

5.3 Results and Discussion

5.3.1 Calculation of Niche Overlap

The percentage time spent by the herbivores in each habitat and the percentage contribution of each grass species in their diet represent the two resource dimensions used to calculate pairwise overlap. The overlap measures were based on the proportional use of six habitats and 35 grass species. Emphasis has been placed on calculating overlap only for the dry season. This was for two reasons, firstly, because of the limited time available, and secondly, because this period is most unfavourable in terms of resource limitation. The importance of measuring overlap during the leaner periods has been stressed by Schoener (1982) as competition between species is most likely to occur during these periods.

5.3.1.1 Single Niche Dimensions

5.3.1.1.1 Habitat Overlap

Habitat overlap was calculated between the white rhino and the four associated large grazers for all seasons (Table 5.1). This was done using the Asymmetrical method presented by Levins (1968) and MacArthur (1972).

Pairwise overlap was generally high for the species, except during the dry season when the ungulates were more susceptible to stress. A decrease in habitat overlap was apparent, especially during the late-dry season when the zebra showed a high preference for the hillside savannas. These habitats, because of their steep slopes are largely inaccessible to the white rhinos. This high overlap between all grazers results from the high selection of all species for the secondary grasslands, valley savannas and thickets.

The overlap estimates indicate that the wildebeest frequent those habitats most similar to the white rhino, and the zebra,

Season	Rhino x Wilde	Rhino x Harte	Rhino x Zebra	Rhino x Impala
Fire	0.79 / 1.06*	0.65 / 0.80	1.09* / 0.87	0.92 / 1.09*
Early Wet	0.92 / 0.93	0.92 / 1.00*	0.83 / 0.81	0.79 / 0.73
Late Wet	0.89 / 1.07*	0.86 / 1.02*	0.90 / 0.93	0.95 / 0.72
Early Dry	0.96 / 0.97	0.90 / 0.75	1.03* / 0.81	0.57 / 0.74
Late Dry	0.83 / 1.09*	0.68 / 0.79	0.44 / 0.35	0.80 / 0.90

Table 5.1 : Seasonal differences in the habitat overlap values using the MacArthur-Levins' Asymmetrical measure. The pairwise overlap estimate relative to the white rhino (rw) is shown on the lower left, with the estimate relative to either the wildebeest (Wild), hartebeest (Hart), zebra or impala on the upper right, ie. w^r , w^h , w^z or w^i , respectively.

the least. Seasonal changes occurred between all species, especially between the white rhino and zebra and the white rhino and impala. The impala, because of their selection mainly for the valley savannas and thickets, tend to overlap the least.

To summarize, all the herbivores show a high degree of overlap with the white rhino, indicating similarities in their habitat use. However, both temporal and spatial differences may be occurring (Bell, 1969), which may affect the overall estimate. For example, herbivores may select similar habitats in different valleys or at different times.

5.3.1.1.2 Dietary Overlap

Dietary overlap between the white rhino and the other grazers was (as described earlier) determined only during the dry season, which is considered to be the period when food becomes a limiting resource.

The overlap measures for the diet were averaged for all habitat types, implying that similar diets were utilized in each habitat type. (The problems associated with this assumption was discussed earlier). The diet was estimated in each of the feeding sites mentioned in section 4.2.1.2.

When using the Asymmetrical method, overlap estimates are given both with respect to the white rhino and also with respect to the other four grazers (Table 5.2). In the first case, the proportion of resource type (k) in species i's diet, i.e. P_{ik} , is that for the white rhino, and in the second, P_{ik} is that for either hartebeest, wildebeest, zebra or impala. A number of points emerge from these measures. Firstly, those species selecting for a narrower dietary range than white rhino (e.g. hartebeest, zebra and impala) tend to have low overlap measures. Secondly, when measuring overlap with respect to a generalist (eg. white rhino which select for a wide variety of grass species), comparatively higher values are recorded, in some cases greater than one. (eg. 1.15 and 1.20).

Season	Rhino x Wilde	Rhino x Harte	Rhino x Zebra	Rhino x Impala
Early Dry	0.82 / 0.76	0.54 / 0.46	0.71 / 0.41	1.20* / 0.28
Late Dry	0.59 / 0.80	0.64 / 0.76	1.15* / 0.40	0.65 / 0.47

Table 5.2 : Seasonal differences in the dietary overlap values using the MacArthur-Levins' Asymmetrical measure. A similar key is used as in Table 5.1.

High overlap values were again recorded between the white rhino and wildebeest. Therefore, in terms of both the habitat and dietary niche dimensions, these species will most likely compete at high densities. Both the zebra and impala overlapped only slightly with the white rhino during the dry season. However, although they selected for similar habitats (see previous section), differences were apparent in their diet. However, whether these differences have resulted so as to avoid competition, as implied by Schoener (1974), is difficult to answer.

5.3.1.2 Multidimensional Overlap

Total niche overlap, based on both habitat and diet, was first determined using the two existing methods for calculating overlap on more than one dimension, i.e. the summation and product methods (Tables 5.3 and 5.4). Total overlap was then calculated using the proposed "weighted overlap" measure (Table 5.5).

With respect to the first two methods, the summation measure in all cases gave higher values than the estimates derived from the product method. However both the two methods indicate that wildebeest overlap the most with the white rhino and zebra the least. This was generally true throughout both the early and late dry seasons.

The "weighted overlap" method is based on the important condition that dietary selection differs between different habitat types. It first calculates dietary overlap in each habitat type and then subsequently modifies these by incorporating the habitat selection coefficients, thus giving rise to a more acceptable estimate. In this case dietary electivities, which are different in each habitat type can now be incorporated in the measures. The results are shown in Table 5.5.

High overlap values were again recorded between the white rhino and wildebeest. Therefore, in terms of both the habitat and dietary niche dimensions, these species will most likely compete at high densities. Both the zebra and impala overlapped only slightly with the white rhino during the dry season. However, although they selected for similar habitats (see previous section), differences were apparent in their diet. However, whether these differences have resulted so as to avoid competition, as implied by Schoener (1974), is difficult to answer.

5.3.1.2 Multidimensional Overlap

Total niche overlap, based on both habitat and diet, was first determined using the two existing methods for calculating overlap on more than one dimension, i.e. the summation and product methods (Tables 5.3 and 5.4). Total overlap was then calculated using the proposed "weighted overlap" measure (Table 5.5).

With respect to the first two methods, the summation measure in all cases gave higher values than the estimates derived from the product method. However both the two methods indicate that wildebeest overlap the most with the white rhino and zebra the least. This was generally true throughout both the early and late dry seasons.

The "weighted overlap" method is based on the important condition that dietary selection differs between different habitat types. It first calculates dietary overlap in each habitat type and then subsequently modifies these by incorporating the habitat selection coefficients, thus giving rise to a more acceptable estimate. In this case dietary electivities, which are different in each habitat type can now be incorporated in the measures. The results are shown in Table 5.5.

Season	Rhino x Wilde	Rhino x Harte	Rhino x Zebra	Rhino x Impala
Early Dry	0.79 / 0.74	0.49 / 0.35	0.73 / 0.33	0.68 / 0.21
Late Dry	0.49 / 0.87	0.44 / 0.60	0.51 / 0.14	0.52 / 0.42

Table 5.3 : Total overlap based on both the habitat and dietary dimensions using the "Asymmetrical-Product method". A key similar to that described in Table 5.1 is used.

Season	Rhino x Wilde	Rhino x Harte	Rhino x Zebra	Rhino x Impala
Early Dry	0.89 / 0.87	0.72 / 0.61	0.87 / 0.61	0.89 / 0.51
Late Dry	0.71 / 0.95	0.66 / 0.78	0.80 / 0.38	0.73 / 0.69

Table 5.4 : Total niche overlap based on the habitat and dietary dimensions, using the "Asymmetrical-Summation method". See Table 5.1 for an explanation of the key used.

Season	Rhino x Wild	Rhino x Hart	Rhino x Zebra	Rhino x Impala
Early-Dry	0.56 0.36	0.25 0.21	0.33 0.36	0.16 1.12
Late-Dry	0.14 0.29	0.49 0.14	0.08 0.04	0.39 0.12

Table 5.5 : Estimates of total niche overlap using the "Weighted Overlap measure". Refer to Table 5.1 for an explanation of the key.

A marked decrease in the overlap values is apparent. For example, the overlap between the white rhino and zebra is now much lower, i.e. 0.36, than the estimates determined using the previous two methods. Differences as large as this can obviously greatly influence herbivore management. These differences can be explained in terms of the herbivores' feeding ecologies. For instance, if two animals utilize similar grass species, but forage in different habitats, then obviously overlap is going to be very low. Similarly, low overlap would also occur if the species forage in identical habitats, but on different grass species. The first case is analogous to the white rhino and zebra where the zebra, by spending approximately 80% of their time foraging in the inaccessible hillside savannas, show low overlap with the white rhino. When using the summation or product methods to calculate multidimensional overlap, fairly high measures (0.8 and 0.51, respectively) are observed as opposed to the "weighted overlap" measure (e.g. 0.04). In addition, another important aspect which must be considered is the dietary differences which are apparent between habitat types (see section 4.3.3). For instance, although the herbivores may depict similarities in their overall diet, the similar grass species may have been utilized in different habitats.

To conclude, the lower overlap values estimated using the "weighted overlap" method probably depict resource overlap more accurately. However all three methods need to be experimentally tested before definite conclusions can be made.

5.3.2 Habitat Overlap Using Discriminant Function Analysis

For the analysis all species recorded in less than ten sites were excluded because of their inadequate sample size. However, only four sites were recorded for impala, but were included out of interest as this species accounted for a large percentage of the total grazing ungulate biomass. Five herbivore species comprising a total of 110 feeding sites were analysed using DFA. An early dry and late dry season comparison was not possible as

insufficient data were collected. Each feeding site was characterized using the habitat variables (e.g. grass cover, grass height and percentage bulk contribution of each of the 35 species) given in Appendix I.

The final analysis was carried out using a matrix of 5 species and 37 variables.

5.3.2.1 Variables capable of discrimination

Appendix J shows those variables for which the between group variance is large compared to the within group variance, measured by the partial univariate F-ratio. A variable is considered for selection only if its F-ratio is larger than a specified value. The partial F-ratio measures the discrimination introduced by the variable after taking into account the discrimination achieved by the other selected variables (Klecka, 1975, Hill, 1979). This therefore identifies which variables are responsible for the separation of the herbivore groups, and the importance of each in this respect. All the variables are significant at the 1% level. The percentage abundance of Panicum deustum, Rhynchyletrum repens and Heteropogon contortus are related most closely with the occurrence of herbivore species.

5.3.2.2 Dimensions of the Community Niche

The analysis produced four discriminant functions with the first three accounting for a total of 90% of the overall variance. Each discriminant function represents a gradient proportional in length to the percentage between species variance accounted for by each (Appendix K). Ferrar and Walker (1974) interpreted these trends of variance along the discriminant functions as representing the primary dimensions of a community niche.

In order to adequately describe the community niche dimensions, it is necessary to know the degree of association between the D.F.'s and each variable. Appendix K represents the degree of associations as standardised weights for each variable, with the

highest positive (near the origin) and negative values (furthest from the origin) arranged in increasing magnitude (Ferrar and Walker, 1974).

The first and primary dimension (accounting for 49.6% of the total variance) represents a gradient from sites dominated by Panicum deustum (PADE) and Cymbopogon excavatus towards fairly tall grasslands dominated by Eragrostis gummiflua (ERGU) and Trichoneura grandiglumis (TRGR). The second discriminant function which accounts for 26.5% of the total variance suggests a trend from areas dominated by Loudetia flavida (LOFL), Digitaria eriantha (DIER) to areas dominated by Perotus patens (PEPA), Tristachya rehmanii (TRRE) and Eragrostis racemosa (ERRA). The third gradient which only accounts for 13.9% of the total variance, indicates a gradient from patches dominated by Cynodon dactylon (CYDA), Heteropogon contortus (HECO), Cymbopogon excavatus (CYEX) and Urochloa mosambicensis (URMO) to patches dominated by E. plana (ERPL), Tristachya rehmanii (TRRE) and Sporobolus pyramidalis (SPPY).

The remaining variance is due either to chance variability, or to variation in the individual variables that are not associated with the common trends (Ferrar and Walker, 1974). None of the gradients could be interpreted with respect to the habitat types classified in chapter 3, although, the first axis may represent a gradient from thickets (dominated by Panicum deustum) at the one end, to secondary grasslands (dominated by E. gummiflua and Trichoneura grandeglumis), on the other. This suggests that the spatial separation of the herbivores is on a much finer scale than that discussed in chapter four.

5.3.2.3 Species Separation and Overlap along the Habitat Niche

Each herbivore's feeding site contributes to a discriminant score along each discriminant function. By plotting each

discriminant score on the relevant D.F., scaled in proportion to the amount of variance extracted, it provides a multidimensional picture of the positions of each herbivore species' habitat niche (Figures 5.3 and 5.4). The extent and nature of species separation (or overlap) is represented by the distances between and location of the species centroids. Page and Walker (1978), interpret these centroids as indicating the species' niche centres. When considering the ecological separation or overlap of species one is more interested in their relative positions or patterns in the canonical space rather than their specific locations, ie., the degree to which two species separate or overlap. Figures 5.3 and 5.4 depict the species centroids and their variance on a two-dimensional space represented by the first three discriminant functions.

The first axis or discriminant function, representing a gradient from short grasslands dominated mainly by Panicum deustum and Cymbopogon excavatus to taller grasslands dominated by Eragrostis gummiiflua and Trichoneura grandiglumis, showed separation only between the impala and wildebeest, and impala and hartebeest. All the other grazers showed little separation. The white rhino showed similarities with all grazers, especially with the wildebeest and zebra. Thus on the one extreme we have the hartebeest specializing on the secondary grasslands, and on the other, the rest of the herbivores depicting little separation.

Separation on the second axis was again incomplete, especially between the white rhino, wildebeest and hartebeest. The zebra showed only slight similarities with the other herbivores, particularly with the impala.

The third gradient again depicts incomplete separation. However when analysed multidimensionally, only slight overlap between wildebeest and hartebeest, and wildebeest and rhino is depicted. it does separate those species which were not distinct along the previous two gradients. These results seem to support the

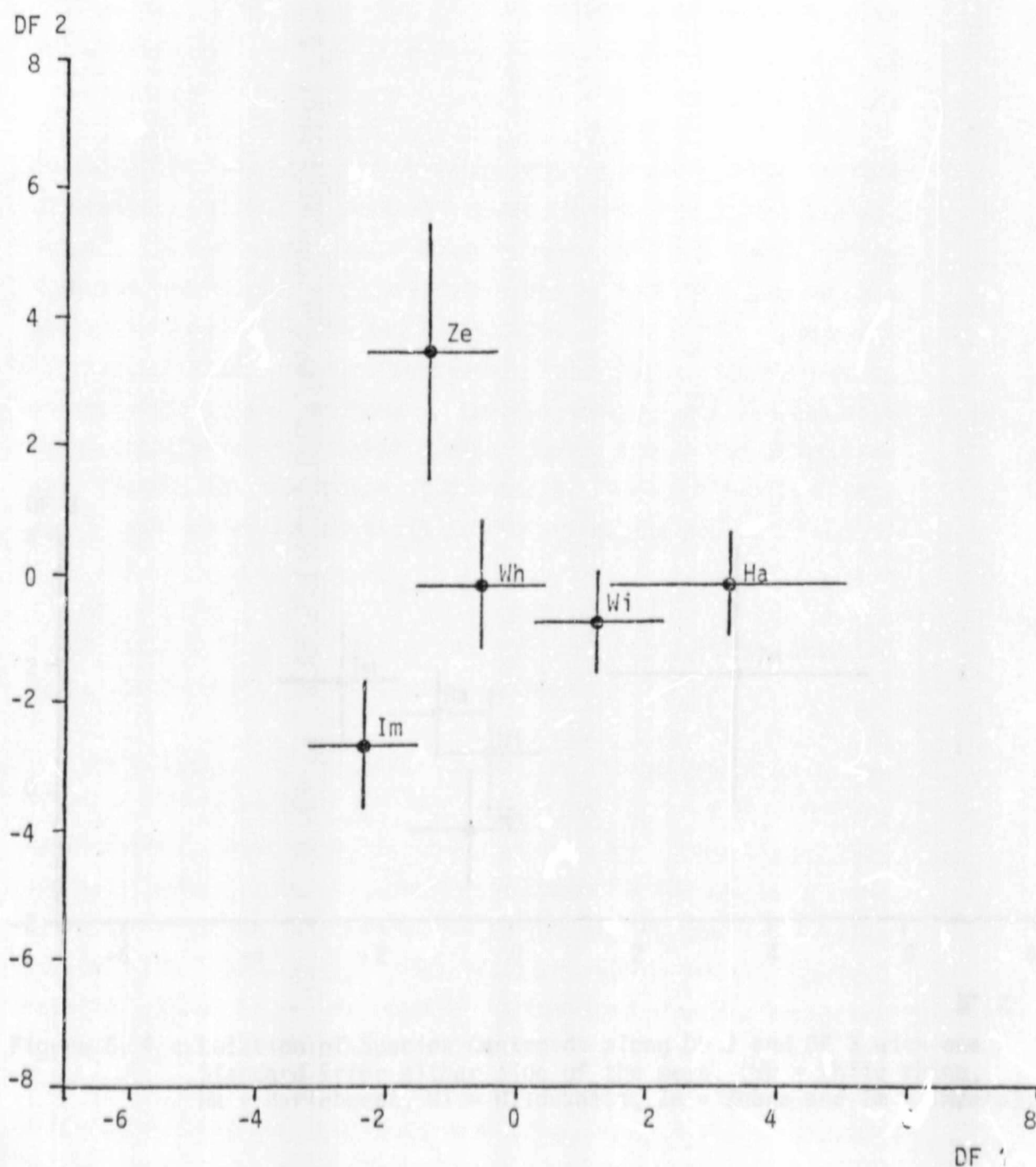


Figure 5.3 : Location of Species Centroids along DF 1 and DF 2 with two Standard Errors either side of the mean. (Wh = White rhino, Ha = Hartebeest, Wi = Wildebeest, Ze = Zebra and Im = Impala).

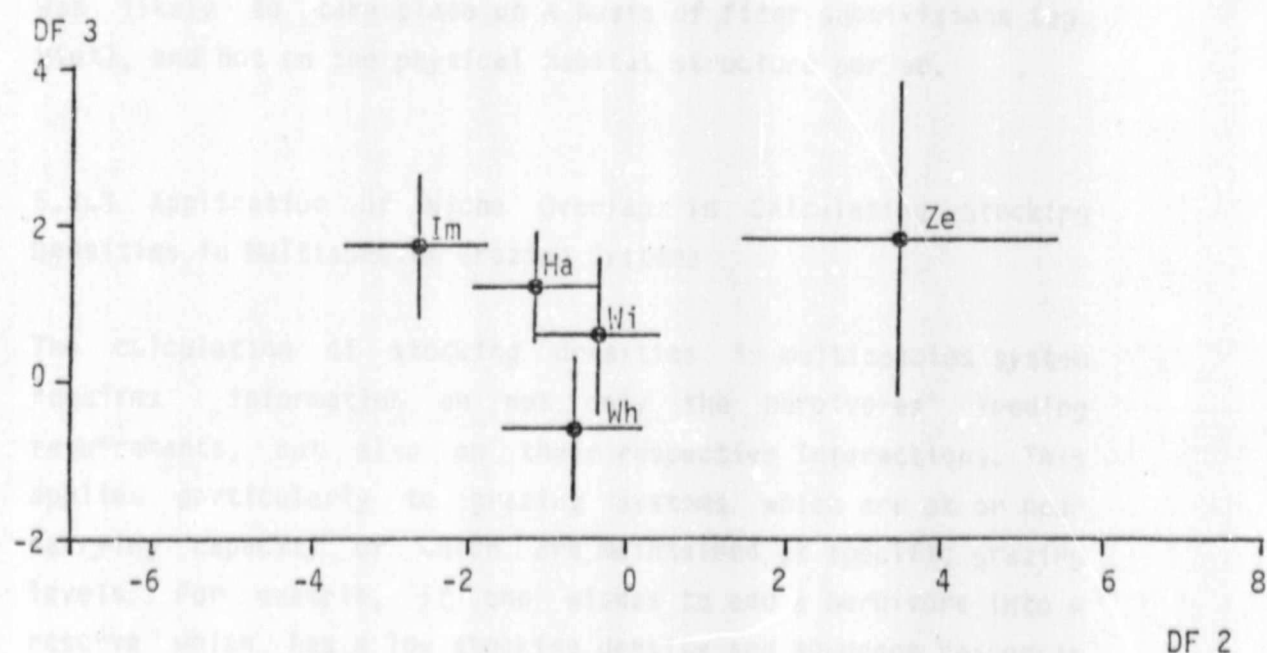


Figure 5. 4 : Location of Species Centroids along DF 2 and DF 3 with one Standard Error either side of the mean. (Wh = White rhino, Ha = Hartebeest, Wi = Wildebeest, Ze = Zebra and Im = Impala).

arguments given by May (1975) against calculating true multidimensional overlap from single dimensions.

Quantitative measures of habitat overlap, along these reduced dimensions, although possible (see Carnes and Slade, 1982), entail complex mathematical calculations. Hence, no quantitative measures were used to estimate habitat overlap. However, the analysis does point out two limitations of the previous methods. Firstly, true multidimensional overlap is generally overestimated, and secondly, species separation may occur at a more detailed level. Ferrar (1973), showed that niche separation was likely to take place on a basis of finer subdivisions (eg. diet), and not on the physical habitat structure per se.

5.3.3 Application of Niche Overlap in Calculating Stocking Densities in Multispecies Grazing Systems

The calculation of stocking densities in multispecies system requires information on not only the herbivores' feeding requirements, but also on their respective interactions. This applies particularly to grazing systems which are at or near carrying capacity or which are maintained at specific grazing levels. For example, if one wishes to add a herbivore into a reserve which has a low stocking density and abundant resources then no interactive effects will be evident. This is because the introduced animal has a negligible effect on the foraging behavior on the resident herbivores. The use of overlap measures become important only when concerned with systems at carrying capacity or when wishing to maintain specific grazing levels within these systems.

The importance of deciding on when a particular overlap value should be used becomes apparent when modifying stocking densities under particular grazing levels. If for example species 1 is the hartebeest and species 2 the white rhino, then the following question may arise when wishing to add a rhino in

the reserve but still keeping the extent of utilization constant. How many hartebeest must be removed? When answering such a question, a decision must first be made on whether one is interested in the effect of species 1 on species 2 (α_{21}) or, the affect of species 2 on species 1 (α_{12}). This is best explained by thinking in terms of how the addition of a white rhino will affect the availability of the food for the hartebeest. In this case the affect of the generalist (white rhino) must be considered, hence, 0.46 (α_{12}) hartebeest must be removed. If one wishes to add a hartebeest then 0.8 (α_{21}) white rhino must be removed. When removing a white rhino (the generalist), then one can only add 0.46 (α_{12}) hartebeest out, when removing a hartebeest then one can add 0.8 (α_{21}) white rhino.

CHAPTER SIX

MEASUREMENT OF CARRYING CAPACITY IN A MULTISPECIES SYSTEM

6.1 Introduction

The concept of Carrying Capacity has been given much consideration in recent literature, and is generally defined as the state of equilibrium between herbivores and plants. The position of that equilibrium is indexed by its characteristic density of animals. In other words, it is the animal density at which the rate of forage production equals the rate of forage consumption (Caughley, 1979).

Sinclair (1981) on the other hand, argued that a population at carrying capacity should not be thought of as one with a stable or constant level. Rather, it is one that is fluctuating, often extensively between certain boundaries. He also stressed that we should be careful not to consider carrying capacity as an average of these random fluctuations - most systems are dynamic one way or another. Firstly, because half the time the population is above the average, and the rest of the time, below and secondly, because the fluctuations may be greater than 50% of the mean. He therefore concluded that in general, a population is at carrying capacity, or equilibrium, if it can persist while fluctuating within certain limits in that environment over a long period of time. The emphasis is therefore on persistence rather than steady state. In addition, it should be noted that although true carrying capacity is viewed as a long-term "equilibrium", in actual fact it consists of a number of short-term equilibria which change as a result of extraneous effects such as fluctuations in the environment, e.g. rainfall variation.

The concept and measurement of carrying capacity has been used widely, especially in range management, where guidelines on the maximization of livestock production are required. A number of workers have applied this concept to estimate the optimal

stocking densities at which animals perform at their maximum growth rate on a particular range or habitat. Danckwerts (1982) for example, described the grazing capacity as the "productivity of the grazable portion of a unit of vegetation, which is the number of animal units that can be maintained per unit area of land in order to maximise animal production per unit input under consideration, but does not permit soil erosion or changes in the botanical composition....this would otherwise reduce the potential of the vegetation to produce animal products".

These agricultural estimates are based largely on surveys of plant densities, vegetative composition, rates of growth, proportions of annual growth removed by animals, and the time trends in these statistics. Their primary aim is to attain equilibria between plants and animals in order to provide maximum yield of wool, milk, meat or hides (Caughley, 1976).

There are therefore two types of carrying capacities. The first, is the density of animals stocked at equilibrium with range conditions, which provide maximum sustained offtake or return, and the second is the density of animals that can be maintained indefinitely. The standing crop providing maximum sustained yield is lower than the maximum sustainable standing crop, because food per head must be kept high enough to generate productive yields (Caughley, 1976).

Although both describe equilibria between animals and vegetation, they are in actual fact two totally different kinds of equilibria (Caughley, 1979). The first differing from the second in its lower standing crop of animals and higher standing crop of vegetation. The agricultural carrying capacity is an equilibrium only because the animals are harvested to maintain a constant density.

The first equilibrium state, in which the net yield or harvest of animals is at a maximum, is termed the "economic carrying capacity". The second equilibrium, which is reached unaided, is known as the "ecological carrying capacity".

It is unfortunate that the difference between these two equilibria are not widely recognised. To the agriculturalist, the vegetation in systems above the economic carrying capacity are judged to be in "poor" condition and "overgrazed" when, in actual fact the system may be below its ecological carrying capacity. It therefore depends entirely on which equilibrium one is referring to.

The aim of this section is to determine the carrying capacity of the reserve for white rhinos at various stocking densities of associated grazers. The carrying capacity mentioned here is some point between the economic and ecological. The estimates obtained will be determined for average rainfall conditions.

6.2 Plant-herbivore Interactions

In order to get a clear understanding of the mechanisms leading to equilibria between two interacting populations (one being the herbivore or predator and the other the forage or prey type), it is important to monitor and analyze their population growth patterns.

Caughley (1979) identified three basic components of this process by which plants and herbivores reach a joint equilibrium;

(i) The growth response of the plants- the rate of increase of plant biomass as a function of the density of plants.

(ii) The functional response of the herbivores- the rate of intake per animal as a function of plant density.

(iii) The numerical response of the herbivores- the rate of increase per animal as a function of plant density (Caughley, 1976).

In grazing system of this type, the rate of change of herbivores is influenced only by the plant density, whereas the rate of change of plants is a function of both the herbivore and plant densities, i.e. the two components are interactive (Caughley,

1976).

The observed trajectory of a growing population can then be described by an equation that summarises the pattern of growth. Caughley (1976) proposed two different approaches. The first, although easier, but less useful, using curve fitting techniques, and the second, using models which simulate the two interacting populations.

The various population models, both simple (e.g. the logistic and delayed logistical equations) and complex (e.g. the interactive model of growth), have been examined in detail by May (1976) and Caughley (1976). The first two models have been rejected because they both treat vegetation and other resources as inert. The third model, the interactive model of growth, is considered to provide the best description of vegetation-herbivores systems. The equations presented below, are essentially those of May (1973) who used them primarily to model predator-prey system. Here they have been slipped down one trophic level (Caughley, 1976).

$$dV/dt = a_1 V (1 - V/k) - c_1 N [1 - \exp(-d_1 V)] \dots\dots\dots 6.1$$

$$dN/dt = N [-a_2 + c_2 (1 - \exp(-d_2 V))] \dots\dots\dots 6.2$$

where, a_1 = intrinsic rate of increase of plants,
 K = maximum ungrazed plant density,
 c_1 = maximum rate of food intake per herbivore,
 d_1 = grazing (searching) efficiency of the herbivore when vegetation is sparse,
 a_2 = rate at which herbivores decline when the vegetation is burnt or grazed flat,
 c_2 = rate at which this decline is ameliorated at high plant density,
 d_2 = demographic efficiency of the herbivore; its ability to multiply when vegetation is sparse,

V = the vegetation biomass, and
N = the herbivore biomass.

The first equation expresses the rate of change of vegetation using two terms, the first depicting logistic growth, and the second, the rate of grazing. The second equation summarises the rate of change of herbivores (N) in terms of their intrinsic rate of increase, as modified by the availability of food.

Figure 6.1 (adapted from Caughley, 1976) depicts the trajectory of a population and its food supply growing as predicted by the above two interlinked equations. The herbivore biomass increases greatly as a result of the super-abundance of vegetation (commonly called an eruption), the vegetation biomass then decreases abruptly, followed by a dramatic reduction in the herbivore biomass (i.e. a crash) which then, converge to an equilibrium with their food supply, through dampened oscillations (Caughley, 1976). These two sets of oscillations are displaced from each other, the animals trailing behind the vegetation. This occurs as a result of the lag effects between the two populations.

Figure 6.2 (adapted from Caughley, 1976) is a phase diagram showing the changing ratio of animals to plants as the herbivore-plant system moves to its equilibrium point ($dV/dt = dN/dt = 0$) of N^* , V^* , a position that can be calculated as;

$$V^* = 1/d_2 \log e (c_2 / c_2 - a_2) \dots \dots \dots 6.3$$

$$N^* = (V^* a_1 (1 - V^* / k)) / (c_1 (1 - \exp(-d_1 V^*))) \dots 6.4$$

An interesting feature of the vegetative equilibrium is its complete independence of the variables of plant growth, the animals alone determining its level. The equilibrium level of the animals, on the other hand, is determined by the characteristics of both the plants and animals. (Refer to Caughley (1976) for a

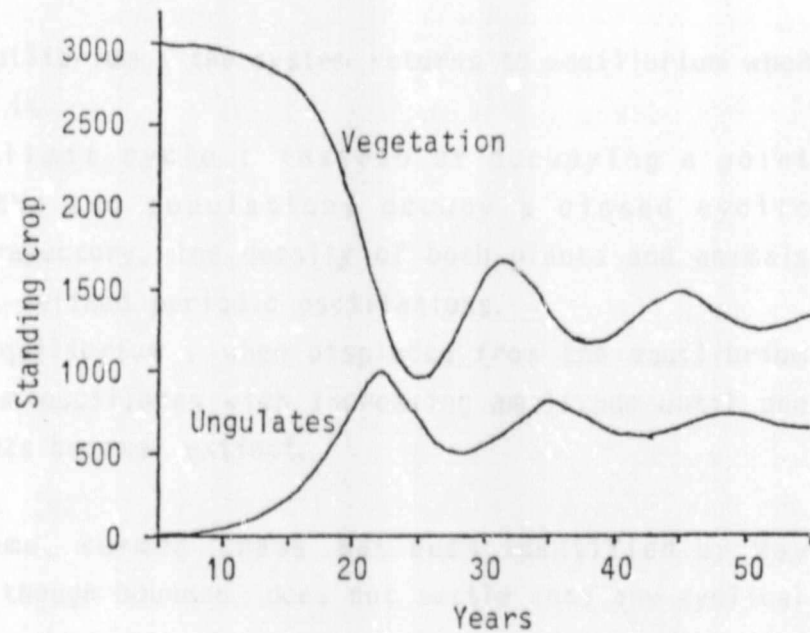


Figure 6.1 : Trends the vegetation and herbivore biomasses modeled by Caughley (1976).

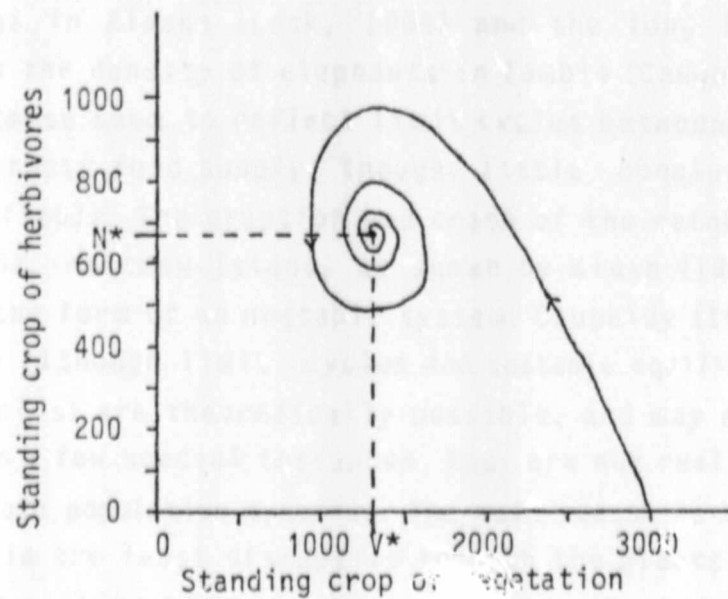


Figure 6.2 : Phases diagram of the relative densities of plants and herbivores as modelled by Caughley (1976).

more detailed explanation of these two interacting formulae).

Caughley (1976) identified three theoretical outcomes from the interactive model depending on the specific parameter values:

(a) Stable Equilibrium : the system returns to equilibrium when displaced from it.

(b) Stable limit cycle : instead of occupying a point equilibrium, the two populations occupy a closed cyclic equilibrium trajectory, the density of both plants and animals exhibiting well-defined periodic oscillations.

(c) Unstable equilibrium : when displaced from the equilibrium point the system oscillates with increasing amplitude until one of the components becomes extinct.

A fourth outcome, termed 'Chaos' has been identified by May (1976) which although bounded, does not settle into any cyclical patterns.

The last two outcomes identified by Caughley, and the additional one identified by May, are foreign to us, although it is becoming more apparent that they may exist; For example, the 4 year cycle of the lemmings in Alaska (Lack, 1954) and the long term fluctuations in the density of elephants in Zambia (Caughley, 1973). Both of these seem to reflect limit cycles between the herbivores and their food supply, though little conclusive evidence is available. The eruption and crash of the reindeer population on St. Matthew Island, as shown by Klein (1968), appear to take the form of an unstable system. Caughley (1976) concludes, that although limit cycles and unstable equilibria (and chaotic cycles) are theoretically possible, and may even have occurred in a few special instances, they are not really a feature of ungulate population dynamics. The main reason is that stable equilibria are least disruptive to both the plants and animals, so that systems of this nature would be selected for. Stable limit cycles and unstable equilibria, on the other hand, increase the probability of populations leading to extinction, and consequently, are selected against.

Unfortunately, Caughley's reasons given for the common occurrence of stable equilibria were largely based from a group selectionist point of view. It is highly unlikely that the populations interact in such a manner so as to always lead to stable equilibria. Instead, I believe that a system's dynamic behaviour is controlled largely by stochastic environmental events and its parameter and variable values.

This finally leads on to the question, of whether or not carrying capacity is a useful concept which can be applied to all systems. It is obvious that for systems, other than stable ones, the concept is extremely difficult to apply. However, for systems which are either stable or which can be managed, it becomes a useful concept. Therefore, before attempting to estimate the carrying capacity of any system, one must be fully aware of the dynamic interactions between the populations. One cannot assume that all systems will eventually become stable if left alone. The Píanesberg grazing system is assumed to follow a stable cycle.

6.3 The Measurement of Carrying Capacity in a Multi-species Grazing System

For any effective management policies to be established, there is clearly a need to develop and refine predictive models, both for climatic variations and animal carrying capacities and protein production. Four different predictive models are described below.

6.3.1 The Rainfall-Metabolic Mass Relationship Method

It has been predicted that climatic variations, particularly in precipitation, affect the production of plant material, and hence the carrying capacity of the ecosystem (Coe, *et al*, 1976). Relationships of a predictive nature have been established between rainfall and primary production (e.g. Walter, 1954; Whittaker, 1970; Seely, 1978) and between actual evapotranspiration and primary production (Rosenzweig, 1968).

Associations have also been made between annual rainfall and large African herbivore biomass (Watson, 1972; Leuthold, 1973; Sinclair, 1974; Western, 1975; Phillipson, 1975, and Coe, et al, 1976). Coe, et al (1976) examined the relationships of both published and unpublished information on standing crop biomass of large herbivores and above ground net primary production (from mean annual precipitation). The hypothesis was proposed that for a majority of savanna systems, particularly those with rainfall less than 700mm, it is possible to establish "statistically significant relationships" which are able to predict large herbivore biomasses, and hence, their carrying capacities. They calculated a linear regression equation which could then be used to predict large herbivore biomasses from annual precipitation. The calculated regression equation for predicting long-term carrying capacities of semi-arid wildlife systems (Coe, et al, 1976), is;

$$\text{Large herbivore biomass} = 1.685(\pm 0.238) \text{ AP} - 1.095(\pm 0.661) \dots 6.4$$

By substituting the average rainfall for Pilanesberg (620mm) into the equation an estimate of 1 AU per 10 ha was obtained. This amounts to a total of 5350 AU in the reserve. (1 AU is equivalent to a large steer weighing 454kg).

6.3.2 The Standard Agricultural Method

The previous method calculates only the total large herbivore carrying capacity for an area. In most multispecies wildlife systems, such as the Pilanesberg Game Reserve, estimates have to be derived separately for each species. The "Standard Agricultural" method, commonly used for cattle systems, has been adapted for wildlife systems comprising of a number of species. The approach used in this method can be summarized as follows;

- (i) the total carrying capacity for an area is first estimated using the relationship between rainfall and metabolic mass,
- (ii) according to food availability, proportions of the

total stocking density are allocated to each feeding class (Mentis and Duke, 1976, and Collinson and Goodman, 1981), and

(iii) finally, proportions of each feeding class are allocated to each of the species being considered.

The last two decisions are largely arbitrary, but do consider the following factors (Collinson and Goodman, 1981);

(i) the type of food and the proportion of each type available in the system,

(ii) the feeding habits (e.g. food type preference, land unit preference, habitat preference, and the tendency to overgraze selected sites) of the animals stocked or being stocked, and

(iii) the ecological and circumstantial objectives of the reserve.

The calculation of the total large herbivore biomass was discussed using the previous method. A stocking density of 1AU per 10ha, was recommended for a reserve with a similar rainfall pattern as that of Pilanesberg. However, as Collinson and Goodman (1981) noted, the range condition in Pilanesberg is generally poor, especially that of the pediment and valley bottoms. They therefore recommended a more conservative estimate of 1AU per 15ha.

Collinson and Goodman (1981) considered two major food types available to the herbivores. These were grasses and sedges in the herb layer, and forbs and woody plants. The range condition for each food type is then evaluated in terms of its quantity and quality, for each season, especially the winter months.

The herbivore species were then divided into four feeding classes, based on their feeding habits and preferred food types. The groupings recognized by Collinson and Goodman (1981), which essentially range from a continuum of grazers, to mixed feeders, and to browsers, are the bulk grazers (e.g. white rhino, buffalo, zebra), concentrate grazers (e.g. wildebeest, hartebeest, mountain reedbuck), mixed feeders (e.g. elephant, impala, eland)

and browsers (e.g. black rhino, giraffe, kudu).

The allocation of the total stocking density, firstly, to each feeding class, and secondly, to each species, was then calculated. As shown in Appendix N (adapted from Collinson and Goodman, 1981), a major portion (45% = 1470 AU's) of the total stocking density was allocated to the bulk grazers, because of their selection for the most abundant, low to moderate quality food source. The rest was then allocated to the other feeding classes, 20% (654 AU's) to the concentrate grazers, 20% (653 AU's) to the mixed feeders, and 15% (490 AU's) to the browsers. The recommended stocking density of white rhinos was 488 AU's or 200 animals.

The major problem with this technique is that the final stocking densities, estimated for each species, rely heavily on both the types of food resources available to the animals, and their preferences. Differences in any of these aspects would lead to differences in the carrying capacity assessments. In addition, by classifying the herbivores into feeding types they are assumed to have identical feeding patterns. This will obviously underestimate the values. The next two proposed methods attempt to calculate carrying capacity using the quantitative feeding data collected during the study. Finally, a model was developed which explores another important aspect similar to the one mentioned by Collinson and Goodman (1981), i.e. the tendency of species to overgraze selected sites, and its influence on carrying capacity estimates.

6.3.3 The Modified Agricultural Method

This approach differed from the previous method in two main aspects. Firstly, the grazing species permissible in the reserve, whether as a result of the habitat potential, or ease of availability (Mentis, 1977), was reviewed. Secondly, with the use of both habitat and dietary overlap coefficients (with respect to white rhino), the divisions of the herbivores into feeding types was unnecessary. Thus, the Standard Agricultural technique was

modified based on the quantitative feeding data collected on the following grazers, in addition to the white rhino;

- (i) wildebeest,
- (ii) hartebeest,
- (iii) zebra, and
- (iv) impala.

The carrying capacity of the white rhinos, given various stocking densities of other grazers and their respective overlap coefficients (for the dry season only), were then calculated using the formula described below;

$$Q_r = \left[T - \left(\sum_{i=1}^n N_i \times C_i \right) / A_i \right] \times A_r \dots 6.5$$

where, Q_r is the carrying capacity of the white rhino,

T is the total permissible grazing animal units of the white rhino, in the absence of other grazers,

i is the grazing animal species, 1.....n,

N_i is the number of individuals of species i ,

C_i is the total overlap coefficient between the white rhino and species i ,

A_i is the animal unit equivalent for species i , and

A_r is the animal unit equivalent of white rhino.

In a multispecies grazing system such as Pilanesberg, caution must be taken when estimating the total permissible animal units in the reserve. Collinson and Goodman (1981) arrived at an estimate of 2124 grazing animal units (Appendix N). However, the total area of the reserve has been recently updated to 53500 ha (Peddie, 1983), as opposed to 49000 ha estimated by Collinson and Goodman (1981). The estimated flat area suitable for white rhino, is approximately 28000 ha thus permitting only a total of 1867 grazing animal units (approximately, 766 white rhino). The less dominant species, such as the buffalo (12), sable (14), waterbuck

(40), etc. (Appendix N), must also be accounted for. Approximately, 130 AU were allocated to these grazers. The mountain reedbuck were not included because of their almost total selection for the summit and hillside savannas. If the white rhino were the only major grazers in the reserve, then the total permissible animal units for this species would be 1737, i.e. approximately, 712 animals.

The present approximate densities of the four major associated grazers (1500 hartebeest, 1500 wildebeest, 1000 zebra and 3500 impala) and the respective overlap coefficients (averaged for the dry season) of 0.37, 0.35, 0.21 and 0.28, respectively were then substituted into equation 6.5. The carrying capacity of the white rhino, under the present stocking densities was calculated as 1011 AU's or approximately 415 animals. This value would obviously change if either the animal numbers or the species mix changes.

However, the final estimate, assuming that the animal densities and the overlap coefficients are accurately determined, relies heavily on the estimate of "T". In the above two methods it is assumed that this value has been accurately calculated. In a majority of cases this is not true.

6.3.4 The Modified Rainfall/Metabolic Mass Relationship

Coe, et al (1976) have pointed out the need for caution when relating rainfall directly to large herbivore biomass. Environmental factors such as the differences in topography, soil type and habitat type, can effect the primary production of an area. It is therefore imperative to analyze these aspects in detail before modifying the carrying capacity estimate obtained from the rainfall/metabolic mass relationship. This was the approach taken in this method.

First, the area under consideration must be divided up into habitat types. Then, depending on the size of the habitats and the mean annual rainfall, carrying capacity estimates are

determined according to the relationship given by Coe, et al (1976). These estimates are now modified, firstly, by a topographical factor (T), secondly, by habitat preference factor (P), and thirdly, by a dietary importance factor (D). Therefore each habitat is weighted depending on its capability to support white rhinos. These weighted factors are calculated for each habitat based on the feeding preferences of the white rhino. For example, hilly areas would support a lower density of white rhino than areas of a less hilly terrain. Habitats dominated largely by unpalatable grass species would again support a lower white rhino carrying capacity than typical "sweetveld" areas dominated by palatable species. Table 6.1 summarizes the white rhino importance factors for each habitat type. These factors are then substituted into the following equation;

$$MCC = (ECC_h \times T_h \times P_h \times D_h) \dots \dots \dots 6.6$$

where, MCC is the modified carrying capacity of white rhino,
 ECC_h is the estimated carrying capacity of white rhino,
 for habitat h, using Coe's, et al (1976) relationship,
 T_h is the topographical factor for habitat h,
 P_h is the preference factor for habitat h, and
 D_h is the dietary importance factor of the plant species
 in habitat h.

All the factors range from 0 to 1 depending on their importance to the white rhino; 0 indicating unsuitable habitats and 1 indicating highly suitable. The topographical factor (T) was given a value of 1 if the habitats were in the valley bottomlands, 0.1 (or near complete avoidance) if on the hill slopes and 0.5 for the other habitats. Values for the habitat preference factor (P) were based on the habitat preference indices discussed in chapter four. The habitat with the highest preference (during the dry season) was given a value of 1 (e.g. the thickets). The dietary importance factor (i.e. the ratio of the palatable to intermediate to unpalatable grass species) was given a value 1 if the dietary selection for a particular forage

Author Borthwick Michael Robert

Name of thesis Habitat Use By The White Rhinoceros In Relation To Other Grazing Ungulates In Pilanesberg Game Reserve, Bophuthatswana. 1986

PUBLISHER:

University of the Witwatersrand, Johannesburg

©2013

LEGAL NOTICES:

Copyright Notice: All materials on the University of the Witwatersrand, Johannesburg Library website are protected by South African copyright law and may not be distributed, transmitted, displayed, or otherwise published in any format, without the prior written permission of the copyright owner.

Disclaimer and Terms of Use: Provided that you maintain all copyright and other notices contained therein, you may download material (one machine readable copy and one print copy per page) for your personal and/or educational non-commercial use only.

The University of the Witwatersrand, Johannesburg, is not responsible for any errors or omissions and excludes any and all liability for any errors in or omissions from the information on the Library website.