water Availability. In 14 of the 15 areas, no areas were greater than c.15km from permanent water. This model could thus not include effects of large areas without water. Instead, for predicting carrying capacities, areas > 15km from water are classed as inaccessible to black rhino except in areas with a large succulent component to the vegetation. Kunene-West does have such areas, but no spatial details were available to allow us to account for this. Hearn (2000) says that currently the rhino are distributed over c. 10 000km2 , with another 10 000km2 used after good rains. Estimates of average rhino densities and range sizes have varied greatly between studies in this region. This did impact subsequent modelling of Kunene-West carrying capacity and adult male range sizes (ie, which density / range size to use?).

Below, measures of variables that were used in this work are discussed:

AVERAGE HOME RANGE SIZE: A SURROGATE FOR CARRYING CAPACITY DENSITY

The average home range size of adult rhino may reflect the carrying capacity of the conservation area, in that each home range must include adequate food and water resources to support each rhino year-round. Examining the relationship between range size and habitat variables should be one way of identifying explanatory variables for a predictive model.

Several studies have suggested that this is a valid assumption. For example, they showed that individual (and average) home range sizes varied with the proportion of thicket and the density of woody plants, and thus presumably browse availability (see below) (Goddard 1967, Hitchins 1969, Mukinya 1973, Frame 1980, Kiwia 1989, Hearn (1999). The distribution of water (eg. Hearn 1999), the presence of inaccessible terrain (eg Wolf 1999, and this study), and the suitability (in terms of species composition) of the vegetation for black rhino (this study - Adcock 1999; Hearn 1999) also affect home range size.

Emslie (1999) described how in Hluhluwe from the 1960's, habitat carrying capacity declined due to vegetation changes and specifically changes in the availability and suitability of browse. This decline was also evidenced by major increases in measured average home range sizes of black rhino in Hluhluwe by Peter Hitchins. Ranges grew from as little as 3 to 5 km^2 in 1962-63 at densities of 1-1.5 rhino/km^2(Hitchins 1969) to around 7.5km^2 by 1971 at c. 0.6-0.8 /km2 (Hitchins 1971, Brooks 1975). Recent Hluhluwe average black rhino home range estimates are around 15-18 km^2 at densities of 0.3-0.4 /km^2 (Hluhluwe sighting data and population estimates supplied to the RMG).

Appendix 1 gives the correlations between average male range size and potential determinants of black rhino carrying capacity measured in the 15 baseline areas. The Appendix 1 and Figure 2.3.1 show how range size does indeed closely correlate with prior ("expert") estimates of CC and model-predicted CC.

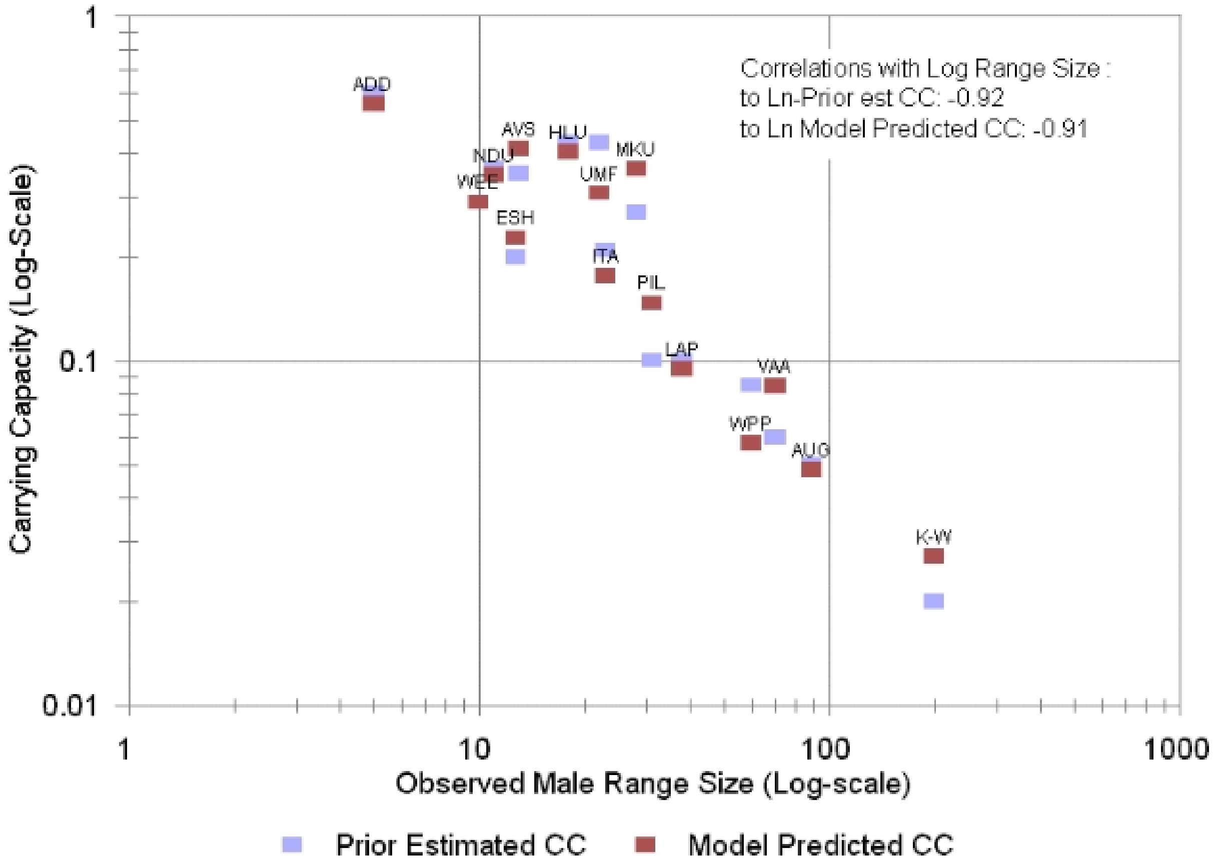


Figure 2.3.1: Correlations between Range Size and Carrying Capacity - also see fig 5.1, section 5.

Measurements of home range size for this model were not without problems. Adult male range size was used mainly because there happened to be more data for males (adult ranges must be used as young animals are usually not yet established, and often range widely). Range measures were based on ranger sighting data in most cases. Possible biases could have arisen due to sightings being mainly restricted to daylight hours, where ranging patterns may differ to night times. The length of time over which sightings were used to estimate range size varied, but in most cases was 3-5 years. The numbers of individual rhino from which the average range size was taken, was usually small (<5-20). In most cases no proper statistical analysis was possible to determine range size (e.g. convex polygon method), due to insufficient sightings. Here, estimation was from hand-drawn polygons around the majority of sightings, but excluded "outlier" sightings.

The possibility also exists that range size may not always reflect the area carrying capacity at very low and very high rhino densities, due to range extension and range compression respectively.

Never-the less the correlations shown in Fig. 2.3.1 suggest a remarkably strong relationship between range size and estimated carrying capacity despite all these measurement problems. This relationship also quite closely "retrospectively predicts" the average range sizes found by Hitchins in Hluhluwe in 1969 and 1971, given the rhino densities found then (try it out in the model spreadsheet file).

BROWSE AVAILABILITY

Some measure of available browse should be fundamental to any assessment of black rhino carrying capacity. Joubert and Eloff (1971) noted how in Etosha National Park, rhino density and distribution were determined by the distribution of denser vegetation types. Fabricius (1994) also described the significant relationship between the relative woody plant density of habitat patches and kudu density, and recommended regressions of resource density against wild herbivore density as a useful way to understand their carrying capacity. The studies referenced in the previous section also related home range size (and thus carrying capacity) to vegetation density, and by implication to browse resource availability.

No detailed quantification of browse availability in each of 15 rhino areas was possible for this work. The author had to depend on either existing vegetation survey data, or rather rapid visits to rhino areas where no data were available, or both, plus consultation with the scientists experienced in each area. A crude availability index was developed by the author which relates mainly to the projected aerial cover, density and "fill" of woody plant and forb parts in the 0-2m height range (see section 3).

Some justification for the field browse availability index used for this work:

The browse availability scoring procedure (section 3) crudely describes the average % "lateral or aerial cover and volume of fill" in a 0-2m high layer across a vegetation type of area x.

"Cover / density"
Where data were available, shrub/forb canopy cover was used as a starting point for the scoring decision, giving % fill in the lateral dimension. Alternatively, shrub/forb density data were used, by building a rough relative relationship between canopy cover and density estimates from several areas and vegetation types. Breebart (2000 - after this work) found that in Weenen NR, the frequency of occurrence (related to density) of plant species provided a realistic index of the actual measured amount of available browse for black rhino: she found a c. 97% correlation between these two parameters.

In a study of the browse carrying capacity of eastern Cape succulent valley bushveld, Stuart-Hill (1991), Stuart-Hill and Aucamp (1993) developed a vegetation "condition" index which represented to a large extent the range from very dense thicket to sparse woody vegetation (along with some differences in dominant plant species and height structures). Their experimental trials with goat browsers demonstrated the positive (but possibly curvilinear) relationship between the condition index and browse capacity, with a c.27-fold increase in carrying capacity from the least to the most dense vegetation conditions. Stuart-Hill also determined that the average of c.9 peoples' judgements should be used for an unbiased score, while in this study one 1 -3 people were involved in scoring rhino areas. The index used here was however more one-dimensional and simple than the concept of "condition score" used by Stuart-Hill.

"Vertical fill"
Average "fill" of the vertical 0-2m height space was ***not accurately*** accounted for (eg, by properly accounting for average shrub heights, leaf/branch densities etc.). During field trials to assign browse availability scores, it was found that observers seem to automatically adjust their "cover" scores to account for predominantly short vegetation in a vegetation type. Available evidence points to the cover and "fill" of the lower height ranges (< 1m) as being the most important to black rhino anyway.

Justification for assessing the 0-2m height range is as follows:

Several studies have shown how most black rhino feeding is done in the 0-2m height range, and how lower feeding heights are preferred.

Percentage of black rhino feeding that occurred at different height levels in the available vegetation:

Study:		**<50cm**	**50cm-1m**	**1-2m**	**cum<=2m**	**>2m**
Breebart (2000)	Weenen	c.38%	c.47%	c. 14.4	99.4%	0.6%
Rossouw (1998)	E.Shores	35.59%	54.45%	8.79%	98.82%	1.17%
(Joubert and Eloff 1971)	Etosha West	Optimum feeding ht. 60-120cm; with a c. 152cm (5ft) browse line (i.e. most feeding offtake was below this height level.)				

Emslie and Adcock (1993) also documented the significant decline in preference of black rhino feeding with plant height in Umfolozi. Plants of 0-1m were most preferred and taller height classes were rejected. However, interference by tall, thick grass in neighbouring Hluhluwe altered the patterns of feeding height, forcing rhino to eat more from taller, less favoured plant size classes.

Other food sources:
Spirostachys africana is one species where feeding on taller plants/parts of 1.75-2.5m is preferred, and makes up a significant part of that plant's contribution to black rhino diet in some Zululand regions. Spindly tree forms of other species are also pushed over by black rhino, and taller tree branches over 2m above the ground are hooked down and the tips eaten. Circumstantial evidence suggests that tree

pushing and breaking down of high branches is not a notably frequent rhino activity in normal conditions. Their incidence seems to increase during dry periods, and when population densities approach carrying capacity.

Trees recently pushed over by elephants can also provide a rhino with an extra meal, although this source probably forms a small % of its annual diet. The occasional toppling of huge *Acacia xanthophloea* trees deserve mention as another unmeasured food supply for black rhino in some areas.

Finally, certain types of marshes and wetlands could provide a major source of “key” (Illius and O’Connor 1999) food resources to black rhino. This food source has not been accounted for in this work. Heavy use of a variety of marsh plants was documented by Goddard (1968)’s feeding studies in Ngorongoro crater (Tanzania). The personal observations of Rob Brett at Solio Ranch (Kenya) noted how black rhino activity patterns were orientated around the central Solio marsh belt. In Ndumo GR, large amounts of reed or marsh-like plant material can be found in some black rhino dung (Adcock pers. obs), and Pete Goodman commented on hearing this that the >1 black rhino /km^2 that Ndumo once carried in an isolated, low-nutrient section of sand forest adjoining the Pongola river marshes, may have been sustained largely by the marsh vegetation. Andy Blackmore has observed that the Eastern Shores wetland shorelines are well- used by black rhino as floodwaters recede.

The need to fine-tune the browse availability index

Improved indexing of black rhino browse availability is an important need for future versions of this model and black rhino carrying capacity / productivity assessments. Never-the-less, the index used in this model is still the most highly-significant predictor of black rhino carrying capacity in the 15 benchmark sites (see appendix 1).

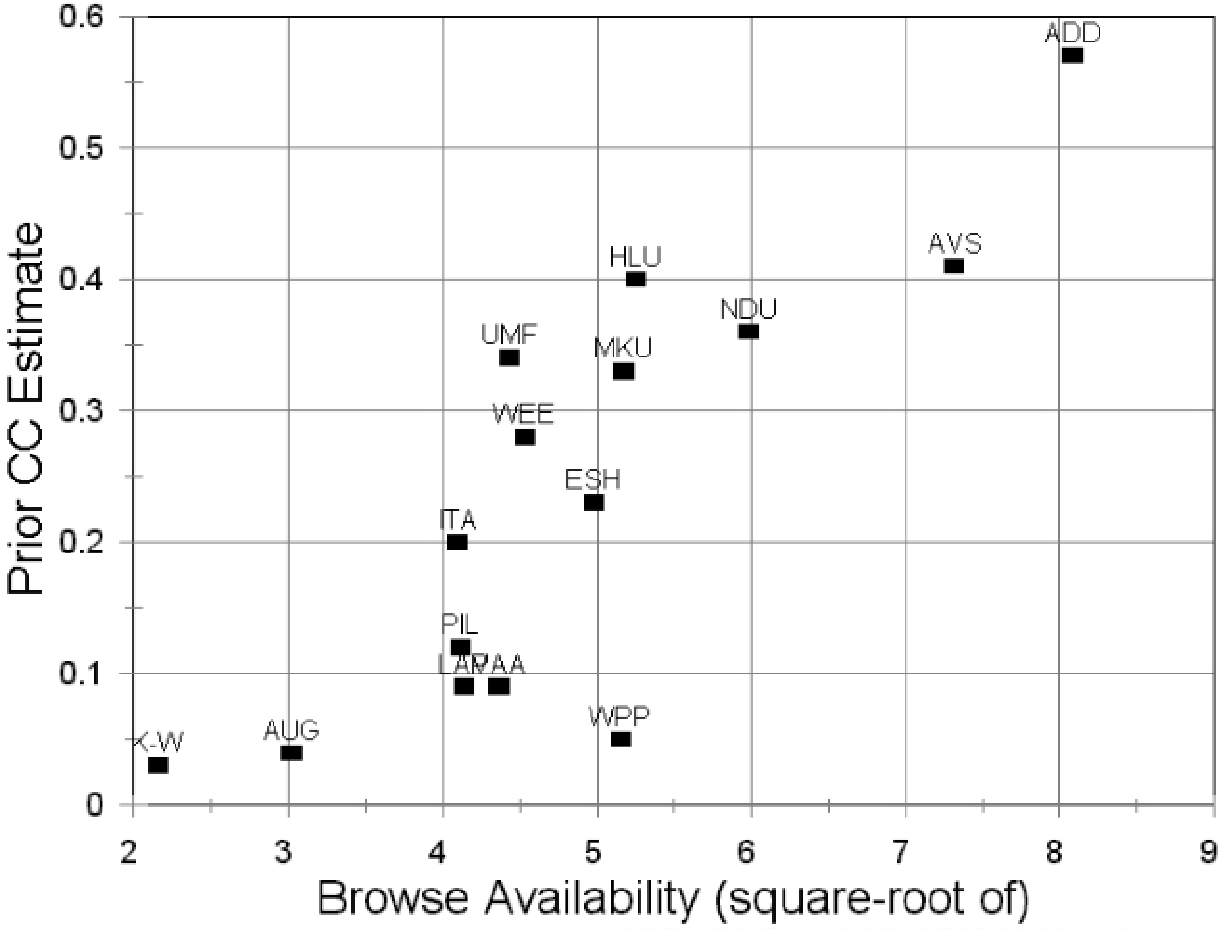


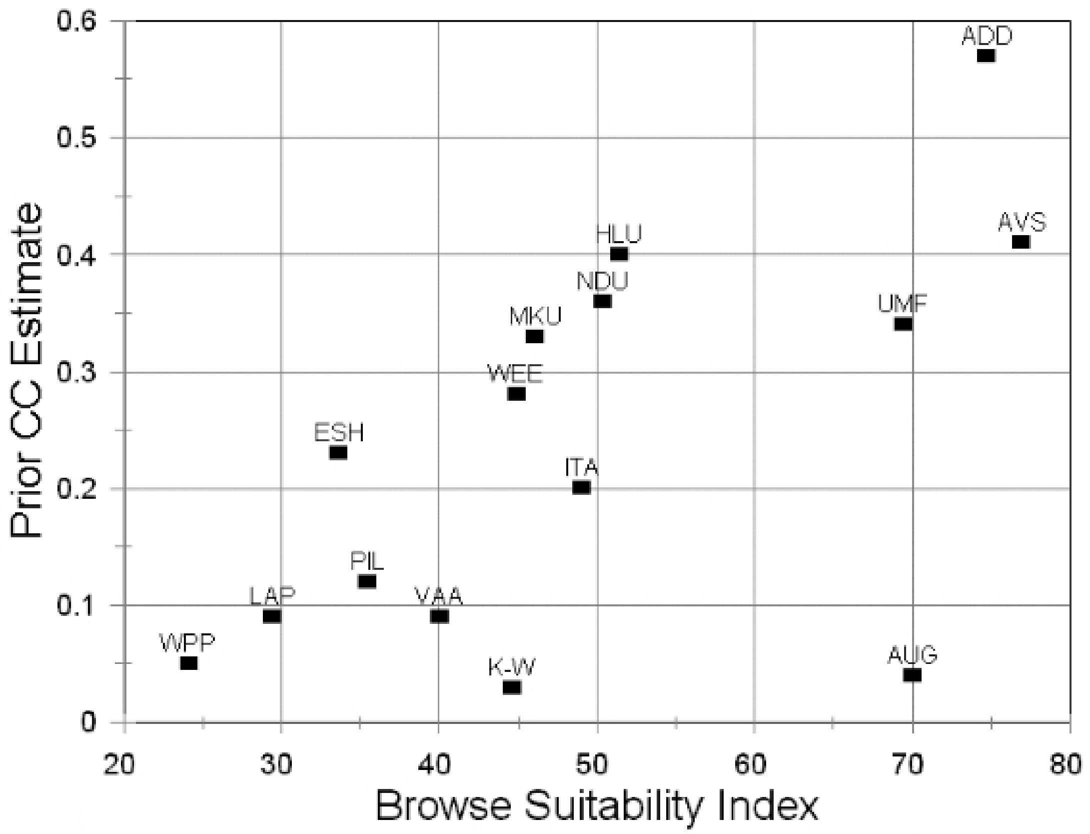
Figure 2.3.2: Graph of Prior estimated carrying capacity versus the Browse Availability Index

BROWSE SUITABILITY

This measure of vegetation palatability and value to rhino was fairly straightforward to construct (see section 3). It is based on actual feeding data from most of the 15 baseline areas. It combined the role of plant species importance (percentage in their diet) and palatability (degree to which the species are selected for versus occasionally chosen or rejected). The palatability information from all available areas' data was taken into account, because the abundance of a species in one area may distort its apparent palatability rating (especially for less abundant species).

Both the overall suitability index, and the proportion of the area with “low browse suitability” were significant in their relationship to range size and prior estimated carrying capacity.

A



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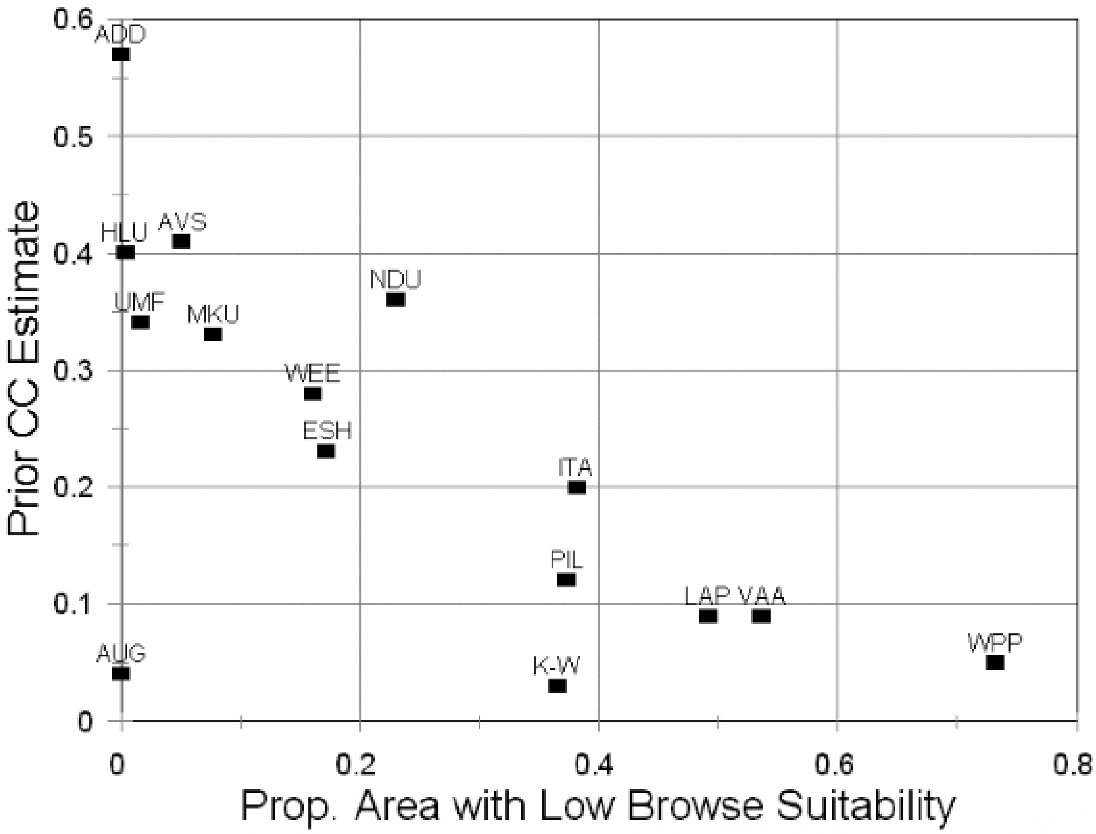

Figure 2.3.3: Graphs of prior estimated carrying capacity versus the Browse Suitability Index or proportion of the areas with Low Browse Suitability

FERTILITY

Besides the somewhat tedious business of evaluating each soil / geology class, this measure (very low to very high on a 9 point scale) was straightforward, and the overall fertility index was significantly related to carrying capacity. Justification for fertility scores will not be discussed here. General explanations are given in section 3. Needless to say, there is room for improvement of fertility ratings for individual soil / geology types.

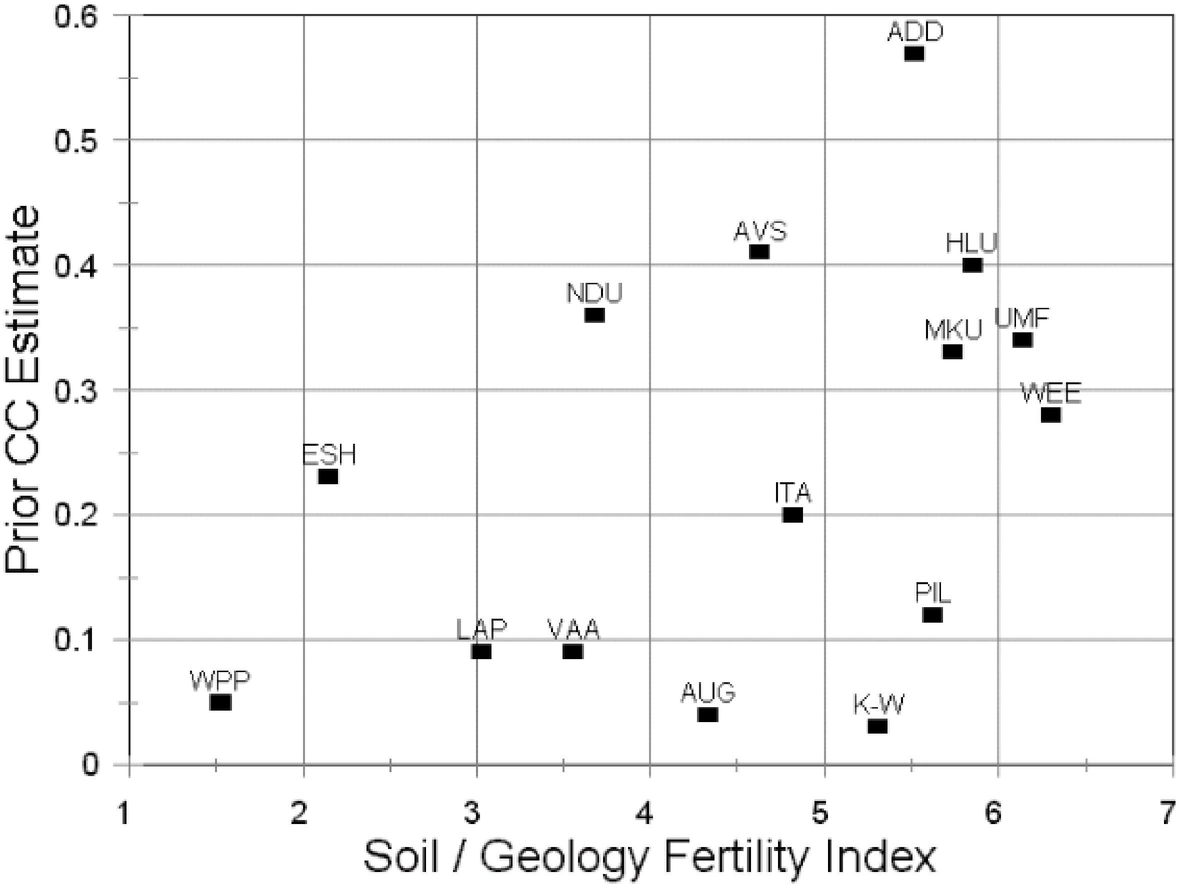

Figure 2.3.4: Graph of Prior estimated carrying capacity versus the substrate Fertility Index

TEMPERATURE

In this work, average minimum July temperature was chosen as the best and most easily obtainable indicator of (i.e. strong correlate of)

- likely frost incidence
- the likely temperature environment affecting carbon and nitrogen assimilation and initiation of woody plant growth.

Minimum July temperature is highly correlated with altitude above sea level in southern Africa, but this effect will decline with latitude, i.e. the more one approaches the equator.

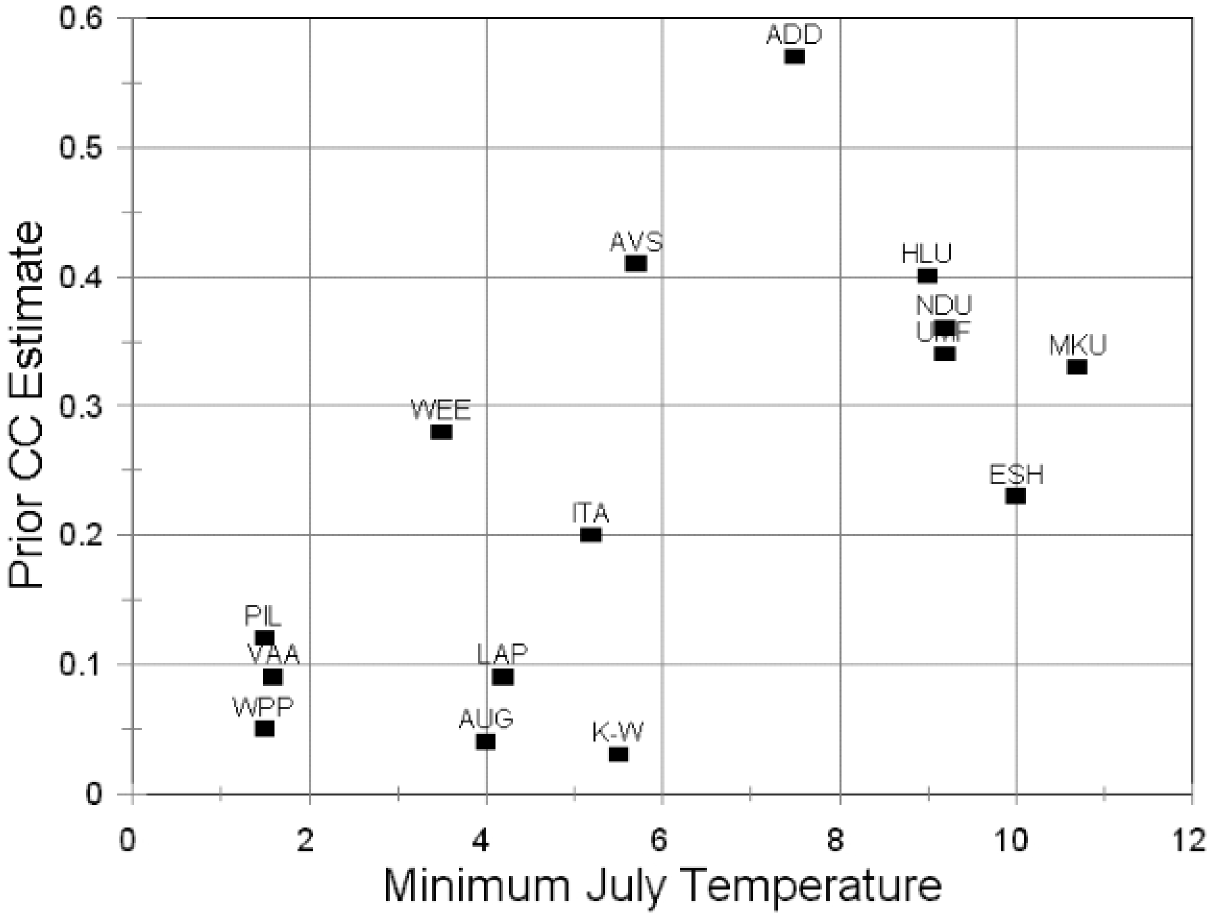

Figure 2.3.5: Graph of Prior estimated carrying capacity versus Minimum July Temperature

RAINFALL TOTAL AND RAINFALL CONCENTRATION

Average total annual rainfall was used as a variable in the model. The co-efficient of variation in annual rainfall was not used due to its very high correlation with average total annual rainfall.

The effects of “rainfall effect modifiers” such as catenal position and soil depth and texture (see section 2.2) on black rhino browse production and thus carrying capacity were not accounted for in more detail than in their general effect on standing browse quantity and plant species composition.

The author developed her own index of rainfall concentration (explained in the spreadsheet file *BrCCDataInput*,) because the one used by Schultz (1997) was rather complicated. This index is based on a standardized standard deviation of average monthly rainfalls, and seems to suitably describe the degree to which rain is concentrated into a few verus all months of the year. A measure of 100% would mean that all annual rain occurs in only one month of the year, while very low values mean that rainfall is spread more evenly though most months of the year.

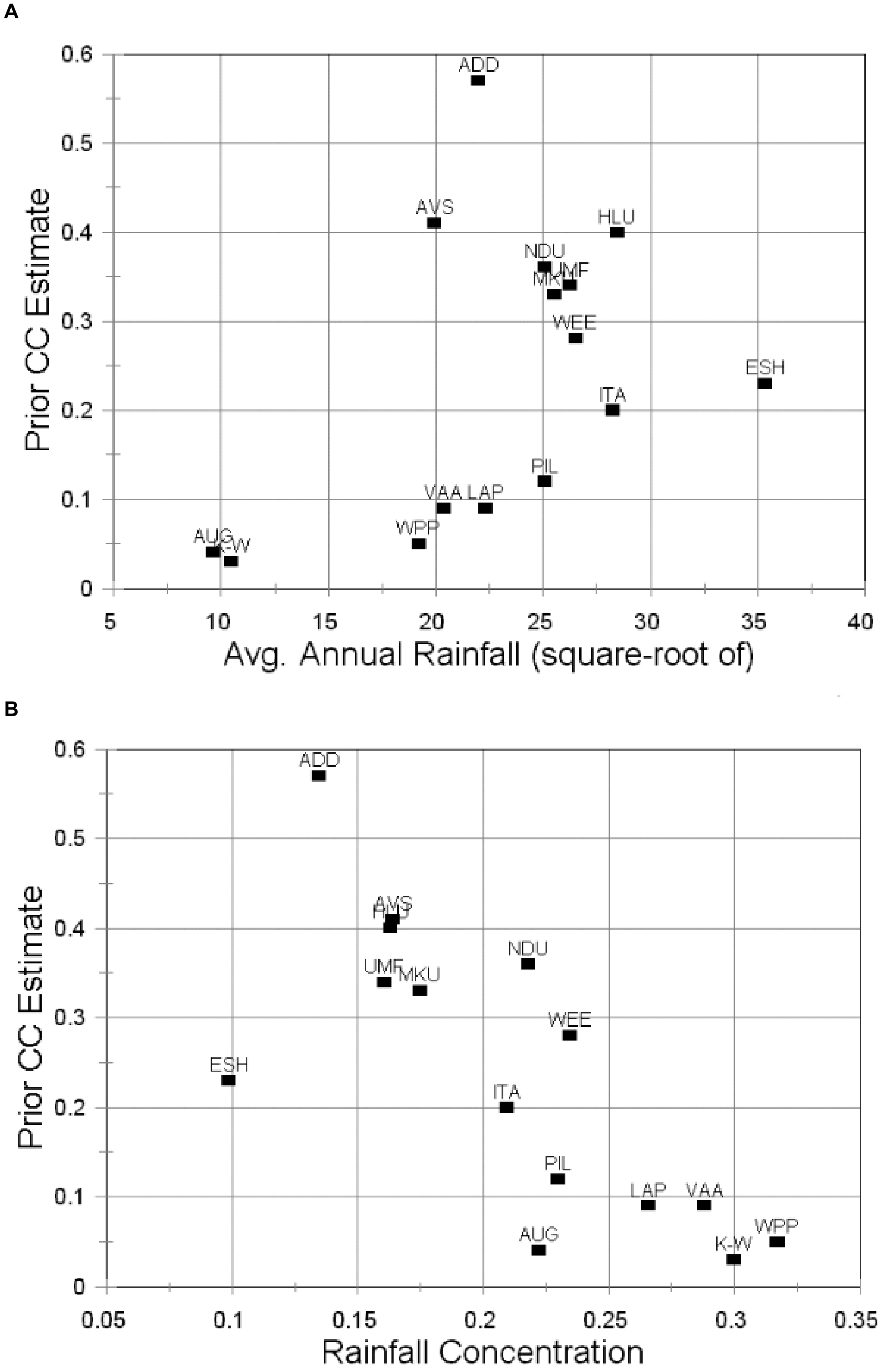

Figure 2.3.6: Graphs of Prior estimated carrying capacity versus Average Annual Rainfall and Rainfall Concentration

2.4. MODEL CONSTRUCTION AND STATISTICAL ASPECTS

The aims of model construction in the context of this work were as follows:

- The model should predict as closely as possible the prior, “expert” estimates of ecological carrying capacities of the 15 baseline areas.
- It should also have a sound theoretical basis, reflecting the known causal links between environmental properties and browser herbivory (e.g., as in figure 2.2).

A multiple regression approach was used to produce the RMG black rhino carrying capacity model, which in the end was comprised of an average of 4 regression equations.

The steps taken to build the regression equations followed the procedural guidelines of Johnson (1980), Williams (1986), Hair et al (1998), using the Statistica Version 5 software package (StatSoft Inc., 1995).

1) Variable transformations: individual variables were examined for linearity of relationship to the dependent variable, and for normality, skewness and kurtosis. The dependent variable (prior) ECC-est. has a curvilinear relationship with several explanatory variables. Thus a natural log transform or a square-root transformation was tried for these. Proportions (such as % of the area with x suitability/browse availability/fertility) were arcsin transformed. Transformed variables were re-examined for linearity of relationship, normality / skewness / kurtosis.

2) A correlation matrix including the transformed and original variables was examined to identify likely significant correlations with male range size (a carrying capacity surrogate) or prior estimates of carrying capacity. In the end a subset of these variables was chosen based on their correlation coefficients and distributional properties.

3) Factor analysis (principal components) was used to examine the structure of the interrelationships (correlations) between the remaining, still-large set of variables. Using factor analysis as a data reduction technique was initially investigated, but was ultimately not pursued despite the known multicollinearity between many variables, for the following reasons: Factor scores are computed based on the loadings of all variables on a factor. Although a factor may be characterized by variables with high loadings on it, there is the additional influence of smaller loadings from other variables, which may not be wanted. I.e. in this context such a composite variable was difficult to justify in theoretical terms. Also factor scores are not easily replicated across studies because they are based on the factor matrix, which is derived separately in each study. In developing a predictive model this is unsatisfactory.

A more appropriate approach would have been to use Path Analysis and Structural Equation Modelling. For this,
1) theory is used to specify the multiple and inter-dependent relationship between all independent, and dependent variables, and
2) these relationships are then turned into a series of structural equations (similar to regression equations) for each dependent variable.
SEM has the ability to represent “unobserved concepts” in these relationships (i.e. those not directly measurable in the field, for example the concept here of “rhino food productivity” influenced by annual rainfall, rainfall concentration, soil fertility, and temperature as outlines in section 2). SEM can also account for measurement errors in the estimation process (Hair et. al. 1998).

SEM is proposed as an important approach to use in future versions of the black rhino carrying capacity model.

4) Multiple-regression equation construction was then undertaken.

Although tried out, neither forward nor backward stepwise procedures were used to select variables for inclusion into the regression. These procedures have a tendency to boot variables out if they were “highly” correlated with any variable already in the model, and thus they are over-dependent on the order in which variables entered the equation.

In the end, variables were selected for the regression model(s) based on

1) theory and
2) variable distributional characteristics, and
3) the degree to which the equation(s) produced acceptable approximations of the prior “expert” estimates of carrying capacity for each rhino area.

Four fairly similar models were arrived at. Because the author had no logical basis to chose between them, all 4 were included the “RMG black rhino carrying capacity model Version 1.0", by using an average of all four's results. The average of the 4 equations was also closer to prior carrying capacity estimates across all 15 sites than any single equation.

Multicollinearity
The models contained 6 explanatory variables, some of which were correlated with each-other (see Appendix 1). However multicollinearity was ignored in this context because:

- multicollinearity is mainly relevant (problematic) when trying to use the regression coefficients of individual independent variables to <u>explain</u> their impact on the dependent variable (i.e. carrying capacity). This was not the purpose of the modelling exercise in this context.

- multicollinearity does <u>not</u> have a substantial effect on the estimated regression variate (i.e. on predicted carrying capacity).

The most critical error in developing theoretically-based models is the omission of one or more key predictive variable (i.e. specification error). The author felt that on a theoretical basis, all 6 variables deserved a place in the models.

The model variables represented the influence of the following on black rhino carrying capacity:

- average annual rainfall
- rainfall concentration (monthly spread)
- coldness or frost incidence
- soil fertility
- available standing browse biomass
- browse suitability or quality

Potential problems with the model

Potential problems with the model are as follows (these will not be expanded upon here....)

Violation of some assumptions
- The standard deviations of every conditional distribution of Y values may not be the same:
- a) Different coefficients of variation in annual rainfall would imply potentially greater fluctuations in carrying capacity in lower rainfall areas.
- b) Different vegetation states or conditions (standing browse biomasses / species compositions) with the same biotic conditions (rainfall/soil) may show different degrees of fluctuations in productivity.
- c) Higher rainfall areas can more easily develop a higher standing biomass of browse, but can also be in a very low biomass state. They can thus potentially change through a far wider range of browser carrying capacities than can more sparse, arid areas.
- Distributional “problems” could not be rectified totally by transformations in some variables.

Measurement error
- Measurement error is present in especially the non-climatic variables. Each of the 15 baseline areas had different levels of detail available of soils, vegetation, etc. Due to lack of budget, each was also “ground surveyed” to a different extent by the author and/or resident researchers. *Improving model data quality is definitely feasible, and is a priority need for future model versions.*
- The dependent variable values of “expert” estimates of carrying capacity are definitely fallible - all “experts” still have much to learn, while carrying capacity itself is a moving target. <u>Some explanations of “Priors” are given in Appendix 3 (for evaluation purposes).</u>

Specification error
- Several other factors influence carrying capacity, but could not be defined and/ or measured well enough, or else seemed not to be powerful enough in effect to include in the model. The role of

"missing predictors" could still however be significant, theoretically. (Eg . extent of competition with other browsers - this was felt to be important, but the measures of "other browser impact" devised during the research proved confusing. Across southern Africa, black rhino densities and CC estimates are positively correlated with the biomass densities of other browsers (which might imply the more other browsers, the better for black rhino). The problem was that there is no information available on general "browser" carrying capacities for the range of areas. These would be needed to be able to say whether or not the observed other-browser biomass densities were excessive, and thus likely to be problematic for black rhino, or not).

Sample size and Power

- The model is only based on 15 cases - a very small sample size. Never-the-less, highly significant adjusted R-squares were obtained with all equations. However, confidence intervals around predictions are large due significantly to the low sample sizes (degrees of freedom).

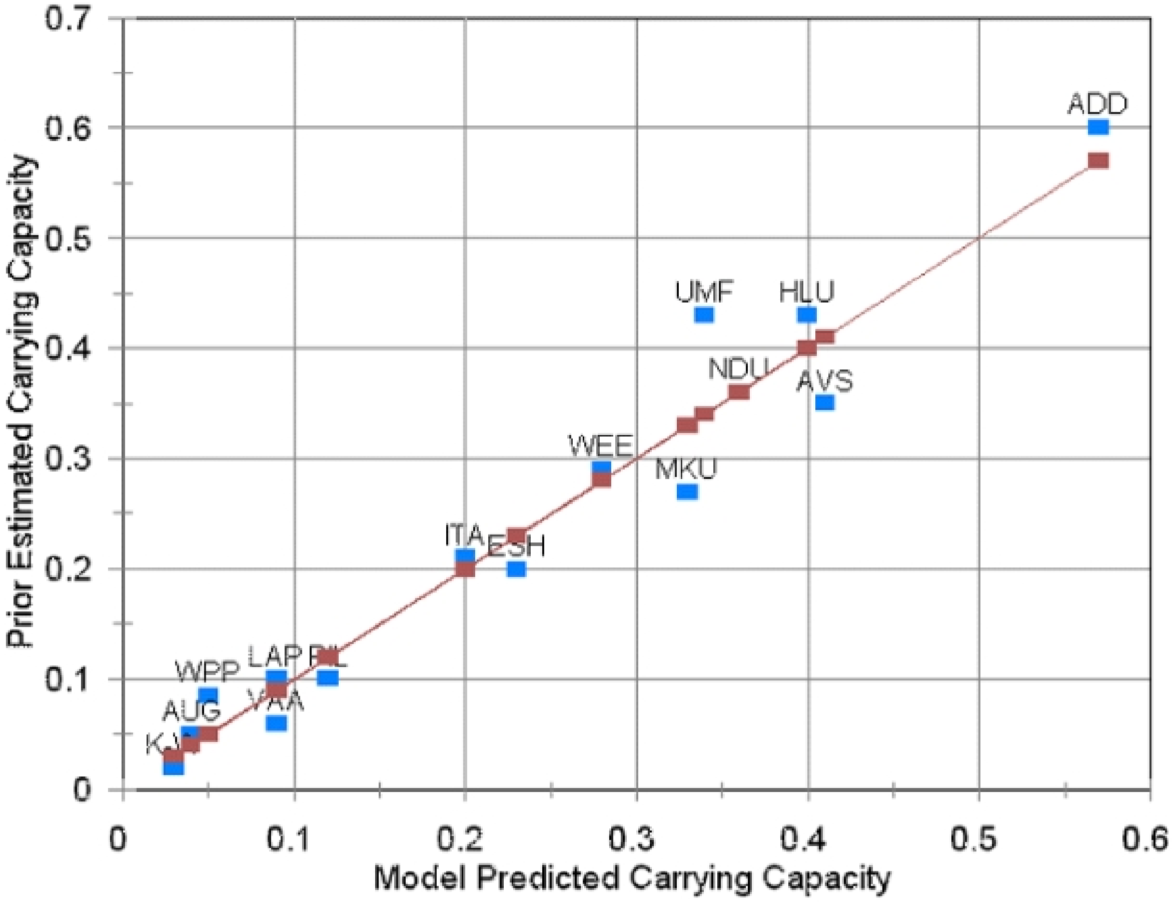

Figure 2.4.1: Graph of Prior estimated carrying capacity versus Model Predicted Carrying Capacity

SECTION 3 -DATA GATHERING FOR CARRYING CAPACITY ASSESSMENT

3.1 CHECKLIST

DATA / MAP INFORMATION TO COLLECT:

1) Topographic map of the area, showing
- **area boundary**
- **contours**
- **location of permanent water**
- **main infrastructure, large water bodies, fenced-off sections etc**

2) Vegetation map of the area
- **Vegetation survey data if available**
- **Vegetation descriptions: species composition, physiognomy etc**

3) Soil and or geology map
- **Soil / geology descriptions etc**
- **Soil analysis data if available**

4) Long-term rainfall data by month, or
- **Average annual total**
- **Average monthly totals**

5) The average minimum July temperature (or that in the coldest month).

Auxiliary data:
6) population estimates over the last 5 or so years for all browsers and mixed feeders
7) Any information on possible mineral limitations / excesses or imbalances found in the area

THINGS TO ASSESS IN THE FIELD (PLUS USING ANY AVAILABLE SURVEY DATA):

- **browse availability**
- **browse suitability or quality**
- **soil / geology, if no information is available on these**

Auxiliary data:
- **Impacts of browsers on the rhino-available vegetation**
- **trends in vegetation size structure changes (fire impacts / successional changes, alien plants etc)**
- **the potential for substantial grass interference with shrub browse over a large proportion of the area**
- **Presence of natural mineral licks or diverse soil types**

3.2 PROCEDURES

Users should make a separate copy of the original data input file (*BrCCDataInput*) and of the model file (*BrCCModel*) for the rhino area to be assessed. These working files can be renamed BrCCDataReservename and BrCCModelReservename., where Reservename is the name of the rhino area to be assessed.

3.2.1 INACCESSIBILITY / WATER

Topographic map of the area, showing

- **area boundary**
- **contours**
- **location of permanent water**
- **main infrastructure, large water bodies, fenced-off sections etc.**

a) Calculate the exact size, in square kilometres, of the total area.

Calculate the area inaccessible to rhino:
b) Calculate the size of places taken up by the main infrastructure, large water bodies, fenced-off sections.
c) Using the contour information, calculate the size of inaccessible terrain patches (slope>=30 degrees, or areas surrounded by inaccessible slopes etc.)
c) Mark off areas > 15 km from permanent water [in areas without a significant succulent component to the vegetation], and determine the size of such places.

Note on water distribution : In general - exclude areas> 15 km from permanent water, especially in areas lacking a significant succulent vegetation component. In succulent vegetation, black rhino can use areas at a far greater distance from water, even going year-round without drinking (eg Goddard 1968).

e) Add up the total amount of inaccessible area, and **determine what percentage of the total area is inaccessible.** This is entered into the Vegetation page of the *BrCCDataInput* file.

3.2.2 VEGETATION

Vegetation map of the area

a) Mark out inaccessible areas from the vegetation map where appropriate. Calculate the accessible area of each vegetation type.
b) Calculate the percentage that each vegetation type (excluding inaccessible parts) makes up of the total area, including inaccessible parts. (I.e., inaccessibility becomes accounted for in the browse indices).

For example: A reserve of 100 km^2 has 3 vegetation types and an inaccessible tourist camp area.

	Accessible	Inaccessible
Tourist Camp (1 km^2):		1 km^2=1% of total area
Vegtype A (17 km^2):	15 km^2= **15%** of total area	2 km^2=2% of total area
Vegtype B (33 km^2):	30 km^2= **30%** of total area	3 km^2 3% of total area
Vegtype C (49 km^2):	48 km^2= **48%** of total area	1 km^2=1% of total area
(Total area 100 km^2)		(Total inaccessible = **7%** of total area)

Field assessments of browse availability and suitability

Time of year for field assessments:

Probably, early winter (+-late June) is the best time, providing indications of both summer and winter conditions (i.e. a reasonable average). Ideally, a summer and a late winter visit should be done. Assessments in full summer only are not advised. as it is then difficult to account for the great decline in browse during the late dry season.

Survey layout

As many different parts as possible of all different vegetation types need to be visited and assessed. Time is usually the constraint on this. The idea is to see enough of the diversity of states / conditions within each vegetation type so as to be able to give each a valid overall average browse availability / suitability score.

Of course, each vegetation type can be subdivided on the map if parts are in very different states to other parts (e.g. size-structure-wise). If this is done, then each part gets treated as a separate vegetation "type" and its proportional area must be calculated.

Browse availability (at < = 2m)

This is a very important index. The one described here is very rough and ready, and a better index and field methodology, along with a set of photographic references, is going to be developed.

- The cover rating is on a scale of 0 to 100% : Print out and use the "browse cover scale" page in the spreadsheet file *BrCCDataInput.*
- This is an index or rating score of the "biomass" of rhino-available vegetation in each vegetation type.
- The score estimate of the projected % cover/density of all vegetation in the <2m height range.
- Average "fill" of the 2m height space is accounted for by giving the vegetation a lower cover rating than its projected aerial % cover rating *where appropriate*. Eg. If a vegetation type is only averaging 1m high in the 0-2m range, the initial aerial cover score is halved.
- **NB:** Species composition is totally ignored.

Implementation:

- Match each vegetation type to a cover class, dealing only with forbs and woody plants in the <2m range and ignoring grass and taller (>2m) parts of the woody vegetation.[Unless such parts are routinely eaten by rhino]

  Adjust your chosen cover class downward, to account for lack of "fill" due to canopy gaps/ short vegetation.- Be careful here as observers do tend to integrate the lateral cover and the "fill' component automatically when deciding on an initial cover score - it is easier to keep these dimensions separately.
- Fill in the relevant data and scores on the page called "*vegetation*" in the file *BrCCDataInput*, following instructions given on this page.

Browse suitability

This accounts for the available browse species composition of each vegetation type.
Browse suitability is rated on a % scale (in increments of 10%) from 10% (very low suitability) to 90% (very high suitability)

10	**v.**	**very low**
20	**v.-l**	**very low to low**
30	**l**	**low**
40	**l-m**	**low to medium**
50	**m**	**medium**
60	**m-h**	**medium to high**
70	**h**	**high**
80	**h-v.**	**high to very high**
90	**v.**	**very high**

- It rates the suitability of the available browse "volume" for black rhino.
- Essentially, it rates the proportion of available browse volume / amount that is comprised of suitable (mainly important + preferred) rhino food. Take seasonal use into account.

We are trying to rate the plant suitability separately from the abundance of browse biomass indexed by the cover-based rating. Thus a vegetation type may be very open and sparse, but contain mostly really good rhino food plants - so it gets a high rating, while a dense thicket may contain very few species actually eaten by rhino.

Implementation:

- Make a list of the most dominant browse plant species in each vegetation type. Note each species' (potential) value to the black rhino diet. Information on this for a large range of species is given on the "black rhino diet" page of the spreadsheet file *BrCCDataInput*. Use available survey data if suitable.
- Order the species from most highly important / preferred to least important / rejected, and present any available form of species abundance data for each vegetation type in columns next to the diet value data. An example of an approach to take is given of page "Suitability Profile" of the *BrCCDataInput*.
- If necessary, forbs can be lumped together, and an overall "edibility" rating made for them.
- Using your above list, once the browse availability (above) has been assessed, ask yourself "what % of this available browse "biomass" (no matter how small or great it is), is suitable rhino food?"

  Also ask "what is the average suitability of the available biomass of browse?"
- Assign each vegetation type a browse suitability score.
- Fill in the relevant data and scores on the page called "*vegetation*" in the file *BrCCDataInput*, following instructions given on this page.

3.2.3 SUBSTRATE FERTILITY

Obtain or draw up soil and geology maps and descriptions/analyses of the area. It is best to use both soil and geology information, but either can be used on their own in the assessment if the other is not available.

Soil and or geology map

a) It is not that vital to take out inaccessible areas from the soil / geology map, but this can be done if these are substantial and will affect overall fertility of the area.
b) Calculate the percentage that each soil / geology type makes up of the total area.

Fertility rating of soil / geology

Here we attempt to rate the fertility of the substrate. Conventional (agricultural) soil fertility rating are often

not usable here.
Fertility is rated on a 1-9 scale (very low to very high fertility). A 5-point or 3 point scale can also be accommodated with this, eg. If you can only rate a soil as high, medium or low fertility) :

1	**v.**	**very low**
2	**v.-l**	**very low to low**
3	**l**	**low**
4	**l-m**	**low to medium**
5	**m**	**medium**
6	**m-h**	**medium to high**
7	**h**	**high**
8	**h-v.**	**high to very high**
9	**v.**	**very high**

The subject of soil and geological fertility is of course complex, but for rhino CC purposes, we are trying to rate the relative ability of the substrate to hold and supply minerals for potential plant growth.

Information on soil type- and geological type- fertility scores for rhino areas are given on the “Soil Info” and “Geology Info” pages of the spreadsheet file *BrCCDataInput*, and under the headings “Soil fertility” and “Geological fertility” below.

Implementation: (users must be familiar with basic soil science and geology, and consultation with experts in these fields is advised where doubt or inexperience exists).

- Rate the fertility of each soil / geology type on the above scale, referring to the information provided below and in the data input spreadsheet. Obtain expert advice where necessary.
- Complete data input (each soil / geology type name, its % of total area, and fertility score) into the “Soil Geology” page of spreadsheet *BrCCDataInput* according to instructions given there.

Soil fertility

- For our purposes, soil depth is ignored.
- Innate soil fertility is a function of the soil’s clay content and its base status.
- Humic content is important in maintaining base status, but is not that relevant in arid areas.
- Soils with an orthic A horizon are generally not fertile.
- Sandy soils are not generally fertile. High-clay soils are fertile - esp. those with “reactive / high-activity” clays.
- Lithic (rock) “soils” (lithosols/Mispahs)are generally rated here as being of medium fertility (minerals are obtained +- straight from rock weathering, yet not leached away); unless the rock is very infertile (eg. aged sandstones) or fertile (dolorite, basalt etc).
- Under low rainfalls, basic cations can be in excess of cation exchange capacity in soils.
- Account for the geological origin of a soil when assigning a fertility score.

Fey (1993) suggests the following algorithms for obtaining a soil fertility score (0-10):

Fertility = %Clay score X Base status score

Clay%	Score
0-<15	1
15-<35	2
35-<55	3
55-100	3.3

Base status rating	Score	(Sum of exchangeable bases)
dystrophic	1	(<5)
mesotrophic	2	(5-15)
eutrophic	3	(15)

(Some base-status ratings are given in McVicar et.al. 1997, 1991).

Geological fertility

Black rhino workers should be familiar with some important references:
Bell (1982) was among the first in sub-Saharan Africa to discuss “geomorphological fertility” in an ecological context. Scholes and Walker (1993) and Scholes (1990) provide a summary of the general relationships between parent geology and soil type and fertility.

GEOLOGICAL TYPE and derived soil and general fertility rating (under compilation)

GEOMORPHOLOGICAL TYPE (after Bell 1982)		**GENERAL FERTILITY**	
Volcanics		High fertility	
Marine sediments		Medium fertility	
Rift Valley Sediments		Medium fertility	
Cratonic sediments		Medium fertility	
Granitic shields		Low fertility	
Kalahari Sands		Low fertility (usually)	
"ROCK" TYPES	**DERIVED SOIL TEXTURES**	**GENERAL FERTILITY**	Dominant minerals/Comments
SEDIMENTARY			
Sandstone	Sandy	Infertile	
Sand (recent, wind-borne)	Sandy	Infertile	
Alluvial deposits	Silty, sandy or clayey	Quite low fertility to highly fertile depending of texture and parent material.	
Shales	Clayey	Moderately fertile	
Mudstone	Clayey	Moderately fertile	
Limestone	-	Medium fertility?	
Conglomerate Breccia Tillite	various	Medium fertility - varies	
IGNEOUS			
Acid lavas			
Felsites	Usually thin, stony, loamy	Low to medium fertility	
Rhyolites, alkalai-Rhyolites	Usually thin, stony, loamy	Low to medium fertility	
Granites	Sandy in upslope positions, can be sandy with clay. Downslope positions, sandy with more clay. Bottomlands: more clayey, excess sodium.	Quite infertile Low-medium fertility Low-medium+ fertility	
Intermediate			
Andesites, Trachytes		Med.-med/high fertility	
Porphyrites (microdiorites) Int. Lamprophyres		Med-high fertility	
Diorites Syenites	Silt/clay, low sand as above	Med-high fertility Low-Medium fertility	
Basic lavas			
Basalt	Clayey (high mineral content, active, vertic, "arid")	Fertile	
Dolerite	Clayey	Fertile	
Gabbro		Fertile	
Recent volcanic Lavas / Ash	?	Very Fertile	
METAMORPHIC			
Marble	?	Med-high fertility	Calcite
Quartzite	Sandy	Infertile	Quartz
Schists	variable	variable	
Gneisses	variable	variable	
Hornfels	variable	variable	

3.2.4 ANNUAL RAINFALL AND RAINFALL CONCENTRATION

Long-term rainfall data by month

Average values or the raw monthly rainfall data are entered into the spreadsheet file *BrCCDataInput*. Using another means or the above spreadsheet....
a) Calculate long term average monthly totals.
b) Calculate the long-term average annual rainfall total (this is automatically done once monthly avg. totals are entered).
c) The spreadsheet then automatically calculates rainfall concentration for you.

3.2.5. JULY MINIMUM TEMPERATURE

The average minimum July temperature (or that in the coldest month).

Find data for the area being assessed. If it has no weather station, use data for similar, nearby areas - (check for altitudinal similarity - consult a climate expert to make adjustments for large differences in altitude).

a) This value in degrees Celsius must be determined.
b) The value must be entered into the spreadsheet file *BrCCDataInput*.

3.2.6. AUXILIARY DATA

Population estimates over the last 5 or so years for all browser and mixed feeder game species. (Note: Buffalo can take substantial browse esp. in valley bushveld type areas).

[still under development]

Provision is made in the spreadsheet file *BrCCDataInput* for calculating metabolic and standard biomass of browsing animals.

- The percentage of browse in each species' diet in that area will need to be confirmed or altered- defaults are given in the spreadsheet.
- Future versions..... (A rough idea will be given of whether this is a potentially high biomass that could compete adversely with black rhino).

Any information on possible mineral limitations / excesses or imbalances found in the area

[still under development]

- Ask about natural mineral lick sites in the area. Ask local veterinary of agricultural workers about mineral issues in the area.
- Ask about the water quality from groundwater, if only groundwater is available to the animals.
- Future versions ....(an appendix will provide background information on mineral issues).

SECTION 4 - ESTIMATING BLACK RHINO ECOLOGICAL CARRYING CAPACITY USING THE MODEL

Use the RMG black rhino carrying capacity model version 1.0 given in the *BrCCModel* Spreadsheet file, on page "*Predict ECC of an area"*.

Once data gathering and entry into the spreadsheet file *BrCCDataInput* is complete, a set of model input variable values is calculated for you on the page "*Final Variable Set*".

These 6 values must be entered by hand into the file *BrCCModel* on page *"Predict ECC of an area"*, in the correct order (as given on the page "*Final Variable Set*" and the model page). (Final variable values can be copied into the model by the "copy", *PASTE SPECIAL* - VALUES" process, but **not** by straight copying to the clipboard and pasting.

Once the variable values are entered, the predicted CC is displayed prominently on the page. Users can also scroll down to view the individual predictions from each of the 4 regression equations which contribute to the average value.

NB NB NB - be careful not to clear values totally from data input fields in the model and the data input pages - this will result in lots of ERR's in spreadsheet workings and the model. Workings should re-instate to correct values once numeric data is re-entered, but rather do not do this!

Using Auxiliary data to adjust the model-predicted ECC

Carrying capacity estimates can be adjusted downwards (eg. by taking the lowest of the 4 regression carrying capacity predictions) in these cases:

Adjust the estimated CC down if numbers of other game species which use browse (impala, springbuck, kudu, nyala, eland, giraffe, possibly bushbuck), taken together, comprise a high biomass for such an area [guidelines are being developed]. Signs of heavy browse pressure and hedging should be evident on the more palatable of the semi- evergreen plants - especially those on termitaria, under big trees etc.

Adjust the estimated CC down if there is only one general type of soil/geology in the area.

Adjust the estimated CC down if there are strong indications of "negative" trends in vegetation size structure: i.e.

- if palatable available browse plants are mostly growing out of the 0-2m height range,
- if fire show signs of heavily impacting browse plants so as to significantly open up the available vegetation in future,
- if there are signs of significant increases in less suitable plant species relative to palatable species, eg. less palatable species include *Euclea* species, *Tarconanthus camphoratus*, *Maytenus senegalensis*, *Croton* species (except where such thickets provide the only available cover/shelter for black rhino).

Adjust the estimated CC down if grass biomass builds up each growing season to a >1m, dense sward over large parts of the area. Such a sward has to substantially interfere with shrub browse availability to black rhino.

It may be better to adjust carrying capacity estimates down if the area has a rainfall coefficient of variation of over 30%.

Productivity of a rhino population:

Areas with predominantly low to very low substrate fertility, and / or where > c.50% of the area has **low** browse suitability, are not likely to carry a productive black rhino populations. (The figure of 50% is a rough guide, and is another subject for review).

SECTION 5 - ESTIMATING CARRYING CAPACITY FOR DOMINANT ADULT MALES USING AVERAGE ADULT MALE HOME RANGE ESTIMATION

Once an estimate of the overall ecological carrying capacity for black rhino is obtained, this CC value can be used in the *BrCCModel* Spreadsheet on the page *Predict Avg Male Range.* The user needs to provide this value along with the total area size, excluding inaccessible areas*. The likely average adult male range size in the area is then determined. An estimate is also made of how many dominant bulls the area could contain.

*Note: To estimate numbers of bulls, the distribution of water must be accounted for. In areas with a low degree of vegetation succulence, areas far from water (say >8km - but this is still under review / debate) must be excluded from the Area Size estimate which you need to enter in the spreadsheet. Personal observations of ranging data from several rhino areas have lead the author to estimate that c.0- 8km from permanent water is the *approximate* area used in dominant, territorial male ranges. Patterns of dominant male range distribution with respect to water do need further investigation.

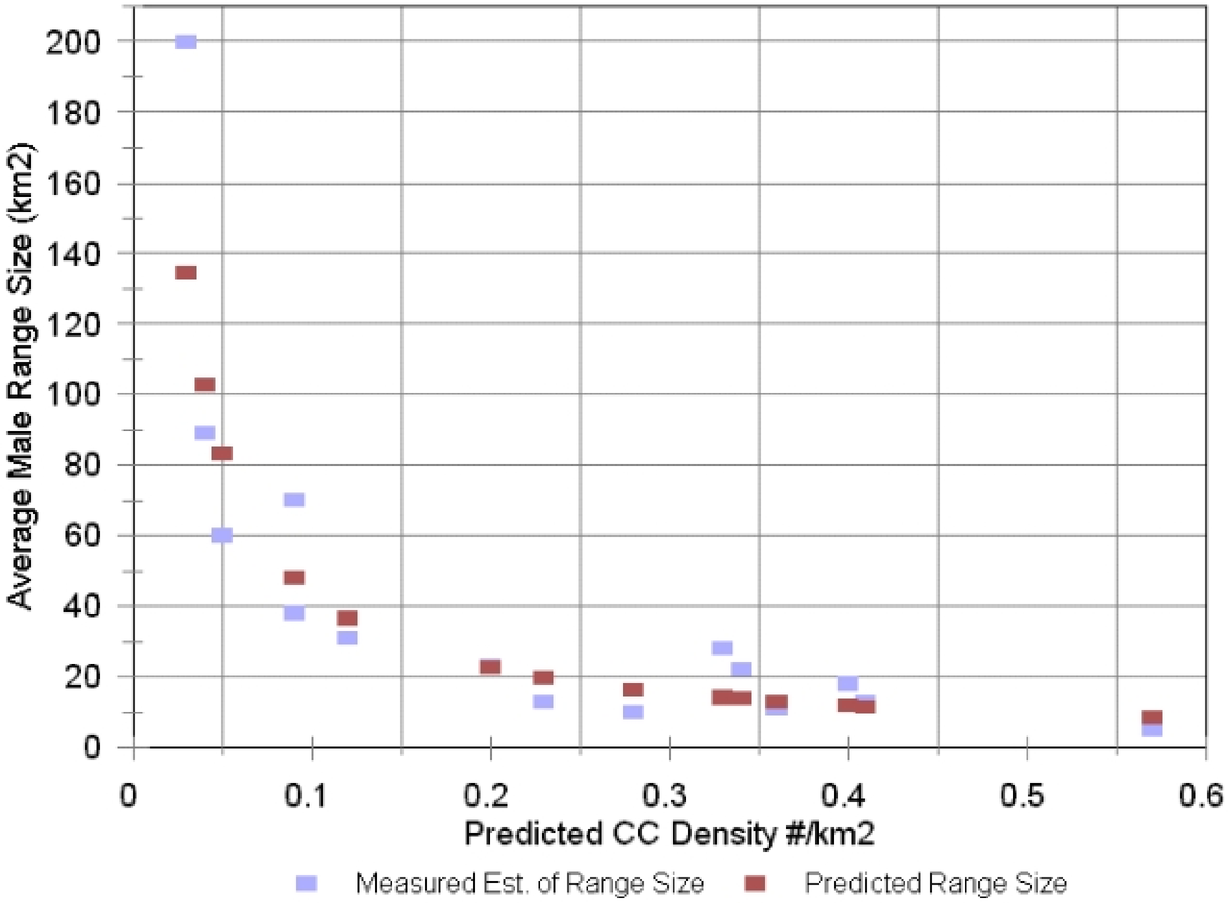

Figure 5.1 Measured and predicted black rhino male average home range size, versus predicted carrying capacity.

APPENDIX 1: Designing model variables: Correlations between independent (habitat) variables and dependent variables (carrying-capacity measures).
(Note: The variables “Primary productivity” and “Overall Browse Value” are to be examined for use in future model versions).

	Maximum Recent Rhino Density	Browse Suitability	Square-Root Browse Suitability	Browse Availability	%area with Veg. of Low Suitability	Square-Root Browse Availability	Primary Productivity Index: Fertility Index Annual Rainfall	Overall Browse Value: x Availability x Suitability	Substrate Fertility index	Rainfall Concentration	Annual Rainfall (avg)	Square-Root Annual Rainfall	Natural log Minimum temperature in July	Male Home Range Size	Log Male Range Size
Variable Name	MAXDENS	BSUITABI	SR_BSUIT	BAVAILAB	LOWSUIT	SR_BAVAI	FERTRAIN	B_ALL	FERT	RAINCONC	ANNRAIN	SQ_ARAIN	LN_JMINT	RngMale	LOG_RNGM
MAXDENS	1.00														
BSUITABI	**0.45**	1.00													
SR_BSUIT	**0.47**	1.00	1.00												
BAVAILAB	**0.5**	0.49	0.46	1.00											
LOWSUIT	**-0.59**			-0.36	1.00										
SR_BAVAI	**0.55**	0.40	0.37		-0.33	1.00									
FERTRAIN	**0.66**	*0.11*	0.15	0.12	-0.44	0.21	1.00								
B_ALL	**0.5**						0.14	1.00							
FERT	**0.39**	**0.52**	**0.57**	0.04	**-0.61**	-0.01		*0.24*	1.00						
RAINCONC	**-0.63**	**-0.51**	**-0.52**	-0.51	**0.79**	**-0.53**	**-0.55**	**-0.53**	*-0.27*	1					
ANNRAIN	**0.47**	*-0.24*	*-0.22*	*0.12*	*-0.18*	0.24		-0.01	-0.03	**-0.63**	1.00				
SR_ARAIN	**0.53**	*-0.24*	*-0.22*	*0.20*	*-0.13*	0.34		0.07	0.01	**-0.59**		1.00			
LN_JMINT	**0.69**	0.40	0.42	0.30	**-0.70**	0.31	0.41	0.33	0.26	**-0.75**	**0.45**	0.40	1.00		
“Dependent” Variables															
RngMale	**-0.64**	-0.16	-0.15	**-0.57**	0.32	**-0.69**	**-0.63**	**-0.47**	-0.06	**0.62**	**-0.67**	**-0.76**	-0.28	1.00	
LOG_RNGM	**-0.75**	-0.33	-0.32	**-0.76**	**0.48**	**-0.81**	**-0.81**	**-0.7**	-0.2	**0.71**	**-0.6**	**-0.67**	**-0.46**		1.00
Prior Est. CC	0.90	**0.61**	**0.61**	**0.76**	**-0.67**	**0.77**	**0.59**	**0.79**	**0.45**	**-0.71**	0.36	**0.44**	**0.63**	**-0.65**	**-0.85**
Ln Prior ECC	0.88	0.43	0.43	**0.7**	**-0.58**	**0.77**	**0.71**	**0.66**	0.32	**-0.74**	**0.58**	**0.67**	**0.58**	**-0.87**	**-0.92**
Model Predicted CC	0.80	**0.58**	**0.58**	**0.82**	**-0.69**	**0.84**	**0.58**	**0.84**	**0.45**	**-0.75**	0.38	**0.45**	**0.63**	**-0.67**	**-0.86**
Ln Model Predicted CC	0.82	**0.42**	**0.43**	**0.71**	**-0.61**	**0.78**	**0.73**	**0.69**	**0.39**	**-0.77**	**0.6**	**0.68**	**0.59**	**-0.85**	**-0.91**

Correlations in **bold** are significant and of particular interest in understanding possible determinants of carrying capacity.
Correlations in *italics* show an interesting lack of correlations between variables - eg. between browse availability and annual rainfall.

Note: The greater the proportion of the land with vegetation of low suitability for rhino, the *lower* the cc.The greater the rainfall concentration (i.e into just a few months of the year), the *lower* the carrying capacityThe greater the average minimum July temperature, the *higher* the cc.

APPENDIX 2 - SOME BACKGROUND INFORMATION ON FIBRE AND SECONDARY PLANT CHEMICALS IN NUTRITION

References: Bravo (1998), Illius and Jessop (1995), Foley, McLean and Cork (1995) Shahidi and Wanasundara (1992), Dearing (1997), Paglia (1999).

1) Effects of a high fibre diet:

- High fibre dilutes the proportion of digestible material and thus nutrients/energy in the diet.
- Fibre makes limiting nutrients even more unavailable by fibre binding to minerals.
- High fibre stimulates the secretion of mineral-rich saliva, and irritate the gut lining, causing the animal to secrete more mineral-rich mucus which is lost in the dung.

2) Effects of a relatively high concentration of "adverse" secondary plant chemicals:

Our understanding of the role of secondary plant chemicals (SPC's) on black rhino is rudimentary. SPCs are ubiquitous in plants and have a huge variety of forms and effects. Defining "adverse" SPC's is difficult due to a limited knowledge of plant chemical contents in black rhino habitats, and rhino metabolic coping mechanisms. However, secondary plant chemicals potentially have major implications for rhino nutrition (and health).

The ability to deal with SPCs varies non-linearly with nutrient intake (diet quality):

* When nutrient intake is about 1.5 to 2 times the maintenance level, the tolerance to the highest concentrations of SPCs is achieved.

* As nutrient intake falls below 1.5x maintenance, only increasingly lower levels of SPCs can are tolerated. At intake levels insufficient to maintain weight / energy balance (sub-maintenance), SPC tolerance is markedly curtailed.

The effects of high levels of SPCs are mainly likely to be felt at diet supplying near- or sub-maintenance nutrition.

3) Some summary information on plant secondary chemicals

Measuring the individual effect of each SPC seems impossible. The mechanisms of dealing with SPCs are however largely common to most vertebrates, and their general effects can be evaluated in terms of existing knowledge about physiological homeostasis and regulation. Enzyme systems of mammals have evolved which are very non-specific and can metabolize a virtually unlimited variety of substances, including phenolics, terpenes, steroids, alkaloids. Once absorbed, SPC's may undergo the following transformation":
Phase I: oxidation, reduction or hydrolysis and introduction or uncovering of a functional group in the SPC. This usually makes the SPC more polar and water soluble.
Phase II: conjugation of the SPC or its phase I metabolite(via a functional group) and an endogenous molecule such as glycine, glutathione, or sulfate or glucuronic acid. This greatly increases excretion of SPCs by the renal (urine) or biliary-fecal (dung) routes.

Most importantly, the process of biotransformation and excretion of the vast majority of absorbed SPCs in mammals result in the need to buffer and excrete a load of organic acids.

The skeletal system and acid buffering: Enormous reserves of alkaline salts are held in bone, and acidemia dissolves bone, releasing calcium salts and bicarbonate from the active bone surface and driving hydrogen ions into the bone matrix. There are large excretions of calcium (and maybe magnesium and phosphorus also as in humans) as a result. Mineral wastage is important in domestic animal production, anecdotal evidence of this exists for wild species.

Urinary excretion of phosphate is the major contribution to titratable H+ excretion. High dietary phosphate helps buffer an acid load. Animals that are phosphate depleted retain H+ ions because secretion of these ions is inhibited in the kidney distal tubules.

During acid loading, ammonium production and excretion in urine increases10-20-fold. (Urinary ammonium arises from the metabolism of glutamine, a process that also generates bicarbonate for acid buffering).

If dietary protein is insufficient, skeletal muscle is broken down to supply glutamine (the maintenance of acid-base homeostasis is all-important). Chronic acidosis could lead to growth retardation. The increased urinary loss of N though ammonium is a clearly measurable cost of biotransformation of SPCs.

A continuum of degrees of acidosis can occurs. In cattle, acute acidosis leads to “Sudden Death syndrome”: cattle wander aimlessly, cannot stand and appear to have “brain damage”. The “brain effects” result because in acute acidosis, the production of thiamine by gut bacteria is impaired, resulting in thiamine deficiency.

Eating soil with high Mg, Na bicarbonate and eating charcoal counteracts acidosis. (Black rhino are noted for eating burnt plants in preference to even lush green spring flush material)

SPC tolerance and browse digestibility (inverse of dietary fibre contents)

A rhino would need to chose a diet of increased digestibility (eg. c. 7% greater?) when SPCs are present to counteract both their dilution of plant nutrient content and the metabolic costs they incur to the rhino. This diminution in the nutritive value of browse caused by SPCs may cause SPC:nutrient ratios to fall below the tolerance threshold, resulting in the diet becoming “intolerable”.

SPCs : Other effects on nutrient depletion and digestion

- Lower body sodium (Na) concentrations through
- lower Na absorption from diet
- increasing faecal Na losses (to 2x) due to increased salivary and intestinal mucosa mucus secretion
- Enlarged adrenal glands
- Depleted kidney fat
- Erosion of the intestinal mucosa
- Nitrogen absorption from diet is reduced, and levels in faeces are elevated.

Getting tannins to bind to protein by increasing gut ionic strength means that tannins that would otherwise erode the intestine, and inhibit protein digestion later on, are neutralised. Tannins bound to proteins in the stomach would not be able to interact with enzymes / bacteria in the small intestine. The high levels of N in the faeces are of endogenous, not dietary origin, ie secreted mucus + eroded intestinal epithelia.

> The presence of Saponins in food (1%) seem to prevent these tannin effects. The above effects may be a mechanism used by monogastrics to acclimatise to tannins.
>
> Eating clay: clay can act as a lubricant, reducing mucus/saliva etc secretion and gut irritation. The clay lattice of high-activity clays can also absorb SPCs and so help to neutralize their effects.

Potential SPC effects on blood physiology

Polyphenols can form strong complexes with metal cations through their carboxylic and hydroxylic groups, and interfere with intestinal absorption of minerals.

In particular, Fe absorption is strongly inhibited. Polyphenolics also affect Zn, Na, Cu, and Al absorption; but supposedly not Mn, Ca or Mg.

The strong chelating ability of the polyphenols is responsible for their *in vivo* antioxidant activity and inhibition of hydroxyl radical production by the Fenston and Haber-Weiss reactions. However, under conditions of high concentrations of phenolic antioxidants, high pH, and the presence or iron, phenolic antioxidants can initiate an auto-oxidation process and behave like pro-oxidants. Given the black rhino's unusual blood physiology, high levels of pro-oxidants could affect the integrity of red blood cell membranes and precipitate a haemolytic event.

APPENDIX 3 - EXPLANATIONS OF PRIOR "EXPERT" ESTIMATES OF BLACK RHINO CARRYING CAPACITY FOR THE 15 BASELINE AREAS

The "prior" carrying capacity estimates used to develop this model, were derived over a period of c.12 years of monitoring in the RMG rhino areas. Although the author did have a *documented* role in developing the CC estimates (Adcock 1995, Brooks and Adcock 1997), her own understanding behind the estimates was influenced by other key people with their own long experience of black rhino in different habitats (see section 1).

The documented estimated CC ranges given in Adcock (1995) and modified in Brooks and Adcock (1997) were drawn up based on discussions with RMG members, field observations and black rhino monitoring data in RMG status reports in some areas. A very crude analysis was made for the 1997 report, of each area's annual rainfall, soil/geology fertility status, likelihood of frost and vegetation / terrain conditions. These 1997 values were used as a starting point to develop a set of "best" ("expert") estimates" of carrying capacity for developing this model. Explanations for the best estimates of each of the 15 baseline areas are given below (A3.2).

A3.1 A brief look at alterative "Prior Carrying Capacity Estimates" and their predictions

During the initial process of CC model design, not only were the ***best*** prior estimates of carrying capacity used, but for each of the 15 areas, maximum and minimum "priors" were also tested (using the same 6 independent explanatory variables). Also, some alternative CC estimates were tested, mainly for Hluhluwe, Umfolozi and Addo.

It is easy to imagine that given the theoretical relationships of rainfall, soils, temperature and browse availability / quality with black rhino carrying capacity, the problem might be to determine the correct height (Y intercept) and "slope" of the regression line describing the relative quantities of these characteristics in each rhino area.

If we assume we knew nothing about the "absolute" values of CC for each area, but could merely order the 15 areas from our assumed lowest CC to assumed highest CC, we could ask "What is the relationship between the order of sites and the various "determinants" or independent variables?" Figure A3: 1 shows a regression using the 6 independent variables against a prior "ordering" of the sites, and the regression results are summarised below:

Regression Summary for Dependent Variable: ECC_ORD
R= .96459209 R^2= .93043790 Adjusted R^2= .87826633
F(6,8)=17.834 p<.00031 Std. Error of estimate: 1.5726

This shows that we could be generally on the right track in understanding the relative CC order of areas, with some possible errors showing up also.

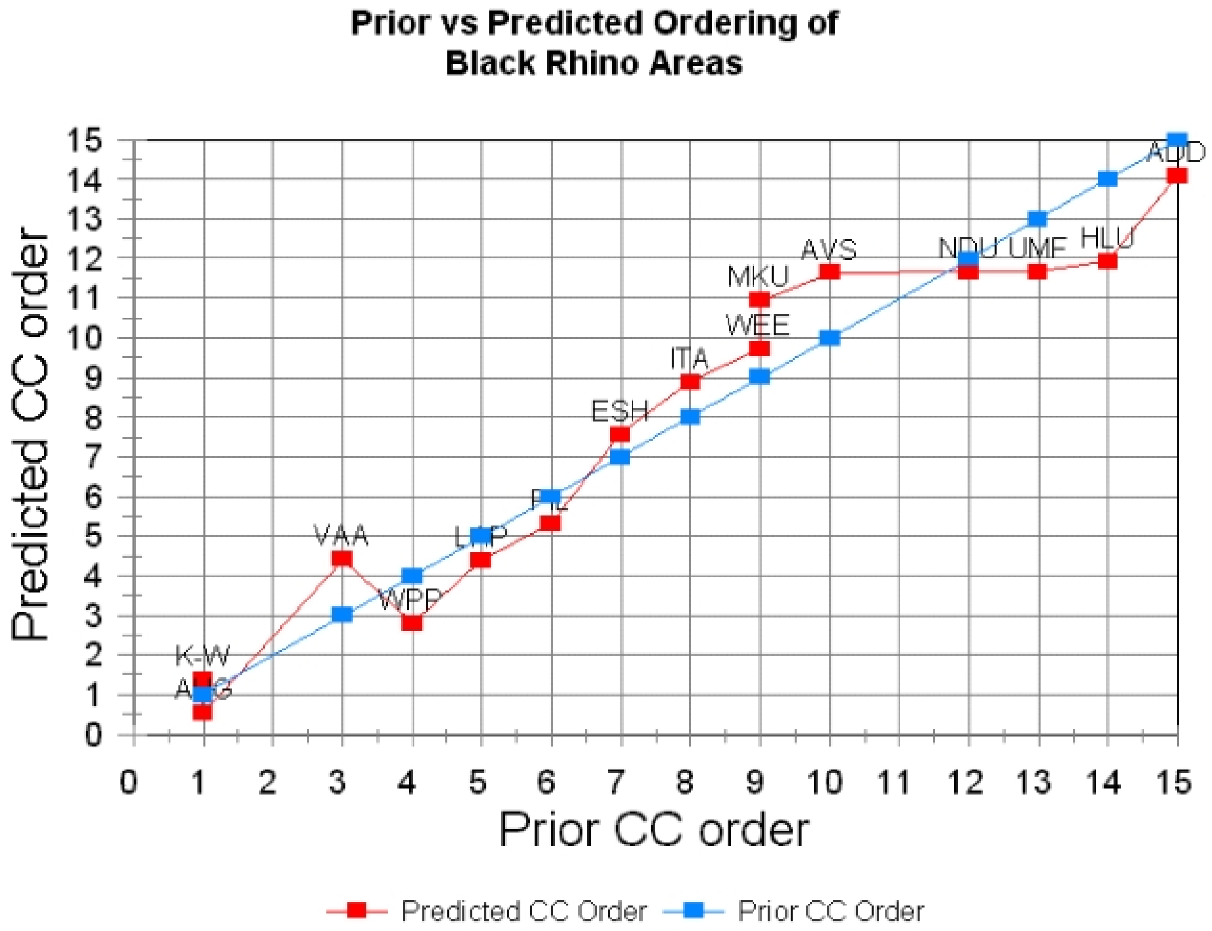

Figure A3: 1 - Simple ordering of site based on prior estiamtes of carrying capacity, versus regression-predicted ordering of sites

Figures A3:2 to 8 show the rhino areas graphed in approximate “prior” carrying capacity sequence from lowest to highest, with various prior CC estimates and then the corresponding regression-predicted CCs.

The minimum priors in fact give the best regression fit, slightly better than the “best” estimates (which were used in the end to build the model). The maximum priors give a very poor fit: they produce an adjusted R-square of 0.58 versus an adjusted R-square of 0.879 using the “best” prior CC estimates. Also, most of the carrying capacities predicted from Maximum priors cannot be justified on a theoretical or empirical basis and are way too high. This suggests that if anything, we should be more conservative in our carrying capacity estimates for most areas, and that higher estimates are less likely to be realistic.

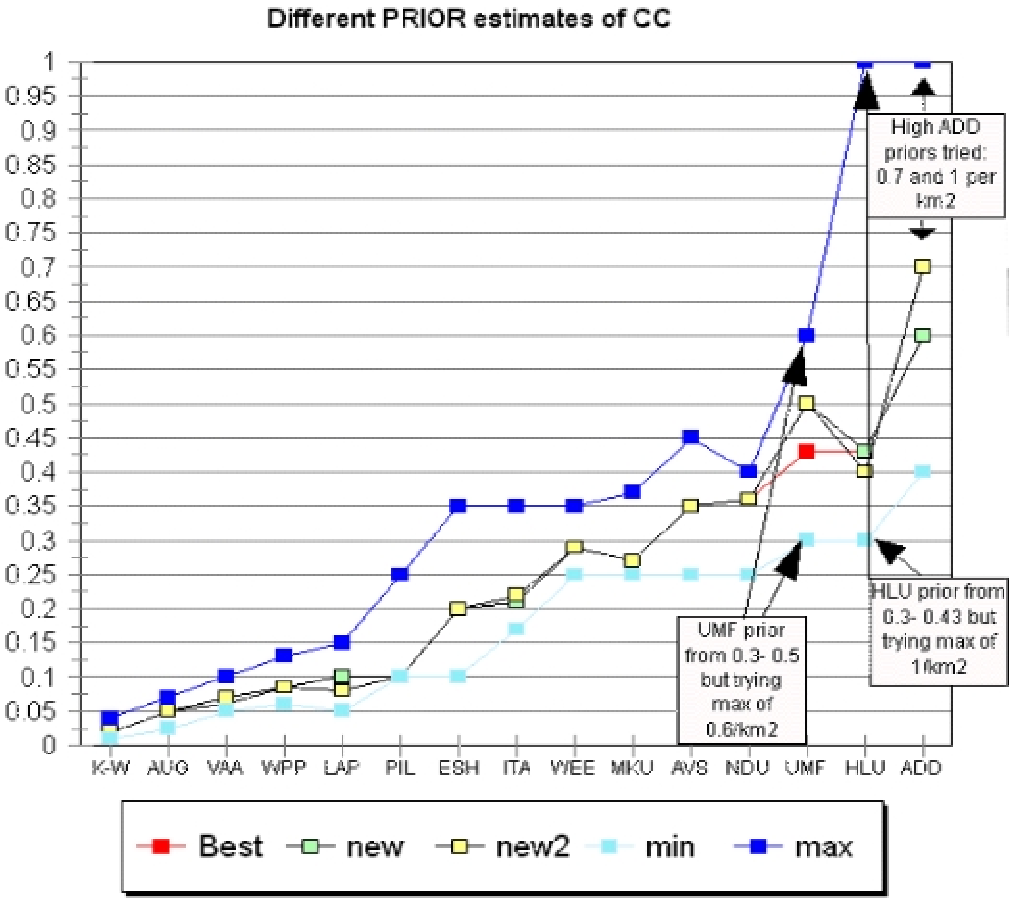

Figure A3: 2

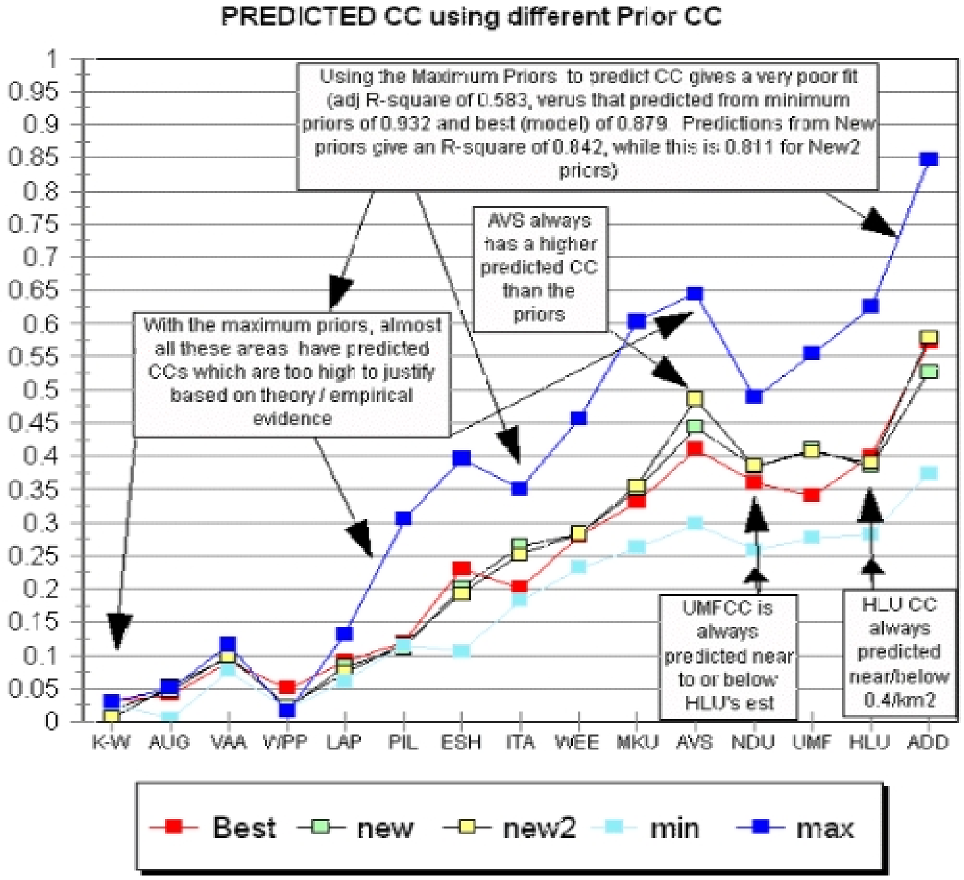

Figure A3: 3

I also tried using prior CC estimates of 0.5 rhino/km^2 for Umfolozi, with Hluhluwe priors of 0.43 rhino /km^2 (the same as the best estimate) and 0.4 (lower). With such priors, the regressions predict CC's near 4 for Umfolozi, and just below 4 for Hluhluwe.

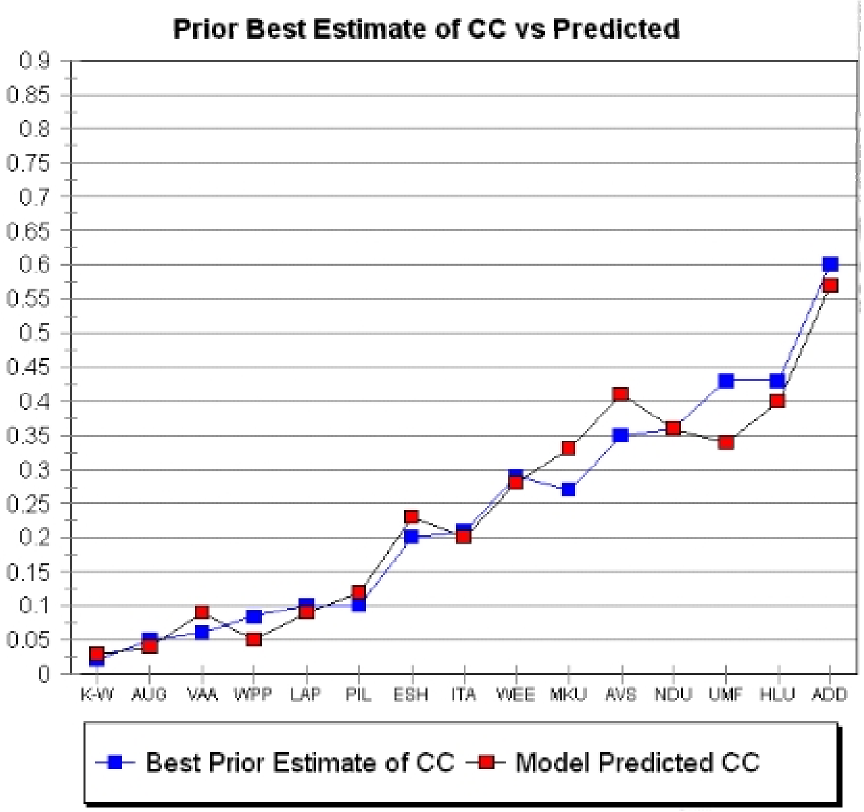

Figure A3: 4

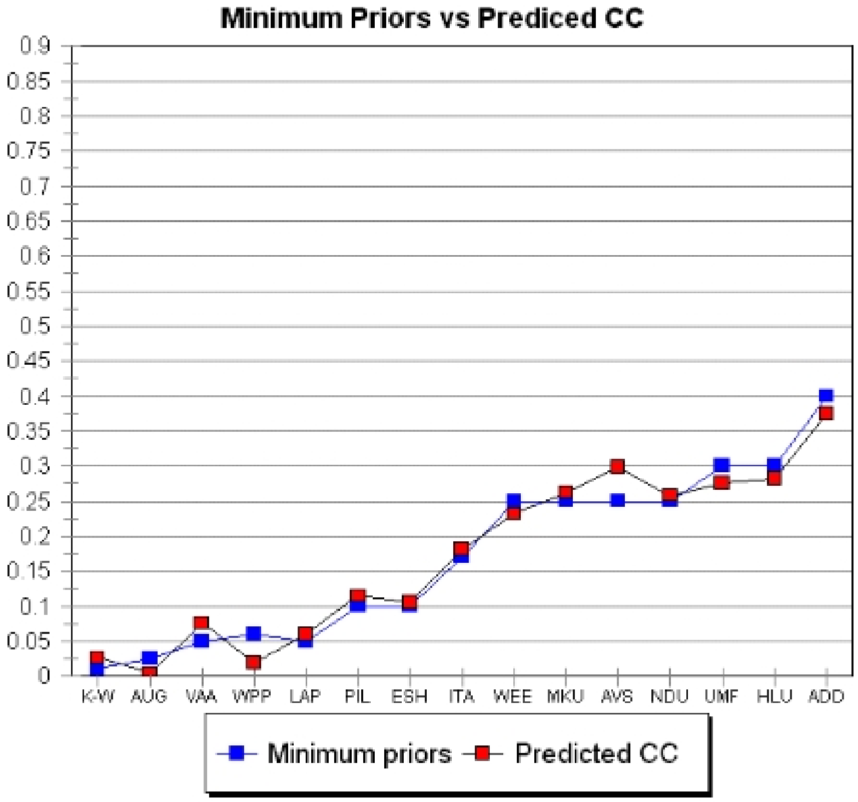

Figure A3: 5

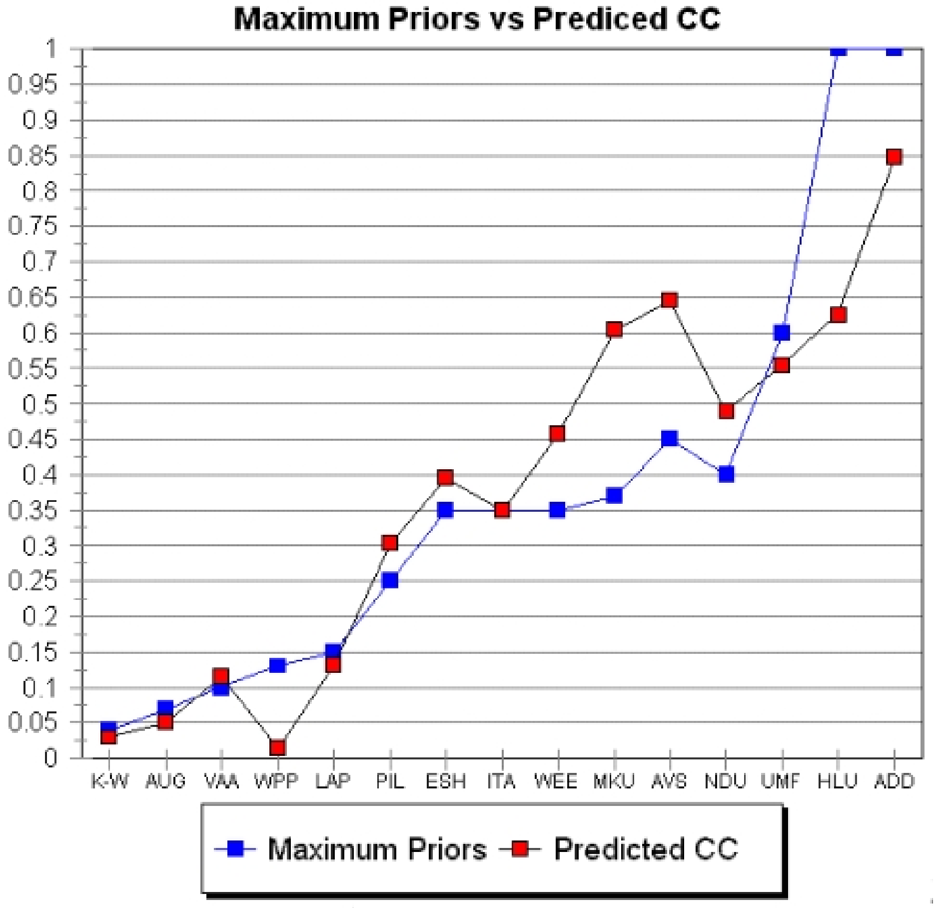

Figure A3: 6

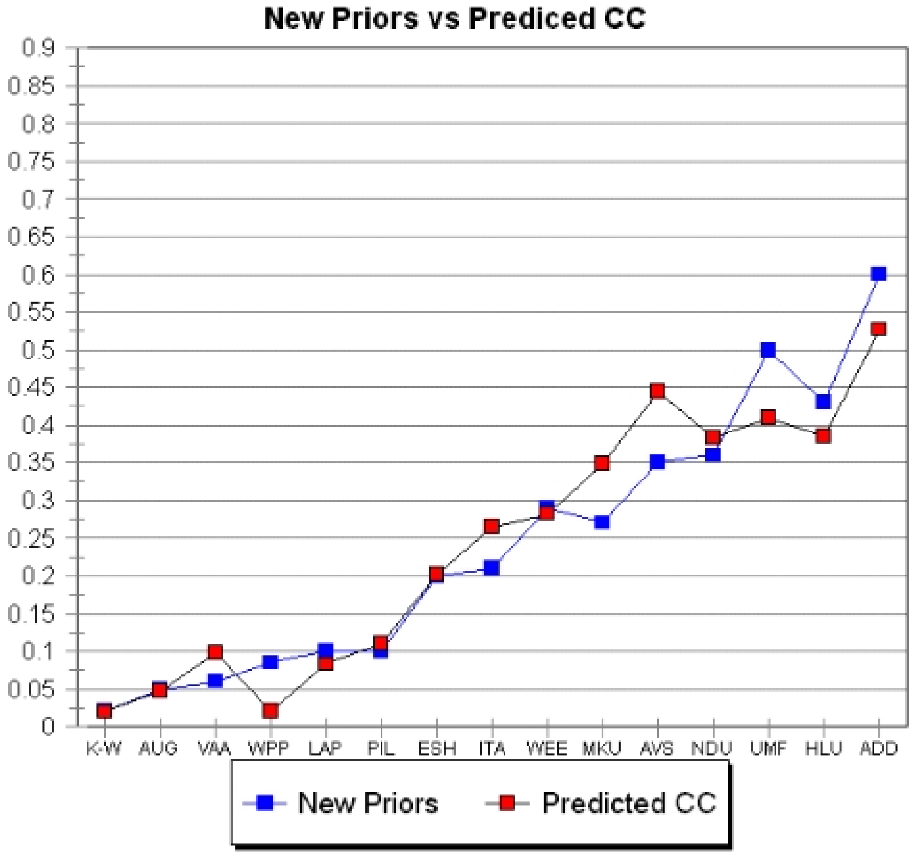

Figure A3: 7

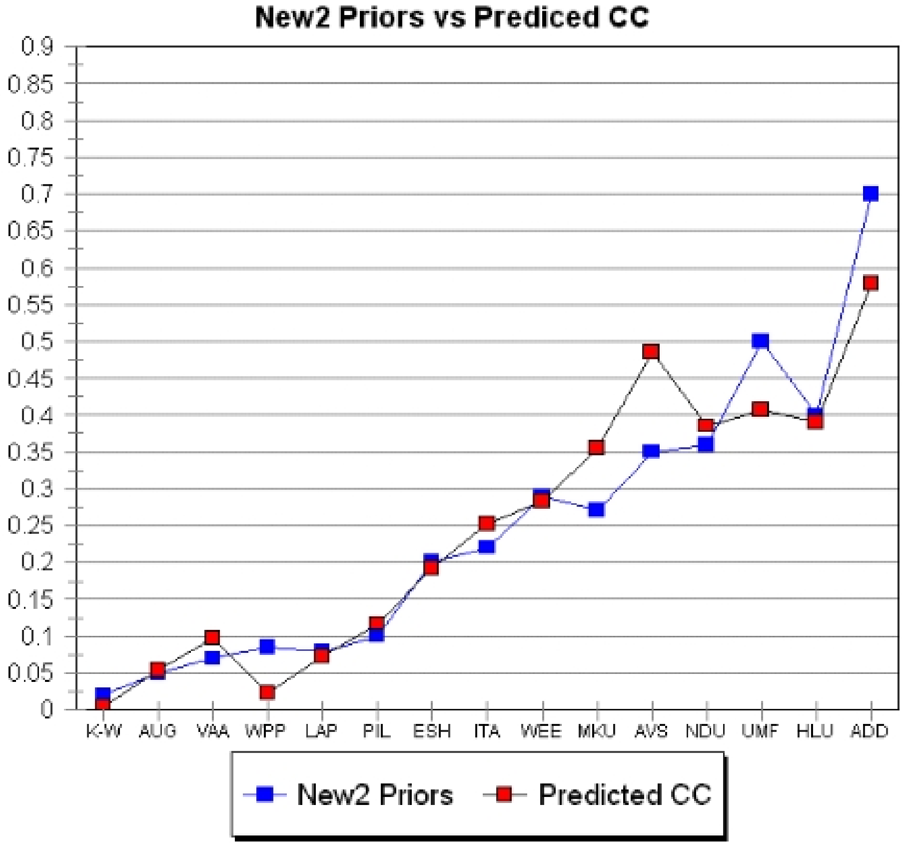

Figure A3: 8

Table A3-1 gives a summary of estimated browse availability and rhino diet data for parts of Hluhluwe and Umfolozi respectively. It suggests that Umfolozi does have less browse available than Hluhluwe - i.e. The Umfolozi study area had only 56% of the quantity of “good” browse and 25% the quantity of “poor” browse, that the Hluhluwe study area had. However this does not account for the impact of severe grass interference in Hluhluwe, which appears to exert additional negative effects on its black rhino carrying capacity (Emslie and Adcock 1993; Emslie 1999). Never-the-less, if we exclude the likelihood of CC estimates near the apparently unrealistic Maximum priors, then the model predicts an Umfolozi carrying capacity near 0.4 rhino /km^2.

A3.2: Prior carrying capacity estimates explained for each area

Untransformed model variate values for the 15 baseline areas.

	Best Prior ESTIMATE	CCBROWSE SUITABILITY	BROWSE AVAILABILITY	Propn. SUITABILITY	LOWFERTILITY	RAINFALL CONCENTRATION	ANNUAL RAINFALL	JULY MIN. TEMPERATURE
K-W	0.02	44.7	4.7	0.37	5.31	0.30	110	5.5
AUG	0.05	70.0	9.2	0.00	4.33	0.22	93	4
VAA	0.06	40.0	19.1	0.54	3.56	0.29	415	1.6
WPP	0.085	24.2	26.6	0.73	1.53	0.32	370	1.5
LAP	0.1	29.4	17.2	0.49	3.03	0.27	500	4.2
PIL	0.1	35.5	17.0	0.37	5.63	0.23	630	1.5
ESH	0.2	33.6	24.8	0.17	2.15	0.10	1250	10
ITA	0.21	49.1	16.8	0.38	4.83	0.21	799	5.2
MKU	0.27	46.2	26.8	0.08	5.74	0.17	652	10.7
WEE	0.29	45.0	20.6	0.16	6.31	0.23	705	3.5
AVS	0.35	76.9	53.6	0.05	4.63	0.16	398	5.7
NDU	0.36	50.5	35.8	0.23	3.68	0.22	630	9.2
UMF	0.43	69.5	19.7	0.02	6.15	0.16	690	9.2
HLU	0.43	51.4	27.6	0.00	5.85	0.16	810	9
ADD	0.6	74.8	65.4	0.00	5.52	0.13	484	7.5

ADD Addo Elephant National Park (Elephant Camp) Best Prior Estimate: 0.6 rhino/km^2

Hall-Martin et.al. 1982 and Hall-Martin and Pentzhorn (1977) documented that from 1962-1977 , the initially introduced black rhino were confined to a c. 210 ha. paddock, at densities averaging 4 rhino /km$^{2.}$ During 15 years, ... “These high densities resulted in serious damage to the vegetation as evidenced by degradation of thicket and its replacement in part by open scrub and dwarf shrub communities.” Intense aggression between rhinos was also evident at densities exceeding 3.3 rhino /km^2

Since release into the larger Addo elephant camp, from April ‘89 to March ‘94 densities averaged 0.311 /km^2 and annual growth averaged 10.6%. From ‘94 to ‘97, densities were similar averaging 0.316 /km^2, but increasingly heavy removals and deaths due to accidents, elephant, old age and capture-related causes took their toll, and avg. growth rate halved. Mike Knight (pers. comm.) thought ECC might be as high as 0.7 /km^2. Brooks and Adcock (1997) gave a likely range of 0.5-0.7.

AUG Augrabies Falls National Park (North Section) Best Prior Estimate: 0.05 rhino/km^2

The area available to black rhino has changed several times since first introductions in 1985. Densities went as high as 0.16, then 0.1 rhino/km^{2,} up to 1991 - these densities were unacceptably high, and were reduced to 0.056 rhino/km^2 around 1994.They have ranged from 0.05 - 0.079/km^2 up to 1998. Female breeding has been very good, but the human manipulation of this population took its toll on overall growth, which has only averaged 3.5% over 10 years. At the time of research for this model, K. Buk had not yet completed his M.Sc. thesis, but reported that in the rhino were severely impacting their food resource density. Knight et. al. (in prep.) recorded that vegetation biomass/densities were now only about half of those of the southern part of Augrabies, although the N and S sections had been of similar densities in the early ‘80's.

rhino/km^2	Reference
0.03	Brooks (1989) in Knight et. al. (1997)
0.075	Knight (1993) in Knight et. al. (1997)
0.04-0.06	Adcock (1995), Brooks and Adcock (1997)

AVS Andries-Vosloo section of the Great Fish River Reserve Complex Best Prior Estimate: 0.35 rhino/km^2

Rhino densities have increased from 0.057 to 0.207 rhino/km^2 since introduction, and growth has averaged 9.9% per year over 10 years. The carrying capacity of this area was estimated based on discussions with Brad Fike, and by comparison with Addo, and was thought to be 0.35-0.45 rhino/km^2 (in Brooks and Adcock 1997).

ESH Eastern Shores - Tewati Wilderness section Best Prior Estimate: 0.2 rhino/km^2

This area’s carrying capacity had been grossly overestimated when 17 founder animals were introduced from 1984-1988. The population declined by 6.1% per year on average up to ‘94, and has declined by 1.5% per year since then. Densities have gone from 0.24 to 0.173 rhino/km^2.

The 1997 carrying capacity range (Brooks and Adcock 1997) was estimated as 0.2- 0.27 rhino/km^2, but at that stage the population size had been overestimated, and subsequent monitoring allowed previous estimates of rhino numbers to be adjusted downwards.

HLU Hluhluwe section of Huluhluwe-Umfolozi Park Best Prior Estimate: 0.43 rhino/km^2

UMF Umfolozi section of the Huluhluwe-Umfolozi Park Best Prior Estimate: 0.43 rhino/km^2

The large area size, large population size, presence of a proportion of clean (unrecognisable) black rhino and the vegetation conditions in Hluhluwe-Umfolozi Park make it one of the most difficult populations to monitor closely. Assessing carrying capacities for black rhino in HUP has been a difficult task: Vegetation conditions can change fairly significantly within half a decade especially in the higher rainfall sections, and a complete field survey of current vegetation conditions in HUP was not possible for this project. HUP has 5 sections each with different climate, main soils and vegetation, and also different rhino densities and removal histories.

Hluhluwe

Rhino numbers in Hluhluwe (which has a north and south section) went from 300 (c.1 per km^2) in the late ‘50's to c. 85 in ‘91/‘92. Vegetation changes were shown to be the main cause of these declines. Since ‘92, numbers have ranged between 80 and 108 (0.266 - 0.359 rhino/km^2). Few removals (or only 4 removals after ‘98?) have taken place in this time.

Hluhluwe Manzibomvu (N) section : 0.292-0.438 since ‘92, avg 0.377 rhino/km^2 in last 5 years
Hluhluwe Nqumeni (S) Section : 0.256-0.359 since ‘92, avg. 0.328 rhino/km^2 in last 5 years

Documented Hluhluwe carrying capacity estimates for ‘90's conditions have been:

Manzibomvu rhino/km^2	Nqumeni rhino/km^2	Reference
0.392	0.5	(Emslie and Adcock 1993)
0.36	0.26	(Goodman et. al. 1996 NPB meeting)
0.3-0.42	0.35-0.5	(Brooks and Adcock 1997)

Umfolozi

In Umfolozi, black rhino were rare in the late ‘50's. Numbers built up during the 80's and early ‘90's up to c March ‘94 where they peaked at c.321. Removals averaged 12.4 rhino per year, or 4.1% of the population from ‘89 to ‘98 (but with more removals in later years). From end ‘94 to the end of ‘98, numbers have varied from c. 319 to c. 283, and annual increment accounting for removals has averaged around 3.5%.

Density range from April ‘94 to Dec. ‘98

Masinda	0.473 to 0.586 rhino/km^2
Mbhuzane	0.346 to 0.442 rhino/km^2
Makhamisa	0.52 to 0.613 rhino/km^2

The average densities in Umfolozi as a whole have been around 0.458 rhino/km^2 since March ‘94.

Documented Umfolozi carrying capacity estimates for ‘90's conditions have been:

Masinda rhino/km^2	Mbhuzane rhino/km^2	Makhamisa rhino/km^2	Reference
0.5	0.5	0.5	(Emslie and Adcock 1993)
0.46-0.5	0.45	0.44	(Goodman et. al. 1996 NPB meeting)
0.4-0.55	0.4-0.55	0.37-0.5	(Brooks and Adcock 1997)

ITA Ithala (ne’ Itala) Game Reserve Best Prior Estimate: 0.21 rhino/km^2

This population derived from 33 animals introduced from ‘75 to ‘85. Only since c. ‘97 have the numbers and history of this population been deduced, based on intensive monitoring efforts by staff, and back-calculations of numbers. The population ranged from 48-53 animals between ‘89 and ‘97, during which time only 4 male removals were made. Growth averaged about 2.3% during this time. 11 rhino were removed in ‘98. Before the removals, densities were thus between 0.18 and 0.2 rhino/km^2 (excluding cliffs). Ithala has been subject to extreme browse pressure from a range of antelope species and giraffe over the last decade.

CC estimates for Ithala exclude a totally inaccessible zone along and above steep cliffs. The ‘97 CC estimate of Adcock and Brooks was 0.22 rhino/km^2, based on unadjusted population estimates. Goodman et. al. (1996) estimated Ithala’s CC at 0.2 rhino/km^2. Wolf (1998) estimated the Ithala black rhino carrying capacity as being 50-55 animals - giving densities of 0.187-0.206 over the whole park (-cliff), but densities of 0.271 rhino/km^{2}over the more available terrain area of 184 km^2. The author considers 0.21 rhino/km^2 to be a reasonable CC estimate.

K-W Kunene West - General **Best Prior Estimate: 0.02 rhino/km^2**
This indigenous population has been recovering from heavy poaching since the late '80's. Estimating rhino densities and carrying capacities has been difficult, as details were not available regarding which parts of this huge area are accessible to the rhino, given water distribution patterns and terrain. Also, rhino ranges have been difficult to estimate as these can change greatly depending on rainfall distribution. Hearn (2000) has investigated black rhino habitat relations in 3 study areas. From his information, recent local densities were approximately calculated as :

Southern area:	0.0117 rhino/km^2
Central area	0.045-0.0658 rhino/km^2
Northern area	0.01-0.015 rhino/km^2

Past rhino densities in these areas are not known to the author. Past records (Blythe Loutit, RMG status report information on breeding covering the '80's and early '90's) had however shown generally good black rhino breeding performance in K-W, but subsequent rhino productivity as reported by Hearn (2000) has been much reduced.

The "Prior CC estimate" of 0.02 should thus not be taken as a solid estimate, but merely as an index of a generally low CC for this arid region.

LAP Lapalala Nature Reserve - (Rhino section) **Best Prior Estimate: 0.1 rhino/km^2**
Lapalala's black rhino were introduced in '90 and '92, resulting in densities near estimated carrying capacity from the start. From '92 densities have ranged from 0.105 to 0.152 rhino/km^2 (avg. 0.124). Over '96-'97, 4 rhino died. Growth has been virtually nil over the years. Although CC was estimated as 0.13 rhino/km^2 (Brooks and Adcock 1997), during a subsequent survey Adcock produced a revised carrying capacity estimate of nearer 0.1 rhino/km^2.

MKU Umkhuze - (ne' Mkuze) - excluding wilderness **Best Prior Estimate: 0.27 rhino/km^2**
The Umkhuze population grew from c. 54 in '89 to 83 in '95, and has since been stable at this number. There were 17 live removals (avg. 3.4 rhino/year or 4.9% of the population) from '89 to March '94, and also 10 rhino poached (at c. 2.8% per year) up to 03/94. There have been 4 rhino poached since 03/94, but no live removals. Population growth declined from c. 11% (April'89-March '94) to 1.5% (April '94-Dec '98).

Carrying capacity estimates from Umkuze seem to be confused by the fact that the rhino do not seem to use the entire area. 347 km2 should be "available" to them, but the area they occupy seems closer to c. 300 km2. For these two cases, densities have been as follows:

In 347km2	in 300km2
0.164 - 0.24 rhino/km^2	0.18-0.28 rhino/km^2

CC has been estimated as high as 0.35 rhino/km^2(Goodman et. al. 1996, Brooks and Adcock 1997's upper estimate from the range 0.25-0.35 rhino/km^2). Based on the recent performance, distribution and numbers of this population, the "best" estimate of 0.27 rhino/km^2 was decided on.

NDU Ndumo Game Reserve **Best Prior Estimate: 0.36 rhino/km^2**
After 10 removals in '89, there were possibly 32 black rhino in Ndumo, however the rhino numbers in Ndumo during the early '90s were not really known. From intensive surveys in '97/98, the population history could be re-constructed back to '94 when another 10 rhino were removed. From '94 to '98, numbers appear to have been between 24 and 26 animals, showing c. 3% growth. This population may periodically have lost a few animals when rhinos wandered over to Mozambique or got washed away in severe floods. Ndumo has very high densities of Nyala. Rhino densities have gone as high as c. 0.42 rhino/km^2 (Conway and Goodman 1989), but were probably 0.31-0.36 rhino/km^2 in the early '90s, and 0.24-0.26 in the mid and late '90s.

CC has been estimated at 0.37 rhino/km^2(Goodman et. al. 1996), and 0.34-0.426 rhino/km^2 (Brooks and Adcock 1997).

PIL Pilanesberg National Park Best Prior Estimate: 0.1 rhino/km^2

Pilanesberg black rhino originated from 19 introduced from '81-'83. Numbers grew to 32 in '89*, then 49 in '98, while 10 animals were removed in 1996. Growth has average 11.3% per year from April '94 to Dec '98. Densities have gone from 0.076 to 0.089 rhino/km^2 since '94. Carrying capacity estimates for Pilanesberg made at the '93 property assessment workshop were 59-69 rhino, or 0.107-0.125 rhino/km^2. Taking into account measurement of the extent of inaccessibility of Pilanesberg's terrain, in 1997, Adcock revised the estimates to c. 0.01 rhino/km^2.

* 3 males were unsuccessfully introduce, and 2 females were successfully introduced in '89.

VAA Vaalbos National Park Best Prior Estimate: 0.06 rhino/km^2

From 6 rhino introduced in '87, densities have varied from 0.03 to 0.072 rhino/km^2 (max. 13 rhino in 1998). The area has been plagued by problems of deaths from male aggression and accidents / disease, especially in early years, when growth was 5-6% versus 17% since April '94. 8 animals were removed from '94 to '98. The Vaalbos population has been totally removed since '98.

CC Estimate rhino/km^2	Reference
0.077	(1993 in Knight et. al. 1997)
0.05-0.07	(Brooks and Adcock 1997)

WEE Weenen Nature Reserve Best Prior Estimate: 0.29 rhino/km^2

This population began from 4 rhino introduced in '83. From 'April 89 March '94, the population grew at 8.4% per year on average, going from 8 to 11 animals (0.18-0.25 rhino/km^2, average 0.21 rhino/km^2). Since then, there has been no growth, and there have been 4 rhino removals. The breeding females in Weenen may be very old. Densities have stayed + or- 0.205 rhino/km^2. The estimated CC density of 0.294 /km^2(Brooks and Adcock (1997), and possibly that of 0.29 made by Goodman et. al. (1996), was made when it was thought the population was 1 higher than it turned out to be. 0.29 was the maximum density achieved with that erroneous extra animal. Based on Weenen's rainfall and soils, the estimate was however still thought to be reasonable.

WPP Waterberg Plateau Park Best Prior Estimate: 0.085 rhino/km^2

27 black rhino were introduced in '89, and two more females were introduced in '94. Survival was poor however, and numbers remained around 25 up to '94. Thereafter growth averaged 4.2% per year, reaching a high of 33 rhino before the two removals in March '2000 (data from Pierre du Preez's thesis). Densities ranged from 0.055 to 0.063 rhino/km^2 up to '94, and from 0.065 to 0.083 thereafter. The author's first CC estimates for the area were 0.08-0.11 /km^2 (Brooks and Adcock 1997), but based on discussions with Raoul du Toit during a brief AfRSG visit to WPP, 0.085 rhino/km^2 was taken as a possible likely CC density by the author.

Appendix Table A3.1 (Data from Emslie and Adcock 1993)

BROWSE AVAILABILITY AND DIET TWO STUDY-AREAS IN HLUHLUWE-UMFOLOZI PARK

	UMFOLOZI (W)		**HLUHLUWE** (N)		
MAJOR "GOOD" FOODS	**AVAILABLE BROWSE UNITS/Ha IN HABITAT**	**% IN RHINO DIET**	**AVAILABLE BROWSE UNITS/Ha IN HABITAT**	**% IN RHINO DIET**	**W Umfolozi's Browse Availability as a % of N Hluhluwe's**
Acacia types					
Acacia's	2782	36.0%	5097	23.4%	54.6%
Dicrostachys cinerea	743	10.0%	2808	10.7%	26.4%
	3525	46.0%	**7905**	34.1%	**44.6%**
Palatable, more evergreens:					
Berchemia zeyheri	17	0.1%	1069	6.0%	
Acalypha glabrata	0.5	tiny	1600	*14.5%*	
Spirostachys africana	2115	24.6%	2100	23.0%	
Other "'Green bite" species	5463	20.7%	5851	8.8%	
Forest palatables	173	0.2%	1739	4.7%	
	7768	45.6%	**12359**	57.0%	**62.9%**
Total "Good" Food	**11293**	**91.6%**	**20264**	**91.1%**	**55.7%**
MAJOR "POOR" FOODS					
Croton menyhartii	2577	0.3%			
Brachelaena illicifolia	706	1.0%			
Scutia myrtina			755	*0.4%*	
Euclea's	2382	0.4%	3830	0.70%	
Diospyros's	32	0.05%	2684	2%	
Lippia javanica	2	tiny	1897	0.50%	
Rhus sp (rej)	293	0.27%	2015	1.10%	
Maytenus senegalensis	135	tiny	1095	0.14%	
Total "Poor" Food	**2843**	**2.1%**	**11521**	**4.8%**	**24.7%**
Ratio of Good to Bad Food	**3.97**		**1.76**		
% Good Food (out of available browse)	**79.9%**		**63.8%**		

APPENDIX 4 - ISSUES AND HYPOTHESES RELEVANT TO BLACK RHINO POPULATION DYNAMICS AND PRODUCTIVITY

POSSIBLE DENSITY DEPENDENT POPULATION DYNAMICS IN BLACK RHINO

Noticeable effects on a rhino population can occur if the densities of black rhino in an area are so “high” that rhino are consuming much of the yearly production of edible (available/suitable) food, or that available during the dry season. Availability of food of adequate quality becomes in short supply, and individual female rhinos (and especially old females) may not maintain sufficient body reserves to easily and repeatedly fall pregnant, carry a calf to full term and successfully wean it. Such calves produced under sub-optimal resource conditions may grow more slowly and weigh less. The chances of these weaned rhino successfully competing for food resources and surviving to adulthood are reduced. Young female age-at first-calving can be delayed from c.6-7 to 9 or 10+ years (e.g. Hitchins and Anderson 1983). The chances increase of older rhino dying. (See Owen-Smith 1988 for more information).

The above effects are density dependent, and occur because numbers have approached ecological carrying capacity. The net result is lowered rhino recruitment and increased mortalities, and thus slowed and perhaps zero population growth. Population numbers need not stabilize at this level of zero growth, ‘though. Habitat conditions affecting food resources may change due to external events (drought, vegetation succession, fire impacts etc.).

Overshooting carrying capacity

Black rhino populations can “overshoot” carrying capacity, especially if their densities initially increased rapidly.

<u>Food resources start to become limiting, ...then</u>

Popn “Growth” Events :->	females fall pregnant *and/or*	a “cohort” of calves are born
Lag Periods :->	a few months to c. 20 months lag (pregnancy / post-natal period)	c. 2 to 8 year lag (calf independence and maturation)
Impacts During Lags -> **which Deplete Resources:**	persistent browse pressure of existing biomass of adults	increasing browse pressure of growing bodies (biomass) of youngsters
Eventual effect -> **on population** :	more pregnancies abort or infants die, conceptions are delayed	more subadults die or ages at first calving are delayed

During the lag periods, rhino biomass can increase to overshoot carrying capacity. The rhino then consume plant resources in excess of annual production, or enough to begin suppressing regrowth and lower productivity per plant. Over time suitable browse supply can decline through lowered standing plant biomass per plant, plant mortalities and induced shifts in plant species composition (e.g. declines in more palatable/important rhino food plants allowing less edible plant species to increase in dominance). If effects on rhino recruitment and mortality rate become even greater, rhino population growth may become negative, and rhino density may decline. This implies a coupling (two-way effect)between the condition and dynamics of the vegetation (rhino food) and rhino population dynamics (i.e. rhino numbers/density/biomass changes).

THE ROLE OF OTHER BROWSERS AND COMPETITION IN BLACK RHINO CARRYING CAPACITY

Black rhino are not the only herbivore species that are eating the browse resources of an area. The "competitive" impact of other browsing game could also result in fluctuations in black rhino food production. An extreme suggestion is that the carrying capacity of a natural ecosystem may only be viewed at the level of all the herbivores combined (browsing herbivores in this context) and not that of the individual species (Prins and Douglas-Hamilton, 1990).This can only be true to the extent to which browsers share exactly the same resources. Black rhino's ability to eat fairly thick twigs and branches (up to c. 3cm) means they can access food unavailable to most browsing animals feeding in its height range. Such a twiggy diet is high in fibre and of low quality, however. Thus competition with in particular kudu, impala, nyala, and eland, for "quality " leafy shoots, has the potential to become a problem. Giraffe are also capable of exerting very significant impact in plants in the 0-2m range (e.g. Itala Game Reserve (pers. obs.), Lewa Downs, Kenya (Craig pers. comm.) and Ol Jogi, Kenya (Kimani, pers. comm. and Kimani, unpublished thesis). Heavy browse pressures, resulting in notable vegetation impacts and changes, are evident in several black rhino areas in southern and eastern Africa. No detailed synthesis of such cases are available as yet.

FLUCTUATIONS IN CARRYING CAPACITY WITH RAINFALL, AND DENSITY DEPENDENT EFFECTS

Because the annual production of available browse itself fluctuates with annual rainfall, so (strictly speaking) does year to year carrying capacity. For long-lived animals with > 1 year gestation periods like rhino, such fluctuations cannot be closely tracked by changes in birth and death rates. Longer-term cycles of above- and below-average rainfall may be more relevant in causing shifts in carrying capacity and resulting changes in rhino recruitment rates and moralities.

The relative length and amplitude of these kinds of dry and wet period rainfall fluctuations may hypothetically determine the degree to which density dependent effects occur in the rhino and plant populations: Rhino numbers may be kept below a theoretical "average" carrying capacity in areas with very high fluctuations in inter-annual rainfall (following the logic of Illius and O'Connor 1999). Increased moralities or large declines in rhino body condition may occur in dry periods, and there may be insufficient time between dry periods for population densities to "recover" or for animals to regain good condition for sustained reproductive output. But although in wetter periods the population growth and recruitment appear relatively healthy as recovery begins, populations that are high (but still below "average carrying capacity" levels) can have extreme impacts on their food base during below-average rainfall periods, with negative consequences for future rhino production potential (as is hypothesised to happen in other some plant-herbivore system - e.g. Milton and Hoffman 1994, Illius and O'Connor 1999).

KEY RESOURCES, BLACK RHINO PRODUCTIVITY AND HABITAT QUALITY

"Key resources"

The fact that different plant components and species in the habitat are of different "quality", is understood to be important to black rhino. As "browse" material usually appears to be super-abundant in their habitats, it is most likely the decline in quality of the food with density that most impacts black rhino. Certain vegetation components are postulated to provide the "quality" in the rhino's diet. These include leafy material, softer shoots, more palatable / digestible plant species, and certain plants which retain dry-season "green-bite"found in or near drainage lines, on termite mounds and in other kinds of bush clumps. Quality vegetation components are higher in available nutrients and energy per bite than other plant components on offer. They have a relatively low fibre content (and thus a high digestibility) and/or a low concentration of adverse secondary plant chemicals. When the abundance of these components in the vegetation drops, black rhino dietary quality declines, potentially to levels where their body condition, health, fertility and survival are compromised and their population performance may drop.

These components of the vegetation, with which the black rhino population is more closely coupled, are termed "Key resources" (Illius and O'Connor 1999). Identifying the details of this coupling remains an important research need in black rhino conservation.

Hobbs and Swift (1985) tackled the problem of determining the role of dietary quality in carrying capacity determination. Their approach requires estimates of the distribution of limiting nutrients within the available forage, i.e. the quantity of forage in each quality class. They showed an inverse relationship between the quality of diets obtainable from a habitat, and the animal density. Even when total "forage" availability was not limiting, increases in animal density could compel deterioration in the nutritional status of the individuals.

The above discussion has potential implications for the relationships between rhino density, productivity and vegetation condition.

Areas dominated by low-quality food

In habitats that supplying only or primarily(?) low-quality food (e.g. Waterberg Plateau Park, Eastern shores), the diet available may be whether there are a few or many animals (i.e. irrespective of the population density). In such cases, the supply of one or more limiting nutrients or energy may be barely sufficient for successful calving, but may be sufficient to maintain adult, non-reproductive animals. Calving success may be low, and may result in only slow population growth. Where calving is too low to replace adult mortalities, a slow population decline may result.

However - The author gets the impression from observing such low-nutrient areas, that even there, low amounts of “key” resources (sensu Illius and O’Connor) occur that provide the quality elements to the rhino diet. This may enable rhino to subsist by filling up with remaining poor-quality but abundant browse, but not to show normal levels of recruitment.

In reality, there may well be a continuum from areas dominated by fertile soils and palatable available browse; to those dominated by infertile soil and/ or low-suitability rhino food.

Areas dominated by high quality food

Areas dominated by high quality food may initially have “high” carrying capacities. Rhino can rapidly build up to very “high” densities, overshoot carrying capacity and over-exploit palatable plants, some of which appear to have low resistance to browse pressure. The system can crash, settle to a lower carrying capacity level and turn into a lower-productivity system with respect to remaining but lower-palatability plant elements (possible examples include Solio Ranch, Kenya and Augrabies Falls NP, South Africa). Alternatively it could crash, allowing palatable elements time to recover and rebuild potential for a higher carrying capacity. Also, some palatable plants may have a ‘refuge”: they may be able to maintain their level of browse production or “browse interest” but due to hedged growth structure, the browse “capital” may be fairly well-protected from over-exploitation. Eastern Cape valley bushveld may provide examples of plants showing low resistance to browse pressure as well as hedged growth forms providing browse refuges.

Finally, we should perhaps ask the question of whether black rhino can, at all or to some extent(?), show induced population-level differences in mean body size or stature in response to gross differences in habitat quality, rather than in mean body condition. This has been found in red deer (Clutten-Brock and Albon 1989), reindeer (Skogland 1990) and moose (Hjelford and Histol 1999), where populations living in poor quality habitats contain smaller-sized adult animals and calves.

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