THE BEHAVIOURAL ECOLOGY
OF THE
WHITE RHINOCEROS

BY

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THE BEHAVIOURAL ECOLOGY OF THE WHITE RHINOCEROS

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Under the supervision of Professor John T. Emlen

A 3 1/2 year field study was carried out in the Umfolozi-Corridor-Hluhluwe Game Reserve Complex in Zululand, South Africa. Vegetation was mainly acacia savanna. Nearly 3000 hours of direct observation were supplemented by radio telemetry; 677 animals were recognized individually. The phylogeny and distribution of the species are outlined. Morphological and physiological characteristics are summarized, and basic motor patterns described.

White rhinos are entirely grazers using their broad lips to pluck grass close to ground level. Short grass areas were favoured for most of the year, while during the late dry season stands of tall <u>Themeda triandra</u> were grazed. Drinking took place only every 2-4 days during the late dry season. Wallowing in mud was fewquent during summer; the mud cover probably inhibits ectoparasites. Peak activity levels occurred during the earlier morning and evening but were modified by prevailing conditions of temperature and insoloation. Animals resorted to shady rest-places on ridge-crests through midday. Feeding occupied a year-round average of 48.8% of the day and resting 36.8%, with more hours

devoted to feeding following spring rains.

Adult males were basically solitary. Adult females were usually accompanied by a single offspring, or alternatively by up to six adolescents. Adolescents were grouped mostly in twos. Territorial bulls occupied mutually exclusive home ranges of 0.7-2.6 km^2 which were coinhabited by 0-3 subordinate adult bulls. Cow home ranges covered 10-15 km^2 with movements restricted to a core area of 6-8 km^2 during optimum grazing conditions. The annual range included corridor extensions to long-lasting water sources.

Ten auditory displays were distinguished. Visual and tactile displays were less conspicuous. Only territorial bulls scent-marked by spray-urination, and dung-scattering at dungheaps. Resident territorial bulls confronted intruders silently horn to horn, while subordinate bulls responded with a defensive snarl displays used also by cows and immatures. Ritualized confrontations took place at territory borders. Territorial bulls also investigated cows while cows and immature animals paid little attention to one another or met nasonasally. Intragroup relationships revealed a close bond between two companions with additional adolescents of bulls more loosely attached.

Reproduction was year-round with seasonal fluctuations. Territorial bulls confined oestrous cows within their

territories for 1-2 weeks, courship advances spanned 24 hours and copulation lasted 16-28 minutes. Subordinate bulls were excluded from reproduction. Gestation period was 16 months and lactation usually continued for about a year. Ontogeny through infancy, juvenilehood and adolescence is described. Females calve at 6 1/2-7 years and males mature mature socially at 10-12 years. Deposed territorial bulls remained within the territory assuming subordinate bull behaviour.

Little notice was taken of other ungulates. Diseases and parasitism had few apparent effects and predation was rare. Confused responses to man are discussed.

Total population size was nearly 2000 with population densities in favourable habitat averaging 5.7 $/km^2$. Population trend showed a constant 9.5% rate of increase. Overall age compositions was 46.1% adults, 32.1% subadults and 21.9% calves. Adult sex ratio was 80 males: 100 females, while secondary sex ratio showed an excess of males. Mortality rates were estimated to be: adults - 2.0%, subadults 3.0%, juveniles 3.5%; pre- and postnatal losses 8%. Intercalving intervals averaged 2.5 years. The absence of population regulatory changes despite habitat deterioration were related to the current prevention of subadult emigration and lower dry season populations of grazing competitors.

It is recommended that white rhino biomass be reduced by one third with increase then controlled by the removal of rhinos settling within selected "vacuum areas".

Approved________________________

Date________________________

I. INTRODUCTION

A. PROLOGUE

The need for this study arose from the continuing expansion of the white rhinoceros population in the Zululand game reserves of Umfolozi and Hluhluwe. The success achieved by the conservation measures taken to save the white rhinoceros from extinction had become somewhat embarrassing. From a relict which supposedly still numbered only about 20 individuals in 1922, the Umfolozi population had increased steadily in size; 912 white rhinos were counted in the 1965 aerial census (later evidence shows that this was an underestimate). The grass cover was deteriorating rapidly. With high population densities, there was the danger of a disease epidemic which could suddenly change the success story.

In 1961, the Natal Parks Board, under the directorship of Col. Jack Vincent, farsightedly instituted a program to translocate a portion of the white rhino population to restock other areas of its former occurrence in southern Africa, and to make specimens available to zoos throughout the world. This dispersal of the stock of the species made it possible for the IUCN to remove the southern white rhinoceros from the Red Data Book of endangered species.

However, the removal program only delayed the dangers of overpopulation which seemed to be looming in the Umfolozi Game Reserve, where the bulk of the population remained concentrated. The distribution of white rhinos and their effects on the habitat were somewhat uneven, and information on the ecology and sociology of the species was clearly needed in order to plan appropriate management steps. Yet, information on the animals remained limited to the short term observations of park rangers and to the notes of early hunters (notably Selous (1881, 1899) and Kirby (1920)). The only recent published accounts were those of Player and Feely (1960) and Foster (1960) for the Zululand population, and of Heppes (1958) and Backhaus (1964) for the Uganda and Congo populations of the northern subspecies. Backhaus' was the only scientific study that had been attempted, but was limited to four months of field observations.

This was the background when I commenced my work in January, 1966. I was then a graduate in chemistry, looking for an opportunity to get into wildlife research. I was initially encouraged by two men: Prof. G.A. Petrides of Michigan State University, then visiting professor of wildlife management at Pretoria University; and Dr. R.C. Bigalke, then Principal Research Officer of the Natal Parks Board. I began with a simple brief, to observe and find out as much as I could about the habits of the white rhino. Underlying questions clearly related to the factors which influenced the distribution and numbers of the species, which are fundamental in the science of ecology. The two factors which seemed to me likely to be of prime significance were food and social relationships. The favorable circumstances prevailing for the observation of individual life histories soon caused me to concentrate particularly on social behaviour.

After a six month initial study period, I spent two years undertaking course work in zoology and wildlife ecology at the University of Wisconsin in Madison. In November, 1968, I returned to South Africa, and spent almost a further three years engaged in full time field observations on the white rhinocerous in the Umfolozi and Hluhluwe reserves. For this, I was extremely fortunate in having the supervision and friendship of Prof. John T. Emlen of the University of Wisconsin.

There are few species of large mammal for which it is not only more pleasant, but also more effective to work on foot. In being able to wander freely exploring the big game wilderness of Umfolozi, I satisfied a personal ambition which had helped impel me into the field of wildlife research. The African wilderness is a vibrant, living world about which it is impossible to be passive. Travelling on foot, one is intensely aware of and impressed by the detailed patterns of trees, grasses, soils and the riffles after rain, the dawn, sunshine and the cool, quiet world of the night, weather and seasonal changes; and of the lives of the numerous animals, large and small which exist there. This subjective confrontation imparts deep empathy for ecological relationships and the phenomenon of life, and influences personal philosophical attitudes to the process of living.

The major results of this study relate simultaneously to both behaviour (or ethology) and ecology. I will consider as behaviour the mechanisms by which an animal responds to its perceived environment, in a manner that can be observed externally. This approach, which can be termed that of behavioural ecology, is here distinguished from physiological ecology, in which internal responses by the organism to environmental factors are considered. In explaining observed behavioural actions, I will generally not relate them to underlying neural mechanisms, but rather will interpret them as consequences of adaptation and natural selection.

In view of the paucity of previous published material on the white rhinoceros, the treatment will be monographic. On account of my own biases, information will be more extensive, and better substantiated, on social behaviour and population ecology than on other aspects of biology. In the remainder of this chapter, I will introduce the background history of the species. Chapter II describes characteristics of the study area, and the research techniques employed. Chapter III summarises basic attributes of the species in terms of morphology and physiology. Chapter IV will cover the behavioural patterns linking individual maintenance requirements to the physical and floristic environment. Chapter V covers in some detail the social organization of spatial dispersion and behavioural interactions. Chapter VI surveys more briefly relationships with other species. Chapter VII considers the consequences of these in terms of changes in distribution and numbers. Chapter VIII discusses management technology, and leads to a set of recommendations.

B. PHYLOGENY AND TAXONOMY

1. Evolutionary origins of the modern Rhinocerotidae

The family Rhinocerotidae included many species representing several diverse lineages during the early to mid Tertiary period (Colbert, 1969; Thenius and Hofer, 1960; Thenius, 1969). Evolutionary trends commonly exhibited by these lineages included (i) an increase in general body size; (ii) the development of broad three-toed feet for support of the heavy body; (iii) a tendency towards molarization of the premolars (in common with other Perissodactyls); (iv) a lengthening of the crowns of the cheek teeth; (v) frequent development of horns on the skull, which were unique in lacking a bony core; their presence may be inferred in fossil remains from the presence of roughened supporting areas on the cranium.

The tendency towards large body size was presaged by Caenopus, an early Oligocene stem form, which stood 1.3-1.5 metres high at the shoulder. Its maximum expression was reached in Baluchitherium, from the Oligocene and early Miocene of Asia, which stood up to 5.5 meters at the shoulder, and is the largest known land mammal. Teleoceras, a squat, heavy bodied North American form, had a single small horn at the end of the nose, while the Diceratheres had two small nasal horns arranged side by side. The Elasmotheres were Pleistocene giants with a huge single horn in the frontal region and high crowned molars exhibiting an extremely complicated enamel pattern, evidently an adaptation for grazing the hard steppe grasses of their Eurasian home.

Forms ancestral to the five extant species of rhinoceros were also represented during the mid-Tertiary period. These may be grouped within three distinct subfamilies: the Dicerorhinae, the Rhinocerotinae, and the Dicerinae (Thenius and Hofer, 1960; Thenius, 1968 and 1969).

The Dicerorhinae can be traced back 40 million years to the tapir sized Dicerorhinus tagicus of the Oligocene. The group is characterised by two horns arranged in tandem on the snout, and by a tendency towards ossification of the nasal septum. Among early Pleistocene representatives were, D. hemitoechus, and Merck's rhinoceros, D. kirchbergensis. However its most striking product was Coelodonta antiquitatis, the wooly rhinoceros which inhabited Europe during the later Ice Ages. In Coelodonta, incisors and canines are completely reduced, molars are high-crowned (hypsodont), and the skull is greatly lengthened, adaptations clearly related to a gramnivorous diet. The living species, the Sumatran rhinoceros D. sumatrensis, differs relatively little from the Oligocene D. tagicus. Incisors and canines persist, while the molars are relatively low-crowned. D. sumatrensis is a relatively small rhinoceros standing only 1.2 metres high at the shoulders, its skin is sparsely covered with short hair, and it is a browser frequenting the forests of south-east Asia. Historically it was once widely distributed from Assam through to Vietnam and the islands of Borneo and Sumatra. Today only about 100-170 individuals are estimated to survive (Fisher et al., 1969), and since these are sparsely dispersed through much of this range, their future is somewhat precarious.

The Rhinocerotinae can be traced back to the Miocene species Gaindatherium browni from the Sivalik hills of northern India. This in turn was probably derived from the Oligocene Caenopus. The two living species, the Indian rhinoceros Rhinoceros unicornis and the Javan rhinoceros R. sondaicus are characterised by a single horn on the end of the snout, and by the retention of lower incisor tusks which are used offensively for biting. R. sondaicus is the more primitive, having altered little since the early Pliocene. It is a browsing, forest-dwelling form standing about 1.5 metres high at the shoulder, and was once distributed through most of south-east Asia from India to the China border and southwards through Sumatra to Java. Currently only about 40 individuals survive, all confined to the Udjong Kulon Reserve in western Java (Simon, 1966). R. unicornis is larger, standing about 1.8 metres high at the shoulder, and is mainly a grazer of flood-plain grasslands, though it also browses forbs (Ullrich 1964). Though formerly more widespread through northern India and Nepal, it is today restricted to the Kaziranga sanctuary and adjacent parts of Assam and southern Nepal (Fisher et al. 1969).

The Dicerinae resemble the Dicerorhinae in having two horns arranged in tandem, but lack the ossification of the nasal septum, while incisors and canines are lacking. Their early phylogeny is obscure. The finding of the aberrant Paradiceros mukirii, showing resemblances to Diceros, in late Miocene deposits at Fort Ternan in Kenya (Hooijer 1968) suggests that the group had an independent African origin (Hooijer and Patterson 1972). The earliest known representatives, Diceros pathygnathus and D. douriensis, occurred in Europe and North Africa respectively at the time of the Miocene/Pliocene transition.

There are two extant species, both entirely African: the black rhinoceros Diceros bicornis, and the white rhinoceros Ceratotherium simum. Ceratotherium evidently diverged from the Diceros lineage during the course of the Pliocene; fossil remains from late Pliocene deposits in Kenya and the Cape Province, tentatively dated to about 4-5 million years B.P., show resemblances to both modern forms, and have been assigned to a separate species C. praecox probably ancestral to C. simum (Hooijer and

Patterson 1972; Hooijer 1972). Post-cranial bones of this form from the Cape are larger than those of the modern C. simum. Early Pleistocene fossils from Bed I and lower Bed II at Olduvai Gorge, Tanzania, are referred to as subspecies C. s. germanoafricanum (Hooijer 1969). Diceros bicornis occurs at Olduvai only in the more recent beds. However, early Pleistocene teeth found in the Usno formation of the lower Omo Basin, Ethiopia, are almost indistinguishable from those of the modern D. bicornis (Howell et al. 1969).

Differences in dentition between the black rhinoceros and the white rhinoceros relate largely to their differing dietary adaptations. The black rhinoceros is a browser and accordingly has high cusped teeth. The white rhinoceros has high-crowned cement covered teeth in accordance with its gramnivorous diet. Other specializations for grazing shown by the white rhinoceros include a greatly lengthened skull and broad lips.

The black rhinoceros is still widely distributed through most of its historic range, which extended from the south-western Cape northwards to Ethiopia and Somaliland. The white rhinoceros had a more limited historic distribution, with separate populations occurring in southern Africa and in north-eastern Africa.

The morphological adaptations for grazing shown by Ceratotherium strongly resemble those of Coelodonta, but were independently evolved. As Coelodonta was the most progressive end-product of the Dicerorhine stock, so Ceratotherium is of the Dicerine lineage. The radiation of Ceratotherium from the Diceros stock was probably related to an expansion in the extent of grassland resulting from the droughts of the African Pliocene. Ceratotherium is exceeded in size only by Elasmotherium among rhinoceroses and the latter may well have taken some browse to carry it through the more northern winter, as is known to have been the case for Coelodonta. All larger Proboscideans were probably at least partially browsers, as are the modern elephants. Thus, Ceratotherium simum may well be the largest entirely grass feeding herbivore ever to have walked the earth.

2. Taxonomy of the white rhinoceros

The first scientific description of the species is that of the French traveller Burchell (1817), based on a specimen obtained in 1812 in the northern Cape Province about 150 kilometres north of the town of Kuruman (Cave, 1967). However, the species was probably known to the Boer settlers before then; Barrow (1801) refers to the supposed occurrence of a white rhinoceros in Namaqualand. Burchell applied the name Rhinoceros simus, and the generic name Ceratotherium was first proposed by Gray (1867).

Thomas (1901) and more recently Ellerman et al. (1953) regarded the species as congeneric with Diceros bicornis. Cave (1962) outlined evidence in support of the retention of the separate genus. Striking differences between the two species are largely cranial, and relate to the differing dietary specializations of the two species. Hooijer (1969) and most other modern workers have followed Cave in accepting the validity of the genus Ceratotherium.

The existence of a northern population of the white rhinoceros was confirmed only in 1900, when a skull was secured from the Lado Enclave of the Sudan. This was separated subspecifically by Lydekker (1908) under the name R.S. cottoni, on the basis of the single specimen. Heller (1913) examined fourteen Lado skulls and nine South African skulls, and supported the subspecific distinction with evidence of a consistent difference in the depth of the dorsal concavity of the skull. This was found to be 50 mm or less in adult Lado specimens, but at least 60 mm in South African material. The greater flatness in dorsal outline of the skull in the northern race is noticeable in photographs of live animals. Hooijer (1969) feels that the differences proposed by Heller are hardly worthy of subspecific distinction. However, an extensive collection of specimens has yet to be examined, and the name C.S. cottoni has generally been retained for the northern form.

The origin of the vernacular name white rhinoceros and its equivalents has been the subject of much speculation. The skin colour of the species is actually grey, similar to that of the black rhinoceros. Several authors have suggested that the name is derived from a corruption of a Cape Dutch name "wijd mond renoster" (meaning wide mouthed rhinoceros). This supposition is entirely conjectural, and etymologically unlikely, since the word "breed" would have been used rather than "wijd" in such a context. A more plausible explanation is simply that the first specimens observed appeared paler in coloration than the black rhinoceroses known from the more humid south-western Cape; perhaps as a result of rolling in calcareous soil. For example, Figuier (1870) quotes Chapman: "its colour is of such a light neutral grey, as to look nearly as white as the canvas till of a wagon"; and Coryndon (1894) states that white rhinos were said to have been much paler in the south-western part of their range than those from further north-east. "Blue" rhinoceroses are also reported from this period, referring to a supposedly distinct form of *Diceros bicornis* (Selous, 1881; Buckley, 1876).

I will use the name white rhinoceros in this report, simply because it is more widely employed and less cumbersome than the more accurately descriptive alternative, square-lipped rhinoceros.

Nomenclature

Scientific: *Ceratotherium simum*, with two subspecies: *C.s. simum* (southern Africa), and *C.s. cottoni* (north-eastern Africa); synonyms *Rhinoceros simus* *Diceros simus*, *Rhinoceros oswelli*, *Ceratorhinus simus*.

Vernacular: English--white rhinoceros, square-lipped rhinoceros, square-mouthed rhinoceros, Burchell's rhinoceros; French--le rhinoceros blanc; German--Breitmaulnashorn; Dutch--witte neushorn; Afrikaans--wit renoster, platbek renoster; Zulu--mkhombe, mkava; Sindebele--mkofo, mhofu; Tswana--tshukuru.

C. DISTRIBUTION AND RECENT HISTORY

1. Distribution of the northern population

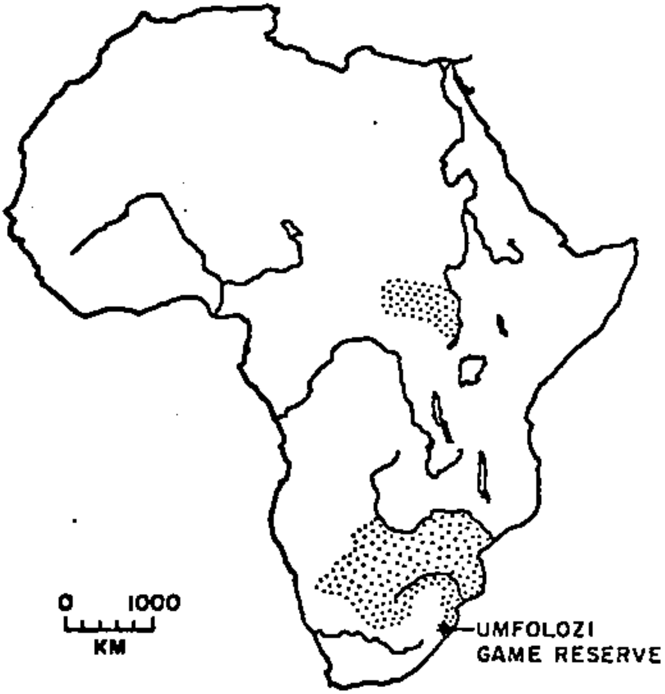
The range of the northern subspecies C. s. cottoni was historically restricted to the west bank of the upper Nile River (Heller, 1913; Lang, 1920; Harper, 1945; Sidney, 1965). The distribution extended from the Ora River just north of Lake Albert in the West Nile District of Uganda northwards for some 480 km to the vicinity of Shambe in the Sudan. Inland it encompassed the Bahr-el-Ghazal and Equatoria provinces of the Sudan, the Uele district of Zaire (the former Belgian Congo), and extended into the borders of Tchad and the Ubangui Province of the Central African Republic (see Figure 1). The maximum east-west extent of the range was about 800 km.

From the description of Heller (1913), and

FIGURE 1.: Historic distribution of the white rhinoceros

Distributional limits of southern population adapted from Huntley (1966)

Distributional limits of northern population from Lang (1920)



photographs of Lang (1920) and Heppes (1958), the northern habitat is apparently an open woodland dominated by trees of the genus Combretum; both Heller and Lang mention the occurrence of rank tall grass growing over 2 m in height during the wet season. Within this geographic range, the species was not evenly distributed, but tended to occur in certain local pockets (Roosevelt, 1910).

In more recent times, the northern white rhinoceros has suffered from the political instability of this region, which extends across the borders of three states. A population of about 1000 individuals occurred in the Garamba National Park in the former Belgian Congo in 1963, but rebels overran the area and fewer than 100 animals survive there (Fisher et al., 1969). In Uganda it has proved impossible to protect the species from poaching in its original West Nile range. Only about 60 individuals persisted there in 1965, while a further twelve were transferred to the Murchison Falls National Park on the east bank of the Nile (Foster, 1967). In the Sudan, as many as 1000 individuals may still exist (Schomber, 1963, 1966), but there is no information on the current situation. A few white rhinos have apparently recolonised the northern Ubangui Province of the Central African Republic (Fisher et al., 1969).

2. Historic distribution of the southern population

When first encountered by the early white explorers, the white rhinoceros occurred over much of southern Africa, from the Orange and Vaal Rivers in the south to the Zambezi River in the north (Fig. 1)(Heller, 1913; Player and Feely, 1960; Bigalke, 1963; Huntley, 1966).

Burchell first discovered the species about 500 km north of the Orange River. The Boer Trekkers in 1836 apparently first met is just north of the Vaal River in the southern Transvaal (Selous, 1899). Harris (1839) on a journey north-eastwards from Kuruman first encountered the white rhino near the headwaters of the Marico River, in the Magaliesberg district of the western Transvaal. However, partially fossilized skulls have been found south of the Vaal River near Kroonstad and Fauresmith in the Orange Free State, and in the Kimberley district of the northern Cape (Bigalke, 1963). In the south-east, Baldwin first met white rhinos in Zululand between the White and the Black Umfolozi Rivers, within the boundaries of the present Umfolozi Game Rerserye (Baldwin, 1855, reported in Player and Feely, 1960). Baldwin (1863) also reports shooting a white rhino cow near Lake St. Lucia in southern Tongaland. Further north, it occurred in Gazaland in western Mocambique (Selous, 1899). Kirby (1899) did not encounter it north of the Zambezi River in Mocambique. In the west, it was first encountered by Galton and Andersson during their journey westwards from Walvis Bay in 1851 about 100 km west of Ghanzi in western Botswana (Galton, 1889). Andersson *1861) mentions eating rhinoceros hump on a subsequent expedition in the vicinity of Omuramba Omatako to the south-east of the Etosha Pan, in present day South-West Africa. According to Castell-Ruedenhausen (1966), the white rhinoceros occurred in South West Africa as far south as Rehoboth and Swartrand in 1836 (reported in Huntley, 1966). Horns of the species have been found in the sands of the Omaruru and lower Ugab Rivers, and from near Usakos (Zukowsky, 1924), and the local Nama Hottentots have a name for it (Shortridge, 1934). It formerly occurred on both sides of the Okavango River, extending northwards a short way into south-eastern Angola at Lujana (Schultz and Hammer, 1877, quoted in Huntley, 1966).

The white rhinoceros seems to have been particularly abundant from the vicinity of Lake Ngami in central Botswana eastwards to the Magaliesberg district of the western Transvaal, and northwards to the Chobe River in Botswana (Andersson, 1856; Livingstone, 1857; Baines, 1864; Selous, 1899). Harris (1838a) reports that he himself saw 80 white rhinos during a day's march in the Magaliesberg district, and that Sir Andrew Smith here encountered between 100 and 150 rhinoceroses, at least half of which belonged to the white species, in a day's journey with wagons. It was also abundant in parts of Rhodesia, though Selous (1908) considers that it was never quite as numerous there as in Botswana. Favoured areas mentioned by Selous include the Dett Valley to the east of the present Wankie National Park; in the vicinity of Bulawayo; between the Gwelo and Umniati Rivers; to the west of the Gwaai River, south of the Zambezi; and in northwestern Mashonaland between the Sebakwe and Manyani Rivers.

This broad geographic range corresponds with the more arid types of wooded grassland which are termed bushveld by Acocks (1953). The species apparently never occurred on the temperate grasslands of the Transvaal Highveld, nor did it extend southwards into the moist grasslands of Natal. Selous (1899) reports that it was partial to broad grassy valleys and open woodlands having a good grass cover. Kirby (1920) suggests that in Zululand it was "more a bush-loving animal than elsewhere." Both Selous and Kirby indicate that the white rhinoceros was always rather localised in its occurrence within the geographic range.

3. The distribution gap

Fossil remains of C. simum occur at Olduvai Gorge in Tanzania from upper Bed II to Bed IV, which date back to the mid-Pleistocene 0.5-1 m years B.P. (Leakey, 1965). However, teeth reported from Kenya by Hooijer and Patterson (1972, in appendix) suggest that the species may have persisted in East Africa into the Quarternary. In South Africa, C. simum is represented in Pleistocene deposits in several localities (Cooke 1950; Hooijer 1958; Hooijer and Singer 1960). Historically, however, there are no records of the species having occurred in central or East Africa between the Zambezi River and north of Lake Albert, a distance of about 2000 km. Evidently, the species disappeared from Kenya and Tanzania some time during the later Pleistocene.

Similar though less extreme distribution gaps occur between the southern African and eastern African populations of oryx (*Oryx gazella*), gazelles (*Antidorcas marsupialis* and *Gazella thomsoni*) and dikdik (*Madoqua kirkii*); all of which are arid country inhabitants. Wildebeest (*Connochaetes taurinus*) and giraffe (*Griaffa camelopardalis*) are absent from the *Brachystegia* woodlands of southern Tanzania and Zambia. In correlation with the Ice Ages which occurred in northern latitudes during the course of the Pleistocene, Africa experienced periods of greater and lesser rainfall, which resulted in expansions and contractions in the extent of forest zones (Moreau 1963, 1966). Moreau suggests that during the height of the last (Würm-Wisconsin) glaciation, montane forest conditions extended in a continuous block from the Cape and Angola through East Africa to Ethiopia, and that such conditions probably persisted over most of East Africa until 12,000 years ago or later. Arid conditions prevailed between 75,000 and 52,000 years B.P., and again

12,000 years ago, when Kalahari sands extended far into the Congo basin. During these dry periods the miombo (*Brachystegia-Julbernardia*) woodlands were probably much fragmented in central Africa.

Since the white rhinoceros seems dependent on more arid forms of grassland, pluvial conditions would have rendered most of eastern and central Africa unsuitable for it. However, present habitat conditions over much of East Africa seem favourable. A significant feature of the historic distribution seems to be the limitation by rivers. While the black rhinoceros is able to swim (Roth, 1969), the white rhinoceros, with its heavy, low-slung head, would have more difficulty doing so. Thus river barriers may have prevented its recolonization of the east African region after one of the pluvial periods.

In the Sahara region, extreme desert conditions have probably developed only over the last 5,000 years. Rock engravings in Algeria (Lang, 1923; Peringuey, 1906) indicate that white rhino may have occurred in North Africa as recently as 5,000-10,000 years ago.

4. Decline in southern Africa during the late Nineteenth Century

By the middle of the nineteenth century the white rhinoceros had disappeared from the Kuruman district where Burchell had first encountered it (Smith 1869); this was attributed to the introduction of firearms among the local Tswana people. However, from the accounts of Gordon-Cumming (1850) and Andersson (1856), it remained still abundant then in the present day Botswana. Selous (1899) reported that by the time of his first visit to southern Africa in 1871, the range of the white rhinoceros had been very much reduced in Botswana, but that it was still abundant then in what is now Rhodesia. This he ascribed to the exploits of white hunters, since up until that time the native people possessed very few firearms (Selous, 1908). He reports that messrs. Oswell and Vardon killed 89 rhinos during one short hunting trip in 1848, most of which probably consisted of the white species. Andersson (1856) accounted for 60 rhinos during his trip to Lake Ngami between 1850 and 1854. Selous (1881) reported white rhinos still fairly plentiful along the Chobe River in northern Botswana in 1874, but in 1877 he could find the tracks of only two, and in 1879 the local bushman people said that there were none left. In 1880 following the declining availability of ivory, rhinoceros horn increased greatly in value. It was said to be used for carving knife handles and ornaments; there is no mention of any Chinese aphrosidiac trade, though this may have had an influence. Selous (1899) reports that one trader alone supplied 400 Matabele hunters with guns and ammunition, and that his store between 1880 and 1884 at times contained the remains of 100 rhinoceroses.

By 1885 only a small pocket of white rhinos remained in north-eastern Mashonaland. Coryndon and a companion shot four here in 1890, and Coryndon (1894) prophesied that "Long before the close of the Nineteenth century, the white rhinoceros will have vanished from the face of the earth" (the rumoured existence of a northern population was then unsubstantiated). Museums made sudden haste to secure specimens, and Eyre collected the last recorded Rhodesian white rhinoceros in 1895 (but see below). The last Transvaal record is of a cow and calf seen in 1895 by Kirby in the Matimhiri bush of the present day Kruger National Park (Kirby, 1896).

In 1894 a small pocket of white rhinos was found to be still in existence near the Umfolozi River in Zululand, and six were then shot (Selous, 1899). In 1897 this population was encompassed within the Umfolozi Game Reserve. Supposedly only ten or eleven individuals survived (Lang, 1924; Sidney, 1966). An additional remnant persisted without outside knowledge until the 1930's in the Nuanetsi area of Rhodesia and adjacent parts of Mocambique (Shortridge, 1934; Harper, 1945; Sidney, 1966). Repeated suggestions that the species still survives in the Kaokoveld of South-West Africa (e.g. Barnard, 1952) are without foundation (G. Owen-Smith, 1971). Guggisberg (1966) reports rumours that it still occurs in Angola, but confirmation has not been forthcoming.

Thus, within the course of about 60 years, the southern white rhinoceros was reduced from an abundant and widespread species, to small relict populations of unknown size in Zululand and in Mocambique.

The reasons for this rapid decline are not hard to find. The white rhinoceros was valued for its horns and tough hide (Andersson, 1856); and its meat was highly regarded by the early hunters, both for its agreeable flavour and abundance of fat. Selous (1899) considered the flesh to be superior to that of any other game animal in southern Africa, and this opinion was shared by many others (e.g. Galton, 1889). The cervical hump of the white rhino was a particular delicacy, being merely inverted over the cooking fire without the need for a vessel. The meat of the black rhinoceros, in contrast, was reported to have a slightly bitter taste and be far less attractive. The white rhinoceros was conspicuous, inoffensive, and easily approachable. By waiting at a watering place in the dry season, it was possible to come into contact with most of the rhinoceroses in the surrounding district; Selous (1908) states that he could easily have killed 100 rhinos of each species in a season by this method.

Selous (1881) reports that native hunters seldom passed by a rhinoceros without attacking it--but this was after guns had been acquired. The animals would have been more difficult to kill by a primitive hunter armed only with a spear or bow and arrow, and, judging by their abundance, the animals were apparently not hunted to any great extent by the native peoples before the advent of firearms. Harris (1839) however records the use of pits to capture rhinoceroses by the Tswana people living near the headwaters of the Marico River. The Bantu tribes, who spread through most of the area south of the Limpopo River only during the Fifteenth or Sixteenth Century, were mostly dependent on their herds of cattle for sustenance, and therefore did not need to devote much effort to hunting. The earlier Bushman inhabitants depicted rhinoceroses in their rock art in Rhodesia, South-West Africa, and in the eastern Cape Province. Their effect as hunters is difficult to gauge; but it would seem that, with their small bands, the extra meat provided by a white rhinoceros would partly be wasted, and thus would not adequately justify the extra effort required to bring down one of these thick-skinned animals with their primitive weapons.

Though the Tswana and Sindebele people evidently ate the meat, the Zulus do not regard the flesh of the white rhinoceros as edible (Foster, 1960). To this fact, together with the prevalence of tsetse flies in the region, may be attributed continued survival of the species in Zululand.

5. Twentieth Century recovery

The Twentieth Century history of the white rhinoceros is intimately tied up with the history of the Umfolozi Game Reserve and surrounding parts of Zululand (see Player and Feely, 1960; John Vincent, 1969 and 1970).

As proclaimed in 1897, the Umfolozi Game Reserve consisted of a wedge-shaped section of land situated between the Black and the White Umfolozi Rivers, encompassing an area of 250 km^2. In 1911 Mr. F. Vaughan-Kirby was appointed as the first Game Conservator for Zululand. In 1922, his estimate was that only about 20 white rhinos remained. However, it seems that this was a deliberate underestimate, intended to arouse stronger support for their protection. The first count was made by Lang in 1929, when 120 white rhinos were recorded within the game reserve, plus an estimated 30 on surrounding lands. In 1932 and 1936, two ground counts made by the veterinary authorities recorded 220 and 226 animals respectively. However, these were made during, and shortly after, a very severe drought, in which over 100 white rhinos are said to have died (Player and Feely, 1960). It thus seems likely that the 1920 population numbered at least 150-200 individuals. It is from this nucleus that all existing representatives of the southern race have been derived.

Because of the prevalence in the area of the tsetse fly, vector of the trypanosome parasites which cause the cattle disease nagana, control of Umfolozi Game Reserve remained in the hands of the Division of Veterinary Services from 1932 to 1952. From 1942 to 1950 a campaign was undertaken to exterminate all potential hosts for the fly, except for the two rhinoceros species. This succeeded in eliminating most of the conspicuous large mammals from the reserve, except for some duiker, bushbuck and bushpig. Between 1948 and 1950 a two mile wide strip along the western and southern boundaries of the reserve was cleared of all woody vegetation. This measure was intended to contain the tsetse fly within the game reserve, by eliminating shade for resting. From 1947 to 1951, aerial spraying with insecticides, initially DDT and later BHC, was carried out. This operation finally eliminated the tsetse fly from the area.

In 1952, the Natal Parks Board assumed control of Umfolozi Game Reserve. An aerial count in 1953 revealed a total of 437 white rhinos. The first tourists were admitted in 1958. In 1962, additional land was added in the south and west, to bring the total game reserve area up to 480 km^2. Fencing along the new boundaries commenced immediately, and was completed in 1965. This fence consists of five strands of heavy duty lift cable supported by heavy wooden posts, and is effectively rhino proof.

The 1960 aerial count yielded a total of 705 white rhinos the Umfolozi Game Reserve and surrounding areas. Concerned by the dangers associated with the increasing population in a limited area, the Natal Parks Board in 1961 instituted a program of live capture and translocation of surplus animals to other areas. This "Operation Rhino" has been described by Player (1967 and 1972). Initially attention was concentrated on removing those animals which had been fenced off outside the boundaries of the reserve, but since 1969 most of the animals have been taken from within the game reserve. Up to October, 1970, a total of 730 white rhinos had been removed. A helicopter count carried out in August, 1970 revealed that at least 1764 white rhinos still remained.

As a result of the translocation program, white rhino populations have now been re-established in several parts of the former range. Significant populations now exist in the Kruger National Park (estimated 157 animals, Pienaar, 1970); Maputa Game Reserve in southern Mocambique (73 animals introduced); Malamala Game Reserve in the eastern Transvaal (43 animals); Wankie National Park, Rhodesia (35 animals); Gorongoza National Park, Mocambique (12 animals by October, 1970, with more being added); Ndumu Game Reserve, Zululand (13 individuals); and Mkuzi Game Reserve, Zululand (6 individuals). Six animals were also transferred from Zululand to the Meru Game Reserve in Kenya. In addition, the original Umfolozi population has expanded its range north-eastwards through the State Land known as the Corridor into the nearby Hluhluwe Game Reserve.

II. THE STUDY

A. METHODS

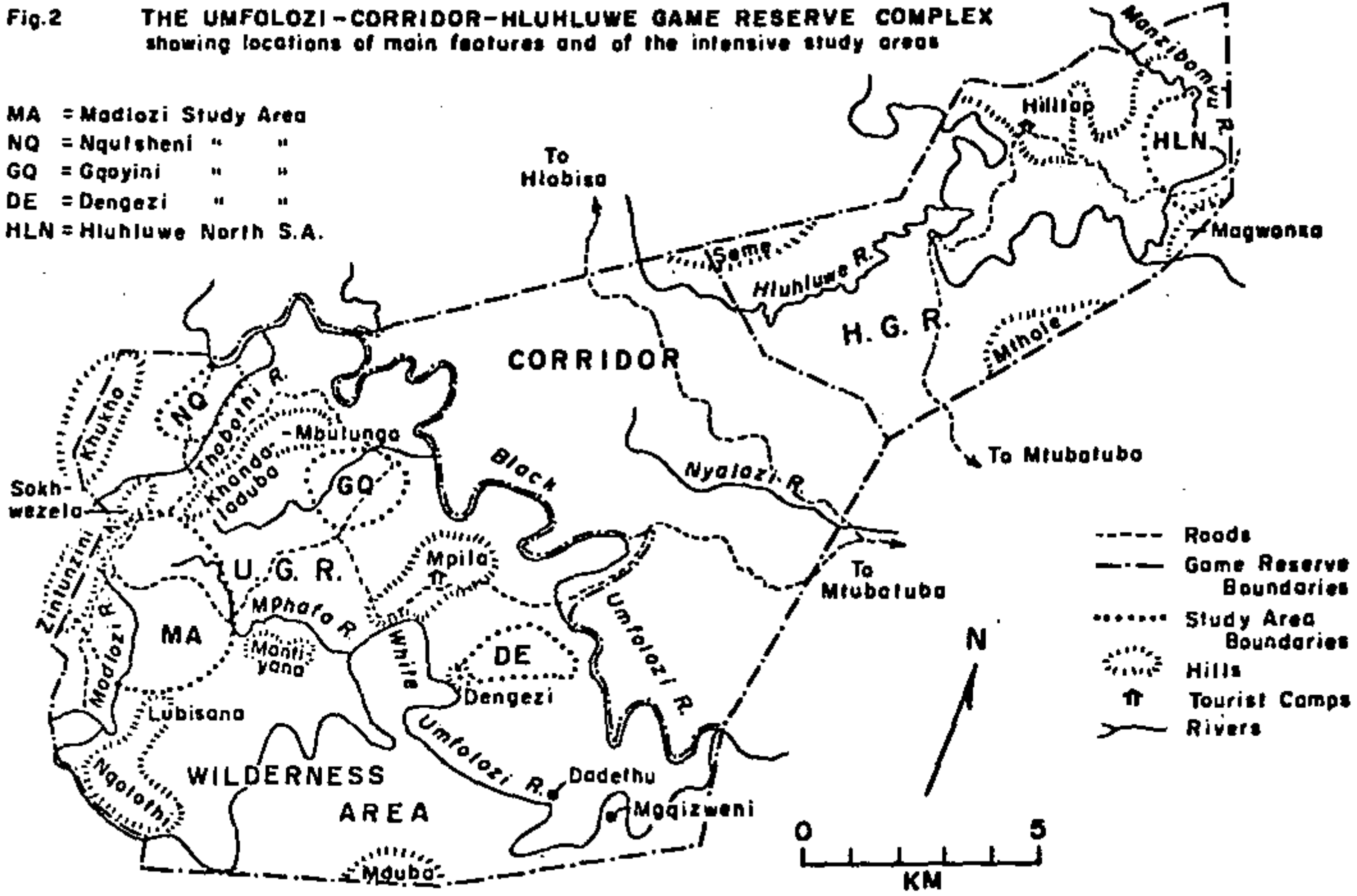
1. Duration and selection of study areas

I commenced work in the Umfolozi Game Reserve on 1 January 1966. After initial exploration, an area for intensive study was selected in the vicinity of the Madlozi game guard camp, near the western boundary of the reserve. There was a good white rhino population in the area, and observation conditions were favourable. I commenced observations here on 12 February 1966, and continued them until 10 July 1966.

On 18 November 1968, I resumed field observations in the Umfolozi reserve, and extended them through to 5 September 1971 without interruption. The limits of the Madlozi study area were extended northwards to include the large numbers of rhinos which grazed the bush-cleared zone below the Zintunzini Hills. In addition I added four comparative study areas. These were selected on the basis of anticipated differences in white rhino population density, and in dispersal opportunities: (i) the Nqutsheni study area near the north-west corner of the reserve was chosen as a second high density area, which dispersal outwards checked both by the boundary fence to the west and the Black Umfolozi River on the north; (ii) the Gqoyini study area was selected as a fairly high density area, centrally situated so that free dispersal was possible in all directions; (iii) the Dengezi study area was located in the eastern part of the reserve where white rhino densities were lower than those in the west; (iv) the Hluhluwe North study area was on the extreme northern limit of the range and had only relatively recently been colonised by white rhinos (colonisation took place only after about 1965).

The locations of these study areas are shown in Fig. 2. My caravan base camp was established centrally in each, and their extent was determined by the area that could adequately be covered working outwards on foot. This usually included the nearest four to five male territories, encompassing an area of 5-8 km^2. At Madlozi there was a central core of intensive coverage of about 8 km^2 extent, but I worked outwards from here following the movements of the rhinos which were regular visitors to the central area. The total area covered with some regularity at Madlozi was about 30 km^2, but no fixed

Fig.2 THE UMFOLOZI-CORRIDOR-HLUHLUWE GAME RESERVE COMPLEX
showing locations of main features and of the intensive study areas



boundaries were assigned.

From November 1968 to May 1969, I spent about a month surveying the rhino populations in each of the study areas. Thereafter, observations were concentrated at Madlozi, and only brief further visits were made to other study areas at intervals to fill in information and check on changes.

The total period spent in field work was thus 3 1/2 years but, because of the interruption, the total time span encompassed by observations is almost 5 3/4 years. During this time I was able to devote my full attention to the study, and about 2,500-3,000 hours was spent in direct observation of white rhinos.

2. General techniques

Observations were carried out mostly on foot, using a pair of 6 X 30 Bushnell binoculars, and recording by means of notebook and pencil. This gave great freedom to move around with the animals. On account of their poor vision, the rhinos usually remained completely unaware of the presence of the observer, provided care was taken not to move while in direct view of the animals and to remain downwind. The usual observation range was about

75 metres, but under favourable circumstances could be 30 metres or less. If, through an unanticipated change in their direction of movement, or an erratic breeze eddy, or through the alarm of associated oxpeckers or other ungulates, rhinos detected my presence, they reacted immediately, either running away, or standing shuffling about alert for about thirty minutes before resuming normal activities.

Vehicular travel off the roads is generally not permitted in the reserve because of the damage it causes to vegetation. Rhinos reacted uneasily to the presence of a vehicle at the ranges which would be necessary to secure a clear view in the wooded habitat.

Observation patrols were basically of two types. Either (i) a general tour was made through an area to survey the various individuals present; or (ii) a particular animal or group was selected and followed continuously in its movements for periods varying between a few hours and all day. Standard information recorded included the location of the animals; their age and sex categories; a description leading to individual identification; and ongoing activities in relation to time of day and weather. Particular attention was paid to interactions occurring between animals.

Locations were described relative to landmarks such as watercourses, ridgecrests, roads and vegetational features, and transcribed each evening onto 1:18,000 mimeographed maps of the study areas. Topographic sectional maps at this scale exist for Umfolozi Game Reserve, in addition to sheets in the Government 1:50,000 series. Accurate location was facilitated by four times blow-ups of the corresponding aerial photographs, which revealed vegetational features in detail. Accuracy of location is believed to be within ± 80 m at most, but usually should be considerably better than this.

Night observations were undertaken over full moon periods, totalling about 75 observation hours. Additionally 30 nights were spent sitting at waterholes. During the last six months of the study, night observations were facilitated by the availability of a Starlite Image Intensifier Scope.

Notebook and pencil recording were supplemented by still photography, using a Leica M3 camera generally with 135 mm lens. Magnetic tape recordings of sounds were made using an Uher 4000 Report S recorder with Uher and later SKV microphones. Towards the end of the study, 7,500 feet of 16 mm movie film was taken, using a Doiflex camera equipped with Angenieux 12-240 mm zoom lens.

3. Identification of individuals

Artificial marking was generally not necessary, since considerable variation in horn shape occurs among individual rhinoceroses. The anterior horn may be relatively long or short, curved or straight, upright or projecting forwards to varying degrees. The posterior horn tends to be worn into an even greater variety of distinctive shapes. Ear tears and other scars are less commonly present than is the case for the black rhinoceros, but can be individually characteristic. Such features enabled me to distinguish individually all of the adults and some of the immature animals encountered in each of the study areas. Initially I estimated horn lengths in relation to the length of the ears, and sketched horn shapes. With time a photographic file of portraits was compiled including all regularly encountered individuals.

Forty-five individuals were marked with identifying eartags. These consisted mainly of immature animals, which lacked distinctive horns and were otherwise difficult to identify. Ten animals were tagged in 1966 at Madlozi, and during the course of 1969 a further 23 individuals were marked at Madlozi and 12 at Nqutsheni. The tags used initially consisted of a plastic "Jumbo Rotortag," together with a strip of woven nylon ribbon ("Sterkolite") knotted through a hole in the ear. Because of poor retention, these were replaced in 1969 by paired discs of coloured "Sterkolite" held in place by a nylon cord inserted through a hole made in the ear, and knotted at each end (Plate 1).

Most of the earlier tags tended to be lost after a few months, though identifying slits still remained in the ears. Experience showed that this was not related so much to the type of tag, as to the position of placement on the ear. Tags inserted through the softer proximate lateral edge of the ear were usually lost. Seemingly this part of the ear was more susceptible to tearing, aided sometimes by infection and necrosis. Tags placed close to the centre of the pinna exhibited the best retention; with four out of six remaining for over a year. The longest lasting tag was still in place after 2 1/2 years, but had become frayed and less conspicuous; several others also still remained on animals at the conclusion of the study.

Including calves, which were identifiable by association with their mothers, 314 different individuals were recorded from the Madlozi study area and environs. Of these, 135 were sufficiently well known to be instantaneously recognisable when seen. During a month spent in each of the other areas, 145 different individuals were recorded at Nqutsheni, 108 at Gqoyini, 75 at Dengezi, and 35 at Hluhluwe North. The sum total of individuals identified in the study areas is thus 677, representing about one third of the estimated total population.

4. Radio telemetry

Radio telemetry was introduced in 1970 primarily to provide information on the extent of movement of adult females and subadults. The transmitters consisted of crystal controlled pulsed oscillators operating at a wave-length of 3.55 m mounted in a cylindrical casing. These were placed into a cavity drilled into the posterior horn of the rhino, and a groove was drilled around the horn to accomodate the loop antenna (Plate 1b). The assembly was then covered over with fibre glass and epoxy resin. The portable receiving set had crystal controlled channels tuned to each transmitter frequency. It included built-in telescoping dipole and half-Yagi antennas to enable animals to be tracked down for direct observation. For long range bearings, a large portable double Yagi antenna was used. This was transported to fixed receiving stations established on the slopes or crests of suitably situated hills. It allowed a directional precision of ± 1/2-1 1/2°, at ranges of up to about 6 km. There was an unavoidable time delay of about 30 minutes between successive bearings from different hills; but locations were carried out at times when the animals were unlikely to be on the move, so that errors from this source were unlikely to be of major consequence. Any unusual locations for a particular individual were investigated further. The equipment was designed and supplied by the South African CSIR, and has been described in more detail by Anderson and De Moor (1971), Anderson (1972), and Anderson and Hitchins (1971).

Ten functioning transmitters were placed on seven adult females and three subadults, while a further two placed on cows failed to operate. The first four transmitters were inserted between March and June, 1970, and the remaining six in August. The large Yagi antenna only became available in late August, and before then it was possible to locate only one or two individuals in a day. Three radio-tracking runs each covering ten consecutive days were carried out between late August and early October. Thereafter locations were only irregularly made until March, 1971, when another ten day run was carried out. By then only three transmitters still functioned. One transmitter operated for 12 1/2 months, the remainder for shorter periods.

Further information on the performance and use of the radio telemetry equipment can be found in Owen-Smith (1972) and Hitchins (1972).

5. The "Territory Occupancy Index"

Calculation of local population densities was based on the knowledge that white rhino territorial bulls were always present somewhere within the limits of their individual territories. Thus, for a set of incomplete randomly located censuses of a particular territory, the ratio of the number of sightings of any particular individual to the number of times that the terrirorial bull was seen, is an estimate of the frequency of occurrence of that individual within the territory. If N_x = number of sightings of individual x, and N_t = number of sightings of the territorial bull, then

$$\text{Territory Occupancy Index for } x = \frac{N_x}{N_t}$$

for that particular territory. This assumes that both the individual x and the territorial bull are equally likely to be seen when present. Random patrols counteract any bias resulting from tendencies by individual rhinos to favour different parts of the territory.

Similarly, for any class of individuals m, the average population present within a particular territory may be estimated by the ratio $\frac{N_m}{N_t}$, where N_m = the total number of individuals of class m recorded in a similar set of random patrols.

Population density is obtained by dividing by the areal extent of the territory. Accuracy is strongly dependent upon knowledge of this. The local population density for an area including a set of territories may be calculated by summing the densities for the individual territories.

The calculations are analagous to those in the mark/recapture or "Lincoln Index" method for estimation of population density. The territorial bull serves as a single marked individual whose presence within the fixed limits of the territory is always known.

Routine patrol tours avoided any set routes, and thus approximated the required conditions of randomness. The "Territory Occupancy Index" will be used to calculate (i) relative frequencies of occurrence of certain individuals within particular territories; (ii) average local population densities of particular age/sex classes of rhinos; (iii) with suitable corrections for differing "sightability," the local population densities of other ungulates within the study areas.

white rhinos population is concentrated, and where I carried out most of my observations. Information is based particularly on the work of Downing (1972).

2. Climate

Climatically the region is characterized by hot wet summers and mild dry winters. The average annual rainfall measured at Mpila camp in UGR is 635 mm, based on records dating back to 1959 (Downing, 1972); that at Hilltop camp in HGR is about 250 mm more. The winter drought is normally broken in September, and during the spring months of October, November and early December, precipitation occurs mainly in the form of soft rain spread over several consecutive days. During late summer (January to March), heavy afternoon thunderstorms are usual. The dry season normally sets in in April or May, though late rains may occur. The winter period is characterised by a succession of clear sunny days. The Umfolozi reserve forms a dry enclave surrounded on all sides by higher rainfall areas.

The mean daily maximum temperatures recorded at Mpila camp are 32.6°C for January, and 25.3°C for July; corresponding mean daily minima are 21.8°C and 13.2°C respectively. The absolute maximum temperature recorded at Mpila is 43.3°C, and the absolute minimum 6.7°C. Downing reports that maximum temperatures at Thobothi, in the western section of the reserve, were usually about 3°C higher than those at the higher elevation of Mpila, and minima about 3°C lower. I personally recorded a highest screen temperature of 44.0°C in October, 1969, and a low of 5.5°C in July 1970. Frost occurs occasionally in the low lying river valleys.

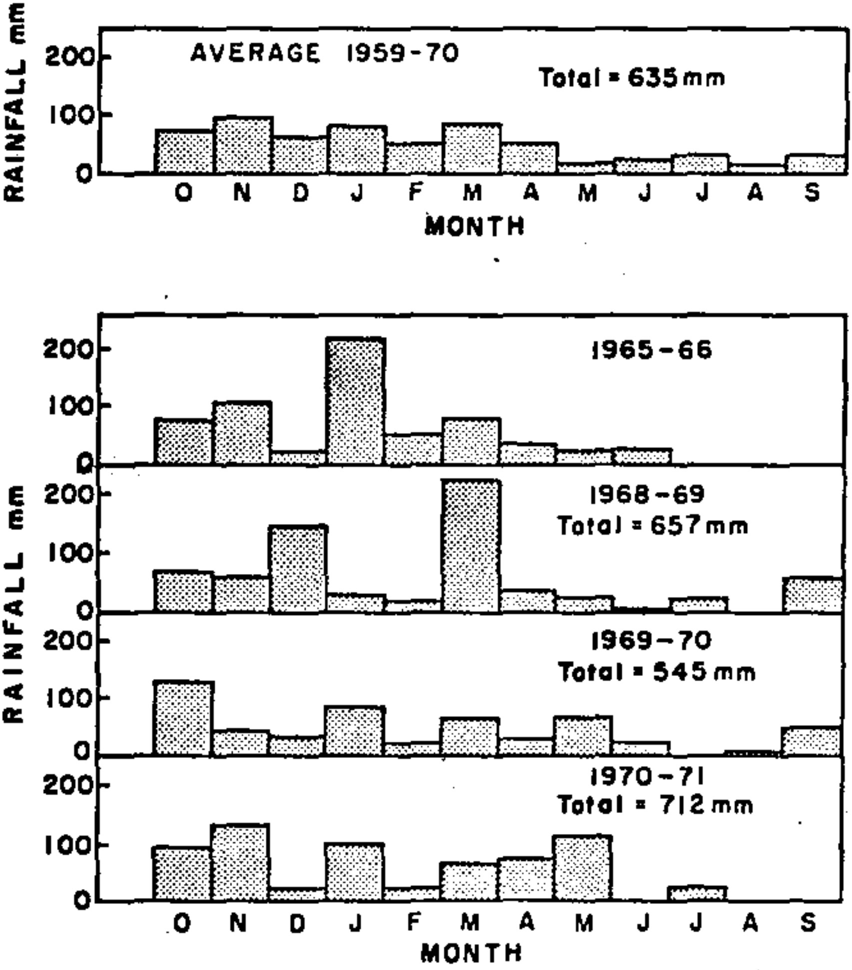
Rain bearing winds are mainly southerly, and the prevailing fine weather breeze is northerly. Warm, drying northerly or westerly winds are not infrequent during August. Relative humidities are tempered a little by the inland situation of the reserve.

Rainfall patterns vary considerably from year to year, and this influences the conditions prevailing during any limited study period. Rainfall patterns during the study period are presented in Figure 3, in comparison with average monthly rainfall. The year 1966 was one of very good mid-summer rains, producing a growth of grass which was said to be the best seen for many years. However, the winter drought set in relatively early. The seasons

FIGURE 3. Rainfall patterns during the study years recorded at Mpila Camp, Umfolozi Game Reserve

Average data 1959-70 from Downing (1972)

Data for study years from NPB files



of 1967 and 1968 during my absence, were bad drought years. The study years 1968 to 1971 were characterised by summer droughts and late rains. The dryest conditions during the whole of the study period prevailed in January, 1970, but this is not evident in the monthly rainfall data as heavy rain fell on the last two days of the month. January and February of 1969 were unusually hot, with periods of several days in succession during which maximum temperatures ranged between 37°C and 42°C. Total annual rainfalls were close to average, but their erratic pattern had a considerable influence on grass growth. Ample rain fell too late in the season to bring the grass on to full height in the summers of both 1968-69 and 1969-70. However, in consequence, the winter droughts were shorter than usual.

3. Geology and soils

Umfolozi Game Reserve is underlaid mainly by alternating Ecca sandstones and shales. Dwyka tillite occurs near the surface in a few places, notably on the western slopes of the Madlozi valley, and there are localised exposures of Table Mountain sandstone near the two

Umfolozi rivers. Localised to fairly extensive dykes and sills of dolerite also occur. In Hluhluwe Grove Reserve and the Corridor, Table Mountain sandstone, in places Basement granite, commonly occur at or near surface level.

Soils derived from Ecca sandstones and shales typically vary between sandy and clayey loams. Soils are shallow (about 50 cm deep) on watershed ridges, while transported soils in valley bottoms may be up to 10 m deep. Frequently a relatively impervious calcareous subsoil layer is present. Localised patches of fairly loose sandy soils occur where sandstone lies at the surface. Dolerite derived soils are clayey and very sticky when wet, but allow a good water infiltration. Soils on slopes and valley bottoms are of medium to good fertility.

An important factor in soil formation is the influence of termitaria, which usually occur as low mounds raised only slightly above general ground level. A large proportion of the soil surface on ridgecrests may be underlaid by active or abandoned termite workings, resulting in a hard, relatively impervious surface layer.

4. Topography

The terrain of UGR is mostly gently undulating, with localised higher hills or hill systems based on sandstone or dolerite formations. Elevation varies from 45 m at the confluence of the two rivers to 579 m at the highest point of the Zintunzini Range on the western boundary. Other notable hills include Ngolothi (429 m), Mbulunga (339 m), Mpila (344 m) and Mduba (355 m). Hill systems occur along the southern and western boundaries of UGR, while on the north it is bounded by the Black Umfolozi River. The Mpila range partly cuts off the eastern triangle from the remainder of the between rivers section further west.

The Corridor is mostly hilly with broadly rolling slopes, while HGR is more steeply undulating with elevations varying from 80 m beside the Hluhluwe River to 540 m at Mpansikazi Hill, Seme Hill, on the western boundary of the Corridor, rises to a height of 586 m, and is the highest point in the Complex.

5. Water Resources

The Black Umfolozi River is a perennial but, in common with many other South African rivers, deteriorating soil erosion conditions in the catchment are resulting in more violent summer floods and reduced winter flow. The exceptionally severe flood of July 1963 deposited large amounts of silt, markedly altering the former fairly deep, swift flowing and rocky nature of the river. In consequence the river is now easily fordable by animals for a much longer period of the year, a factor of significance in relation to animal movements between the Corridor and UGR. During the winter of 1970, surface flow ceased for the first time on record.

The White Umfolozi had typically been a relatively clear meandering river with a wide sandy bed, but now floods with brown murky water regularly during the summer. While surface flow formerly persisted through most winters, nowadays only scattered pools remain along its course during the dry season.

Between the two rivers there are only temporary watercourses which carry flowing water for a few hours, or at most a few days, after heavy rain. Small permanent springs occur in the Nyonikazane (a tributary of the Madlozi Stream), Thobothi and Ntshiyana streams in the west, on the slopes of Ngolothi Hill, and at several sites to the south of the White Umfolozi River. However, only the Nyonikazane produces any extensive flow, for a distance of about 100 m. A small spring on the upper Madlozi Stream which produced a steady flow in 1966 had entirely dried up by the winter of 1971. Springs are said to have been more numerous in the past. However, no part of UGR is more than 8 km from one of the two perennial rivers. The water from all springs is reportedly fairly "brack" or saline.

Numerous animal formed depressions (or "pans") carry water for varying periods into the dry season. At Gqoyini, a set of pans has been artificially supplied with water by pumping through the dry seasons of most years. A tourist observation hide was constructed here in 1970. Small semi-permanent lakes occur at Mgqizweni and at Dadethu, but because of their proximity to the White Umfolozi River are not particularly significant as water sources.

In the Corridor there are several permanently flowing streams, while the Hluhluwe River and several of its tributaries are perennial.

6. Vegetation

Most of the area of UGR is covered by a wooded grassland or savanna, with low trees predominantly of the genus Acacia. It falls within the unit "Woodland and Savanna--Undifferentiated Relatively Dry Type" of Keay (1959), and within the categories "Zululand Thornveld" and "Tropical Lowveld Savanna" of Acocks (1953).

In the Corridor several of the larger hills are covered by open grassland. Much of HGR is characterised by grassy hills with small pockets of coastal forest on the wetter south-east facing slopes. The lower south western part of the reserve however has Acacia woodland, similar to that occurring in UGR.

The vegetation of UGR has been analysed by Downing (1972), and the following account is derived largely on his description, unless otherwise stated.

(a) Woody vegetation

Downing (1972) distinguished nine woodland communities, designated by their characteristic tree species:-

(i) Acacia tortilis community: widespread on shallow well-drained soils, usually on ridgecrests; forms an open savanna with tree spacing varying from 20 to 100 m and average tree height of 5-6 m; in addition to A. tortilis with its characteristic spreading flat-topped crown, other common trees include A. gerrardii, A. karoo, Sclerocarya caffra, and Zizyphus mucronata; shrubs are sparsely present. (ii) Acacia nilotica community: extensive on deeper soils overlying shale; tree spacing highly variable, but tending to form a parkland, with clusters of trees with crowns fairly closely spaced separated by about 100 m from other such clusters, with some intervening single trees: tree heights mostly 5 m or less; tight clumps of taller evergreen trees are commonly associated with termite mounds; on heavier soils the 2-3 m high evergreen shrub Euclea daphnoides may densely fill the spaces between the trees, restricting visibility; commonly associated with A. nilotica are A. tortilis, A.gerrardii, A. senegal, and Zizyphus mucronata; other shrubs include Dichrostachys cinerea, Maytenus senegalensis and Euclea shimperi. (iii) Spirostachys africana community: grows as a closed canopy woodland flanking streams and drainage lines; associated trees include the tall evergreen species Schotia brachypetala, Pappea capensis, Olea africana, Sideroxylon inerme, and Mimusops africana, and a variety of shrubs occur, of which Euclea shimperi and Maytenus senegalensis are most common; average tree height is 8-9 m.

(iv) Acacia grandicornuta community: a closed woodland of 7-8 m average height on deep soils of alluvial terraces; A. grandicornuta predominates; associated with it are Spirostachys africana, Pappea capensis, A. tortilis, Zizyphus mucronata, and the shrubs Acacia luederitzii, Euclea undulata, Schotia capitata and Maytenus senegalensis, while spin creepers of the genus Asparagus are common.

(v) Acacia caffra community: restricted to upland hill slope areas usually above 270 m in elevation, where soils are shallow and stony; generally an open savanna; A. caffra grows mostly as a multi-stemmed bush rarely exceeding 3 m in height; A. nilotica, A. karoo, A. gerrardii, A. tortilis, Ozoroa paniculosa, Zizyphus mucronata, Dombeya rotundifolia, Sclerocarya caffra, Matenus heterophylla and Rhus pentheri also occur.

(vi) Acacia burkei community: occurs on sandy soils overlying sandstone, usually in localised areas on ridgecrests A. burkei grows as a fairly tall (about 7 m) spreading tree, frequently in clusters; *Peltophorum africanum* and *Strychnos spp* are characteristic species, but other trees common in the *A. tortilis* and *A. nilotica* communities are also likely to be present.

(vii) *Acacia nigrescens* community: characteristic of the heavy dolerite derived soils, but only below 145 m; forms an open woodland or savanna with trees usually about 8 m high; other trees include several of the species common to other communities, but shrubs of the genus *Grewia* are typical.

(viii) *Combretum ap iculatum* community: grows as a straggly open woodland associated with sandstone terraces; *Spirostachys africana*, *Zizphus mucronata* and several other common species also occur; tree height varies between 5 and 8 m.

(ix) *Acacia robusta* community: occurs on loose alluvial sands where there is a high water table, as bordering the two rivers; A. robusta grows as a tall spreading tree, with *A. tortilis*, *Spirostachysafricana* and *Schotia brachypetala* common associates, while an avenue of *Ficus sycamorus* up to 16 m high line the banks of the two rivers; the palm *Phoenix reclinata* is sometimes present.

Over much of UGR there is a regularly repeated catenary sequence intergrading from open A. tortilis savanna on the ridgecrests through more wooded A. nilotica savanna on the slopes to Spirostachys woodland alongside the drainage lines. Other communities are interspersed in more localised areas in association with particular conditions of soil and bedrock. While the boundaries of A. grandicornuta woodland are usually sharp, other communities tend to intergrade, and several tree species are widely distributed among the communities.

(b) Grass layer

The grasslands through most of UGR are dominated by the species Themeda triandra (rooigras or red oats grass), which grows as a medium tall, densely tufted grass, attaining culm heights of 0.7-1.2 m. A mature stand of rufous awned rooigras undulating in the breeze in late summer or autumn is a particularly attractive sight. As it grows in dry thornveld as at Umfolozi, it forms what is known as "sweetveld"--a term implying that the forage remains relatively nutritious for livestock during the dry season. Themeda triandra has been eliminated from the natural grassland over much of South Africa through overgrazing, on account of its palatibility for cattle.

Nine grassland communities were distinguished by Downing (1972); their physiognomic characteristics are listed in Table 1:-

(i) Themeda Community: this is the tallest and most lush grassland, and is confined to the slopes and crests of higher hills; associated with Themeda triandra are other tall growing species, including Cymbopogon marginatus, Panicum deustum, Digitaria macroglossa, Diheteropogon amplectens and Setaria sphacelata, and also the common shorter growing Eustachys paspaloides;

(ii) Themeda-Panicum Community: forms the most widespread and extensive tall grassland generally on clay soils; invariably associated with Themeda triandra is Panicum coloratum, stoloniferous species which is able to reach light by trailing over more robust grasses; other common tall grasses include Cymbopogon plurinodis, Digitaria spp, Panicum deustum, P. maximum, and medium height Eustachys paspaloides and Eragrostis capensis (Plate 2a);

(iii) Themeda-Urochloa Community: generally kept closely cropped, thus presenting the aspect of a short grassland

TABLE 1. Physiognomic characteristics of nine grassland communities in Umfolozi Game Reserve

(from Downing 1972).

	Community	mean grass height (cm)	mean aerial cover %	mean forb cover %	mean grazing pressure* %
i.	Themeda	78	59	2	13
ii.	Themeda-Panicum	59	39	3	30
iii.	Themeda-Urochloa	45	27	7	45
iv.	Panicum coloratum	24	16	25	80
v.	Themeda-Aristida	40	18	9	35
vi.	Trichoneura	84	28	4	18
vii.	Panicum maximum	50	10	30	47
viii.	Bothriochloa	60	34	18	32
ix.	Cynodon	59	21	11	55

*crudely estimated on basis of degree of defoliation and extent of denudation either interspersed with (ii) or growing over more extensive areas; commonly associated with *Themeda triandra* are four short growing species *Urochloa mossambicensis*, *Panicum coloratum*, *Digitaria argyrograpta* and *Digitaria polevansii*, taller growing *Panicum maximum* and *Bothriochloa insculpta* are also sometimes present (Plate 2 b);

(iv) *Panicum coloratum* Community: a sparsely covering short grassland occurring both on ridgecrests and in bottomlands; comprised mostly of the stoloniferous or short tufted species *Panicum coloratum*, *Urochloa mossambicensis*, *Sporobolus smutsii*, *S. nitens* and *Tragus berteronianus*, anth some taller *P. maximum*;

(v) *Themeda-Aristida* Community: a medium height grassland occurring on looser sandy soils; commonly associated with *Themeda triandra* are *Aristida congesta*, *Eragrostis capensis*, *Panicum coloratum*, *Heteropogon contortis*, *Eustachys paspaloides*, *P. maximum* and *Digitaria spp*;

(VI) *Trichoneura* Community: of limited distribution on loose sandy soil; it is comprised of both tall and short species including *Trichoneura grandiglumis*, *Eragrostis spp*, *Aristida congestis*, *Pogonarthria aquarosa*, *Sporobolis pyramidalis*, and locally the tall thatching grass

Hyperthelia dissoluta;

(vii) Panicum maximum Community: occurs on heavily grazed bottomlands in wooded areas, as a sparse grass cover associated with many forbs; common species include Panicum maximum, P. deustum, Urochloa mossambicensis and Enteropogon monostachyos;

(viii) Bothriochloa Community: grows mainly in isolated patches of medium height grassland; commonly includes Bothriochloa insculpta, Aristida spp and Panicum maximum;

(ix) Cynodon Community: forms a lawnlike cover on loose riverine sands; common species include Cynodon dactylon, Panicum maximum, Urochloa mossambicensis and Dactyloctenium giganteum.

The most important grasslands from the viewpoint of grazing ecology are the four claysoil communities (i)-(iv). In general (i) and (ii) have the aspect of a tall grassland, while (iii) and (iv) present a short lawnlike cover. A trend is shown from Ii) to (iv) towards decreasing occurrence of Themeda tiandra, and increasing representation of shorter growing species, correlated with increasing grazing pressure. In the field, I separated these grasslands physiognomically either as tall grassland ((i) and (ii)) or short grassland ((iii) and (iv)). Community (v) was referred to as the sandy soil community, and (vii) as woodland grassland; (vi), (viii) and (ix) were of limited occurrence in the study areas.

The detailed composition of grasslands occurring in the bush cleared zone at Madlozi was sampled by the wheel-point method of Tidmarsh and Havenga (1954) for comparison with grazing records. Points falling within the typical phase of a grassland type were separated from those falling within localised sub-communities of too limited extent to be mapped separately (e.g. termitarium sites, tree canopies, etc.). Hillslope Themeda grassland may be referred to Downings' community (i), and tall Themeda grassland on the flats to his community (ii). Short grass grassland includes both communities (iii) and (iv), with the former predominating. Results are presented in Table 2.

Some grass species tend to be dispersed on localised sites. Panicum maximum generally grows under the shade canopy of trees, Sporobolus smutsii is commonly associated with termitaria, and Dactyloctenium australa forms mats

TABLE 2: Composition of the grasslands in the Zintunzini bush-cleared zone
Determined by Tidmarsh wheel-point sampling, recording nearest grass if no strike was obtained, 18 Jan- 6 Feb, 1971.; Figures represent relative abundance in percent

grass species	hillslope themeda grassland typical	hillslope themeda grassland map phase unit*	themeda grassland on flats typical	themeda grassland on flats map phase unit*	short grass grassland typical	short grass grassland map phase unit*	termitarium sites only#
Aristida barbicollis	0	0	0	0.5	0	0.4	0.3
Bothriochloa insculpta	0.8	2.0	0.4	1.4	2.8	3.4	3.9
Chloris virgata	0	0	0	0	0	0.4	0.3
Cymbopogon spp.[1]	4.2	3.6	3.0	2.5	0.4	0.7	0.3
Digitaria argyrograpta	1.6	1.4	4.5	4.5	18.7	15.1	5.3
Digitaria spp.[2]	18.3	16.4	11.7	11.9	9.8	8.4	7.4
Diplachne eleusine	0.2	1.5	0	0.1	0	0	0.7
Eragrostis superba	0	0	0.2	0.2	0	0	0
Eragrostis spp.	0.2	0.1	0.2	0.2	1.5	1.3	0
Eustachys paspaloides	2.4	2.0	1.4	1.7	0	0.1	0.3
Heteropogon contortis	0	0.2	0.2	0.2	0	0.1	0
Panicum coloratum	5.8	10.2	16.1	17.8	29.6	26.0	25.8
Panicum deustum	2.2	4.7	0.2	0.5	0	0	1.0
Panicum maximum	0.3	2.7	0.5	2.1	1.0	1.9	1.4
Setaria flabellata	0.3	0.2	0	0	0	0	0
Setaria sphacellata	2.0	1.5	0	0	0	0	0
Setaria woodii	0	0	0.4	0.3	0	0	0
Sporobolus nitens	0	0.2	0	0.1	0.2	1.8	4.2
Sporobolus smutsii	0	0	0.4	1.5	5.2	9.8	20.3
Themeda triandra	60.8	51.7	60.2	53.6	19.4	15.3	9.9
Tragus berteronianus	0	0.4	0	0.1	0.8	1.2	1.4
Urochloa mossambicensis	0	0.4	0	1.3	10.7	13.9	17.3
Total points	649	854	824	1027	675	911	283
% basal cover	13.1	41.7	13.5	42.7	14.4	42.6	8.5

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*including also localised subzones such as termitarium sites, watercourses, tree canoples, and small short grass patches within themeda grassland.

[1] Cymbopogon sp pres. C. marginatus occurs in hillslope grasslands, C. plurinodis is general elsewhere.

[2] D. polevansii, D. pentzii, D. macroglossa including and others.

#within both tall and short grassland map units.

in shady sites on sandy soils.

With the exception of Cymbopogon spp and Bothriochloa insculpta, which contain aromatic resins, most of the grasses are regarded as palatible to grazers. All of the grasses mentioned are perennials, except for Tragus berteronianus, though Urochloa mossambicensis also commonly grows as an annual.

The current fire policy is to burn grasslands whenever there is notable litter accumulation; this results in burning of taller grasslands at intervals of a few years. The short grasslands do not sustain a fire. However, burning policies have been irregular in the past (see Vincent, 1970).

7. Large mammals

The anti-tsetse fly shooting campaign of the 1940's virtually eliminated all large mammals from Umfolozi Game Reserve, with the exception of the two rhinoceroses and secretive species such as duiker and bushbuck. No wildebeest or zebra remained, and there were only very nominal populations of waterbuck, kudu and impala (Vincent, 1970). However, animals remained protected in the nearby Hluhluwe reserve by the Natal Parks Board in 1952, there was a slow but steady recolonisation movement southwards through the Corridor. Most of the movement of wildebeest, zebra and impala back into UGR has taken place only within the last ten years, with the eastern section being colonised first. When I commenced my work in 1966, there were still few individuals of any of these in the west.

Currently, however, large numbers of some nineteen ungulate species occur throughout the Complex (Table 3). Considering that counts of several of these species are undoubtedly incomplete, overall large herbivore biomass in the Complex in excess of 6372 kg/km^2, with UGR carrying a biomass of at least 7190 kg/km^2, over half of which is made up by the white rhino.

In an attempt to control the impact of ungulate populations on the vegetation, the current policy is to carry out heavy culling of warthog, wildebeest, zebra and impala, both by shooting and live capture, while the white rhino capture program has removed increasing numbers of this species.

Among predators, hyenas are numerous, and leopards

TABLE 3. <u>Ungulate populations in the Umfolozi-Corridor-Hluhluwe Game Reserve Complex</u>

Data derived from the Natal Parks Board helicopter census of August, 1970 (Vincent, 1970). Areas: UGR (south of Black Umfolozi River) - 456 km^2; HGR - 215 km^2; Corridor - 270 km^2; Complex - 940 km^2

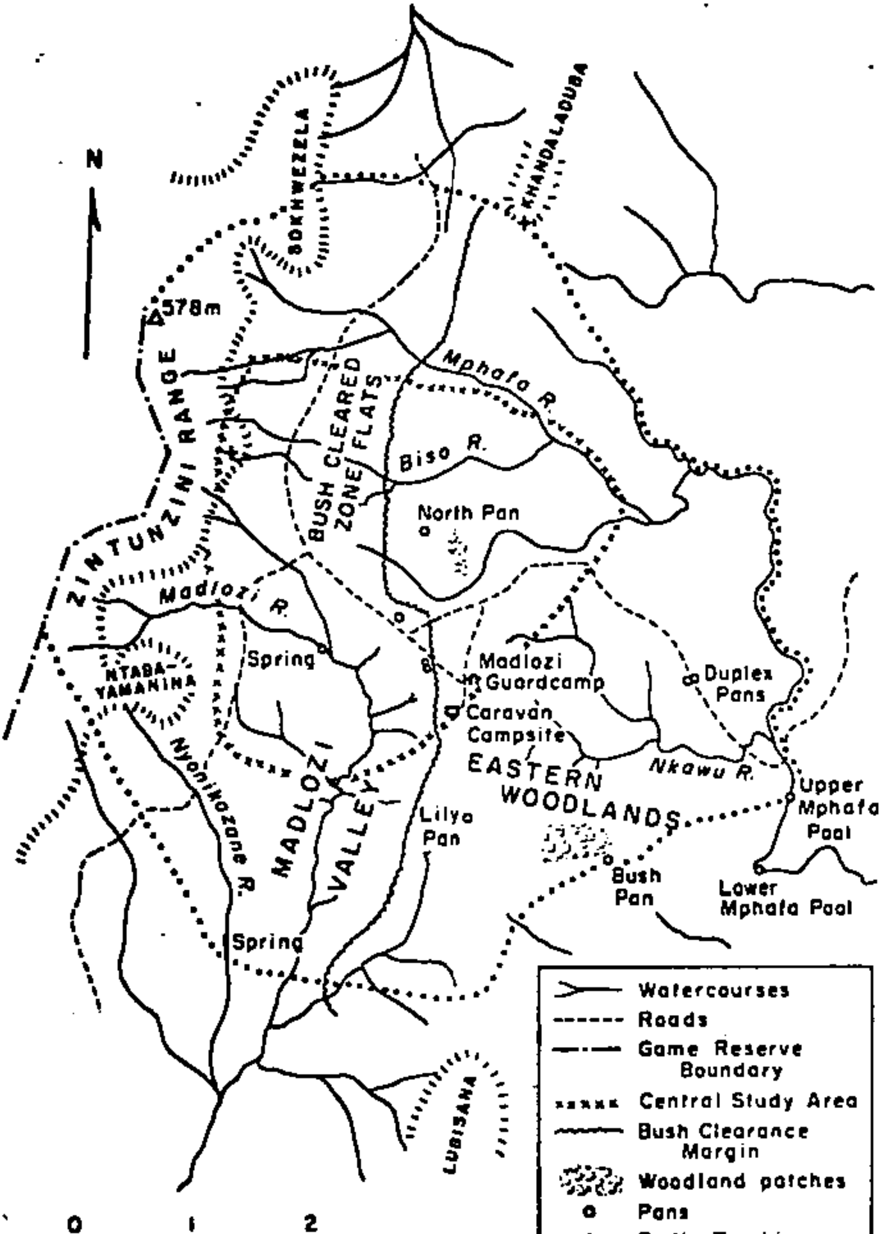
	estim. aver.	numbers				Biomass (kg/km^2)			
<u>species</u>	weight[1] (kg)	UGR	Cor	HGR	TOTAL	UGR	Cor	HGR	TOTAL
White rhinoceros	1350	1361	313	90	1764	4028	1565	568	2532
Wildebeest	160	3367	1954	1042	6363	1180	1160	775	1080
Buffalo	410	426	640	651	1717	384	974	1240	750
Zebra	210	821	1046	877	2744	378	814	858	612
Impala	40	1253	2057	4925	8235	110	305	918	350
Nyala	55	1317	348	2180	3845	159	71	557	224
Waterbuck	155	1045	264	26	1335	355	152	19	220
Black rhinoceros[2]	700	40	50	200	290	61	130	650	218
Kudu	165	840	57	221	1118	305	35	169	197
Warthog	40	1673	569	881	3123	147	85	164	132
Giraffe	800	17	0	17	34	30	0	63	29
Reedbuck	45	473	38	5	516	46	6	-	24
Mountain reedbuck	30	109	4	10	123	7	-	-	4
TOTAL						7190	5297	5981	6372

Not censused: bushbuck, bushpig, grey duiker, red duiker, klipspringer, steenbok.

[1] equals 3/4 of average adult weight for most species; for white rhinoceros based on known age structure; weights from Hitchins (1968), Wilson (1968), Smithers (1971)

[2] not censused, estimated population from Bourquin et al (1971).

Fig. 4 THE MADLOZI STUDY AREA



varied from open Acacia tortilis woodland on the watersheds through less open A. nilotica woodland on the slopes to strips of Spirostachs africana woodland bordering the watercourses. Two more extensive patches of Acacia grandicornuta closed woodland are indicated in Fig. 4, and other areas of denser woodland occurred around the junctions of some of the watercourses. An open Acacia caffra woodland covered the slopes of the Zintunzini Hills. Included within the study area was part of the bush-cleared zone. Here trees were regenerating but remained scrubby, and most of the terrain remained open, offering excellent visibility. The slopes of the Zintunzini Hills were covered with dense Themeda grassland. Elsewhere there was a mosaic of fairly distinct areas of Themeda dominated taller grassland and short grass grassland. On the eastern slopes of the Madlozi valley, and alongside the Madlozi stream, the grass cover was badly degraded and soil erosion was prominent. Permanent water was available at the Nyonikazane spring in the south, and the two Mphafa Pools on the east retained water for most of the dry season. A small spring in the upper Madlozi Stream flowed in 1966. There was a profusion of smaller pans, of which the Lily

Pan carried water for the longest period into the dry season.

(b) Ngutsheni. Elevation of the Ngutsheni study area varied from 135 m near the Black Umfolozi River to 275 m. The vegetation was largely a confused admixture of most of the main communities, with the sandstone favouring types prominent. Most of the area had a fairly sparse cover of short grass, but taller grassland occurred on the slopes of the Khukho Hills to the west.

(c) Gqoyini. The terrain was generally low-lying varying from 120 to 185 m. The dense Euclea phase of the Acacia nilotica community was the predominant vegetation, though some of the best developed Acacia burkei woodland in UGR occurred to the west of the Gqoyi Stream. Acacia nigrescens woodland occurred on dolerite based slopes in the east. Grasslands were mainly short, with relatively small areas of tall grass. Water was available year round from some pans which were kept supplied with water by pumping, and the Bekapansi tourist viewing hide constructed here in 1970, offered favourable conditions for night observations.

(d) Dengezi. This area was situated between the two

Umfolozi rivers, and consisted mainly of a series of hills and long relatively steep-sided ridges. Elevations rose from 60 m at the Black Umfolozi River, to 303 m at the Dengezi beacon overlooking the White Umfolozi River. The ridges were largely dolerite based, and vegetation consisted mainly of an open woodland of *Acacia nigrescens*, which was replaced by *Acacia tortilis* woodland at higher elevations. Tall *Themeda triandra* dominated grasslands prevailed, with only localised areas of sparse short grass.

(e) *Hluhluwe North*. This area was characterised by large steeply rolling hills separated by flat grassy valleys. Elevations varied from 106 m to 378 m at the crest of Magwanxa Hill. Hillslopes were generally open and grassy, with a few small patches of poorly developed coastal forest. Sections had been invaded by *Acacia karoo* which formed a straggly woodland. Hillslope grasslands were of mixed composition with coarse species prevailing, and *Themeda triandra* predominated only in local areas. Tall *Panicum maximum* was prominent in some of the bush invaded sections. Short grass areas were limited to small patches of *Dactyloctenium australe* in some shaded spots. Permanent water was available from two pools in the Manzibomvu Stream. The whole aspect of the country contrasted rather strongly with that in Umfolozi.

9. Study area ungulate populations

All ungulates encountered on patrols were tallied during the first part of the study period. Local ungulate population densities within each study area were calculated using the "Territory Occupancy Index," based on the ratio of animals seen relative to sightings of the resident white rhino territorial bulls (Table 4). Year-round data are available for Madlozi, but records for the other study areas are limited to the month long period of the initial survey. These indicate the approximate large herbivore biomasses being carried by each of the study areas, while the varying species composition reflects their differing habitat qualities. For example, the predominance of wildebeest and zebra in the more open country of Madlozi and Dengezi may be contrasted with the prevalence of impala and nyala at Gqoyini.

White rhino population densities ranged from 4.6/km^2 to 7.0/km^2 in the three western study areas, but the

TABLE 4. Ungulate populations in the study areas

Estimates calculated by "Territory Occupancy Index" (see text), except for Hluhluwe North which is derived from helicopter census.

study area		Madlozi	Madlozi	Madlozi	Nqutsheni	Gqoyini	Dengezi*	Hluhluwe North
extent (km^2)		6.3	8.9	8.9	5.1	7.5	6.1	66.8
time period		Feb-July 1966	wet cond. 1968-71	dry cond. 1969-70	Jan-Feb 1969	Mar-Apr 1969	May 1969	Aug 1970
species	sightability correction factor	Numbers per 10 km^2						
white rhinoceros	1.0	53	57	46	70	51	37	5
Black rhinoceros	2.0	0.1	1.6	0.2	0	2	0.1	4.5
Buffalo	1.25	5	5	0	0	6	30	66
Bushbuck	3.0	8	0	0	1	0	3	-
Giraffe	1.0	0	1	3	0	0	0	0
Grey duiker	4.0	61	26	23	57	88	28	-
Impala	1.5	6	32	52	48	115	7	130
Kudu	1.5	23	17	21	10	24	13	8
Mountain reedbuck	2.0	0	0	0	0	0	6	0
Nyala	2.0	7	2	5	23	73	32	107
Reedbuck	1.5	53	37	27	4	3	16	0
Steenbok	3.5	15	21	19	29	20	15	-
Waterbuck	1.5	20	3	1	15	28	47	0
Warthog	1.4	34	29	40	25	121	121	40
Wildebeest	1.25	16	107	137	1	60	423	34
Zebra	1.25	0.1	24	14	8	12	89	53
BIOMASS (kg/km^2)		8975	10970	9750	10370	10715	16385	6960

*population densities believed to be overestimated by about 50%

exceptionally high population density recorded at Nqutsheni is probably partly due to an influx of animals to the vicinity of the Black Umfolozi River resulting from the dry conditions prevailing during February 1969. White rhino population density at Dengezi was about half that in the western study areas, and at Hluhluwe North only 10% as great, but a large part consisted of hilly country little used by the animals. Overall large herbivore biomass was fairly constant among the five study areas. Only the estimate for Madlozi can be accepted as accurate on a year round basis; here the local biomass was over 10,000 kg/km^2.

III. THE ANIMALS

A. MORPHOLOGY AND PHYSIOLOGY

1. External appearance

The white rhinoceros exhibits typical graviportal construction, with an extended barrel-like rib cage and short thick-set limbs (Plate 4). Characteristic features include (i) wide, squared-off lips, (ii) lengthened head, (iii) nuchal hump, and (iv) pre-sacral vertebral crest. The head is held low, the mouth almost touching the ground, in relaxed posture. The pointed-tipped ears are fringed with hairs, but the remainder of the body appears hairless except on close examination. The skin colour is basically a neutral "battleship" grey, but is usually modified by the colour of the soil last wallowed in. There are prominent folds of skin on the shoulder and on the flank just anterior to the upper hind limb.

Two mamary teats are present inguinally in females; males exhibit a pair of prominent mammillae just anterior to the prepuce. While there is no true scrotum, a male is readily distinguished posteriorly by the presence of a prominent inguinal fold of skin, while the vulva is conspicuous in females. Males tend to be slightly larger and more heavily built, but otherwise there is little sexual dimorphism in general body appearance. Males tend to have shorter and more thick-set horns than females, and do not exhibit the forward projecting horns possessed by some females. The anterior horn is usually considerably longer than the posterior one, but there is much individual variability in the sizes and shapes of the two horns.

The black rhinoceros (Plate 4c) differs in its shorter head and fingerlike and prehensile upper lip. The head is usually held appreciably higher than in the white rhino, there is no nuchal hump, the ears are more rounded, and the pre-sacral crest is more posteriorly located so that the animal appears saddle-backed. In basic skin colour, black rhinos in Zululand are a darker browner grey than the white rhino. In the black rhino, both horns are not infrequently of approximately equal length, and the base of the anterior horn is rounded in front; in the white rhino it is straight-edged.

2. Size

Estimates of the size of the white rhinoceros have usually been much exaggerated by previous writers. Following Player and Feely (1960), shoulder heights of up to 198 cm, and weights of 2700-4500 kg, have been quoted.

It is evident that shoulder height rarely exceeds 183 cm (six feet) from the fact that this is inside height of the crates used by the Natal Parks Board to transport the animals. Kirby (1920) gives the following shoulder heights of two specimens selected for their large size: Male, 179 cm; female, 177 cm. Foster (1960) lists the shoulder heights of four specimens (sex not stated) as 171-185 cm. The tallest mounted specimen measured by Heller (1913) was 188 cm in shoulder height, but from Kirby's observations would have taped about 2 cm less in the flesh. The height at the crest of the nuchal hump with the head raised may exceed shoulder height by about 10 cm.

Various measurements made on animals captured for marking during the course of the present study are listed in Table 5. More extensive data are available in rhino capture records in Natal Parks Board files.

Fully adult males are estimated by Natal Parks Board officers engaged in the rhino capture operations to

TABLE 5. Measurements of adult white rhinoceroses taken during marking operations

Data on animals 1 and 2 from Natal Parks Board files; animal 3 supplied by P. M. Hitchins; remaining animals measured by the author.

All measurements in centimetres

No.	sex	ident.	spine len.[1]	hd. len	tail	sh. ht.	heart girth	hd. circ.[2]	ant. horn len.	post. horn len.	ant. horn circ.
1.	male	P	277	94	71				62	27	72
2.	male	Q	277	95	70				66	27	71
3.	male	A	268		120	174	283		64	39	77
4.	male	H	284				328		64	26	76
5.	female	HH	268				286	135	82	20	65
6.	female	O	250					127	75	26	65
7.	female	MM	273					136	62	16	68
8.	female	AL	248					131	76	18	
9.	female	P	248					126	66	21	

[1] occiput to base of tail

[2] taken posterior to second horn across anterior part of eye

weigh 2040-2260 kg (4500-5000 lb) and adult females about 1600 kg (3500 lb). However, to my knowledge there is only a single measured weight for an adult wild specimen. A male, sectioned and weighed in the field for the purpose of calculating drug dosages, totalled 2130 kg (4700 lb) (J. Clark, pers. com). This individual was a young adult, with the last molar not fully erupted.

The record length for a white rhino horn is 158 cm (5 ft 2½ in) for a South African female (Best, 1962). There is a photograph of this horn illustrating Selous' article in Bryden (1899). The largest male horn, from the northern race, measured 120 cm (4 ft 11 in) (Best, 1962). Of my study area animals, the longest horned female was estimated, from photographs, to have had an anterior horn length of about 90 cm, while the longest male horn was about 72 cm.

The white rhinoceros is generally regarded as being the third largest land mammal, exceeded in size only by the two elephants. The Indian rhinoceros attains approximately the same shoulder height, but Heller's (1913) data suggest that the white rhino tends to be slightly the taller of the two species. However, an adult male hippopotamus has been weighed at 2660 kg (Meinertzagen, 1938), which exceeds the maximum weight estimated for a white rhino bull. The black rhinoceros attains shoulder heights of up to 165 cm, but its maximum recorded weight is only 1313 kg (Meinertzagen, 1938). In the black rhinoceros, there is no appreciable size dimorphism between the two sexes (Hitchins, 1968).

3. Skeleton

The skeleton is massively built to support the heavy weight. There are 18 rib-bearing vertebrae, and the vertebral spines are greatly extended in the shoulder region, and to a lesser degree also in the posterior thoracic region.

The skull is characterized by the long backwardly extended occipital crest, rugous areas in the nasal region which support the two horns, and absence of labial teeth. The adult dental formula is I 0/0, C 0/0, P 3/3, M 3/3. The deciduous dentition includes four premolars. The front deciduous premolars are the last to erupt, but are not replaced when lost during adolescence. Occasionally they persist into early adulthood. There is no record of the presence of even vestigial incisors and canines, as sometimes occur in the black rhinoceros (Goddard, 1970).

Further details of skeletal morphology may be obtained from Heller (1913), and Cave (1962). Groves (1972) has a good illustration of the skeleton.

4. Visceral anatomy

Cave and Allbrook (1959) have remarked on the extraordinary density, toughness and inelasticity of rhinoceros skin. The dermis consists exclusively of collagen fibres, and the epidermis is well keratinized. These authors report a thickness of 1 mm for the epidermis, and 18-20 mm for the dermis. Skin thickness is variable over the body; I measured a total skin thickness of 24 mm in a fresh sample taken from the dorsal shoulder region. The skin is highly vascularised. The usual type of sweat gland is lacking, and instead there are scattered large apocrine sweat glands with myoepithelial cells arranged around the ducts, seemingly designed for the rapid and copious discharge of liquid. I observed that several animals which had run some distance before going down after darting became suddenly covered in droplets of sweat over the head and body regions. The only other circumstance in which I saw an animal sweat noticeably in the field was during a prolonged fight.

The lower lip bears a hardened pad which assists in grazing.

Cave (1969) reported a general absence of body hairs in zoo specimens, though hair follicles were present containing the shaft bases of hairs. However, as already noted by Alexander and Player (1965), wild specimens of the southern form do retain a sparse covering of hairs at least into early adulthood.

Both Cave and Allbrook (1959) and Selous (1899) comment on the large amount of subcutaneous fat present. This may form a layer up to 50 mm thick on the abdomen.

Rhinoceros horn is similar to hair in being an epidermal keratinous derivative, but differs in its construction. While hair fibres are solid, the horn is made up of a mass of tubular filaments which adhere together (Ryder, 1962). In this it resembles the structure of the outer casing of bovid horns and of hooves, but differs in fraying into tubules instead of sheets. The bases of the two horns retain a fuzzy appearance in young animals, but become worn quite smooth distally. The horns grow continually throughout life.

The nuchal hump consists of a skin callus up to 49 mm thick, a fatty pad 30 mm thick, and beneath this a large muscular-ligamentous mass (Alexander and Player, 1965). The presence of the hump seems due to hypertrophy of the nuchal ligament and associated muscalture for raising the heavy head. Three separate pads are noticeable externally.

The penis is muscular and as in equids, lacks a penis bone. There are laterally projecting lobes related to extensions of the corpus cavernosum, and the tip terminates in an enlarged flattened flange (Cave, 1964). The testes are situated close to the skin between the prepuce and the mammillae. The white rhinoceros differs from other living rhinoceroses in have a well-developed preputial retractor muscle, and in the presence of numerous papillae on the glans, prepuce and ventral preputial skin. Cave (1966) describes the association of these papillae with unusual eccrine sweat glands and lymphoid tissue, and suggests that they may be scent glands of sexual significance.

Though pedal scent glands occur in the genus

Rhinoceros (Cave, 1962) no external glands have been described in either Ceratotherium or Diceros apart from the preptial glands.

There are additional papers on the foramen ovale (Cave, 1959), visceral histology (Aumonier and Cave, 1960), and lymph node histology (Cave, 1962b). However, the white rhinoceros still remains poorly investigated anatomically.

5. General physiology

Body temperature is relatively low and somewhat variable. Allbrook et al. (1958) found that the rectal temperatures of free-ranging tame animals varied from 34.5°C at sunrise to 37.5°C at sunset, on sunny days; in the shade, rectal temperatures remained fairly constant at 35.4°C. A minimum rectal temperature of 33.6°C was recorded at night when the ambient temperature dropped to 5°C. Wallach (1969) recorded rectal temperatures between 29.4°C and 35.0°C for a juvenile animal.

Normal pulse rate is between 30 and 40 beats per minute (Allbrook et al. 1958).

The urine is usually milky in appearance, apparently from suspended albuminous material (van den Bergh, 1955, and personal observations). Van den Bergh reported that the urine was highly odoriferous, particularly that of males, but in the field I was able to detect only a milk "medicinal" odour.

The milk is very low in fats. Wallach (1969) reported a fat content of only 0.6% in the milk of a cow with a five month old calf.

6. Drug immobilization

Over one thousand white rhinos have been captured by means of the drugged dart technique to date, with negligible mortality (Wallach, 1966; Player, 1967; Keep, 1971). Etorphine hydrochloride (M.99) is used as the immobilizing drug. A dosage of 1.5-2 mgm is dissolved in a solution of the tranquilliser Acetylpromazine, with the optional addition of hyoscine. The time taken for action is 8-20 minutes. The most effective drug antagonist is Nalorphine hydrochloride (M.285); while black rhinos, elephants, zebras and bovids rise quickly to their feet and are alert within a few minutes, white rhinos experience great difficulty in rising, and remain phlegmatic towards external stimuli for several hours.

7. Genetics

There are 82 diploid chromosomes (Heinichen, 1969). This is the same number as is present in the Indian rhinoceros (Wurster and Benirschke, 1968), while the black rhinoceros has 84 chromosomes (Hungerford et al., 1967). These seem to be the highest chromosome numbers recorded for any mammal so far investigated.

Blood proteins in the Zululand white rhinos showed greater variability than those of black rhinos from the same area (Osterhoff and Keep, 1970). It was suggested that the black rhino population might be more "inbred" than that of the white rhino.

B. GROWTH AND AGEING

I initially recognised eight size classes based on field impression of height relative to that of an adult female supported in younger categories by the degree of development of the horns (Table 6). Later it became possible to estimate the approximate age ranges of these classes from photographs taken of known individuals at regular intervals over the 2 3/4 year main study

TABLE 6. Size classes used
Size classes based on fiels impression of height relative to adult female, supported by horn development in younger classes. Age estimates based on repeated photographs of known individuals.

Class	field impression of height	horn length (in earlengths) ant.	horn length (in earlengths) post.	estim. weight (kg)	estim. age (mo.)
Juvenile J_1	below cow's shoulder fold	bump	none	65-110	0-2
Juvenile J_2	slightly larger, still lacking of posterior horn	lump	none	110-180	2-4
Juvenile J_3	pre-sacral crest not more than half way up side of cow	1/4	discernible	180-400	4-9
Immature I_1	pre-sacral crest up to top of cow's flank fold	1/2	bump	400-600	9-18
Immature I_2	pre-sacral crest up to top of cow's iliac projection	3/4-1	knob	600-800	18-30
Subadult S_1	pre-sacral crest not above cow's sacrum	1-1 1/2	knob	800-1100	30-70
Subadult S_2	discernibly smaller than adult	1 1/2-2	1/5-1/2	m. 1100-2000	70-120
				f. 1100-1400	70-85
Adult	full grown	1 3/4-4	1/4-1 1/4	m. 2000-2400	
				f. 1400-1600	

adult earlength = 25 cm

period (Plates 5 and 6). The size classes did not correspond to unitary year classes.

Weights are routinely estimated by Natal Parks Board officers engaged in rhino capture work, in order to assess approximate drug dosages. Estimates agreed closely with the measured weights of eight young individuals that were transported to Rhodesia (Condy and Davison, 1966). The weight ranges presented in Table 6 are based on these estimates, but since I had no opportunity to weigh any animal that I saw, they are approximate only. There are three records relating to birth weight:- (i) the wild-born female "Zuluana" taken to the Pretoria zoo weighed 48 kg at 6 days of age; (Bigalke et al., 1950); (ii) a male white rhino born at Hanover zoo was estimated to weigh 40 kg at birth, by direct comparison with known weight black rhino calves (Dittrich, 1972); (iii) an estimated 2-day old calf found abandoned by its mother in the field weighed 75 kg (P.M. Hitchins, pers. com.).

Bigalke et al. (1950) present data on the growth of the calf "Zuluana," but her development seems abnormally slow, probably on account of artificial rearing. The data given for the Hanover calf (Dittrich, 1972) appear more consistent with natural growth. Wallach (1969) presents further measurements on a young calf.

Juveniles grow very rapidly for the first few months of life, after which growth slows down considerably. Males become indistinguishable from mature adults by about 12 years of age, and females at around 8 years of age.

C. ACTION PATTERNS

1. Locomotion

Howell (1944), Hildebrand (1965), Gray (1968) and Dagg and de Vos (1968a and b) have presented terminologies for describing the gaits of different animals.

My descriptions of white rhinoceros locomotory patterns are based on field observations supported by examination of movie film footage.

Despite its heavy body and short thick-set limbs, a white rhinoceros can appear surprisingly light and agile on its feet. A striking feature in movement is the marked degree of flexure by the carpal joints, the foot being bent so that the sole almost touches the lower part of the forelimb. This seems to be an adaptation facilitating the clearance of obstacles on the ground by the rather short forelimbs.

(a) The walk. The movement of the limbs during walking is basically similar to that in the horse and most other ungulates. The sequence of footfalls is right hind--right fore--left hind--left fore. At normal walking speeds three-point support is maintained for most of the time, the forefoot not being lifted off the ground under the ipsilateral hind foot has already been placed down (Plate 7a); during a rapid walk there are moments of ipsilateral two-point support. During a steady walk, about 35 strides per minute are made by each limb. Ten animals, all adult males, were followed for distances of 2.7 to 4.7 km while they walked steadily towards a waterhole. Calculated rates of movement along the paths followed vary from 2.6 to 3.7 km/hr, but all walking speeds of over 3.2 km/hr are attributable to one particular individual. These calculations do not take into account minor windings of the paths followed, nor brief pauses, for example to check dungheaps. Thus actual walking speeds maintained were probably 3.0 to 3.8 km/hr. Stride length was not measured directly, but is calculated to be about 1.6-1.8 m on the basis of the above data.

(b) The trot. This is the gait normally employed for rapid movement, as when making off in alarm. The marked flexure of the carpal joints gives a high-stepping appearance to the action, while the hind limbs swing back and forth as propulsive levers (Plate 7b). The body bobs slightly up and down, more markedly at lower speeds. The head is usually held raised looking ahead, but is dropped at intervals apparently to sniff at the ground. Bushes or other obstacles in the path may be avoided, or crashed through. A forelimb leaves the ground before, but is placed down slightly after, the contralateral hind limb. At a rapid trot, there are instants when both fore limbs are off the ground simultaneously, but one of the hindlimbs always retains contact with the ground. Measurements made from a photograph indicate that the stride length during a trot is about 2 m. Player and Feely (1960) timed a trotting speed of 29 km/hr from a vehicle. The trot can be maintained for some distance; certain individuals shot with drugged darts trotted 4 to 5 km with only brief pauses when the drug did not inject.

(c) The gallop. This is employed by adult animals only under extreme provocation, and then only for short distances. Small calves not infrequently gallop to keep ahead of the mother (Plate 6c). I have no movie film footage of the gallop, and thus a detailed analysis is not possible. Player and Feely (1960) quote a top gallopping speed of 40 km/hr.

2. Rising and recumbency

Before lying down, the feet are shuffled, then one of the hindlimbs is transferred inwards under the body, and the weight of the hindquarters collapses on this flank. Finally the forelimbs are shifted forwards to allow the forequarters to sag onto the thorax. Occasionally a rhinoceros may remain for periods of several minutes in the intermediate sitting posture. Zannier-Tanner (1965) has published photographs of the action of a black rhinoceros in lying down; the movements seem identical to those of the white rhino.

In rising, the forelimbs first push the forequarters up into a sitting posture. Assistance is sometimes given by pushing downwards with the head against the ground; this action was especially prominent when an animal was trying to rise from an awkward posture, as was the case with some of the animals that had been drugged. Rising is completed by extending and moving outwards the hindlimb that had been under the body to take the weight of the hindquarters.

During recumbency, an animal usually lies with the weight of the body resting slightly to one side of the sternum, with one hind limb crossed under the body (Plate 7d). The forelimbs may be extended forwards, on either side of the head, with a flexure of the carpal joints so that the soles of both feet rest on the ground, or one of the limbs may be pushed across under the chin. Lying flat on one side may also occur, but is normally not sustained for than ten to fifteen minutes by adult animals.

3. Elimination

(a) Defecation. Before defecation, cows, non-territorial bulls and immature animals first stand. The tail is curled into a upward spiral; then, as the first dung boluses drop, first one hindleg then the other is shifted anteriorly, so that the hindquarters lean backwards (Plate 8a). Upon completion, the animal walks away. Occasionally, the hindlegs are pushed backwards alternately several times after defecation, but this is done slowly, so that the dung pile is disturbed little or not at all. In contrast, territorial bulls make vigorous backwardly directed kicking movements both before and after defecation, which break up and scatter the dung pile. These actions will be discussed more fully in a later section on territory marking.

Defecation by one animal in a group has a stimulatory effect on its companions to do likewise. Defecation is also stimulated by an encounter with the dung of another rhino. Thus, large dungheaps exist in localities that are frequently visited by rhinos, and passing animals commonly add further contributions. Dungheaps may vary in size from the clustered deposits of only two to three animals to large seemingly permanently maintained accumulations three to four metres in diameter (Plate 8b).

Three sets of evidence were used to estimate frequency of defecation: (i) I checked all the dungheaps on the territory of one particular bull daily over a five day period, and found that five or six of these bore fresh marks of use each day; (ii) while under continuous observation for three of these days, this bull was seen to defecate each day at about 0800, 1200 and 1700 hours;

(iii) I tallied the number of defecations recorded per observation hour for other animals that were watched for extended periods; this yielded the following results expressed in terms of observation hours per defecation: adult males--4.6 (N = 24), adult females--4.25 (N = 26), subadults--4.35 (N = 22). The latter records are however based mainly on periods while the animals were active, usually feeding. Actual intervals recorded between successive defecations varied from 33 minutes to 8 hours 43 minutes, with no notable clustering. It may be concluded tentatively that defecation occurs about 5 to 6 times per 24 hour period, with the interval between successive defecations somewhat variable.

(b) Urination. Cows, non-territorial bulls and immature animals first splay the hindlimbs apart, then stand with upcurled tail urinating backwards in a steady stream (Plates 8c and d). Urination durations varied from 10 sec to 2 minutes, with the following means: non-territorial bulls--55 sec (N = 11); cows--32 sec (N = 27); subadults--31 sec (N = 17). Territorial bulls only occasionally exhibited such non-ritualized stream-urination. Usually they urinated instead in powerful pulsed sprays (Plate 8c) and preceeded urination with horn wiping and scraping actions with the legs. This spray-urination appeared to function in territory marking and will be discussed more fully in this context. In a few instances, immature males were also seen to urinate in several weak sprays. In one instance, a three-week old male calf urinated in a squatting posture (Plate 8f).

Urination usually took place independently of defecation, and no social facilitation was evident.

Data on urination intervals are fragmentary. For cows, the mean number of observation hours recorded per urination was 10.2 (N = 10); for subadults, 5.8 (N = 11). However, urination was inconspicuous and could easily be overlooked. Recorded intervals between successive urinations varied from 43 minutes to 6 hours 53 minutes. It may be inferred tentatively that urination occurs about 3-5 times daily. Territorial bulls commonly spray-urinate repeatedly at short intervals while patrolling their territories, but each burst lasts only a few seconds.

4. Ear and tail movements

The ear pinnae keep up an intermittent restless movement. Usually they are moved independently, one ear being twisted to face backwards, held there for several seconds, then flicked forwards again. These movements persist while the animals are lying down apparently sleeping, and occasional ear flicking movements may be made even while the animals are heavily narcotised, suggesting a considerable degree of autonomic control. While advancing attentively, both ears are held facing forwards. While walking backwards, the ears are faced hindwards. The ears orientate quickly to face any strange sound, and movements thus seem related at least partially to auditory attentiveness. However, the pinnae also have a well-developed vascular supply, and the continual movement of the exposed surface could assist in heat elimination as is suggested to be the case for the African elephant (Buss and Estes, 1971).

The tail is relatively short, and has only a sparse fringe of hairs. It is usually flicked from side to side at intervals while animals are active. The action is one of twisting the tail to one side against the rump, then allowing it to swing to and fro a few times; or the tail may be moved actively from side to side several times. Tail movements were infrequent during early morning periods when flies were less active, suggesting that movements may function to inhibit flies around the anal region.

D. SENSES

The animals apparently rely largely on olfaction for orientation and detailed knowledge of their surroundings. The white rhino is macrosmatic, with the nasal sinuses taking up a considerable portion of the anterior part of the skull. Olfactory sensitivity is acute. I noted animals respond with alertness when downwind at ranges of about 800 m, under conditions when a steady breeze was blowing directly across to them. They always reacted immediately to human scent, but took little notice of rhinos and other animals passing by upwind. Much attention is paid to investigating odours encountered on the ground. Rhinos running away from human intruders dropped their heads repeatedly apparently sniffing at the ground. A rhinoceros bull was able to track down by scent a cow he had left 1 1/2 hours earlier, following her tracks for a distance of 700 m.

Much of the time rhinos do not seem alert to sounds, possibly because these are masked by the noise of their own movements. This is particularly the case while grazing. However, when they were attentively listening, I found it impossible to move a foot without eliciting an immediate orientation of the ears, at ranges of the order of 30 m. Their hearing abilities are thus clearly sensitive.

The poor visual discrimination of rhinoceroses is generally acknowledged. When running away, animals sometimes did not seem to notice bushes until these were only about 10 m in front of them. There is very little binocular overlap, and individuals tend to peer first with one eye, then with the other. Moving objects are more readily responded to, and rhinos reacted to a person walking by in clear view at ranges of about 80 m. However, at such distances, their identification of the object seen appeared uncertain. Only at ranges of under about 50 m did rhinos react consistently with flight to a moving person. More specific observations showed that stationary forms were only discriminated at ranges of 15-25 m, and even then might not be identified clearly:-

(i) I stood near a tree but in full view as a rhino bull grazed towards me; at 15 m range he suddenly stared, trotted away 5 m, then stood uncertainly; I remained quite still, and after 5 minutes he resumed grazing paying no further attention to me; (ii) A rhino cow and calf suddenly turned and walked towards me, without giving me an opportunity to move to concealment; as separation distance decreased from 30 to 20 m, the cow looked towards me several times, but did not respond; at 20 m range, I swayed slightly sideways; at this the cow immediately noticed me, and the pair ran off 100 m; (iii) An adolescent female grazed across my scent track, and stood looking around nervously; I stood in the open in clear view only 15 m away, but she did not respond until I moved.

IV. INDIVIDUAL ECOLOGY

A. FOOD SELECTION

Introduction and methods

The white rhinoceros is commonly regarded as a short grass grazer (Player and Feely, 1960); Foster (1967), however, noted grazing of long grass by individuals of the northern subspecies in Uganda. In Umfolozi Game Reserve, white rhino concentrations are commonly associated with regions having a lawn-like cover of short grasses, and these are the favoured grazing areas for much of the year. However, the short grass cover largely reflects the intense grazing pressure, and it is not immediately apparent to what extent this choice is based on the inherent qualities of such grasslands. Long term observations furthermore reveal seasonal shifts in the degree of utilization of different grassland zones.

I obtained detailed records of food preferences by direct observation of grazing animals. I watched a grazing rhinoceros from close range (usually 20-40 m), then chased it away and inspected the site where it had been feeding. A unit sample patch was defined by the area I could touch with the fingers of my right hand while standing with legs straddled over the grazing pathway; this covered about 0.8 m^2. Within this, I tallied the number of "plant bites" taken from each species of grass or other plant. Unit "bite" width was defined by the spread between my extended thumb and middle finger. This distance of 19 cm closely approximates a measured bite width of 20 cm. While the grass was green, freshly torn leaf cuticles were readily distinguishable, and circumstances in which there was possible interference from other grazers were avoided. Signs of fresh grazing were more difficult to detect when the grass was brown. After recording in detail from one such patch, I paced back either three or five steps and repeated the procedure at from one to four further patches, depending upon how readily the grazing pathway could be discerned. Additional information recorded included the height of the grass after grazing, and the height of an untouched stand judged to be similar to that which had been cropped. The height recorded was the prevailing leaf canopy height above soil level, and emergent culms were ignored. I also noted the general condition of the grassland in terms of degree of greeness or browness, the type of grassland and woody vegetation communities within which the site was located and whether or not it was located on a termite mound. A reference collection of grasses and other plants supporting species identifications has been lodged at the University of Wisconsin herbarium.

In all 191 grazing sites were examined including 536 patches and recording 6103 plant bites. The 191 sites were distributed among the five study areas as follows: Madlozi, 124; Nqutsheni, 15; Ggoyini, 24; Dengezi, 14; Hluhluwe North, 4; other areas, 10. Seasonally, 139 sites were inspected during the summer months October-March, and 52 during the winter period April-September. Records are thus biased towards the Madlozi area and the wet season. However, conditions at Madlozi seemed typical of those prevailing through a large part of the western section of UGR.

1. Feeding action

The white rhinoceros lacks incisors, and uses its lips to pluck grass. The moveable upper lip is extended over a grass tuft pressing it against the cornified lower lip, and the tuft is broken off by an inward movement of the two lips. Slight jerking movements of the head may assist in this, particularly if the grass is tall and fibrous. The head is kept low, and grass may be cropped as close as within 1 cm. of soil level. Weakly rooted plants are sometimes uprooted. When feeding in taller grass, leaves and culms are usually gripped and pulled off near the base, so that inflorescences and leaf tips dangle from the mouth if the head is raised. Detection of the presence of a grass tuft seems to be by contact with the anterior surface of the upper lip. The wide nostrils maintain close contact with the ground layer of vegetation, and are thus well situated to relay olfactory information about it. For example, I watched a rhinoceros hesitate upon encountering a tuft of unpalatible _Cymbopogon_, then transfer its grazing attention elsewhere. White rhinos usually grazed carefully around any weedy forbs present among the grass, through occasionally small forb plants were broken off and taken in along with a bite of grass.

Feeding rates averaged about 72 bites per minute in short grass. Chewing seemed to be synchronised with the plucking action. Occasionally a rhinoceros lifted its head, and munched noisily for several seconds. There is, however, no chewing of the cud as in ruminants. The bite width of an adult female revealed in short grass having a heavy dew covering about 20 cm (Plate 9b).

While standing in one spot, the head was moved in an arc to crop the grass within reach, then a step forwards was taken and a new arc covered (seePlate 9a). In this way a swathe up to 1 metre wide was grazed down along the meandering path of movement. Feeding rhinos sometimes paused to concentrate attention on one particularly attractive stand of grass, while at other times they passed head low over evidently less attractive grassland before resuming feeding. Rates of movement by grazing rhinos averaged 12.7 strides per limb per minute, but varied widely between extremes of 2.6 and 30 strides per minute. Rates of movement were slower in tall grass, where more grass was ingested per bite, than in short grass. While grazing the ears tended to be held with the orifices directed postero-laterally, though ear flicking movements backwards and forwards were still made.

Concentrated feeding was usually maintained for spells of from one to three hours, with only brief interruptions to transfer attention from one locality to another. Sometimes animals remained grazing in one locality for a period, following a meandering course; at other times a steady directed movement was kept up while feeding.

2. Food selection by plant species

At least 30 different grass species were recorded in the food, the exact number depending upon species identification (Table 7). However, 12 species comprised about 95% of the food intake, and 74% was made up by the 4 most important species: *Themeda triandra* (35.5%), *Panicum maximum* (17.1%), *P. coloratum* (12.4%), and *Urochloa mossambicensis* (9.0%) The proportion of *Themeda triandra* recorded would have been even higher had sampling been more equitably distributed through the dry season. However, neither of the indices "relative abundance" and relative quantity" as defined here corresponds truly to quantitative intake in the diet. Though rhinos ingest more per bite when feeding in tall grass, they take fewer bites per unit time than when feeding on short grass. The proportional dietary contribution made by different

TABLE 7. Relative importance of different plant species in the diet.

Based on examination of feeding at 191 sites including 536 sample patches and recording 6103 "plant bites".

frequency = proportion of patches in which species was grazed; relative abundance = proportion of total "plant bites" recorded; relative quantity = abundance x mean grass height difference

species (growth form*)	freq. %	rel. abund. %	mean ht. (cm)		rel. quant. %
			bef.	aft.	
grasses:					
Thumeda triandra (tt)	43.4	24.4	12	5	35.5
			(green)		
			25	10	
			(brown)		
Panicum maximum (tt)	25.7	11.2	17	6	17.1
Panicum coloratum (stol)	49.4	17.1	8	3	12.4
Urochloa mossambicensis (stol)	34.4	12.4	8	3	9.0
Panicum deustum (tt)	7.1	3.1	30	14	7.2
Digitaria spp (stol & tt)	15.1	4.4	13	8	5.1
Digitaria argyrograpta (st)	17.4	7.1	6	3	3.1
Bothriochloa insculpta (mt)	11.2	2.5	13	5	2.9
Enteropogon monostachyos (mt)	6.1	2.2	12	6	1.9
Sporobolus smutsii (stol)	13.6	5.6	4	2	1.6
Dactyloctenium australe (stol)	5.0	2.5	6	3	1.1
Eustachys paspaloides (st)	3.9	1.0	9	4	0.7
Eragrostis spp (m-tt)	1.7	0.7	10	3	0.7
Diplachne eleusine (tt)	1.9	0.4	23	13	0.6
Sporobolus nitens (st)	4.3	1.0	7	4	0.4
Aristida barbicollis (mt)	2.2	0.4	9	4	0.3
Eragrostis superba (mt)	4.7	0.8	5	3	0.2
Chloris virgata (ann)	2.6	0.5	3	2	0.1
Setaria flabellata (st)	0.6	0.2	-	-	-
Setaria sphacellata (tt)	0.7	0.2	-	-	-
Cymbopogon plurinodis (tt)	0.7	0.1	-	-	-
Heteropogon contortis (mt)	0.7	0.1	-	-	-
Sporobolus spp (tt)	0.9	0.1	-	-	-
Aristida spp (m-tt)	0.4	0.1	-	-	-
Tragus berteronianus (ann)	0.9	0.1	-	-	-
unidentified grasses	-	0.4	-	-	-
Cyperaceae	-	0.2	-	-	-
forbs	-	1.0	-	-	-

*st, mt, tt = short, medium or tall tufted; stol = stoloniferous; ann = annual grass species would thus be intermediate between the two measures.

Other important species include Panicum deustum, which was uncommon but well favoured where present; and Digitaria argyrograpta and Sporobolus smutsii, which were commonly grazed, but because of their short height make up a lower proportion by quantity. Other Digitaria species were also favoured. Dactyloctenium australe occured only locally, but was well grazed where present.

A measure of the degree of preference shown for different species may be obtained by comparing their relative abundance in the diet with grasslands composition. Such data are available only for the Zintunzini bush-cleared zone; it is assumed that wheelpoint sampling of grasslands gives an equivalent measure of relative abundance to recording food selection in terms of "plant bites" (in Table 8).

The representation of most species in the diet does not differ widely from their availability in the grassland. Highest preference ratios are exhibited for Panicum deustum, P. maximum and Urochloa mossambicensis. However, the short transition period at the beginning of the wet

TABLE 8. Relationship between availability and representation in the diet of various grass species, by grassland type

Based on comparison of grazing records from the Zintunzini bush-cleared zone, in terms of no. of plant bites recorded (N = 45 sites, recording 2271 plant bites), with grassland composition from the same region, determined by wheelpoint sampling (see Table 2).

species	short grass grassland		tall Themeda grassland		hillslope Themeda grassland		mean preference ratio
	avail. %	eaten %	avail. %	eaten %	avail. %	eaten %	
Themeda triandra	15.3	13.5	53.6	53.2	51.7	45.3	0.9
Panicum maximum	1.9	5.6	2.1	5.2	2.7	4.3	2.3
Panicum coloratum	26.0	19.7	17.8	20.0	10.2	6.0	0.8
Urochloa mossambicensis	13.9	23.0	1.3	2.3	0.4	0	1.6
Panicum deustum	0	0.7	0.5	0	4.7	21.5	4.3
Digitaria spp.	8.4	2.5	11.9	6.6	16.4	8.3	0.5
Digitaria argyrograpta	15.1	10.8	4.5	5.8	1.4	1.9	0.9
Bothriochloa insculpta	3.4	6.3	0.5	0.1	2.0	0.2	1.1
Sporobolus smutsii	9.8	12.9	1.5	0.2	0.2	0	1.1
Eustachys paspaloides	0.1	0.2	1.7	0.7	2.0	5.7	1.7
Eragrostis spp.	1.3	0.2	0.2	2.9	0.1	0.6	(2.3)
Diplachne eleusine	0	0	0	0	1.5	0	-
Sporobolus nitens	1.8	0.9	0.1	0	0.2	0	0.4
Aristida barbicollis	0.4	0	0.5	0.1	0	0	0.1
Eragrostis superba	0	1.5	0.2	1.1	0	0.4	-
Chloris virgata	0.4	1.4	0.1	0	0	0	(2.8)
Setaria flabellata	0	0	0	0	0.2	2.4	-
Setaria sphacellata	0	0	0	0	1.5	2.4	(1.6)
Cymbopogon spp.	0.7	0	2.5	0.1	3.6	0.7	0.1
Tragus berteronianus	1.2	0.1	0.1	0	0.4	0	0.1

season when rhinos concentrated temporarily on the hillside grasslands. High preferences suggested for other rarer species (shown in parentheses) are probably influenced by spurious sampling. The positive selection indicated for short grass species in tall Themeda grassland is related largely to the concentration of grazing attention on termitarium sites; 28 of the feeding records in such grassland were based on termitaria, which made up only 7% of the available grassland.

Cymbopogon plurinodis, a fairly tall, coarse grass with a strong resinous odour when crushed, was consistently avoided, and commonly remained as isolated tufts within short grass areas. Bothriochloa insculpta also has a characteristic resinous odour, and is generally regarded as an unpalatible species. It was, however, well grazed by white rhinos where it was short and mixed in with other species, and I also on several occasions observed rhinos grazing into taller stands of Bothriochloa during the dry season.

There were some variations in the dietary representation of different grass species among the study areas. At Nqutsheni and Gqoyini, Themeda triandra was less common in the short grass areas and hence in the food records than at Madlozi, while woodland grasses such as Panicum maximum, Dactyloctenium australe and Enteropogon monostachyos were better represented. At Dengezi, short grass areas were of limited extent, and Digitaria polevansii and Panicum deustum, more common on doleritic soils, were more prevalent in the food records. At Hluhluwe North, where short grass areas were confined to the occasional termite mounds and to localised lawns of Dactyloctenium australe in shaded sites, the mainstay of the food seemed to be Themeda triandra, Panicum maximum and Dactyloctenium australe.

Sandy soil grasslands of the Themeda-Aristida community were poorly represented at Madlozi. However, observations from other study areas indicated that these were not favoured for grazing.

Other grasses of localised distribution are poorly represented or absent from the feeding records. Heteropogon contortis was confined mostly to patches of more stony soil, but where present it was closely cropped and evidently being grazed. Echinochloa sp. grew on raised mounds in the pans, and I observed rhinos feeding on it on occasions. However, less use than expected was made of it, considering that it remained green longer than most other grasses. Cynodon dactylon and Chloris gayana are other palatible species which were rare in the study areas, and hence unrepresented in the feeding records.

Forbs made up only about 1% of the food intake, and in most cases seemed to be taken in merely accidentally when mixed in with grasses. However, at one early dry season site I found that several plants of the small lily Scilla sp. had been freshed grazed, though I was not able to substantiate the record by direct observation. Sedges were rare in the vegetation and insignificant in the food. On one occasion, I watched a white rhino pull a vine of the family Cucurbitaceae out of the grass, and spend some time chewing on it. I also observed a rhino chew on a freshly pulled off branch of the shrub Euclea daphnoides, and Player (1962) records a white rhino stripping off and swallowing bark from the root of a Schotia brachypetala tree. Similar chewing was also observed on occasions on old dry branches and even on iron fencing standards. The nutritional significance of such actions is thus questionable, and they may be related more to exercise of the jaw muscles and teeth.

3. Seasonal trends

In Table 9, results have been analysed in relation to grass condition, estimated in terms of degree of greenness. An orderly trend from sprouting green grass in early summer to generally brown grass towards the end of the dry season would be typical of an average year. In any specific year, this trend is confused by the erratic nature of prevailing rainfall patterns. Since food selection seemed to be based more on choice of grassland type than on individual species preferences, grasses have been grouped in terms of the community types within which each most characteristically occur.

In the Zintunzini bush-cleared zone, on account of excellent long range visibility, it was possible to map the distribution of grazing rhinos among different grassland zones without bias. These data are presented in relation to specific prevailing conditions in Table 10, and have been averaged by month in Figure 5.

During the whole of the wet season, white rhinos concentrated their grazing attention on the short grass

TABLE 9. Trends in food selection in relation to forage condition

	FORAGE CONDITION					
	early green	late green	mainly green	mainly brown	brown	brown green
Duration (as % of year)	17.5	28.5	23.5	14	12	4.5
No. of records:						
sites	41	78	34	9	19	10
plant bites	1634	2230	988	249	672	330
Mean grass height (cm):						
before grazing	7.5	13	10	17	21	31
after grazing	3	5.5	3.5	6	9	15
Representation in diet, by grass species group (as % of total plant bites grazed						
(i) Themeda grassland species						
Themeda triandra	21.7	16.2	19.4	51.0	48.8	38.8
Digitaria spp	3.1	4.7	6.0	4.8	0.3	12.7
Other species[1]	1.8	0.2	1.3	0	0.9	6.9
TOTAL	26.6	21.1	26.7	55.7	50.0	58.4
(ii) Short grassland species						
Panicum coloratum	19.6	19.7	15.2	15.7	13.4	1.2
Urochloa mossambicensis	13.9	17.9	9.5	0	5.7	0
Digitaria argyrograpta	14.2	4.4	6.4	1.6	5.8	0
Sporobolus smutsii	6.7	4.7	11.5	2.7	0	0
Other species[2]	2.5	8.0	2.8	0	0.5	0
TOTAL	56.9	54.7	45.4	20.0	25.4	1.2
(iii) Shade grassland species and woodland						
Panicum maximum	9.1	14.1	14.4	10.4	4.6	6.4
Panicum deustum	0.2	2.8	0.5	0.8	3.6	28.2
Enteropogon monostachyos	1.3	2.3	2.8	8.4	2.1	0
Other species[3]	0	0.5	0.1	0	1.6	0
TOTAL	10.6	19.7	17.8	19.6	11.9	34.6
(iv) Miscellaneous species						
Bothriochloa insculpta	4.3	2.0	3.4	0.8	0.6	0
Other species	0.5	2.2	4.0	1.2	7.2	0
Sedges	0.2	0.6	0.4	0	0	2.4
Forbs	0.7	0.2	1.9	5.2	1.8	0.3

[1] Cymbopogon spp, Setaria Sphacelata, Eustachys paspaloides.

[2] Dactyloctenium australe, Sporobolus nitens, Tragus berteronianus, Chloris virgata.

[3] Diplachne eleusine, Setaria woodii.

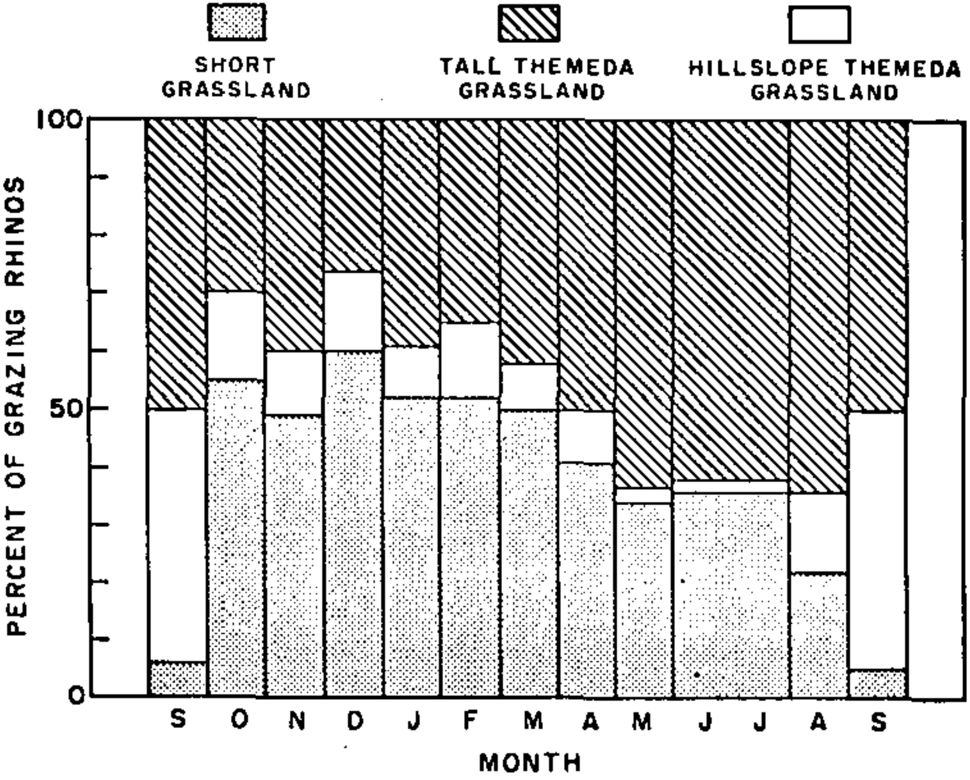
TABLE 10: Shifts in the distribution of grazing white rhinos among the different grassland types in relation to prevailing conditions

Based on mapping locations of grazing rhinos in the Zintunzini bush-cleared zone.

period	condition of grassland	Tot. rhinos rec.	Aver. rhinos present	% on short grassland	% on themada grassland	% on hillslope themada grassl
21 Nov-12Dec'68	hillside grasslands burnt, flushing green	140	14	30	30	39
13Dec-12Jan'69	grass growing green after good rains	154	13	62	37	1
11July-15Aug'69	early winter, grass becoming dry and brown	35	6½	43	54	3
16-31 Aug'69	mid-winter, grass dry and brown	120	11	33	59	8
1-30 Sept'69	late winter, grass dry, first rains at end of month	59	5½	7	59	34
1-31 Oct'69	early spring, grass green commencing growth	137	8½	49	32	19
1-30 Nov'69	mid spring, grass growing lush and green	257	14	70	23	7
1-25Dec'69	late spring, grass green slight drying	45	10	73	16	11
26Dec-30Jan'70	summer drought, grass drying mgrmbr	61	8	44	43	13
31Jan-18Mar'70	drought broken, but rains and grass growth erratic	54	11	59	22	18
19Mar-May'70	grass drying mainly green mainly brown	114	9	41	50	9
9May-20June'70	grass green after late rains	23	9	30	70	0
1-31 Aug'70	mid-winter, grass brown and dry	34	6	12	68	21
1-13 Sept' 70	late winter, grass dry	37	5	0	35	65
14Sep-2Oct'70	first rains, grass sprouting green shoots	91	7	4	43	53
3-31 Oct'70	early spring, grass growing green	33	8	61	27	12
1-30 Nov'70	mid-spring, grass growing lush and green	105	10½	35	50	15
1Dec-11Jan'71	summer drought, grass drying m-green	42	8½	55	26	19
12Jan-4Mar'71	good rains bring themeda into full flowering, then drying mainly green	64	6½	44	48	8
5-31Mar'71	good rains, grass green	104	12	47	53	0
	MEAN		9	41	47	12

FIGURE 5. Seasonal shifts in the distribution of grazing rhinos among grassland types in the Zintunzini bush-cleared zone

Average monthly distributions obtained by combining data for individual years from Table 10.



grasslands. In consequence, the composition of the food while the grass is green closely approximates that of the available grasses in this community type (Tables 8 and 9). The short grass areas on the Zintunzini flats were especially favoured during this period, attracting large numbers of grazing rhinos (Table 10). Most of the grass selected then was under 15 cm in height, though some attention was paid to taller stands of *Panicum maximum*. *Themeda triandra* was kept closely cropped generally only where it was mixed in with short growing species, and stands where it predominated grew into long grass.

As conditions became dryer, increasing use was made first of *Panicum maximum* growing under tree canopies, then of woodland grasslands characterised by *P. maximum* and *Enteropogon monostachyos*. This trend is not clear out in the data presented in Table 8, since I collected fewer records from woodland areas; but is supported on many hours of direct observation. Furthermore, during the period 19 March- 8 May 1970, I made almost daily observations on the activities of one particular cow-subadult pair. The animals were located each day by radio-telemetry and then watched for several hours, so that an objective time sample expended the apparent extent of short grass. Later rhinos were observed grazing within areas having a general cover of tall Themeda of 30-50 cm leaf canopy height. However, they continued to nibble away at the short grasslands through the dry season, so that these were ultimately reduced to stubble.

Towards the end of the dry season, increasing use was made of the less accessible tall Themeda grasslands growing on hillslopes (Table 10). The Madlozi data are supported by more extensive observations made during the aerial census of rhinos in mid-August, 1970. In 1970 there was a striking influx of rhinos onto hillside areas immediately following the arrival of the first spring rains, which fell on 13 September. This is not evident in Table 10, since the animals favoured an area a short distance to the north of the Madlozi study area. The feeding records assigned to the transitional period of brown grass tending to green were mostly obtained during this period (Table 9, column 6). The grasses particularly favoured then were Panicum deustum and a tall Digitaria species, probably either D. pentzii or D. macroglossa. These two species were the first of the tall grasses to sprout green shoots within a few days of the rain. Lesser attention was paid by rhinos to short grass areas until these had put on significant growth, then the hillslope grasslands were largely abandoned.

The hillslope Themeda grasslands were also being extensively utilized by white rhinos when I returned to Madlozi in November 1968. This area had then been freshly burnt, and the grasses there were sprouting succulent green shoots, while poor spring rains had not yet produced much growth in the short grasslands. Animals ranged as high as the crestline of the hills at 500 m. Some of the individuals observed at this time were strangers not subsequently encountered in the study area. Following the arrival of the first good rains in early December, the rhinos abandoned the hillsides and transferred their attention to the short grass areas below.

Conditions during the study period 1968-71 were to some extent atypical, as a result of the cumulative effects of the series of drought years running from 1967 through 1970. An increasing extent of what had been tall Themeda grassland was kept in a closely cropped state year-round. Consequently an increasing degree of utilization of areas mapped as tall Themeda grassland earlier in the season is evident over this period (Table 10). In 1966, a year of good summer rains, I noticed little use being made of Themeda dominated grasslands until late May. During March, 1971 at the end of the wet season, the distribution of rhinos among grassland types was similar to that recorded over the period late July-early August, 1969, under mid-dry season conditions. Extensive sections of formerly tall Themeda-Panicum grassland by 1971 presented the aspect of a short grassland.

4. Quantity of food eaten

I had only a single opportunity to weigh stomach contents. The wet weight of the grass in the stomach of an adult female which had died two days earlier from peritonitis was 72 kg. This would represent about 4.5% of body weight. The cow was either non-pregnant, or in only the early stages of pregnancy, and was not lactating (the uterus had been destroyed by vultures).

Discussion

The white rhinoceros is a gross feeder adapted for the rapid intake of the large quantities of food necessary to support its great bulk. Selectivity is confined mainly to the choice of particular grassland types.

For most of the year, white rhinos favour short grass areas which offer freshly sprouting shoots of highly nutritious forage. These areas contain a variety of grass species growing closely interspersed. Creeping grasses such as *Urochloa mossambicensis*, *Panicum coloratum* and *Sporoblus smutsii* have a relatively low ratio of structural cellulose to cellular contents, and thus offer high nutrient levels. The same applies to the leafy material available from closely cropped rosettes of *Themeda triandra* and *Digitaria argyrograpta*. *Panicum maximum* and *P. deustum*, though basically tall-growing, are "soft" grasses with a high leaf to stem ratio. Analysis of material collected by Downing showed that they offered protein levels averaging almost twice that of whole plant samples of tall *Themeda triandra* (Table 11). Thus, white rhinos clearly concentrate on the most nutritious grasslands available, Diversity may be an additional factor in choice.

Such short grass areas are not only highly favoured by white rhinos, but are also probably to a large extent

TABLE 11. Protein contents of whole plant samples of three grass species from different soil types (data from Downing, 1972)

SPECIES	SOIL TYPE illuviated bottomland clay soils	eluviated hilltop clay soils	sandy soils
Themeda triandra	7.8	4.4	5.9
Panicum maximum	14.9	9.6	11.7
Panicum deustum	12.6	7.8	15.9

created by their sustained grazing pressure. Erect growing tufts of _Themeda triandra_ incur proportionately greater defoliation than decumbent species. Thus the vigour of plants of Themeda is reduced, and they may be prevented from reaching seeding stage. With the opening up of the leaf canopy by grazing, more light reaches soil level and further stimulates the growth of shorter species. Thus a trend is initiated towards decreasing representation by _Themeda triandra_ and increasing abundance of short growing species. In the absence of grazing pressure, short grass grasslands would probably be restricted in their occurrence to localised patches on termite mounds and to shallow soils on ridgecrests. The effects of the heavy grazing pressure exerted by white rhinos and other ungulates are clearly evident at the fenced-in grazing exclosure plots set up in 1967, and is also demonstrated by the extensive areas in Umfolozi which retain only a short grass cover.

Soil type also influences the nutritive content of grasses. Grasses growing on fertile bottom-land soils exhibit considerably higher protein contents than plants of the same species growing on eluviated upland soils or sandy soils (Table 11). Downing (1972) suggests that the paucity of the grass cover on the deep alluvial soils characterised by Acacia grandicornuta woodland is a result of excessive grazing pressure on the more palatible grasses growing there. The grasslands in the bush-cleared zone below the Zintunzini range, a highly favoured grazing area during summer, are based largely on illuviated soils transported from the dolerite-based hillslopes; here, in contrast, the grass cover generally seemed to be standing up well to the intense grazing pressure. In the east of the Madlozi study area, a section of tall Themeda-Panicum grassland based on sandier soils was relatively little used by white rhinos. Extensive areas of tall grassland around Mpila and in other parts of the reserve which were little frequented by white rhinos were associated with largely sandstone based soils.

The short grass grasslands provide food only during the growing season. To carry them through the dry season, the white rhinos are dependent on remaining reserves of tall Themeda grassland. This dry forage is probably submaintenance in protein levels (see Thornton, 1968), and the animals thus lose condition steadily while feeding on it. Subcutaneous fat deposited during the wet season (see Selous, 1899) probably assists in carrying the animals through this period. Critical conditions could arise should the period for which the animals are forced to rely on this substandard diet be unduly prolonged.

Bell (1971) and Jarman (1973) discuss comparative food-seeking strategies among ungulates. Non-ruminants are less efficient than ruminants in utilizing food ingested, but compensate by faster rates of food passage through the digestive system. The more rapid food processing may allow non-ruminants like the rhinoceroses to extract more protein per unit time from low quality fibrous forage. Furthermore, because of lower metabolic rates, animals of large body size lose weight relatively more slowly on submaintenance diets than smaller-bodied species. Thus a large-bodied non-ruminant should be able to survive better than other competitores on coarse forage of low nutritional content. This relationship between forage choice, body size and digestive techniques has been termed the Bell-Jarman principle (Geist, 1973).

The hippopotamus is the largest bodied species with ruminant digestion, though it does not chew the cud like Artiodactyls. Like white rhinos, hippos show a preference for a leafy short growing grasses (Field, 1966, 1970). The African buffalo, which is the next largest African ruminant, feeds largely on taller growing coarser grasses (Field, 1966)--in contradiction to the predictions of the Bell-Jarman Principle. However, Field relates the food choice by the hippo to its relatively inefficient digestive system (in comparison with other ruminants); and to the use of the lips to crop the grass (coarse fibrous grasses tend to slip between the lips). Hippos are year-round grazers, but rely largely on grasses growing on the presumably more fertile alluvial soils bordering major rivers. Buffalo do some browsing of shrubs such as Capparis tomentosa during the dry season.

Elephants are the largest non-ruminant herbivores. The African elephant feeds on tall coarse grasses for much of the year, but during the dry season favours browse and the basal parts of certain grasses, which then offer highe- protein contents (Field, 1971). The white rhinoceros is thus the largest entirely gramniverous non-ruminant. From examination of fecal material, it is evidently a poor digester relying on rapid throughput to secure its nutritive requirements. However, seemingly in violation of the Bell-Jarman principle, it shows greater selectivity for more nutritious forage than either the zebra (Bell, 1970) or buffalo, both of which may be characterised as long grass grazers. However, the Bell-Jarman Principle does not imply that large-bodied non-ruminants should prefer coarser forage; only that they are better able to survive on it. The lip feeding technique of the white rhino allows it to crop grass more closely than either zebras or buffalos, both of which rely on the incisors. This enables it to make better quantitative utilization of short grasses. Since these offer higher nutrient levels, it is natural that the white rhino should prefer to feed on such grasses as long as they offer a sufficient quantity of food material.

During the dry season the white rhinoceros feeds relatively non-selectively on tall dry grass of low nutritional content. Its low body temperature and slow pulse rate (Section III.A.5), coupled with its large body size, indicate that its metabolic rate is probably considerably lower than that of competitor species except for the elephant. It thus incurs a relatively slower rate of decline in body condition when subsisting on such forage.

The white rhinoceros is hence especially well adapted to survive periods of feeding on submaintenance diets. Its grazing competitors rely instead on some browse or other high quality food to supplement the diet during critical periods; or, in the case of zebras and wildebeest, use high mobility to seek out areas of better quality grassland.

However, there must be lower limits to the nutrient levels that the white rhino can tolerate in the winter forage, below which loss in body weight would become critical before the return of the wet season. This probably explain the distributional absence of the species from the more productive grasslands of the wetter regions,of southern Africa. Grasses in such areas tend to grow taller, and thus to have higher fibre content, making them relatively less nutritious when dry.

The white rhinoceros actively transforms extensive areas of grassland into the short grass aspect which offers it the highest food productivity, in terms of amount of palatible food produced per unit area. At the same time, it is dependent on reserves of better quality tall Themeda grassland to carry it through the dry season with the minimum weight loss. It is the decreasing extent of the latter that is likely to become the critical factor in the ability of the vegetation at Umfolozi to support the white rhino population. The increasing attention being paid to poorer quality hillslope grasslands must lead to a more rapid loss in weight during the course of the dry season, so that a less prolonged drought would be needed to cause this to reach serious proportions.

B. OTHER MAINTENANCE ACTIVITIES

1. Drinking

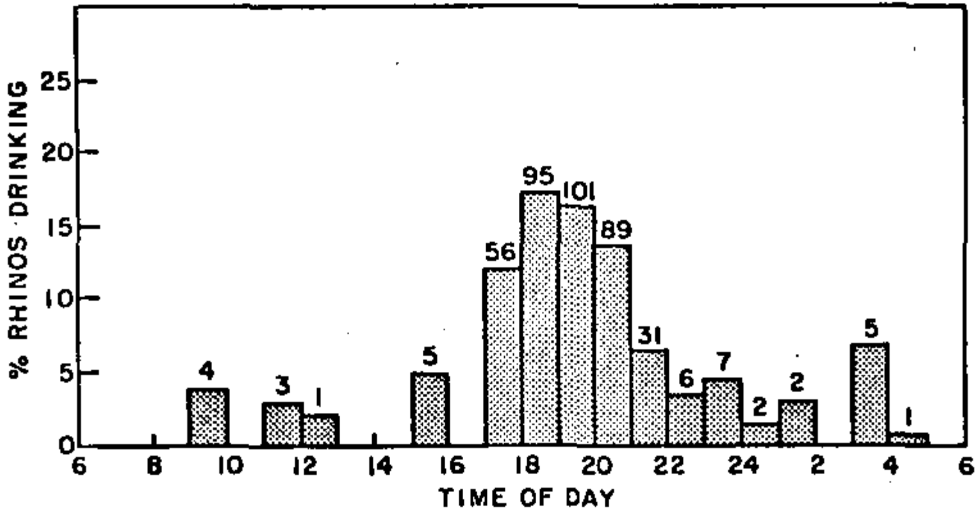
During summer, when pools were plentifully scattered, rhinos paused to drink at any time of day when they happened to be passing one of the pans. Some rhino groups were seen to drink twice during the course of a day under such conditions. Usually drinking then lasted only a minute or two.

During the course of the dry season water supplies became increasingly restricted, and rhinos were forced to undertake a special journey to one of the remaining waterholes. The trip to water usually commenced in the late afternoon, and peak numbers of rhinos arrived at water at dusk and during the early part of the night (Figure 6). Records indicated that an average of 60% of the rhinos drinking in any one day arrived at water between 1700 and 2100 hours. A further 26% appeared during the remaining part of the night, and only 14% drank during daylight hours. The exact timing of the drinking peak depended upon preceeding weather conditions. On a cool, overcast day, rhinos became active earlier in the afternoon, and began arriving at waterholes before dusk. After a hot day, the afternoon resumption of activity was delayed, and peak numbers of rhinos were not recorded until 2000-2100 hours. Animals arriving at water during the day were likely to be local residents, usually bulls. Rhinos coming from afar were more likely to be late arrivals, though locals sometimes also appeared late.

Rhinos, particularly bulls, sometimes remained standing quietly in the vicinity of the waterhole for several minutes before moving down to water. Animals drank deeply with lips immersed for several minutes at a time, interrupting such spells to pause briefly with head lifted (Plate 10). After drinking they departed whence they had come. Occasionally wallowing took place following drinking.

FIGURE 6. <u>Schedule of drinking activity at waterholes, late dry season</u>

Compounded from indpendent observations at different waterholes on different days; figures indicate total number of rhinos recorded drinking in each time interval.



The total time spent at water varied from 2 to 25 minutes, with a mean of 12 minutes.

During a 24-hour continuous watch carried out at the Madlozi Spring Pool over 4-5 July 1966, when this was the most favourably located water source for rhinos in the study area, 42 different rhinos appeared at the water. During three all night watches carried out at the upper Mphafa Pool during July and August of 1969 and 1970, from 14 to 27 rhinos were recorded. The only alternative water source within study area limits then was the Nyonikazane Spring. It was not feasible to count rhinos drinking at the spring, because of the extended distribution of the water. Study area animals were known to divide their attention between these two water sources during the late dry season. The upper and lower Mphafa Pools carried water until late August or early September during the study years, while the Nyonikazane Spring flowed year-round. Beyond this, water was available only at the two rivers, 2.5-4 km beyond study area limits. At the Gyoyini Rhino Hide pan, on 16 August 1970, 80 rhinos were recorded drinking between 1710 and 2335 hours.

The numbers and identification of animals recorded drinking at waterholes, in relation to the known rhino population of about 200 individuals in the Madlozi study area, made it clear that rhinos did not need to resort to water daily. Four separate lines of evidence were used to estimate the late dry season intervals between successive waterhole visits:-

(i) From 8-12 August, 1970, I monitored the approach to the Mphafa Pool radio-telemetrically during the peak drinking period. One transmitterised cow (O) was recorded drinking three times at two day intervals: at 2050 hours on 8 August, at 1958 hours on 10 August, and at 2020 hours on 12 August. A second transmitterised cow (P) drank twice with a three day interval: at 1730 hours on 9 August, and at 1740 hours on 12 August. To confirm that drinking did not take place elsewhere on alternate days, I radio-tracked the cow P on the evening of 13 August. Her movements before being located led away from water, and when found at 1850 hours she had lain down to rest, still 4 km away from the Mphafa pool. A radio signal was also received the same night from the cow O from further to the north, even further away from water.

(ii) Over the ten day period 26 August-4 September 1970, I determined the positions of all transmitterised animals three times daily by radio-telemetric triangulation. The cow P showed distinct movements to and from the direction of the Mphafa pool at 4 day intervals (see Figure 25). The movement patterns of other individuals were less easy to interpret, but were suggestive of 3 day intervals between drinking.

(iii) I carried out watches at the Lily Pan on 6 out of 7 consecutive days over 29 July-4 August 1971, and at the Mphafa Pool for 8 out of 9 consecutive days over 27 August-4 September 1971, during peak drinking hours. Analysis of the intervals between the reappearance of recognisable individuals indicated the following distribution of drinking intervals (N = 26): 1 day--17%; 2 days--19%; 3 days--46%; 4 days--18%. However, some individuals could have drunk elsewhere, or at other times, during the interim.

(iv) There appears to be a rough correlation between time spent drinking and the interval between reappearances (see following page). These data suggest that about 5 minutes is spent drinking for each day absent. On this assumption, records of time spent at the water by drinking rhinos indicate the following distribution of drinking intervals (N = 69): 1 day--23%; 2 days--32%; 3 days--23%; 4 days--22%.

interval between reappearances	time spent at water (min)
1 day	5, 3, 7, 6, 11, 5
2 days	13, 5
3 days	13, 11, 8, 14
4 days	22, 18

Reconciling these various observations, it seems that the late dry season interval between successive waterhole visits varies between 1 and 4 days, with a 2-3 day interval being most usual. Animals that happen to be feeding close by waterholes are those likely to drink at 1-2 day intervals, while those that have further to travel may drink only every third or fourth day.

Individual animals were however not consistent in their usage of different waterholes, nor in their times of drinking, over longer periods. There are year to year variations in the periods for which different waterholes may hold water. For example, in 1966 the Lily Pan dried up in late March, but was partly refilled by subsequent rain and then held water until late May. In 1969 and

1970 it held water until July, and in 1971 into early August. Very small seeps of water from springs may also be used. In August 1969 the Madlozi Spring filled only four very small pools measuring 30 to 50 cm across, and not more than 5 cm deep. During an all night watch, four rhinos drank there. The animals sucked the pools dry, then stood patiently waiting for them to refill, spending about three hours in all in the vicinity. In 1970, this spring had run dry.

Drinking places at the two rivers are usually located where rock ledges jut out to the water's edge. These offer the rhinos a more secure footing than loose river sands (Plate 10b).

Schenkel (1969) found that black rhinos in Tsavo National Park, Kenya, drank only every 4-5 days. However, in Hluhluwe Game Reserve, where water is plentifully distributed, individual black rhinos drink nightly (Hitchins, 1971).

I have no data on the quantity of water drunk. Van den Bergh (1955) reported that white rhinos in the Antwerp zoo drink 60 litres of water per day in winter, and 80 litres per day in summer. If wild animals have the same water needs, and drink only every fourth day, they would need to take in 320 litres (i.e., 15-20% of adult body weight) at a time--which seems impossibly high. Probably white rhinos are able to get by with reduced water intake during the dry season. Though they do not need to drink daily, as is the case for the African elephant (Laws, 1970), they remain water dependent, and this has consequences for their dry season distribution.

2. Mineral Requirements

I occasionally observed white rhino calves nibbling at and apparently ingesting the soil from around termite mounds. However, adults were not seen doing this. No mineral licks are known within UGR. Soils in bottomland areas carry high concentrations of calcium and presumably other minerals, and springs are reportedly usually fairly saline. Presumably the animals are thus able to satisfy their mineral requirements adequately from their food and water.

3. Wallowing

Wallowing is a common activity during the wet season. Two forms of wallowing need to be distinguished: (i) rolling over in mud; (ii) merely lying in a pool of water.

Before mud wallowing, a rhino enters and then lies down in one of the pans having a shallow pool of muddy water. It then rolls partially over, first on one side then on the other. Sometimes individuals merely rolled briefly on each side, then left the wallow. On other occasions, rhinos rolled over almost on the back with the feet in the air, so that the whole body became plastered with mud, except for a narrow strip down the median dorsal line; and remained lying in wallows for a total period of up to 15-20 minutes, rolling over several times. Most commonly, mud wallowing lasted from 2 to 10 minutes.

Pools which had evaporated down so that only a thin layer of water covered a thick deposit of mud were especially favoured. These were stirred to the consistency of liquid mud by the movements of the rhino, and gave a well adherent coating of thick mud plastering the body (Plate 10c). In mid-summer, when most pools were well filled with water, only a thin mud covering was obtained. In several cases, a rhino dug its horn vigorously into the mud before wallowing. This action seemed to serve to test the consistency of the mud. Sometimes, when the mud was very thick, wallowing did not follow, and the rhino walked off with a large blob of mud adhering between the two horns.

Immediately following a mud wallow, rhinos spent 10-20 minutes rubbing various parts of the body against suitably shaped stumps or inclined trees. Special attention was paid to the groin and axillary regions, also to the underside of the belly, the insides of the legs, the neck and sides of the head, and the flanks. Animals sometimes squatted to bring the pubic region in contact with a stump, then swayed back and forth in this awkward posture. As a result of usage by rhinos, stumps and inclined tree trunks in the vicinity of pans exhibit smooth polished surfaces. Projecting boulders may also be used, but were rarely available at Umfolozi. The remains of ticks may be found in the mud rubbed off on stumps.

Rubbing of parts of the body against trees also occurred independently of wallowing. The horns were frequently rubbed against trees, particularly on cloudy days when the animals spent less time sleeping. Such horn rubbing appeared gentle and was not frequently observed, yet the horns exhibit considerable wear. In one case, the protective fibre-glass covering placed over a radio transmitter assembly had been worned down sufficiently to open up the transmitter cavity fifteen months after placement. Bulls which had cable fences within their territories exhibited characteristic grooves on the anterior surface of the second horn, evidently from rubbing against the fence line.

In pool wallowing, a rhino merely lay down quietly in a pool of water 0.3-0.6 metres deep for periods up to several hours (Plate 10d). Rhinos also sometimes lie in shallow water in the two rivers.

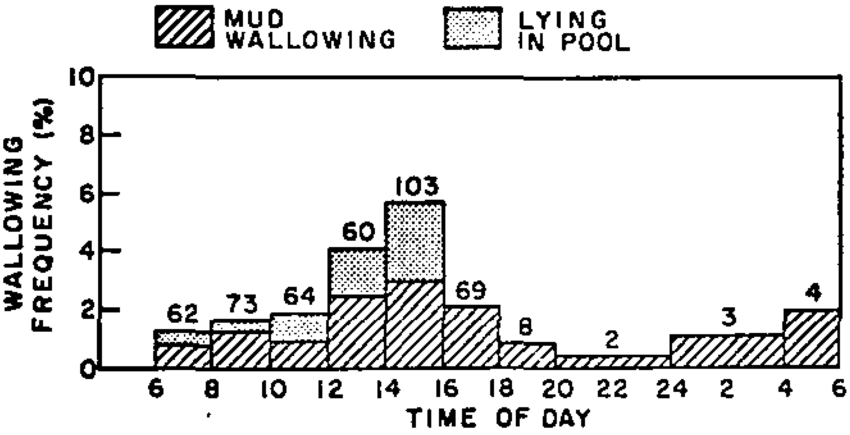
Rhinos frequently lay down in patches of loose sandy soil, but did not roll over, and did not secure any dust cover. Dust wallowing, as reported for black rhinos in East Africa, (Schenkel 1969) was not observed.

Mud wallowing was most often observed during the midday period, either just before the animals settled for the midday rest, or more commonly at the commencement of the afternoon activity period (Figure 7a). However, wallowing was also commonly performed at other times of day. I observed it in the early morning, at dusk on a cool overcast day with a steady wind blowing, and at various times of the night. Lying in a pool was more

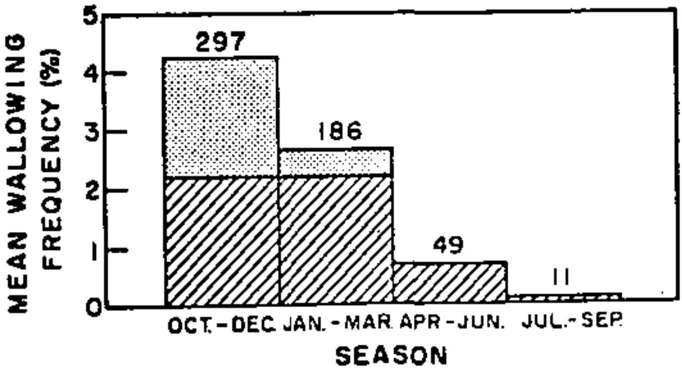
FIGURE 7. Wallowing frequency

a. Diurnal variation in wallowing frequency

Figures represent sample sizes



b. Seasonal variation in wallowing frequency



closely tied to the midday period, though occasionally it occurred at other times of day.

Most rhinos encountered during the summer months exhibited a fresh mud cover, or the dry remnants of an old one. During the winter months, when pans became dry, wallowing was infrequent (Figure 7b). Mud wallowing was observed with equal frequency during the early summer and late summer months. Lying in a pool in contrast occurred more frequently during the early part of summer, when the animals were more active over the midday period (see next section).

Lying in pools may function in getting rid of excess body heat, since water temperatures over midday are likely to be lower than air temperature. Application of a damp mud coating to the body could have the same effect, through evaporative cooling. However, only a weak relationship between mud wallowing activity and ambient temperature conditions was noted. During the summer drought of 1969-70, all pans ran dry, and rhinos were unable to wallow. Despite temperatures of up to 40°C, they showed no obvious ill effects.

The availability of pools offering the ideal consistency of mud seemed to be a special stimulus for wallowing. The action appeared directed particularly towards the acquisition of a thick coating of mud. Swarms of biting flies are usually associated with rhinos (Section VI.C), and the mud covering could function in inhibiting their attentions. Ticks are removed by the rubbing action. Ectoparasites may be presumed to be less active during the cooler winter months, when wallowing was infrequent, though flies occurred on rhinos over this period.

Wallowing is also frequently indulged in by black rhinos, elephants, buffalos and warthogs. These are all species in which body hair is either sparse or lacking. Special heat regulation problems exist for large-bodied species like the rhinoceros and elephant, but not for warthogs. All are however particularly vulnerable to the attention of blood-sucking flies.

It thus seems that the prime function of mud wallowing is to reduce the irritating attentions of ectoparasites, and that functions in heat regulation are secondary. A similar conclusion was reached by Schenkel (1969) for the black rhinos.

4. Resting

Spells of feeding were interrupted by periods of one to several hours spent resting. Usually rhinos lay down to rest; at other times they rested standing with heads held low, almost touching the ground. In 157 observations in which resting posture was recorded, 122 or 82% of the animals were resting lying down. During resting, diminished responsiveness to the surroundings was shown, and the eyes were usually closed. Ear movements continued, though at a slower frequency than when alert. Resting rhinos frequently revealed their presence to me by deep sighs or intestinal rumbles. They seemed to spend most of the resting period dozing between light and deep sleep. Resting rhinos could readily be approached closely from downwind, but an upwind approach or sharp sound startled them into wakefulness. At intervals they shifted position, or stood up for several minutes, before lying down again. One adult male watched resting from 0807 to 1707 hours stood up for periods of 10-35 minutes at 0823, 1155 and 1600 hours. An adult female watched from 0807 to 1120 stood up briefly for 4-15 minutes at 0940, 1030 and 1058 hours. Another adult female watched from 1021 to 1330 rose briefly at 1132 and again at 1248.

During the night and early morning, and on cool cloudy days, rhinos usually lay down to rest wherever they happened to be. During the night and at dawn, patches of loose sand, such as occur in sandstone localities, in the beds of watercourses and on riverbanks, were favoured locations. Presumably this avoided the dewiness of grassy areas.

A long midday rest running through the hot hours of the day lasting several hours was normally taken during warm sunny weather. For this purpose, the animals resorted to certain favoured rest places, marked by the bare soil under several adjacent shady trees (Plate 10f). These were usually located on the crests of low ridges, a situation which is cooler and more breezy than lower lying areas. Resting places did not belong to any one individual, but were used communally by most of the rhinos that had been grazing in that vicinity earlier in the morning. Animals congregated in great slumbering heaps, lying spaced a few metres apart under the same tree or in the shade of adjacent trees. In January, 1969, I recorded 12 separate individuals or pairs totalling 21 rhinos all lying within a diameter of about 100 metres. Under the milder temperature conditions of winter, the movement to especially favoured resting areas was less marked, and frequently any handy shady tree was accepted for a shorter midday rest.

Hitchins (pers. com.) noticed that black rhinos nearly always lay facing downwind, an orientation which would allow them to detect an intruder approaching from behind by scent. However, resting orientations recorded for a sample of white rhinos showed no striking relationship to wind direction (Figure 8).

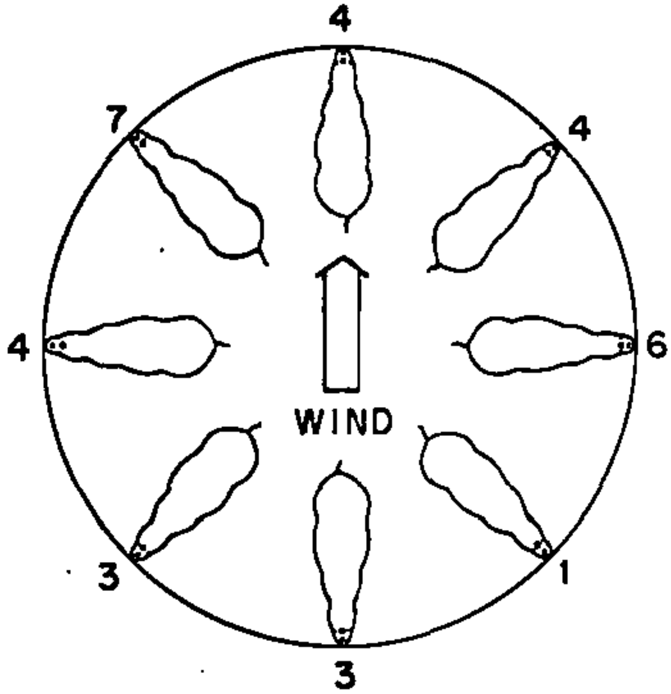
5. Movements

Much movement occurred while grazing. Sustained periods of steady walking were restricted mostly to journeys to and from waterholes, or towards resting areas.

Clear trails radiate inwards towards drinking pools and less strikingly towards rest-places. Rhinos usually followed such trails when travelling to water, walking slowly with head held low. Sometimes broad sinuous marks were found in sand where the mouth region had dragged along the ground for several metres, suggesting that

FIGURE 8. Resting orientation in relation to wind direction

figures indicate number of times each orientation was recorded, in 45° intervals (N = 32 observations)



tactile contact might assist the following of trails at night. The nostrils also maintain close contact with the ground, and can presumably detect olfactory stimuli from the passage of other rhinos. One bull was watched at a three way trail fork, exploring sniffing along one branch, shifting across to sniff at a second, then choosing the third branch. Some of the trails leading to the Nyonikazane Spring could be followed for distances of over 5 km.

Distinct trails also cross high ridges and hills and presumably aid long distance movements, such as may be made to the vicinity of the rivers in the late dry season. Other trails led through patches of dense woodland, but became less clear on leaving the woodland.

Rhinos were sometimes seen moving in the direction of water without following any trail. However, in these cases the individuals concerned were resident territorial bulls, which were undoubtedly familiar with the location of nearby waterholes. It would seem that the network of trails could be valuable in assisting the navigation of individuals less familiar with the region. Since most trails eventually lead to waterholes, it would be possible for a stranger to locate water simply by selecting and following a trail marked with abundant fresh rhino scent.

6. Responses to unfavourable weather

On cool cloudy days with a strong wind blowing rhinos were hard to find. Those that were located were frequently standing quietly in patches of denser woodland such as those flanking watercourses. I kept a watch on one group for several hours on a mild overcast day with a brisk wind blowing. The animals remained within a low-lying well-wooded area where abundant *Euclea* shrubs broke the force of the wind. They fed and rested in short spells, but moved around little.

No avoidance of rain was observed. Rhinos often continued feeding through a rainstorm, though during very hard rain they simply stood or lay down where they happened to be. I watched one group of three rhinos during a heavy early morning thunderstorm which was coupled with a hard driving wind; the temperature was about 22°C. The animals stood heads low in the open, though thicker woodland was present close by. An orientation of about 100° to wind direction (i.e. side-on) was maintained. After standing in this way, with a little shuffling around, for 48 minutes the animals resumed feeding in the rain.

Playfulness and activities such as rubbing the horn on a tree were commonly observed on rainy days, possibly because it was not necessary to spend as much of the day sleeping as during hotter weather.

C. TEMPORAL PATTERNING OF ACTIVITY

Introduction and methods

The 24-hour diel cycle is associated with fluctuations in conditions of light and darkness, in ambient temperatures and in radiant energy flux. Thus, certain times of day are likely to be more favourable for particular activities than others. White rhinos are most conspicuous during the earlier morning and late afternoon, and may also be encountered moving around near the roads at night. During the midday period, animals are mostly seen lying down in the shade of trees.

I noted the activity of all rhinos encountered, and kept an ongoing record of the activities of all animals maintained under continuous observation. Eight activity categories were distinguished: (i) *feeding*--major attention devoted to ingesting food, sometimes coupled with directed movement; (ii) *walking*--sustained locomotion with little or no feeding; (iii) standing--remaining stationary but alertly aware of the surroundings; (iv) resting--either lying down, or standing drowsily with head low, displaying diminished attention to the environment; (v) wallowing and subsequent rubbing; (vi) drinking; (vii) various social interactions; (viii) disturbed by my presence. Weather conditions were noted as follows:- (i) degree of sunshine: fine--clear unobscured sky; fair--occasional clouds passing over the sun; partly cloudy--roughly equal spells of sunshine and cloudiness; cloudy--only occasional sunshine; overcast--completely obscured sun; in the subsequent analysis, fine or fair days represent sunny conditions, and cloudy or overcast days cloudy conditions; (ii) temperature categories were estimated subjectively and correlated with the following ranges: rather hot--42°C+; hot--37-41°C, rather warm 32-36°C, warm 27-31°C, fairly warm 22-26°C, mild 17-21°C, cool 12-16°C, cold 11°C-; (iii) wind speeds were estimated in terms of the Beaufort Scale of wind force.

The major activity categories of resting and feeding were usually engaged in for spells of several hours. Accordingly a unit activity period of 15 minutes was used in analysing results. Thus, a group of 4 rhinos watched for 3 hours would yield 12 data units. Interruptions of activity occupying 7 minutes or less were not counted. Single brief observations of activity were regarded as occupying the whole of the 15 minute interval in which they were recorded. Activities of juvenile animals were inconsistently recorded, and are omitted in calculations. A sum total of 18,891 fifteen minute activity units was recorded.

1. Basic daily activity schedule

On a sunny day, a rhino group typically showed the following sequence of activities (see Figures 9 and 14): (i) at dawn, during the wet season, some animals lay down resting while others grazed; (ii) there was a midmorning feeding spell commencing shortly after dawn and running through the mid-morning hours; (iii) as conditions became warmer during the later morning, the animals moved in towards the resting areas; here they dozed through the hot midday hours; (iv) as temperatures cooled off during the later afternoon, the animals became active again, and there was a second feeding spell running into the evening;

(vi) during the dry season, when water supplies were restricted, the trip to the drinking pool was commenced at around dusk; (vii) during the remainder of the night, animals grazed and rested in alternate spells; there was a predominance of feeding during the early part of the night, passing over into a predominance of resting during the second part, which continued through to dawn (Fig. 11).

2. Seasonal variations

Seasonal changes in temperature and in rainfall as reflected by forage condition (Fig. 10) were associated with variations in daily activity patterns (Fig. 9).

During the hot late summer months (January-March) a long midday rest was taken, and fewer than 50% of rhinos were active between 1900 and 1530 hours. On hot sunny days some individuals commenced dozing soon after 0800, and did not rouse again until 1600 hours (Fig. 14a). Less overall time was spent in feeding during daylight hours than at other seasons; but this may be compensated during the night, for which I have little information.

Temperature conditions were milder during the autumn and early winter months of April-June, but average forage quality was similar to that recorded in summer, on account

FIGURE 9. Diurnal activity pattern - seasonal variations (sunny conditions only)

Figures indicate sample sizes in 15 min.rhino activity units

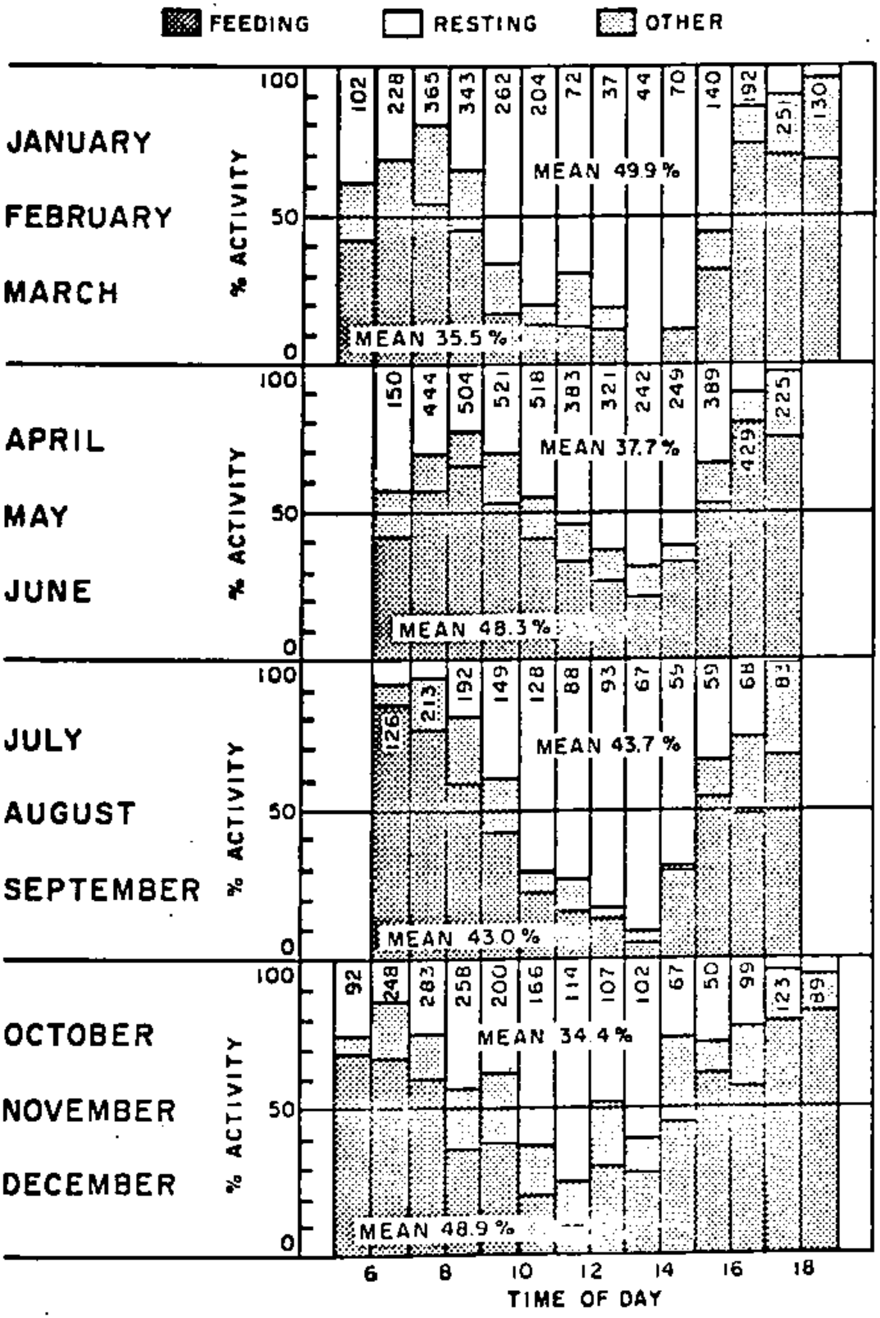


FIGURE 10. Seasonal variations in weather and forage condition during the study period

Average conditions prevailing between Nov.1968 and Aug.1971.

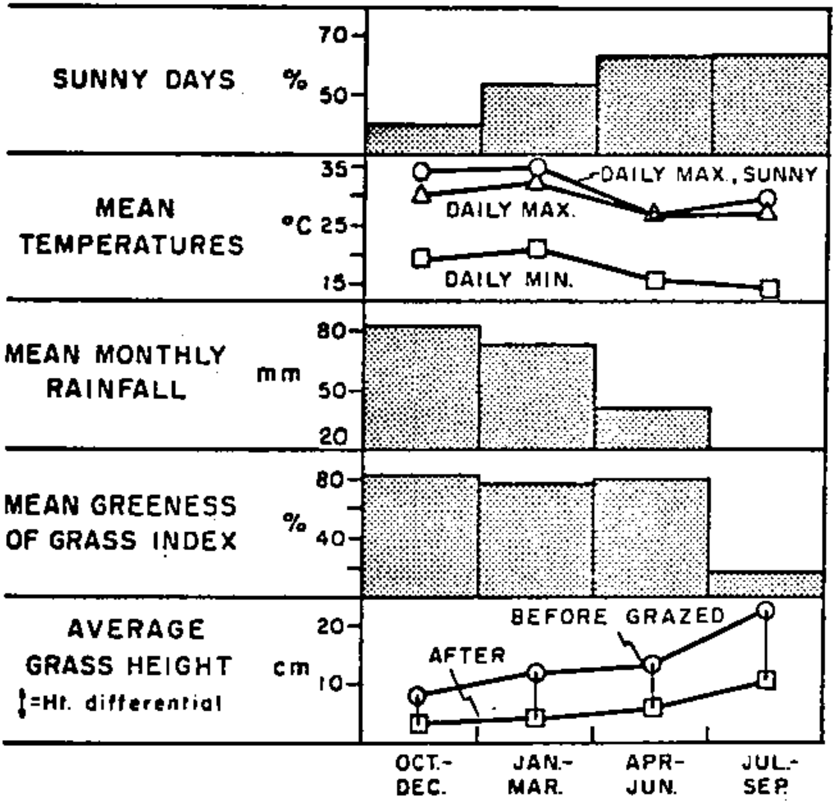
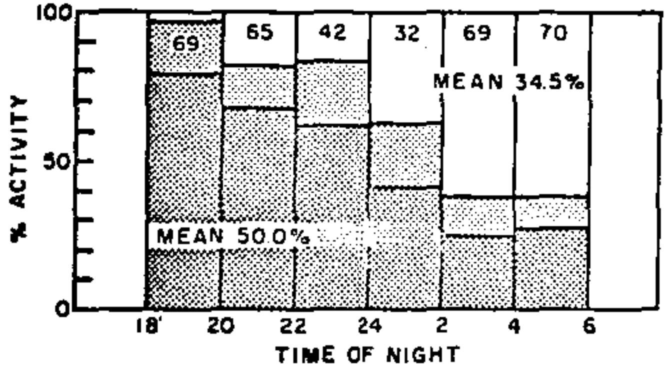


FIGURE 11. Nocturnal activity pattern

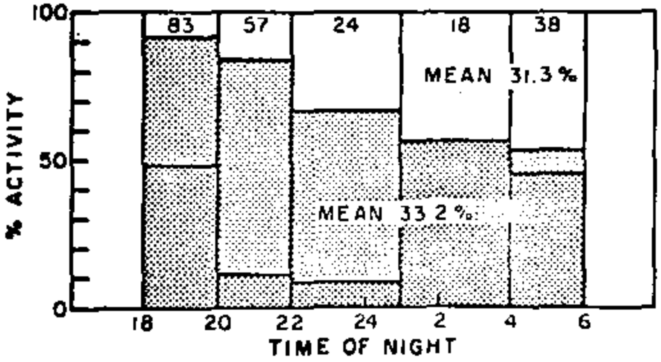
Figures represent total sample sizes, in 15 min. rhino activity units.

▨ FEEDING ☐ RESTING ░ OTHER

a. Wet season conditions (data mostly March-June)



b. Dry season conditions (data derived from June 1966 and July 1969, and biased towards neighbourhood of waterholes)



of the summer droughts and late rains that characterised the study period. During this period, fewer than half the animals were active only from 1100 to 1450 hours. On mild sunny days with maximum temperatures under 26°C, some animals grazed through the midday period (Fig. 14c).

Over the late winter months of July-September, temperatures averaged slightly higher then those for April-June, and forage was restricted mainly to tall dry grass. Less time was spent feeding during the day than over the preceeding three month period, and the early part of the evening was taken up with the journey to and from waterholes (Fig. 11). Results however exaggerate the latter effect, since more night observations were made in the neighbourhood of waterholes where more rhinos were likely to be encountered. Other observations (Section B) indicated that only about one third of the animals were likely to drink on any one night. Higher levels of feeding occurred during the second half of the night, and the dawn resting period disappeared.

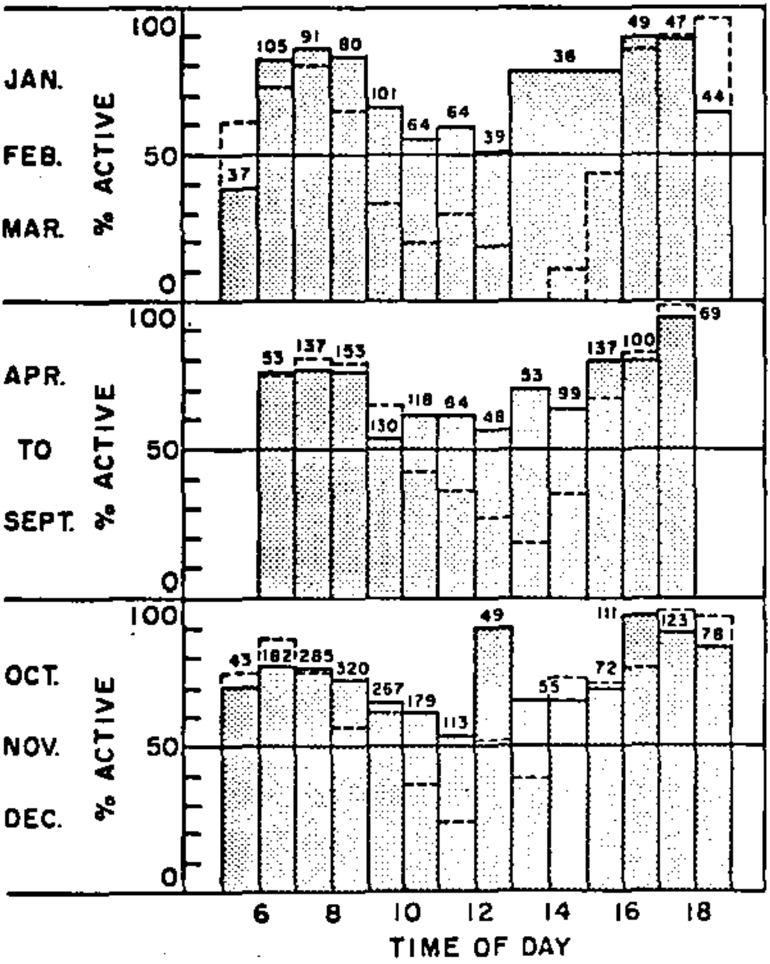
The first spring rains usually arrived in late September, initiating a growth of fresh green grass. Under these conditions a considerable amount of restless feeding activity continued throughout the day (Fig. 9 and 14d), despite temperatures which averaged almost as high as those over January-March. Animals lay down to rest in the earlier morning, but frequently resumed feeding again for short spells through the midday period, and became active again relatively early in the afternoon. As large a proportion of the daylight hours were devoted to feeding as during the far milder conditions of April-June. The grass being grazed then was mainly very short, so that a lesser height difference was cropped than at other seasons.

3. The influence of cloudy weather

Under cloudy conditions there was no distinct midday rest period, and rhinos fed and rested in spells throughout the day (Fig. 12 and 14c). More feeding still occurred during the day in early summer than in late summer, but there was little difference in the cloudy weather time devoted to feeding between late summer and the dry season months (though cloudy weather was more infrequent over the latter period).

FIGURE 12. Diurnal activity pattern, cloudy weather

Results expressed in terms of percent rhinos active, i.e. not resting. Dotted outline = activity levels under sunny conditions.
Figures indicate total sample sizes, in terms of 15 min. rhino activity units.



4. The influence of temperature

Lower temperatures were associated with higher levels of midday activity, but the influence was not as striking as that of cloud cover (Fig. 13). A 43% level of midday activity exhibited at ambient temperatures of about 24°C was depressed to only 10% activity by temperatures of 34°C. However, in cloudy weather an 81% level of midday activity was maintained at 24°C.

5. The influence of moonlight conditions

Night observation patrols were restricted to moonlight periods, and under such condition activity continued in spells throughout the night (Fig. 14f, 14g). At my caravan base camp, more rhinos were recorded passing by under moonlight conditions than when there was little or no moon (Table 11), but differences were not striking, and some animals were active under conditions of no illumination.

	full moon	last quarter	new moon	first quarter
1900-2400 hours	-	9	-	7
0000-0500 hours	-	11	-	4
total	8	20	7	11

FIGURE 13. Relative influence of ambient temperature and insolation on activity

Figures indicate sample sizes in 15 min.rhino activity units

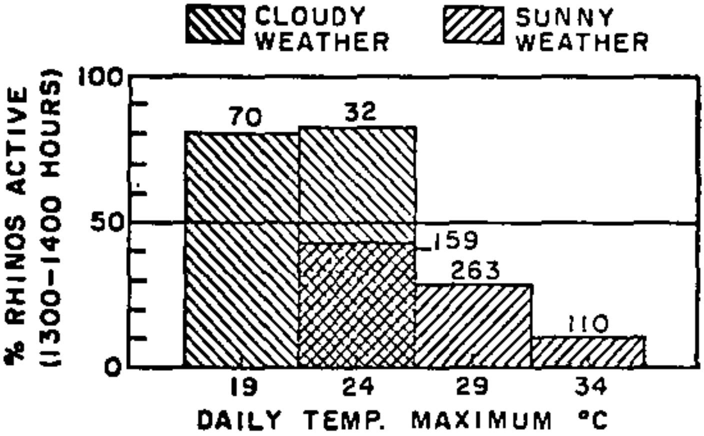
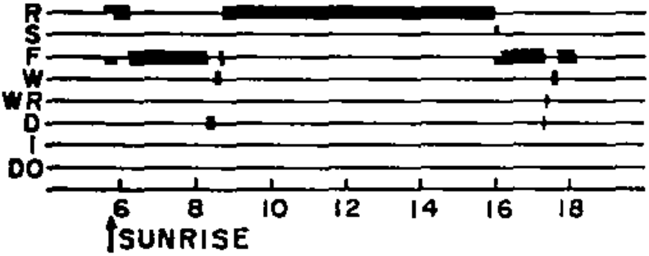


FIGURE 14. Temporal patterning of activity: individual examples

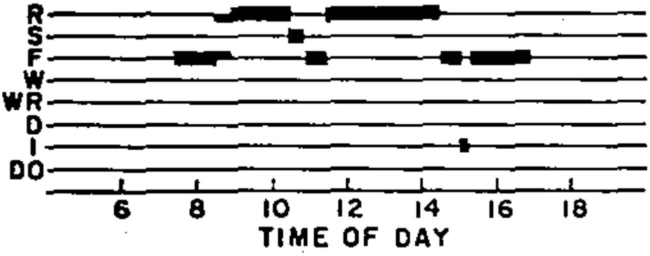
Broad band indicates ongoing activity; where different rhinos in a group engaged in different activities, the band has been subdivided.

Activity categories: R- resting (standing or lying); S- standing (alert); F- feeding; W- walking; WR- wallowing or rubbing; D- drinking; I- interaction; DO- disturbed by observer

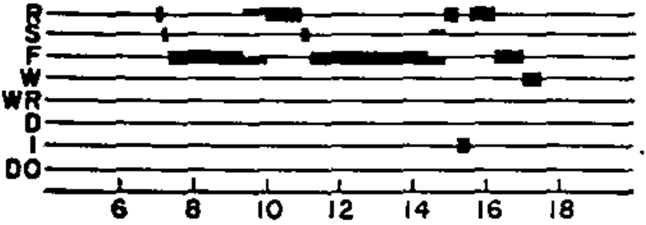
a. LATE WET SEASON: 15 Mar'66: fine, rather warm, fresh breeze; group of 5 rhinos



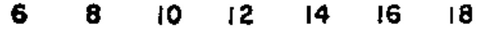
b. EARLY DRY SEASON, showing midday rest. 14 June'66: fine, fairly warm, light breeze; group of 3 rhinos.



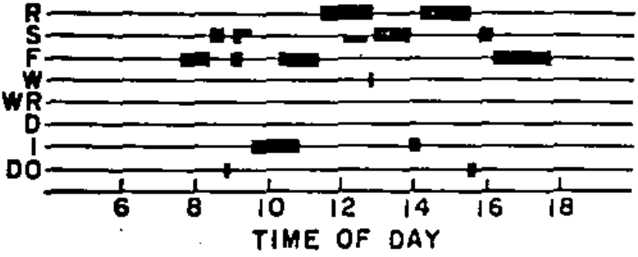
c. EARLY DRY SEASON, showing midday feeding. 17 June'66: fine, fairly warm, breeze gentle becoming fresh p.m.; group of 3 rhinos



d. EARLY WET SEASON. 12 Dec '68: fine, hot(39.5°C), gentle-moderate breeze; group of 4 rhinos

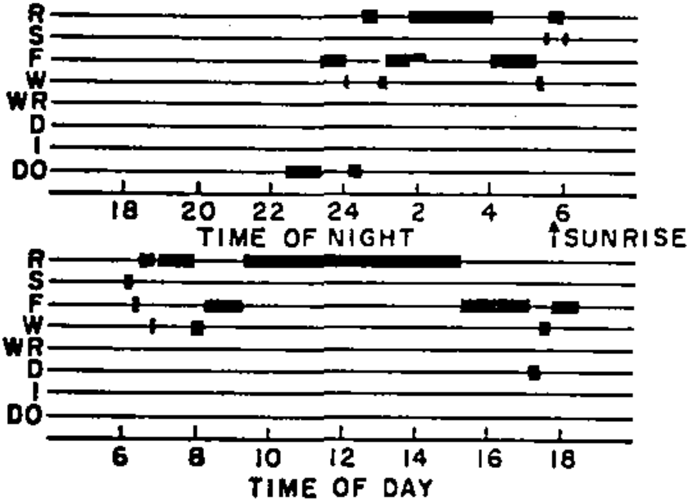


e. CLOUDY WITH RAIN. 13 June'66: overcast, cool, moderate breeze, steady to intermittent drizzle; group of 3 rhinos.

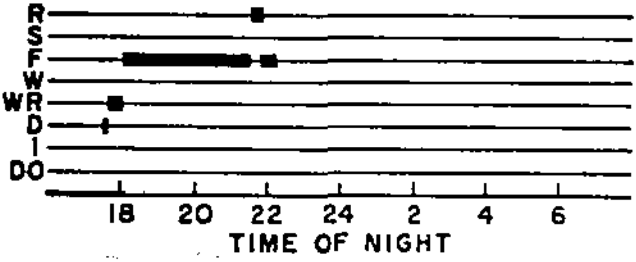


(contd- FIGURE 14)

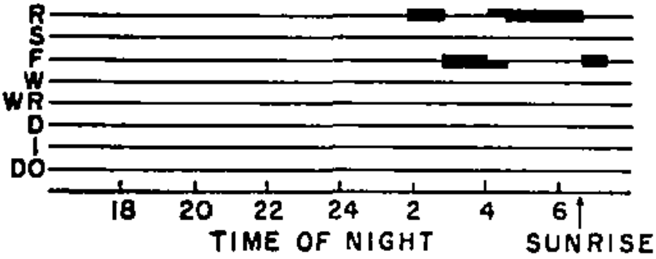
f. 20 HOUR SCHEDULE, LATE WET SEASON. 7-8 Mar.'66: fine, becoming cloudy p.m., rather warm (34.5°C), breeze becoming fresh p.m.; group of 4 rhinos



g. EARLY NIGHT, LATE WET SEASON. 5 Mar:'66: precceding day fine, rather warm, moderate breeze; 1 rhino



h. LATE NIGHT, MID-DRY SEASON. 31 July'69: night clear, mild, moderate breeze; group of 3 rhinos.



Full moon activity is underestimated in the above data as I was more often out on patrol during such conditions.

6. Day to day repetitivity

One bull watched over three successive days repeated very similar activity schedules; (Fig. 15a) but a second bull observed over a three day period when weather conditions were more variable exhibited differing day to day activity schedules (Fig. 15b). A cow and subadult companion observed on six successive days through the morning alternated between feeding and resting through midmorning for 5 days, but then repeated a midmorning feeding period on the sixth. Individual day to day patterns seem influenced mainly by weather conditions, and there is evidently no regularly repeated activity schedule.

7. Duration of activity spells

Most feeding spells tended to last from about 1 1/2 to 3 hours (Fig. 16). Data are however derived mostly from either the morning period on sunny days or from cloudy days; late afternoon-early evening grazing spells are under-represented, and may commonly be longer.

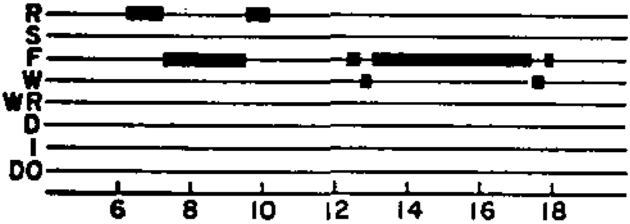
Most resting spells likewise tend to last from 1 1/2

FIGURE 15. Day to day repetivity of individual schedules

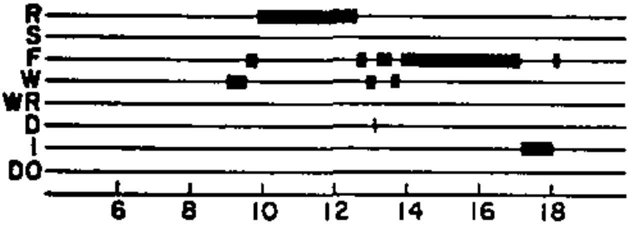
Legend as in Figure 14.

a. Territorial bull I over three consecutive days

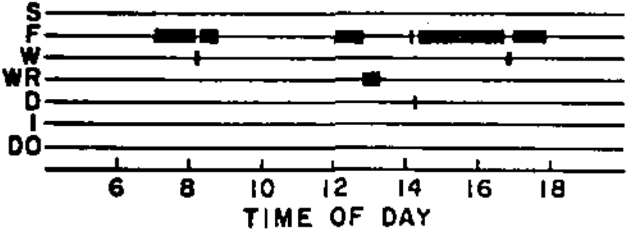
30 Mar.'71: partly cloudy, f. warm(25°C), mod. breeze



31 Mar.'71: cloudy, f. warm(26°C), moderate breeze, a few brief showers

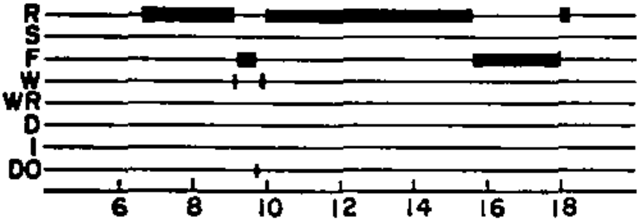


1 Apr.'71: fair, warm (28°C), gentle breeze

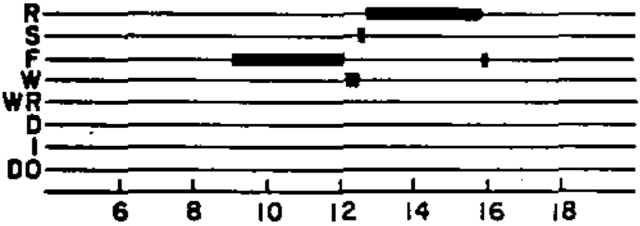


b. Territorial Bull (P) observed on 3 consecutive days

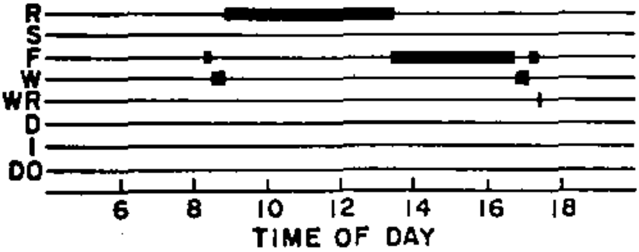
18 April'66: fine, warm, light breeze



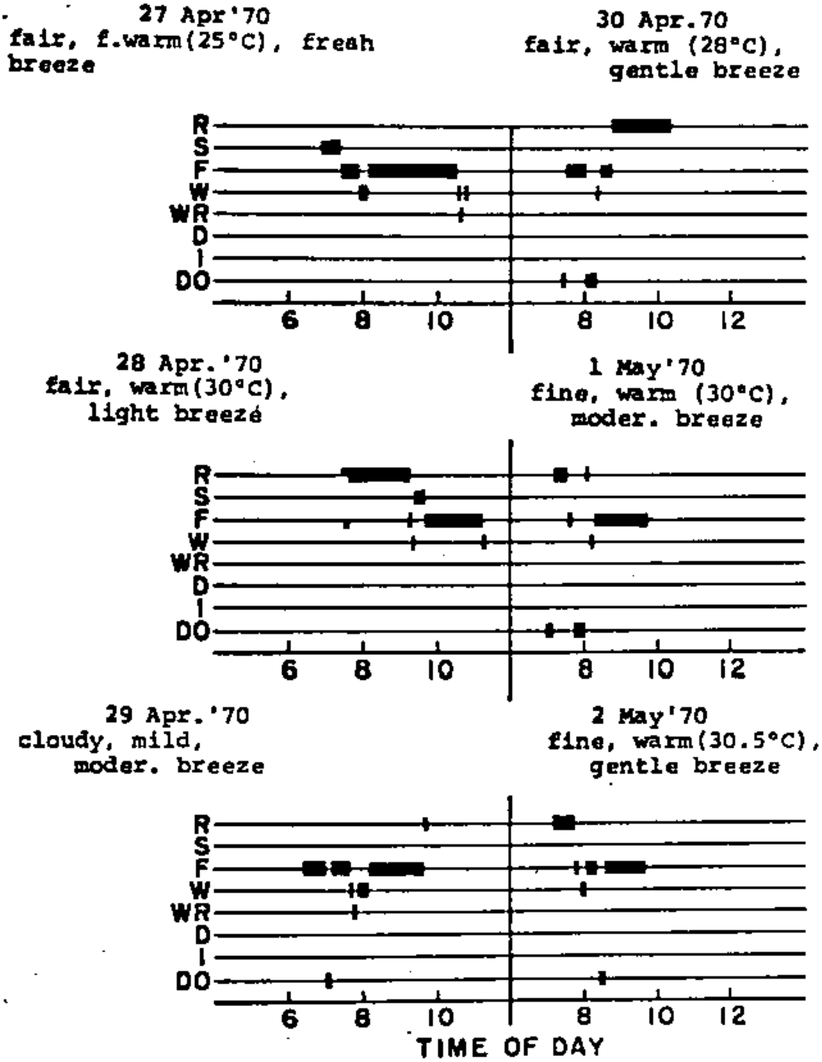
19 Apr.'66: cloudy, mild becoming cool, mod.-fresh breeze, rain commencing 1530 hours



20 April'66: cloudy becoming fair p.m., mild, gentle breeze



c. Cow-subadult pair observed on 6 consecutive mornings



27 Apr'70
fair, f.warm(25°C), fresh
breeze

30 Apr.70
fair, warm (28°C),
gentle breeze

28 Apr.'70
fair, warm(30°C),
light breezé

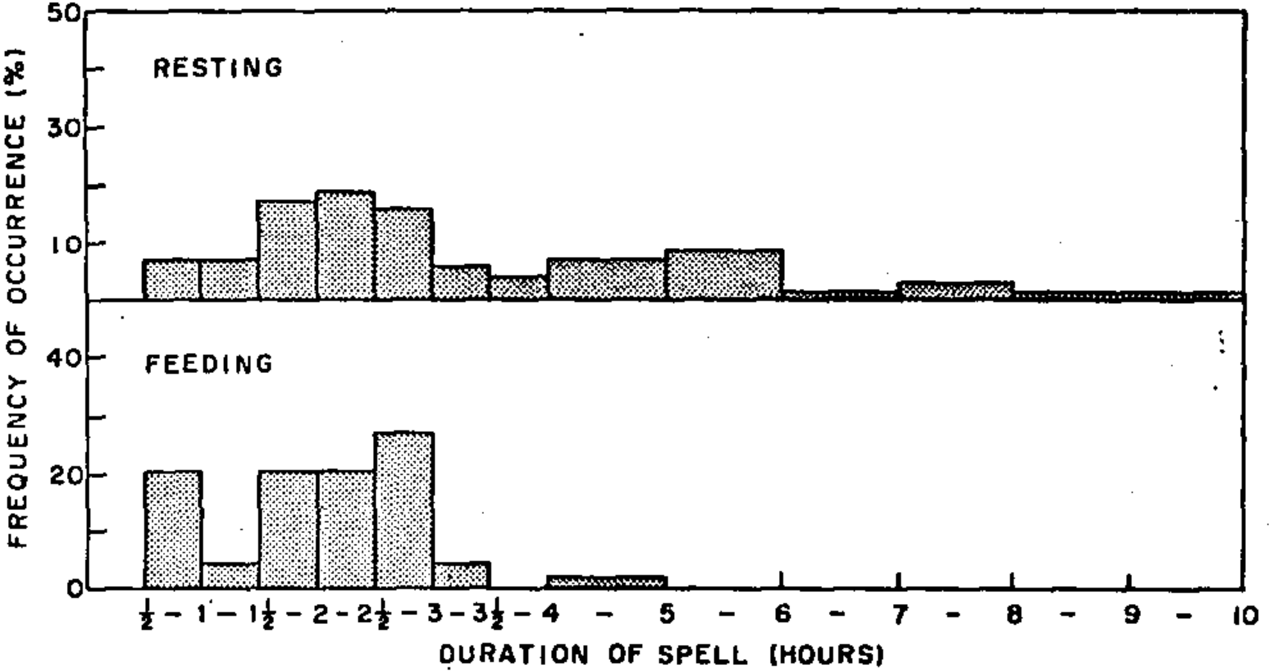
1 May'70
fine, warm (30°C),
moder. breeze

29 Apr.'70
cloudy, mild,
moder. breeze

2 May'70
fine, warm(30.5°C),
gentle breeze

FIGURE 16. Duration of activity spells

Only bouts of activity lasting at least 30 mins are considered, and interuptions lasting less than 30 minutes are ignored



to 3 hours, but longer rest periods are associated with the midday period. Some of these may extend as long as 10 hours.

8. Age/sex class differences

There are no striking differences between the activity patterns exhibited by adult males, adult females and subadults, despite differing body sizes (adult males 2000-2300 kg, adult females 1500-1700 kg, subadults 800-1800 kg) (Fig. 17 and 18). Subadults maintained slightly higher activity levels during the hotter part of the day, and devoted slightly more overall time to feeding (52.7% vs 47.4%, $N = 12.224 + 5741$, $X^2 = 44.1$, $df = 1$, $p \ll 0.001$). Cows devoted more time to feeding than bulls from January to June (47.0% vs 43.0%, $N = 3124 + 4066$, $X^2 = 11.8$, $df = 1$, $p \ll 0.001$), but less time from July to December (48.1% vs 51.0%, $N = 2493 + 2545$, $X^2 = 4.37$, $df = 1$, $0.025 < p < 0.05$). Since March, April and May are the peak calving months, the longer feeding time may be related to the increased food demands associated with pregnancy and lactation. A breakdown in the records for cows by age of associated calf (Table 12) suggests that

FIGURE 17. Age/sex class differences in activity pattern

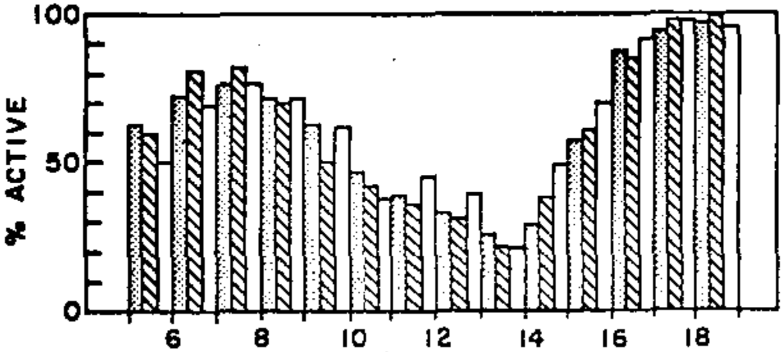
Results expressed in terms of percent rhinos active, i.e. not resting. Individual sample sizes vary between 52 and 423 15 min rhino activity units

░ ADULT MALES ▨ ADULT FEMALES ☐ SUBADULTS

a. Sunny conditions (all seasons)

Mean daytime activity levels:-

ADď - 60.9% AD ♀- 59.9% subad - 60.5%



b. Cloudy weather (all seasons)

Mean daytime activity levels:-

ADď - 72.0% AD♀ - 69.9% subad - 72.0%

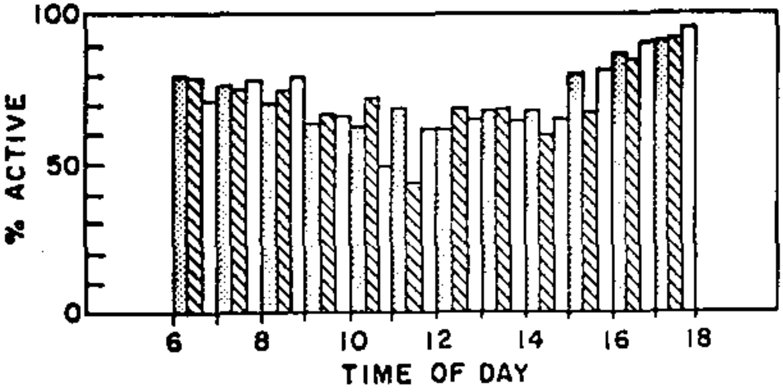


TABLE 12. Activity levels of cows in relation to reproductive status

Data refer to the period April-May-June

Age of accompanying calf	feeding %	resting %	other activities %
6-18 months	46.3	36.8	15.8
18+ months	52.3	32.8	14.8
under 6 months; or cow known to be pregnant and near full term	52.4	30.6	17.0

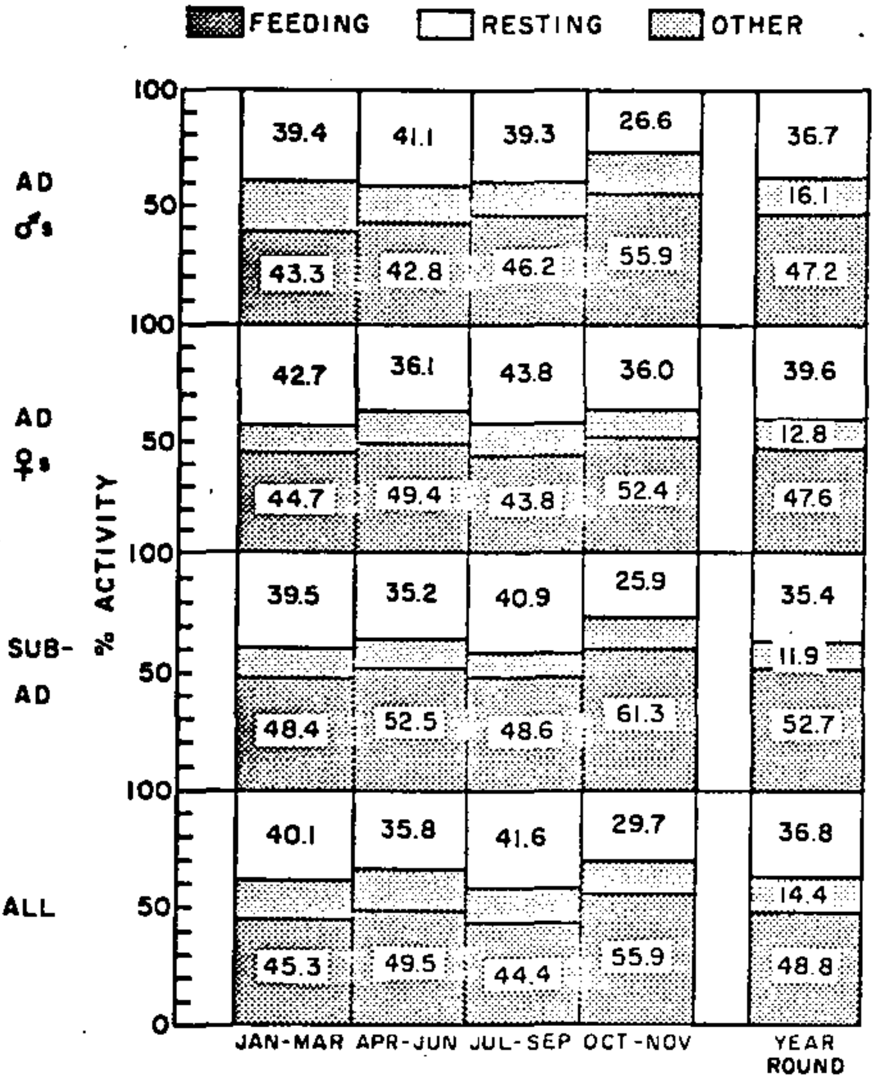
females with calves aged 6-18 months spend less time feeding than those with older or younger calves or known to be near full term pregnancy; but sample sizes are limited, and results are significant only at the 10% confidence level (cows with calves aged 6-18 mo. vs cows with calves aged 18+ mo.: 46.3%, $N = 721 + 716$, $X^2 = 5.15$, $df = 1$, $p \angle 0.025$; cows with calves aged 6-18 mo. vs cows with calves aged $\angle$ 6 mo. or pregnant: 46.3% vs 52.3%, $N = 721 + 394$, $X^2 = 3.62$, $0.05 \angle p \angle 0.10$). The first category includes cows in the later stages of lactation or post-lactation, while the other two categories include animals that were either known or likely to be either pregnant or in early lactation. Adult males devote more time to miscellaneous activities than do females and subadults, probably related partially to patrolling territories by territorial bulls.

9. Overall activity budgets

White rhinos of all age/sex classes devote a year-round average of 48.8% of the daytime hours to feeding (Fig. 18). Adequate night data are available only for the period April-June, and indicate that during this

FIGURE 18. <u>Overall daytime activity budgets</u>

Mean proportion of daylight hours devoted to major activity categories over all seasons and weather conditions.



season over a 24 hour period 49.7% or 12 hours are spent feeding, 35.2% or 8 1/2 hours resting, and the remaining 3 1/2 hours are devoted to other activities (walking, standing alert, wallowing, and social interactions).

One particular group followed continuously for 20 hours over 7-8 March 1966 (Fig. 14f) spent 6 1/2 hours feeding, 11 1/2 hours resting, 1/2 hour walking and 1 1/2 hours standing disturbed. Probably most of the missing 4 hour period running though the early evening was devoted to grazing, suggesting a total of 10-10 1/2 hours spent feeding during the 24 hours. The least time devoted to feeding in this example may be a result of the vigorous summer growth of grass experienced in 1966.

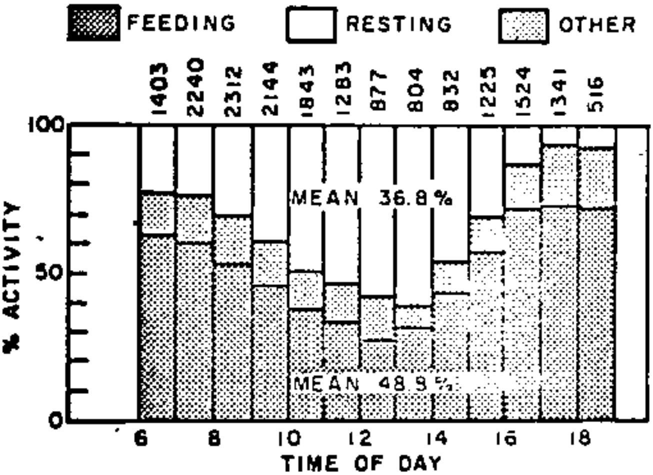
Discussion

The basic individual activity schedule consists of alternating spells of feeding and resting of about 1.5-3 hours duration. The diel fluctuations in ambient temperatures and insolation impose a bimodal pattern on activity levels, with activity peaks occurring during the early morning and early evening periods (see Figure 19). However, this cycle becomes indistinct under conditions of

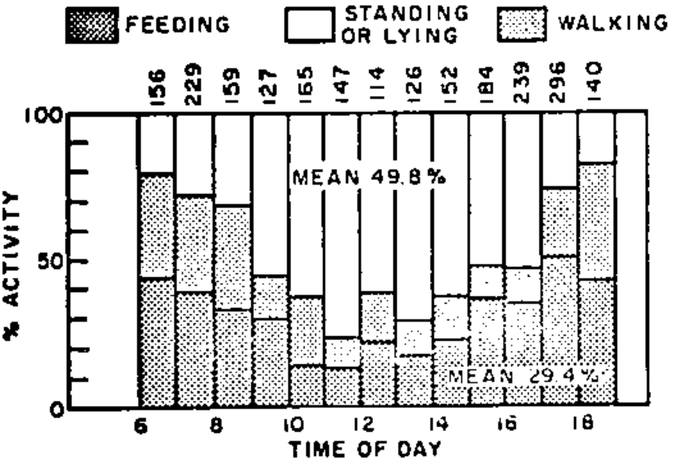
FIGURE 19 . Diurnal activity pattern: comparison between white rhinoceros and black rhinoceros

Figures indicate sample sizes

a. White rhinoceros schedule, all conditions



b. Black rhinoceros schedule, all conditions
(combined data from Goddard 1967)



These differences presumably arise from the differing actions of a browser devotes a portion of its time to walking from one discrete bush to another while a non-selective grazer such as the white rhino can feed steadily as long as it is located in a suitable stand of grassland. The consequent limitations in rate of intake of food per unit time by browsers may be the basis of the smaller body size of the black rhino.

The African elephant is reported to spend 16 hours per day feeding, 1 hour drinking, 1 3/4 hours walking, 3 hours standing and 2 1/4 hours lying down (Hendrichs, 1971). Presumably it is able to be more active through the day than the white rhino on account of having more efficient heat radiators, in the form of its large ears. The extra amount of time it is able to devote to feeding may be significant in allowing it to attain a larger body size than the white rhino. Innes (1958) found that giraffe spent 55-83% of the daylight hours feeding. Waterbuck fed for 43-64% of the day and 17-38% of the night (Spinage 1968), and warthogs devoted 24-77% of the day-time hours to feeding, resting in holes at night (Clough and Hassam, 1970, and Bradley's (1968) data as quoted by them). The white rhinoceros seemingly devoted a slightly greater proportion of its time on a 24 hour basis to feeding than these species, but this difference may be related to decreased food availability at Umfolozi on account of grassland degradation.

Time budgets for the late dry season period indicate that the white rhino does not respond to the prevailing conditions of food stress by spending more time searching out optimum food. Rather, the animals simply fill their bellies quickly with the coarse dry grass which is readily available, though this may be submaintenance in nutrient levels. The unusually ample fat deposits built up over summer probably assist in carrying the animals through this lean period. Selous (1899) reported that "Towards the end of the rainy season, in February and March, white rhinoceroses used to become excessively fat, and would often keep in very good condition until late in the dry season. I have seen them so fat, that between the skin and the flesh over the greater part of the body there was a layer over one inch in thickness, whilst the whole belly was covered in fat two inches thick."

The major period of environmental stress is at the commencement of the wet season. The animals are then in poorest condition, having passing through the winter dry season. To take advantage of the freshly sprouting but still very short grass, they are forced to be more active during the hot part of the day, causing further problems through potential heat stress.

D. SPATIAL PATTERNS OF HABITAT UTILIZATION

Introduction and methods

Observations soon revealed that certain individuals tended usually to be found in particular localities. This characteristic was more strikingly apparent in white rhino bulls than in cows or subadults. Evidence will be presented in the next chapter to show that the movements of adult males are strongly circumscribed by social pressures. In this section, attention will be focussed on the relationship between movement patterns and habitat requirements. In particular, the movement patterns of cows will be considered, since these seem little influenced by social factors. Consideration of the ranging patterns of bulls, and of the relationships between the ranges of different individuals, will be deferred to the succeeding chapter on sociology.

The locations and movements of all rhinos encountered were mapped, and these data provide the basis for the estimation of individual home ranges. Cows and immature animals moved over a greater area than could adequately be surveyed on foot, and radio-telemetry was introduced especially to determine the extent of the wanderings of a sample of females and subadults. Six adult females, one subadult female, one subadult male and two young adult males were equipped with functioning radio transmitters (see Section II.A.4), but radio-tracking was only possible for a period of one year between March 1970 and March 1971, while individual transmitters functioned for shorter periods. Radio-telemetry in principle allows the unbiased determination of individual locations on demand. In practice, while the two main tracking stations used gave excellent coverage over the northern part of the Madlozi study area, transmitter signals were frequently blocked out by the steep sides of the Madlozi valley, and extra effort was needed to locate animals there. Thus, relatively fewer locations were obtained for this section. Furthermore, radio-tracking periods were sporadic, and do not encompass all environmental conditions. Radio-telemetrically determined locations supplement more extensive data obtained by chance locations during foot patrols, and correct to some extent bias in the latter towards the central study area.

Areas of home ranges were determined by connecting outlying points and measuring the enclosed area planimetrically. Since all home range distributions are to be considered incomplete, all areas quoted should be regarded as minimal estimates.

1. Home ranges of adult females

Maps of the distribution of locations of individual cows (Fig. 20, a-h) reveal that each has a preferred area of occupancy which is different from that of other individuals, though there is extensive overlap between the various ranges. The sample of eight cows for which range maps are presented represent those individuals whose ranges are believed to be the most comprehensively recorded, in six cases through the aid of radio telemetry. A further seventeen cows regularly frequented the Madlozi central study area, and another 25 were recorded as occasional visitors. Partial home ranges for some of

FIGURE 20. Home ranges of cows and subadults

1-3 points have been plotted for each day seen

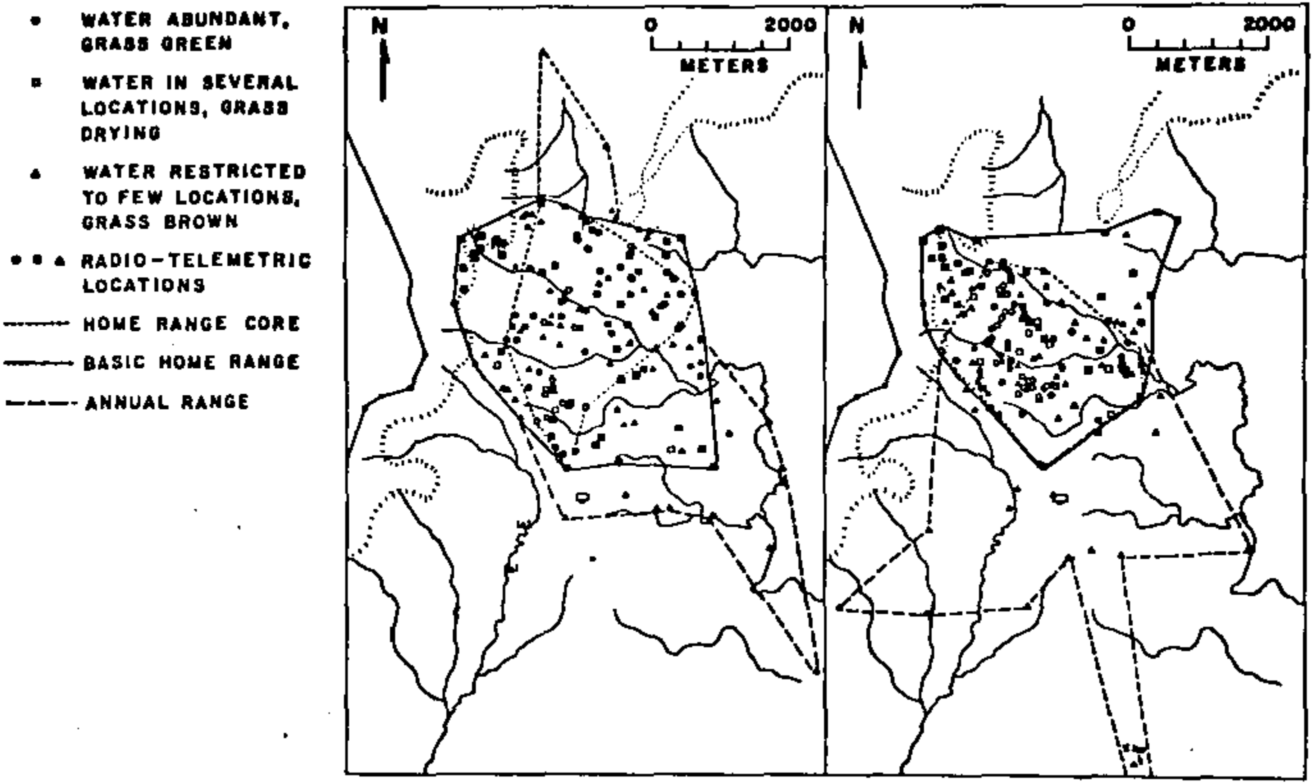
Total number of points, observation duration and home range areas for each individual are presented in Table 13.

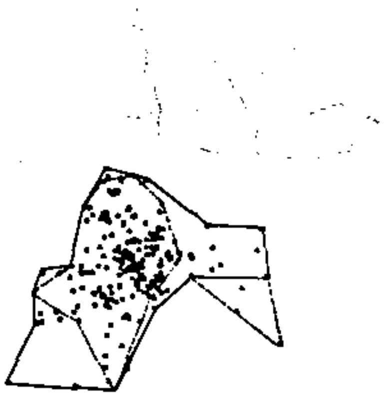
Opposite:-

left, Fig. 20a, ADf-P
right, Fig.20b, ADf-O

HOME RANGE DISPERSIONS FOR TWO COWS

MADLOZI STUDY AREA, 1 DEC. 1968 – 4 SEPT. 1971





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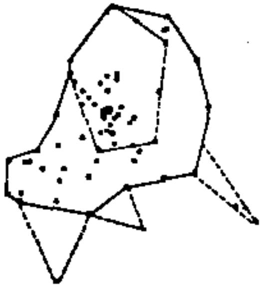

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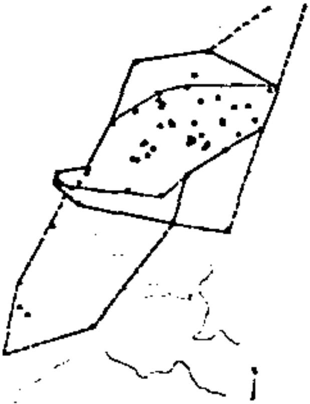

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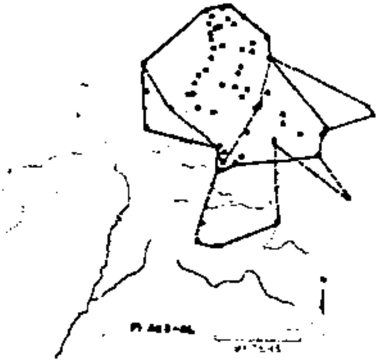

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these individuals confirm this general pattern.

There were differences in the extent of the area utilized under differing seasonal conditions. When grass was green and water abundantly available, individual cows restricted their movements to within an area of about 6 to 8 km^2 (Fig. 20, Table 13), which will be referred to as the home range core. With deteriorating forage quality (grass mainly green to mainly brown), movements were extended further afield, bring the extent of the area utilized up to about 10 to 15 km^2. This area will be termed the home range. When all temporary pools within the home range ran dry, animals were forced to make special drinking excursions towards one of the long-lasting waterholes--at Madlozi, usually either towards the Nyonikazane Spring in the south, or the Mphafa Pools in the south-east. An excursion by the cow P to the north (Fig. 20a) is related to the presence of a small spring in the Thobothi Stream. With the drying up of the Mphafa Pools towards the end of the dry season, animals relying on this source were forced to continue on to the White Umfolozi River, about 5 km further south, in order to drink. However, drinking excursions were only temporary, lasting less than a day,

TABLE 13. Sizes of home range of eight cows and two subadults

Areas measured planimetrically from maps presented in Fig. 20.

Map	indiv.	method	period	no. location points:- conditions: (1)	(2)	(3)	all	core area	area (km^2):- home range	annual range
20a	ADf.P	r-t	Aug'70-Mar'71	28	39	43	110	5.7	11.4	18.2
		total	Dec'68-June'71	55	41	62	158			
20b	ADf.O	r-t	Apr'70-Dec'70	13	34	42	89	5.3	9.1	19.6
		total	Dec'68-Sep'71	58	42	73	173			
20c	ADf.U	r-t	Mar-Dec'70	27	43	17	87	7.9	14.7	16.1
		total	Feb-July'66, Dec'68-July'71	82	89	32	203			
20d	YADf.V	r-t	Sep'70-Aug'71	21	19	2	42	5.3	13.6	16.2
		total	Sep'70-Sep'71	30	22	20	72			
20e	ADf.ZZ	r-t	June'70-Mar'71	23	13	6	42	7.4	10.9	20.5
		total	Aug'69-June'71	25	17	12	54			
20f	ADf.AL	r-t	Aug'70-Jan'71	13	22	22	57	6.3	10.2	14.7
		total	Aug'70-Jan'71	15	24	23	62			
20g	ADf.J	r-t	-	-	-	-	-	9.6	14.0	15.3
		total	Jan-June'66, Dec.68-Aug'71	51	24	39	114			
20h	ADf.AA	r-t	-	-	-	-	-	6.4	8.9	8.9
		total	Dec'68-Aug'71	69	14	17	100			
20i	sam.r+	r-t	Aug'70-Jan'71	9	5	12	26	5.0	7.0	7.3
	saf.d	total	Jan'70-June'71	41	7	16	64			
20j	samb	r-t	-	-	-	-	-	4.3	4.3	6.1
		total	Dec'68-Sep'71	21	3	15	39			

r-t = radio-telemetric

Conditions: (1) grass green, water abundant; (2) grass drying, water in several locations; (3) water restricted to major waterholes.

and animals returned to within their usual home ranges in between such waterhole visits. The range traversed was thus extended during the late dry season by corridor extensions leading to long lasting sources. The total extent of the animal range covered, including such movements, was 20 km^2 or more in some cases. However, those cows whose home ranges adjoined permanent water sources (e.g. U and AA, Fig. 20 c and h), did not exhibit such striking range extensions.

Some individuals may move over even larger areas. A distinctive cow with a missing right ear was an occasional visitor to the Madlozi study area from the south-east. Ranger M. Behr reported that he had seen her twice in the vicinity of the White Umfolozi River, once to the south of the river in the Mpekwa area. The distance between the latter sighting, and the furthest north record at Madlozi, is 13 km.

Two of the transmitterised cows (P and O) are known to have moved to the vicinity of the White Umfolozi at the end of the dry season where they were, except under favourable conditions, beyond radio-telemetry range. These excursions were not prolonged more than one to two days; but it is possible that, had the arrival of the spring rains been delayed further, the cows may have stayed in the vicinity of the river longer. No signal was received from the transmitter of another cow (ZZ, Fig. 20e) for much of the dry season of 1970, and she had evidently moved away beyond the range of the equipment, presumably either to the vicinity of the Black Umfolozi River or the Gqoyini Pans to the north-east.

Other cows that were regular visitors to the study area during summer were not recorded there during the late dry season. Without the aid of radio-telemetry, it was not possible to establish the extent of their movements. However, by comparison with the movement patterns exhibited by the transmitterised animals, it is presumed that they had moved away no further than a few kilometres to one of the hill systems offering abundant long grass. As is evident in Fig. 20, the cows P and) concentrated their late dry season grazing on the slopes of the northern part of this range, AL used the vicinity of Mantivana Hill, and ZZ was recorded in the region of the Mbulunga Range.

Temporary excursions well beyond the usual range may occur under unusual circumstances. Among the rhinos grazing the slopes of the Zintunzini Hills in November 1968, when the grassland was sprouting freshly green after a burn, was a distinctive cow with a broken off anterior horn. This cow was not seen subsequently at Madlozi, but an animal which may have been the same individual was seen once by me and several times by other observers between Mpila Camp and the Black Umfolozi bridge, 28 km to the east. No other broken-horned cow was known to me; suggesting that this animal had wandered westwards for this distance at the end of the 1968 dry season in search of favourable grazing conditions. Rangers reported that, before the reserve was fenced, rhinos sometimes appeared during the months of September and October well to the south of their usual haunts.

I have only one example of what may have been a shift in home range. An ageing individual HA, readily recognisable by her unusually projecting anterior horn, was not seen in the Madlozi study area prior to March 1970. However, I recorded her once from the road some 6-7 km further north. In April 1970 she appeared at Madlozi, in oestrus and being accompanied by one of the study area territorial bulls, and she was mated there a week after her appearance. Subsequently she was fairly regularly seen at Madlozi, ranging as far south as the Lily Pan.

The cow J (Fig. 20g) exhibited an unusually large home range core area. This is related to several sightings of her in the Madlozi valley made over a short period under wet season conditions. In 1966, when I covered this section regularly, she was never seen there. This movement could thus represent a temporary extension. She was probably familiar with the region from visits to the Nyonikazane Spring made under dry season conditions. No other cow whose history was followed over an extended period exhibited any notable shift in home range. Eleven of the cows that had been known to me in 1966 could be recognized again after by return 2 1/2 years later. All were occupying the same localities as before.

Home range limits were indistinct, except where related to topographic features. Several of the cows that regularly frequented the northern part of the Madlozi study area seldom entered the Madlozi valley (e.g., P and O, Fig. 20 a and b), while the Zintunzini Range provided a natural boundary on the west. In other cases, location records simply became increasingly sparse towards home range limits. This is best illustrated by the cow AA (Fig. 20h), whose northern range limits coincided with the most intensively covered section of the study area. She was regularly encountered in the Madlozi valley, and was less frequently seen on the southern part of the bush cleared zone flats below the Zintunzini Range. Location records become increasingly scattered further northwards, and she remained only for a day or less before returning southwards. I watched the cow U (Fig.20c) at the apparent northern limit of her home range graze in a semicircle veering back southwards. Other cows whose home range were peripheral to the study area (e.g. ZZ and AL, Fig. 20 e and f) were recorded as occasional visitors to the central study area. They were encountered there over one or several successive days, then disappeared again.

2. Home ranges of subadults

Subadults usually did not move about singly, but joined up with other subadults or with adult cows. Those that attached themselves to adult females adopted the home ranges of the latter for the period of association. Only a few subadults remained regular inhabitants of the

Madlozi study area for an extended period without being associated with a cow for much or all of this period. Some of the disappearances of younger subadults may be related to the rhino capture operations being carried out on the periphery of the study area, while the dearth of older subadults was probably a consequence of rhino removals carried out here in the past. Information on the ranging patterns of subadults is accordingly limited.

The range distributions of two subadult males have been plotted in Fig. 20 g and h. The radio-equipped individual r was a 7-8 year old male accompanied by a 5-6 year old subadult female companion. This pair was recorded over a range of 7.3 km^2, though this is probably an incomplete estimate because of difficulties associated with receiving a radio signal from the Madlozi valley area they favoured. The 3-5 year old male b was generally accompanied by a subadult male companion of similar age. Apart from one brief excursion to the north, he was seen only in the Madlozi valley, and records encompass an area of 4.3 km^2. Another pair of slightly older subadult males was also encountered frequently in the Madlozi valley, but was never seen elsewhere.

Other observations on subadult ranges are available from 1966, though these span a time period of only five months. Two approximately 7 year old males moved as a pair over two adult male territories, encompassing an area of 2.2 km^2. A pair consisting of a roughly 7 year old male accompanied by a 3 year old female were encountered only within a single adult male territory covering an area of 2.1 km^2. Another pair consisting of a six year old female together with a six year old male wandered over the whole 4.3 km^2 extent of the Madlozi valley, and were also seen to the north of the limits of the 1966 study area.

The female V was fitted with a radio transmitter as a 6 1/2 year old subadult, but bore her first calf a month later. Her subsequent range has accordingly been plotted with those of the adult cows (Fig. 20d). While a subadult, she had been a constant companion of the cow U, whose home range is presented in Fig. 20c, for at least 11 months. Following the birth of a calf to U, V remained independent for two months, then attached herself to another adult female (VV) for the month preceeding the birth of her own calf. The subsequent home range adopted by V was similar to that of the cow U, but she ranged further northwards than either U or VV.

These observations indicate different ranging patterns for subadult males and females. Subadult females moved over fairly extensive home ranges resembling those of adult cows, while subadult males restricted their movements mainly to one or two adult male territories. When a subadult male was associated with a similar aged subadult female companion the home range seemed determined by the female.

Some subadults apparently had no fixed home range. Several recognisable individuals appeared in the Madlozi study area, were seen there regularly over a period of a few days or several months, then were not recorded again. Two animals ear-tagged in the study areas were later located 10-15 km away. Thus, a segment of the subadult population is apparently semi-nomadic, remaining in one area for a period of weeks or months, then shifting on elsewhere. Permanent home ranges are probably not established by females until after the birth of their first calf, and by males probably not until the acquisition of their first territory (see next chapter).

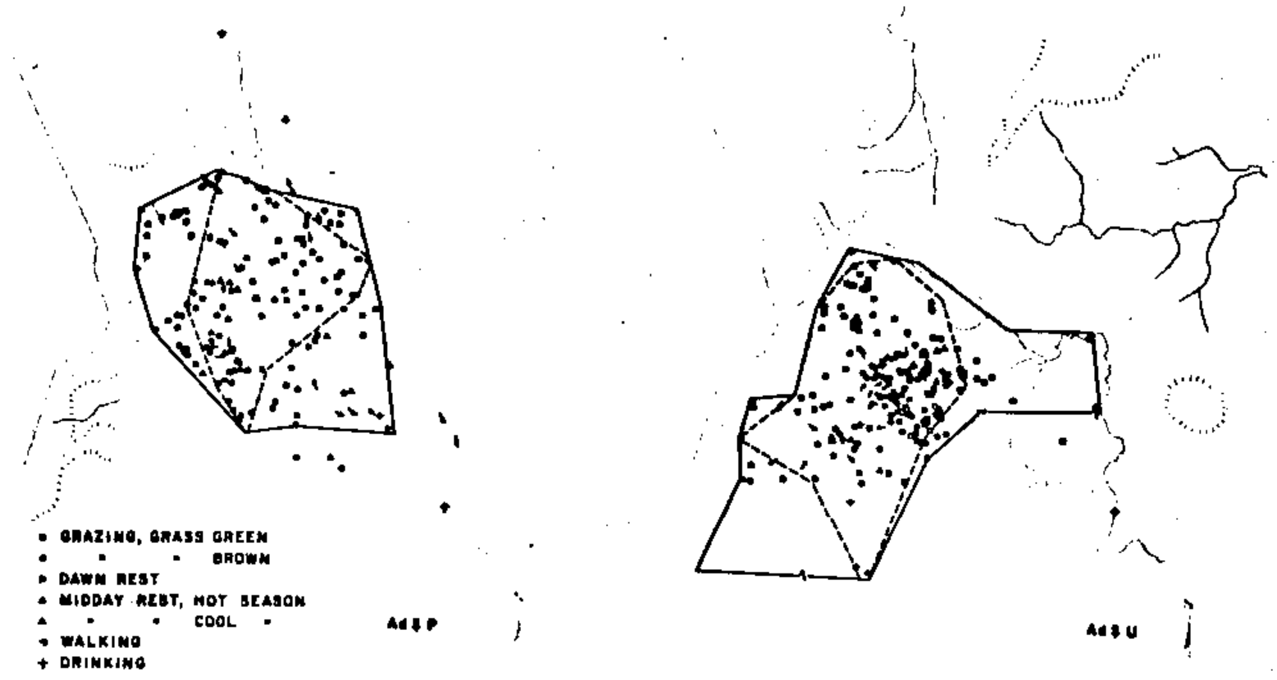
3. Activity distribution within the home range

Further information is revealed by considering the activities that were being performed by the animals when located (Figure 21).

Wet and dry season grazing areas were interspersed through a typical home range, reflecting the mosaic of long and short grass areas prevailing at Madlozi; there were no clear seasonal distinctions in areas utilized, except for the concentration on hillslope areas during the late dry season. The cow P then favoured the hillslope grasslands in the north-west, while the cow U favoured hillslope grasslands in the south-west. For the midday rest during the hot season, each cow had certain favoured ridgecrest localities, but different resting localities were used on different occasions. Cows did not restrict themselves to any particular sites at these localities, and shared these rest areas with many other cows. Steady walking was generally in the direction of one of these rest places, or to or from one of the long-lasting water holes. The cow U was known to use both the Nyonikazane Spring and the Mphafa Pool; P did not visit the Nyonikazane Spring, instead drinking at either the Mphafa

FIGURE 21. Activity dispersion within the home range

All single observations plus locations at 15 minute intervals plotted for periods of continuous observation, have been plotted.


● GRAZING, GRASS GREEN
● " " BROWN
▸ DAWN REST
▲ MIDDAY REST, HOT SEASON
▲ " " COOL "
→ WALKING
+ DRINKING
Ad♀P
Ad♀U

Pools or at the small Thobothi Spring to the north, or when these ran out at the White Umfolozi River. During summer a profusion of small pans offered water throughout most of the home range, and these pools were used also for wallowing.

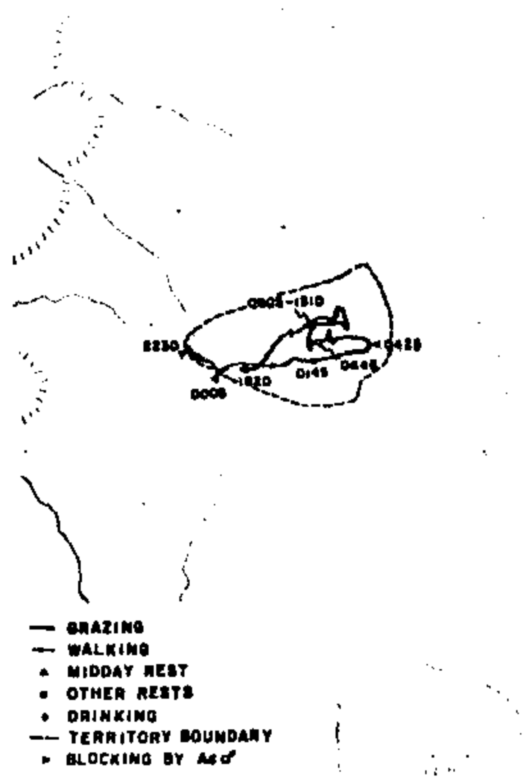
4. Pattern of movements about the home range

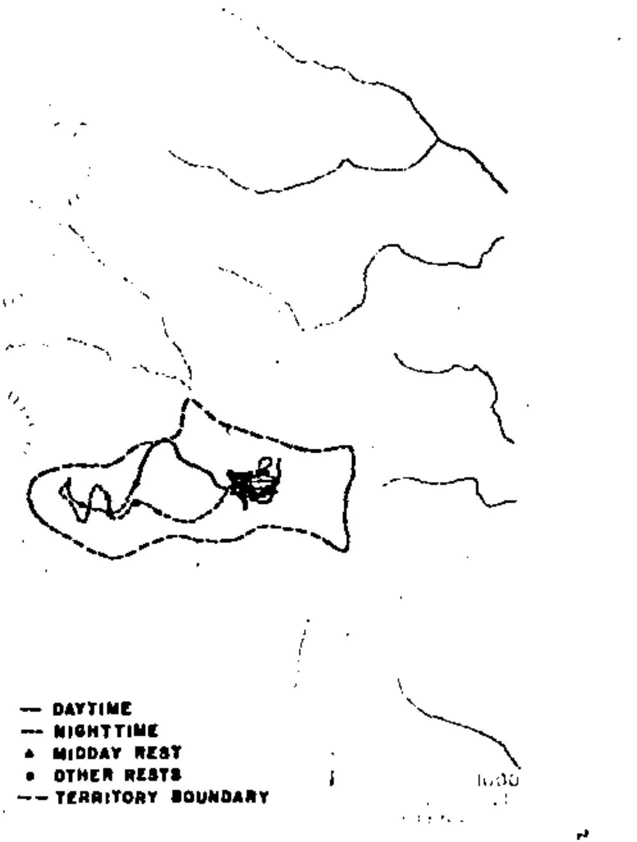
On one occasion I kept a watch on the movements and activities of a rhino group continuously for 20 hours; on another occasion, with the aid of members of the Fieldwork Section of the Wildlife Society, a group was kept under observation for 40 hours with only short interruptions. The movements of the former group are mapped in Fig. 22a, and correspond to the activity schedule presented in Fig. 14f. The total distance covered along their path of movement during the 20 hours was about 4 km. During the 40 hour period, the second group covered about 8 km, mostly accomplished while grazing in circles in one locality (Fig. 22b). Both groups included an oestrous female that was being accompanied by a territorial bull, and their movements were circumscribed by the blocking actions of the bull whenever they approached his territory boundary.

FIGURE 22. Details of movements of particular groups over short periods

Left: Movements of group consisting of tADm + 2 ADfs + saf during 20 hour period, 2230-1820 hours, 7-8 March 1966.

Right: Movements of group consisting of tADm + ADf + calf during 40 hour period, 0715-0032 hours, 5-7 April 1966.


0805-1310
2230
0008
1820
0145
0445
0425
— GRAZING
— WALKING
▲ MIDDAY REST
● OTHER RESTS
◆ DRINKING
-- TERRITORY BOUNDARY
► BLOCKING BY A₆♂


— DAYTIME
-- NIGHTTIME
▲ MIDDAY REST
● OTHER RESTS
-- TERRITORY BOUNDARY

Free ranging cows might move over greater distances.

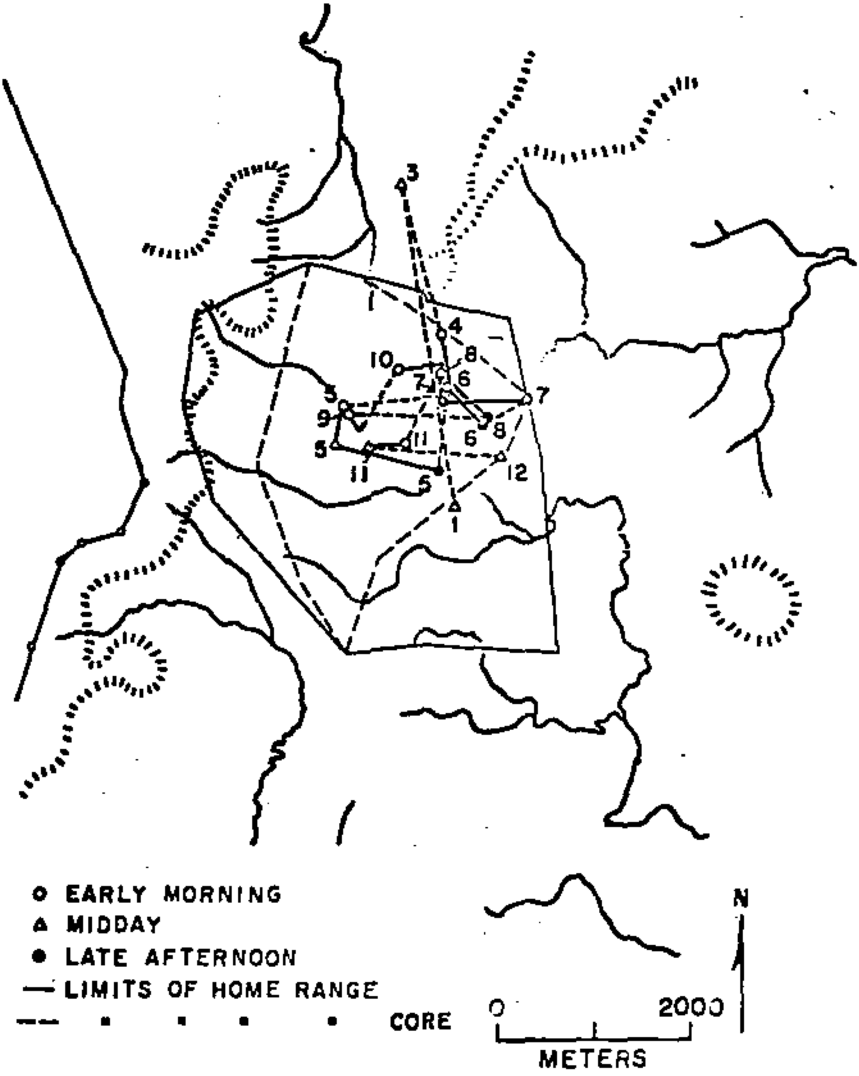
Later, with the aid of radio-telemetry, I located the cow U almost daily over 30 consecutive days, and on 10 consecutive days her detailed movements during the morning and late afternoon periods were watched. Further information on movement patterns was obtained by radio-tracking the locations of all transmitter bearing animals for periods of 10 consecutive days.

None of these periods covers optimum midsummer conditions, and were approached most closely over part of the period covered in Fig, 23. A dry spell, during which most pans ran dry, was broken by heavy rain falling on March 2 (day 3), which brought the grass back to full greenness within 2-3 days. The cow P had evidently moved northwards to drink at the Thobothi spring on day 3, but with the return of favourable conditions she limited her movements to within a small part of her home range. The area encompassed by connecting outlying points from day 4 onwards is about 1.5 km^2. Generally, when grass was green and water plentifully available, individual cows were reencountered over several successive days in the same grazing localities of about 1-2 km^2, and cows evidently

FIGURE 23. <u>Movement pattern during late wet season</u>

Radio-telemetric locations determined three times daily are shown for ADf-P over 12 consecutive days, 28 Feb.-11 Mar. 1971.

A dry spell was broken by heavy rain falling on Mar. 2 (=day 3); thereafter grass was green and water plentiful.


3
4
8
10
7
6
5
7
9
8
6
11
5
12
11
5
1
○ EARLY MORNING
△ MIDDAY
● LATE AFTERNOON
— LIMITS OF HOME RANGE
— — ▪ ▪ ▪ ▪ CORE
0
2000
METERS
N

moved around relatively little under such conditions.

The autumn or early dry season period covered in Figure 24 is characterised by an alternation of drying and greening up periods in the grassland. Over the period 25 April-4 May the grass was sprouting freshly green after light rain, but some drying out commenced over the last few days, and the cow U clearly oriented her movements around one particular midday resting area. She grazed outwards from here in the late afternoon, and back inwards towards it again during the morning grazing spell. Overnight movements probably completed the circuit. An alternative midday resting site was used only on day 5, when conditions were cool and cloudy. The total area encompassed by her daylight movements over this period was 2.4 km^2.

The 30 day period covered in Fig. 24b includes a succession of drying and greening periods. No regular pattern of movement is discernible. During drying periods, probing movements outwards towards the extremities of the home range were made, while during periods of grass growth, movements were confined to a smaller area near the central part of the home range. It seemed that the cow explored around until she located favourable grazing, then settled

FIGURE 24. Movement patterns during early dry season

A. Left: Daytime movements and activities of the cow ADf-U over the 10 day period 25 Apr.-4 May 1970. (= days 13-22 of Fig. 24b)

b. Right: Locations of the cow ADf-U over the 30 day period 13 Apr.-12 May 1970; locations are for the early morning in most cases.

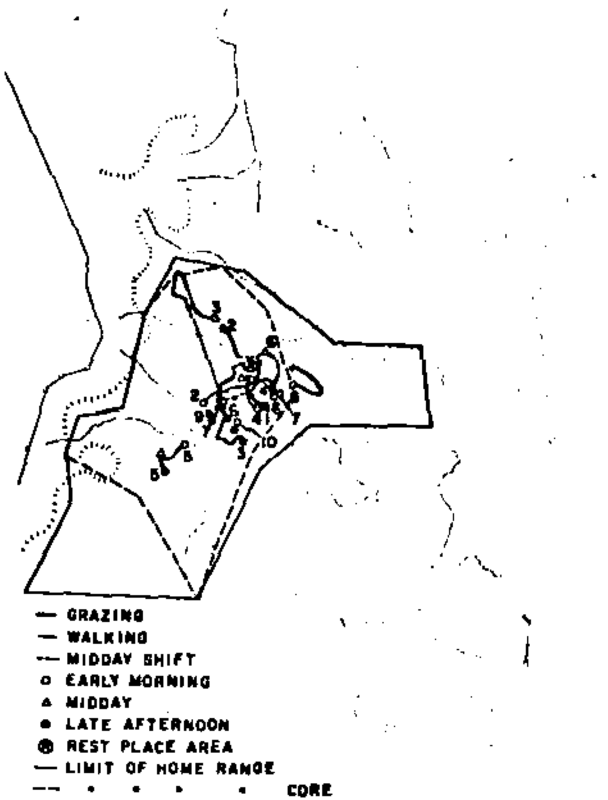
Prevailing conditions:

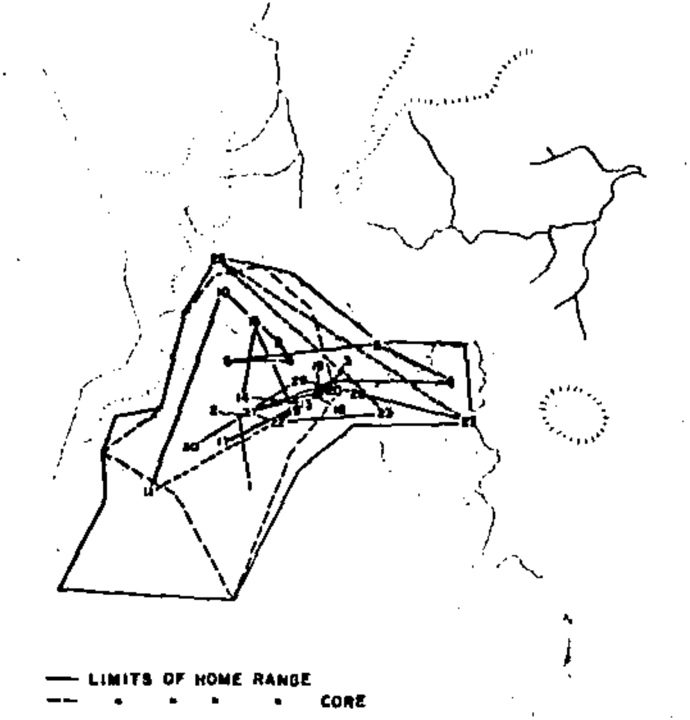
Days 1-4: grass mainly brown, pools dry

Days 5-19: light rain results in scattored pools and freshly sprouting grass

Days 20-26: pools drying up, grass drying off.

Days 27-30: rain creates many pools, grass sprouting green again.


GRAZING
WALKING
MIDDAY SHIFT
EARLY MORNING
MIDDAY
LATE AFTERNOON
REST PLACE AREA
LIMIT OF HOME RANGE
CORE


LIMITS OF HOME RANGE
CORE

A69-U

in this vicinity for a period of several days (e.g. days 18-22). As grazing conditions deteriorated once more, movements were again pushed further afield.

Drying conditions seemed to provide a stimulus for a general shuffling in the rhino population. Individuals that had been seen repeatedly in the same vicinity over several successive days disappeared, and new individuals made an appearance. A prolonged drying spell was likely to bring an influx of "strangers", individuals which were only occasionally seen in the study area. No regular pattern was discernible, as some individuals moved in while others moved out. The arrival of rains breaking a dry spell promoted a similar shifting around by the rhino population.

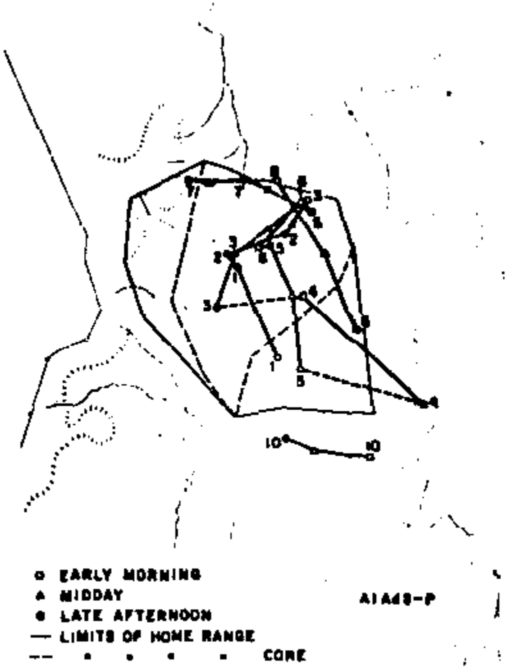
A feature of late dry season movements (Figs. 25 and 26) was the extensive movements to and from the direction of one of the major waterholes every few days. During the initial part of the radio-tracking period covered in Fig. 25, the cow P was evidently drinking at the lower Mphafa Pool at 4 day intervals (the upper pool was then dry). Movements from the pool back towards the central home range are evident on days 1 and 5, and outwards in

FIGURE 25. Movement patterns during the mid-dry season

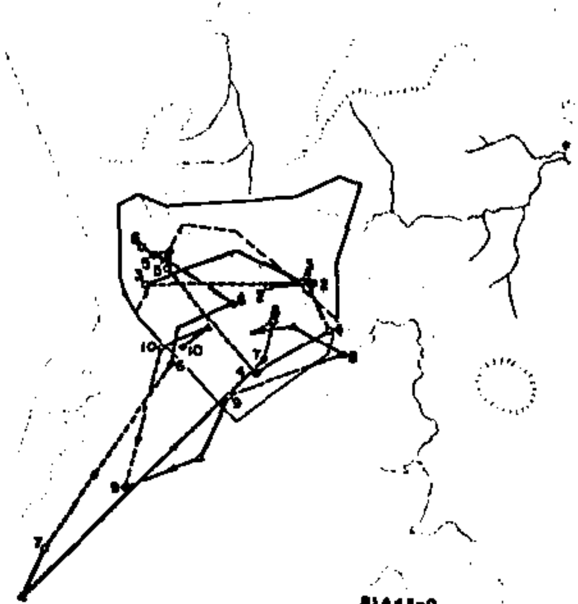
Radio-telemetrically determined locations obtained three times daily over the 10 day period 26 Aug.-4 Sept. 1970 are shown for two cows:

a. left ADf-P

b. Right. Adf-O



A1A48-P



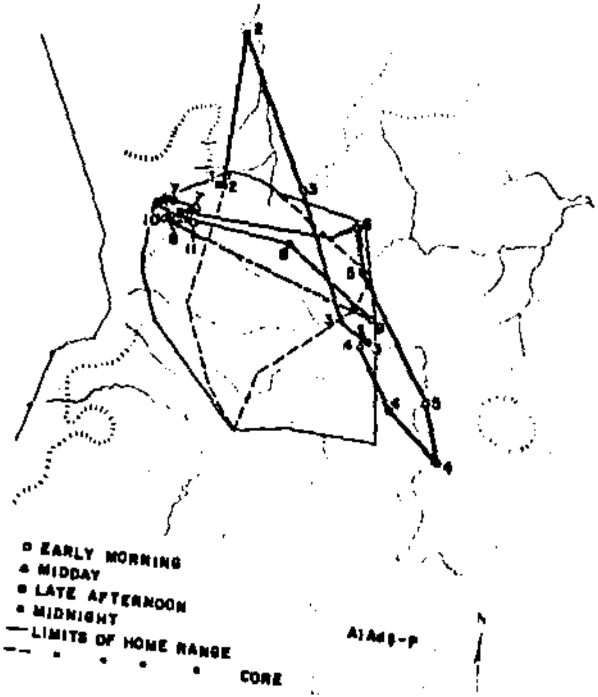
B1A48-O

FIGURE 25. Movement patterns during period covering termination of the dry season

Radio-telemetrically determined locations obtained three times daily over the 11 day period 10-20 Sept. 1970 are shown for two cows; the winter drought was broken by a heavy thunderstorm falling on the night of 13 Sept. (= day 4).

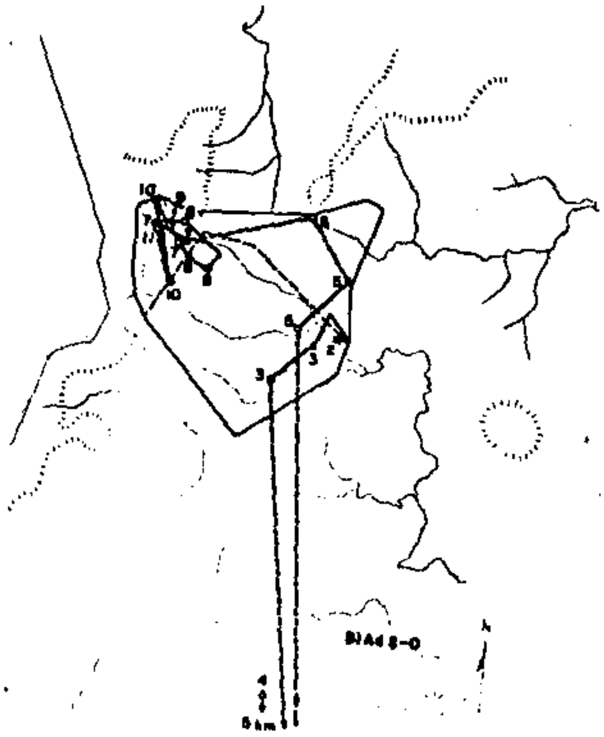
a. left ADf-P

b. right ADf-O



□ EARLY MORNING
▲ MIDDAY
● LATE AFTERNOON
▪ MIDNIGHT
— LIMITS OF HOME RANGE
– – • • • • CORE

A) Ad 8-P



B) Ad 8-O

the direction of the water on the evenings of days 4 and 8. On day 9 no signal was received from her transmitter, and a check of the lower Mphafa Pool revealed that it had run dry. On day 10 P reappeared again, working her way back slowly towards her usual range. Evidently she had continued to the White Umfolozi River on finding that there was no water at the pool. Over the same period, the movements of the cow O are indicative of journeys to the vicinity of the Nyonikazane Spring at intervals of 2 or 3 days. Both cows moved fairly widely over an area of 10-15 km^2.

The period covered in Fig. 26 spans the breaking of the winter drought by the first spring thunderstorm, which occurred on the night of 13 September (day 4). The cow P was moving in the direction of the White Umfolozi River when located at 2100 hours on the night of the storm; the next day, with water plentiful, she moved back into her normal range. Thereafter, she concentrated her grazing in a small area of hillside grassland. Over the same period, the cow O moved away to the vicinity of the White Umfolozi River on the night of 12 September. When seen 1735 on the evening of 12 September, she was feeding slowly southwards, still within her usual range. At midnight, no signal could be received from her transmitter, and she had evidently moved beyond the range of the equipment. The next day, she was located by telemetric triangulation in the vicinity of the Nqolothi beacon, overlooking the White Umfolozi. The straight line distance covered overnight was about 11 km. On the morning of 14 September, following the rainstorm, she was back within her usual range. The reason for this sudden journey is not clear, since water was still available at the Nyonikazane Spring, where she had been drinking up until then.

The night position records obtained on six days over the period 10-20 September showed that there was only limited movement during the nights when no trip to water was undertaken.

Discussion

Interpretation of ranging patterns

The most useful discussions of home range terminology with relevance to large mammals are those of Jewell (1966) and Walther (1967 and 1972). Jewell restates Burt's

(1943) definition as follows: "home range is the area over which an animal normally travels in pursuit of its routine activities." Walther considers home range to be the area "in which an animal or group stays long enough to become familiar with the area and establish a space-time system within it." The total area used by the animal including temporarily used migration routes and occasional excursions, Jewell terms the "lifetime range" and Walther the "aktionsraum" or "action area." However, the term "annual range" (Jay, 1965) seems to me preferable when the time span of study is short relative to the potential lifespan of the animal being observed. Within the home range, Jewell refers to a possible "core area" or several "foci of activity" which is more frequently used than the remainder of the area; and he suggests the use of the term "monopolised zone" for those parts of the home range the use of which is exclusive to one particular individual or group.

The home range reflects a relationship between the individual animal and the ability of the habitat to supply its life requirements. It is the area which presumably has become known to the animal, and which is normally able to supply all its needs in terms of food, water, and shelter from the elements and from enemies, at least for an extended period of time (say several months).

However, wandering further afield may be inhibited, not by decreasing familiarity, but by social pressures from conspecifics. When social inhibition is strong enough to result in strictly exclusive sharply bounded home ranges, these are appropriately termed territories.

Difficulties arise in trying to assign boundaries to the "familiar area" within which the animal "normally travels." In the absence of social pressures, home range boundaries are likely to be diffuse and revealed only by a diminishing frequency of occurrence of the occupant. Any limits drawn to measure enclosed areas are hence somewhat arbitrary.

Such characteristics are shown by the home ranges of white rhino females. Nevertheless, it is clear that white rhino cows do not wander at random, but tend to localise their activities within certain preferred regions of the available habitat. Individual differences in the areas utilised appear merely to be the result of individual idiosyncracies in the localities with which each animal has become familiar. There are no exclusively monopolised zones, and as will be shown in the next chapter, females are generally tolerant of one another in meetings.

However, differing degrees of preference are exhibited for different parts of the range, and these vary seasonally. I have distinguished a core area, not by intensity of utilization as is usually done, but rather on the basis of prevailing environmental conditions. When both good quality food and water are abundantly and widely dispersed, there is no incentive for an animal to move from its most favoured section of its home range. This approach avoids problems in deciding on the particular intensities of usage appropriate for delineation of a core area. All parts of the core area may be covered by white rhino females only at intervals of several weeks, and no regular pattern of movement within the core area was discernible.

More peripheral parts of the home range may not be visited for several months while habitat conditions remain optimal. Some sections may be temporarily subjected to intensive utilization for short periods of days or weeks, for example hillslope grasslands during the late dry season, and seemingly the animal knows that it may find suitable forage there under these conditions. Usage of other parts may be more irregular and opportunistic, as if the animal were searching nearby regions for suitable forage when this was not readily obtainable within the central home range.

Corridors leading to nearby major waterholes may be traversed regularly at intervals of 3-4 days during the late dry season, and the animals are undoubtedly familiar with these routes from previous use. These are not considered part of the home range, since this usage is restricted to special circumstances, and since the animals preferentially return to within the usual home range between such journeys. This exemplifies some of the subjective difficulties in applying definitions based on "normality" and "familiarity," and I suggest that these are best overcome by considering patterns of utilization in relation to prevailing conditions as above.

It is also clear that many subadults do not exhibit established home ranges that accord with the above definitions. Rather, it seems that they have still to become sufficiently familiar with the resources of one particular region to preferentially restrict movements to it. This raises important considerations concerning the applicability of the terms "lifetime range" and "annual range". The former term by implication must include the potentially extensive wandering or dispersal movements made during the period of subadulthood. If only the occasional wandering sallies and temporary range extensions exhibited by adults are to be considered, then the term "annual range" is more appropriate. This term is preferable to the more ambiguous "action space" of Walther (1972).

Comparisons with other ungulates

Goddard (1967) reports that home ranges for black rhino cows vary between 2.5 and 88 km^2, with an average of 14.6 km^2 at Ngorongoro and 34.4 km^2 at Olduvai. However, from his method of recording, these are equivalent to what I have termed the annual range, the extent of which is considerably influenced by the distribution of water supplies. Preliminary findings of Hitchins (1971), using radio telemetry, revealed home range sizes of 5.8-7.7 km^2 for three Hluhluwe black rhino cows. These are closely similar to the areas of 5.3-9.6 km^2 found for the home range core areas of white rhino cows, but are smaller than the full extent of the home range of the latter. Both Hitchins (1969) and Goddard (1967) show that black rhino home range sizes are considerably influenced by habitat type. Hitchins (1969) found a home range size of only 3 km^2 for a black rhino cow inhabiting mainly thicket, compared with 5 km^2 for a cow in a nearby largely savanna area. Goddard (1967) reported home range sizes in the Lerai forest in Ngorongoro of about 2.5 km^2, compared with an average of 15 km^2 for other parts of the crater. Larger home ranges at Olduvai were related to sparsely scattered water supplies.

Thus one may conclude that white rhino female home ranges in favourable habitat, tend to be larger than those of black rhino females under similar conditions. This difference may be related to the larger body size of the white rhino, and to differences between grazing and browsing food seeking strategies. Local grassland conditions are sensitive to unpredictable variations in year to year rainfall distribution, and to take advantage of these a grazer needs to be opportunistic in its movement patterns. In contrast, woody plant growth is more strongly tied to regularly recurring seasonal factors, and hence offer a more predictably seasonally changing food source. White rhino females feed over a wider area during the dry season, whereas black rhino home range sizes in Ngorongoro are contracted during the dry season; though Hitchins (pers. com) found no significant differences at Hluhluwe. Goddard relates the more extensive wet season range in the case of the black rhino to feeding directed towards forbs such as clover.

McNab (1963) related home range size in mammals to body weight and hence metabolic needs, though his data were limited largely to small mammals. His correlation $R = 3.02\ W^{0.69}$ for "croppers," where R = home range size in acres, and W = body weight in kilograms, predicts a home range size of about 500 acres (200 ha) for a white rhino cow. This corresponds approximately to the observed size of the home range core area, but not to the complete home range as I have interpreted these terms. The home range core area of a white rhino female can thus be regarded as the basic home range related to metabolic needs, and the home range extensions during periods of deteriorating forage quality as special strategies for seeking food under such conditions.

Female home range sizes for most African antelopes typically vary between 2 and 10 km^2, though a few species exhibit strikingly larger home ranges (Table 14). Species whose home ranges exceed those of the white rhino in size include the American bison (up to 30 km^2), wapiti (up to 35 km^2), sable antelope (up to 50 km^2), roan antelope (up to 100 km^2), African elephant (up to 250 km^2), and plains zebra (up to 600 km^2). The high mobility of such species may be seen as a special adaptation permitting individuals to locate optimal food over an extensive area. The white rhino exhibits such a capacity to only a limited degree.

TABLE 14. Female home range sizes for various ungulates

Figures quoted are for seasonal home ranges where these differ from the annual range

Species	locality	home range size (km^2)	reference
mule deer	California	0.4-1.6	Dasmann & Taber, 1956
warthog	Sengwa	0.6-3.3	Cumming 1972
lesser kudu	Tsavo	1-3.5	Leuthold 1973
wildebeest	Ngorongoro	2.5	Estes 1969
gerenuk	Tsavo	2.4-4.5	Leuthold 1971
moose	Grand Tetons	2.5-5	Houston 1973
impala	Nairobi	2-5	Leuthold 1970
red deer	Rhum	4	Lowe 1966
Thomson's gazelle	Serengeti	1-9	Walther 1964
waterbuck	Queen Elizabeth Park	6.5	Spinage 1969
black rhino	Hluhluwe	2-8	Hitchins 1969 and 1972
	Ngorongoro	2.5-25	Goddard 1967
white rhino	Umfolozi	10-15	this study
American bison	Yellowstone	30	McHugh 1958
wapiti	Montana	4-35	Knight 1970
sable antelope	Angola and Kenya	7-50	Estes 1973
roan antelope	Kruger Park	60-100	Joubert 1973
African elephant	Tsavo	125-250	Laws 1970
plains zebra	Ngorongoro	80-250	Klingel 1967
	Serengeti	300-600	"

V. SOCIOLOGY

A. INTRODUCTION

In this chapter, a fundamental approach to the analysis of social organization will be adopted, such as to provide a basis for valid cross-species comparisons. The social system of the white rhinoceros will be described in terms of the spatial dispersion of individuals in the population, and of the ongoing dynamics of the interactions occurring between them. Consideration of the spatial structuring of the population leads to the identification of certain groupings of individuals that tend to be associated together, to the spacing both within and between such groups, and to the relationships between the ranges of different individuals or groups (Brown and Orians, 1971). These spatial patterns are influenced by the behavioural actions displayed by individuals both in direct visual encounters, and in indirect encounters through the media of audition and olfactory signs. Special sets of interactions are those leading to gametic transfer from male to female, and those related to nurturing of dependent progeny. Long term changes in the behavioural actions displayed by particular individuals, resulting from the processes of ontogeny, maturation, ageing and social transitions, will finally be considered.

In interpreting social patterns, five social categories or "castes" (McBride, 1964) of individuals will be distinguished. These may be characterised as follows:-

(i) *calves* (c_m, c_f): immature individuals still with their mothers;

(ii) *adolescents* (adolm, adolf): individuals independent of the mother, which have not attained socio-sexual maturity;

(iii) *cows* (AD_f): females of calf-bearing age;

(iv) *territorial bulls* (tAD^m): adult males exhibiting particular behavioural patterns associated with dominance within a certain spatial section of the habitat;

(v) subordinate bulls (sAD_m): adult males which do not show these behavioural patterns (the term "subsidiary bull" (Owen-Smith 1971 and 1972) is equivalent).

These categories are basically age/sex classes, except for the distinction between two classes of adult male. A territorial bull cannot reliably be distinguished from a subordinate bull by appearance, only behaviourally. While differences will become clearer in the ensuing sections, the following "quick field test" will be mentioned now. Territorial bulls nearly always urinate in a powerful pulsed spray; subordinate bulls generally urinate in a stream, in the manner of cows and immature animals.

Further subdivisions may be made. Infant calves, completely dependent nutritionally on the mother, may be differentiated from juvenile calves, which still nurse but are capable of feeding independently. Since the usual inter-calving interval is 2-3 years, all immature individuals judged to be over three years of age, whether associated with a cow or not, will be regarded as adolescents. Among the independent immature individuals, a distinction could be made between the younger prepubertal animals, and older individuals that are sexually potent but not yet sexually active, for social reasons. Walther (1972) used the terms adolescent and subadult to differentiate approximately these two categories. However, there were no striking behavioural changes to mark the time of puberty in the white rhino, and the terms adolescent and subadult will here in most cases be used interchangeably. The former will however be based on behavioural characteristics, while the latter will be applied to an age class differentiated by physical appearance. Thus, some males that are not readily physically distinguishable from adults may remain behaviourally still adolescent. All females will be classed as cows after the birth of their first calf, even though they may still be distinguishable physically as young animals.

B. SPATIAL DISPERSION

1. Groupings

White rhinos may be encountered singly, or in clusters of varying size and cohesion. Clustering may result merely from the congregation of several individuals in a favourable grazing area or at a rest-place. If animals are watched closely, however, it may be observed that some individuals orientate towards one another's movements, and hence tend to remain together; whereas others move independently, and thus separate with time. Associations of individuals exhibiting cohesion will be regarded as groups. Observations indicated that such associations were likely to stay together for at least several hours.

Upon a disturbance, several different individuals or groups that had been feeding or resting in the same vicinity frequently ran together, giving the false appearance of belonging to the same large "herd." Such alliances were however only transient.

When the history of particular groups was followed through time, it was found that certain individuals stayed together for extended periods, while other groups dissociated after shorter periods. Groupings of particular individuals which cohered for one month or longer will be regarded as stable associations. Such individuals were likely to remain close companions for several months or even years. Groupings persisting for shorter periods will be referred to as temporary association.

The analysis of grouping patterns may be approached in two-ways: (i) by considering the size and composition of the various groups encountered (Table 15); this is the conventional approach used by most workers; (ii) alternatively the frequency with which individuals of each social class occur in groups of particular size and composition may be analysed (Table 16); as emphasized by Jarman (in press), this more accurately reflects individual behavioural experience and choices.

The following types of group occur in the white

TABLE 15. Group size and structure

(a) All associations: groupings maintaining cohesion for at least several hours.

N = 1432 groups, from repeated sampling of study area populations with 75% of records from Madlozi.

Results are expressed as percentages of number of groups.

Composition	Size						
	1	2	3	4	5	6	7
ADms	25.5	0	0	0	0	0	0
ADm+ADf+(c, adol)	-	-	5.9	0.6	0.2	0.1	0
ADm+ adols	-	0.6	0.8	0.2	0.1	0	0
ADf+c,+(adol)	-	36.4	4.3	0	0	0	0
ADf + adols	-	5.3	0.8	0.6	0.4	0.1	0.1
1-2ADfs, +(adols)	0.2	0.6	0.1	0.1	0.1	0	0
adols	1.6	13.8	1.3	0.7	0.3	0	0
All	26.8	56.8	13.1	2.1	1.0	0.2	0.1

(b) Stable associations only: individuals remaining together for one month or longer

N = 935 monthly records from following history of particular groups, mostly at Madlozi.

Results are expressed as percentages of number of groups

Composition	Size					
	1	2	3	4	5	6
ADms	33.3	0	0	0	0	0
ADm+ADf+c	-	-	0.1	0	0	0
ADm+adols	-	0.1	0	0	0	0
ADf+c, +(adol)	-	35.1	1.9	0	0	0
ADf+adols	-	9.6	0.4	1.4	0.6	0.2
1-2ADfs, +(adols)	1.4	0.8	0.1	0.2	0	0
adols	5.7	8.1	0.6	0.3	0	0
All	40.4	53.7	3.2	1.9	0.6	0.2

TABLE 16. Associations formed by individuals of particular social castes

Figures represent percentage of individuals associated with companions of each social class.

(a) by adult males

(i) All associations, maintaining cohesion for at least several hours

Territorial bulls

Group size	1	2+	companions
tADm+	61.5		none
			ADm
		30.6	ADf+
		7.7	adol.

Subordinate bulls

Group size	1	2+	companions
sADm+	91.8		none
			ADm
		6.1	AD f+
		2.0	adol.

(ii) Stable associations, remaining together for one month or longer.

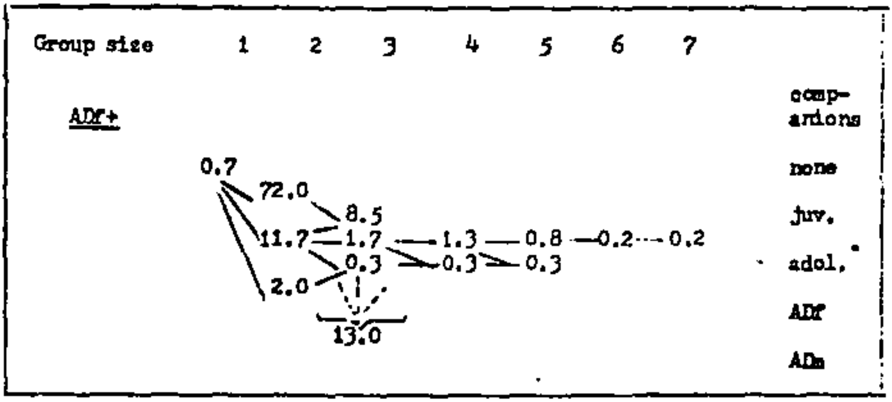
all adult males

Group size	1	2+	companions
all ADms	99.4		none
			ADm
		0.3	ADf+
		0.3	adol.

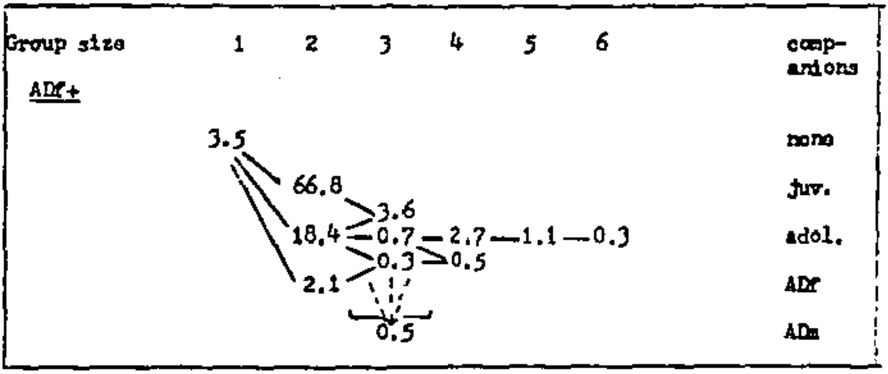
(cont. - Table 16)

(b) by adult females,

(i) <u>All associations</u>, maintaining cohesion for at least several hours

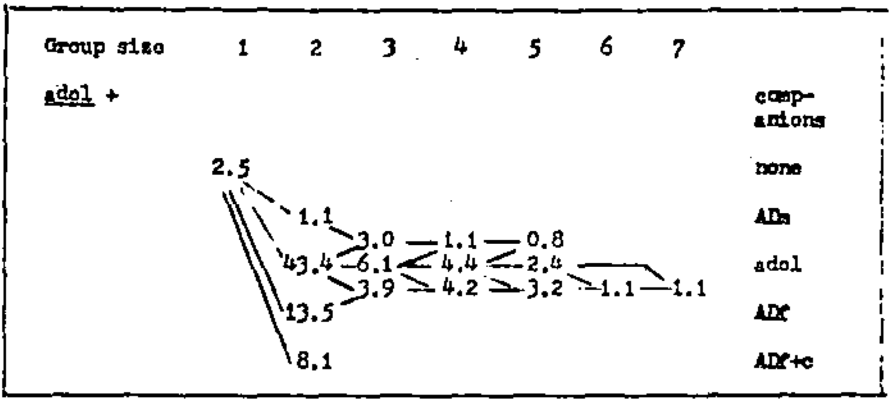


(ii) <u>Stable associations</u>, remaining together for one month or longer

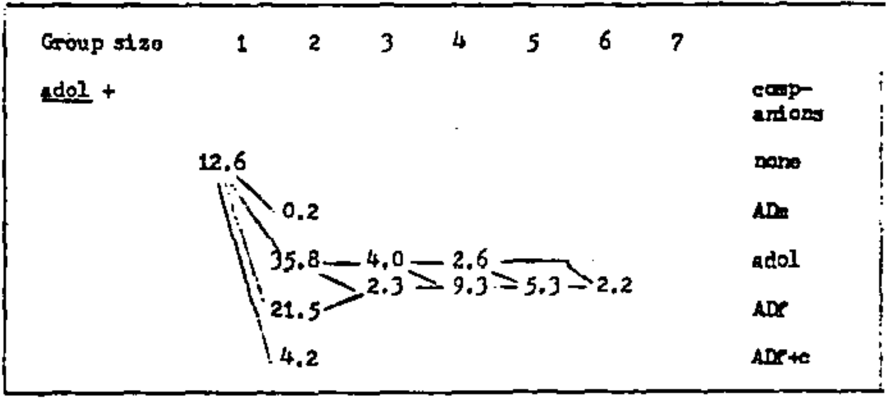


(c) by adolescents

(i) All associations, maintaining cohesion for at least several hours



(ii) Stable associations, remaining together for one month or longer



rhinoceros:-

(i) Cow-calf pairs; most adult females were accompanied by only a single offspring. Sometimes an additional, usually unrelated, adolescent attached itself temporarily to a cow-calf pair.

(ii) Cow-adolescent groups: a cow without a calf (commonly the result of the rhino capture operations) readily accepted the company of one or more adolescents. The higher proportion of cow-adolescent pairs apparent among stable groups (Table 15) is largely the result of a heavier bias in the latter records towards the Madlozi area, in which vicinity the rhino capture team had been more active. The largest stable group encountered in the study areas numbered 6, consisting of a cow with 5 adolescent companions aged 2 1/2-4 years, which remained together for at least 6 months. A sixth adolescent was temporarily associated with them for a period of a few days. Elsewhere in UGR I encountered a seemingly cohesive group of 9 individuals, mostly adolescents (detailed composition could not be established); Research Officer P.G. Stewart informed me that this group had been together at least a month, and had numbered 12 individuals before 3 were caught and removed.

(iii) Adolescent groups: most adolescents were associated with one or more similar aged adolescents of either sex. Groups of more than two individuals tended to be less stable, though a temporary group comprising 5 individuals and a stable group of 4 were recorded. Lone adolescents were seldom seen, but some individuals were only temporarily attached to particular groups.

(v) Solitary males: all adult males were basically solitary, but sometimes attached themselves temporarily to cows or to adolescent female containing groups. While territorial bulls were associated with a female on 38.3% of all sightings (N = 345), subordinate bulls were seen with a cow only 8.1% of the time (N = 114). An association of a subordinate bull with a cow rarely persisted longer than part of a day, whereas territorial bulls commonly attached themselves to cows for periods of 2-3 weeks. As will be shown later, such enduring associations indicated that the cow was approaching oestrus. In two observed cases in which a bull and cow stayed together for longer than a month, this was apparently because the cow did not conceive at the first oestrus period.

I also observed occasional persistent associations between two males that seemed almost adult in physical appearance. However, these I could distinguish to be young adults, so that I have regarded them as behaviourally still adolescent. Another young adult male was several times seen together with a territorial bull and a cow and calf, but again this seemed to be due merely to the persistence of adolescent grouping tendencies; it was never observed of older males. Outside the study areas, I twice recorded an association between a full adult male and a subadult male, but their histories could not be followed.

Discussion

Most white rhino groups seem based on a mother-offspring bond, or on a "surrogate" bond formed between a cow and an adolescent. While in some cases the attached adolescent may have been a former offspring, this was doubtful or known not to be so in several examples; conspicuously those in which several similar aged adolescents were associated with the same cow. Adolescents avoid moving about singly, and attach themselves to a companion of similar age or any other group that will accept them. There is no enduring association between a bull and a cow, except for the period of oestrus and mating.

Several writers have contrasted the more sociable white rhinoceros, supposedly living in family groups or herds of up to 14, with the relatively solitary black rhinoceros (Guggisberg, 1966; Ripley, 1958; Heppes, 1958). In fact, white rhinoceros grouping patterns are not very different from those recorded for East African black rhinoceroses (Klingel, 1966; Goddard, 1967; Schenkel and Schenkel-Hulliger, 1969), except that in the black rhino solitary adolescents are of more frequent occurrence, and groups tend more often to be smaller. The largest black rhino group reported is one of 5 individuals seen by Klingel in Ngorongoro Crater. This included an old cow and a young cow together with a cow and calf and a bull, which remained together for 4 days. The largest group observed by Schenkel at Amboseli consisted of 4 individuals: an old cow and a young cow, together with an adolescent female and a bull. In Hluhluwe Game Reserve, Hitchins (in lit.) found that only 1.7% of black rhino groups (N = 1907) included more than three individuals (compared with 3.4% for the white rhino, my study). He recorded one group including 7 individuals, but this may have been merely a transient feeding aggregation. The slight differences in group size may be partially due to the much higher white rhino population densities prevailing in Umfolozi (5/km^2), compared with those usual for the black rhino (e.g. 0.3/km^2 at Ngorongoro and 0.8/km^2 at Hluhluwe).

Most open country grazing ungulate species form substantial sized multi-female herds with males grouping in smaller "bachelor herds" (Jarman, in press). The white rhino is a notable exception. The occasional associations of two cows or of two young adult males or of an adult bull with a subadult presage the more elaborate herds formed of other species. In most cases where two cows had joined together, one of the individuals was clearly younger, and could have been a progeny; but in one case both females appeared similar aged; and a genetic relationship is clearly also not a necessity for cow-adolescent bond formation.

Jarman (ibid) relates herd formation to feeding styles and the degree of interference resulting from the proximity of conspecifics; and to the influence of predator defence. The white rhinoceros is a relatively unselective grazer, in Jarman's terms, and nearby conspecifics do not so greatly reduce food availability for others. However, adult white rhinos are almost invulnerable to predation (see Chapter VI). Though the grouping patterns of adolescents may be at least partially an anti-predator strategy, the major factor proposed to explain the formation of multi-female units in other open country ungulates is not operative in adult white rhino. The African elephant is likewise predation free when adult; but in contrast to the white rhino occurs in multi-female family units which may join into larger units up to 1000 strong (Laws, 1970). An additional possible advantage in group formation is the accumulation of collective traditional knowledge of the habitat. This could facilitate navigation over the extensive home ranges utilized by the elephant and most other unselective grazers (see Table 14). In comparison with the home range of 125-150 km^2 covered by an elephant group (Laws, 1970), white rhino females limit their movements to relatively small annual ranges of 10-25 km^2.

2. Inter-group spacing

White rhinoceros groups may be encountered isolated from other groups, while on other occasions several groups may be found feeding in the same vicinity. Such aggregations of several groups seemed at least partially the result of locally favourable grazing conditions. As referred to earlier (Section IV.B.4), during the midday rest period in hot weather, population distribution is highly clumped; most or all groups resort to one or another of certain favourably situated resting areas. Here they lie spaced a few metres apart in the shade of the same tree, or 10-30 metres apart under adjacent trees.

To investigate in more detail the dispersion of freely moving animals, the daily mapped distributions of grazing rhinos in the Madlozi bush-cleared zone were analysed by distance to nearest neighbouring group (Clark and Evans, 1954) (Table 17). A significant tendency towards aggregation with other rhino groups was shown by groups of all types. However, adult female and adolescent groups were more strongly aggregated with respect to other groups than were adult males. If particular group types are considered separately (e.g. distance measured from a cow group to the nearest neighbouring cow group), cow groups remain strongly aggregated with respect to one another. In contrast, territorial bulls show a tendency towards a

TABLE 17: Analysis of inter-group spacing

Distance to nearest neighbouring group analysed by method of Clark and Evans (1954).
Data from dispersion of grazing rhinos in the Madlozi bush-cleared zone.
Estimated mean rhino density = $6.4/km^2$ (calculated by territory occupancy index); mean group density = $3.3/km^2$.

(a) All groups considered

	tADm	sADm	ADf+	adol
Mean distance to nearest neighbouring group r_a (m)	227	224	147	125
Sample size N	42	39	178	24
expected r_e in random distr (m)	276	276	276	276
ratio r_a/r_e	0.82	0.81	0.53	0.45
$\sigma (r_e)$	23.3	24.1	10.78	29.3
standard normal variate z	2.10	2.16	12.0	5.15
signif. of difference from random	$p \angle 0.05$	$p \angle 0.05$	$p \angle 0.01$	$p \angle 0.01$

(b) Only groups of same class considered

	tADm/ tADm	sADm/ tADm	sADm/ sADm	ADf/ ADf
Estimated mean density $/km^2$	0.62	0.62	0.62	2.15
Mean nearest neighbour distance (m)	891	406	409	195
Sample size N	48	75	28	168
expected r_e if random	635	447	447	342
r_a/r_e	1.40	0.91	0.91	0.57
$\sigma (r_e)$	48.0	36.0	62.7	13.8
standard normal variate z	5.33	1.14	0.61	10.7
signif. of dif. from random	$p \angle 0.01$	n.s.	n.s.	$p \angle 0.01$

uniform dispersion with respect to other territorial bulls. The distribution of subordinate bulls with respect to either nearest neighbouring territorial bull or subordinate bull was not significantly different from random (for this I considered only territorial bulls and subordinate bulls sharing the same territory; see next section).

Since some degree of contagion undoubtedly results from patchiness in the most favourable grazing localities at any one time, it is the differences between the patterns for different social categories that are of most interest. Though cow groups move separately, there is evidently some degree of social attraction towards the proximity of other cow groups. The average separation between cow groups is a little over half that expected from a random distribution. In contrast, territorial bulls and subordinate bulls sharing the same range move more or less independently. The even spacing out of territorial bulls results from range relationships to be considered in the next section.

3. Individual ranges

In Section IV.D., the ranging patterns of cows and adolescents were considered in relation to habitat factors.

In this section, attention will be focussed on the relationships between the ranges of different individuals, and in particular on patterns of spatial utilization by adult males.

3.1. Territorial bulls

(a) The territory mosaic

Early in the study, it was evident that individual adult males tended to be found in fairly localised areas. Once the distinction between territorial bulls and subordinate bulls was recognised, it became clear that the ranges occupied by territorial bulls were mutually exclusive.

Figure 27 presents location points for the six territorial bulls in the central Madlozi study area for a period of a little over a year. The year-round home ranges occupied by individual territorial bulls did not overlap apart from a few outlying points, except in a narrow border zone. These mutually exclusive home ranges will be referred to as territories. All outlying points can be related to dry season movements to an from water situated at the Nyonikazane Spring in the south.

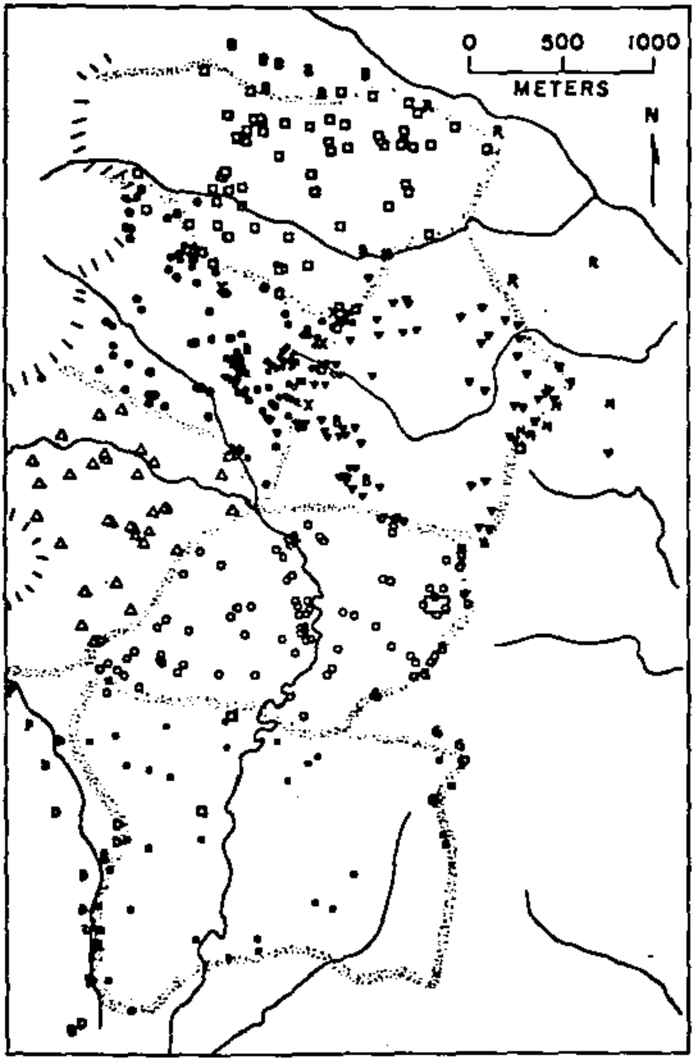
Similar distribution patterns prevailed during other

FIGURE 27. Home ranges of six territorial bulls at Madlozi, June 1970 - Sept. 1971

All single sightings of each bull have been plotted. Where bulls were kept under continuous observation, the first and last locations for that day have been plotted. Additional locations have been included where they are of significance in relation to boundaries. Territory boundaries shown are based on more extensive observations.

HOME RANGE DISPERSIONS OF TERRITORIAL BULLS

MADLOZI STUDY AREA, 1 JUNE 1970 – 4 SEPT. 1971



INDIVIDUAL	□	•	▼	△	○	■
NO. LOCATION RECORDS	74	114	70	34	78	34

X = LOCATION OF CONFRONTATIONS BETWEEN 1♂'s

······ TERRITORY BOUNDARIES

time periods. The interval covered in Fig. 27 represents one during which there were no changes in the identities of the individual territory holders. Fig. 28 shows changes in the territory mosaic that occurred at Madlozi during the study period.

Territories were contiguous with no unclaimed land, except for the steep slopes of the Zintunzini Hills in the west.

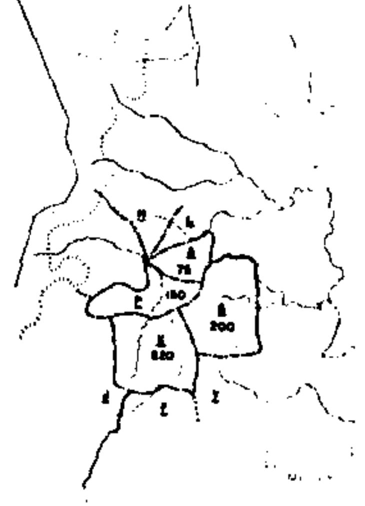
A similar territorial pattern existed in the other three Umfolozi study areas, though individual boundaries could not be mapped so precisely. At Hluhluwe North, two or possibly three adult males behaved as territorial bulls, but they were not seen sufficiently frequently to confirm spatial exclusion.

There was considerable variability in territory size, both at Madlozi and between the study areas. The smallest territory at Madlozi was that occupied by the bull A in 1966, which covered 0.75 km^2. This bull had shifted to a larger territory in 1968. The largest, that of H in 1971, covered 2.60 km^2. For other study areas, only an average territory size can be quoted. Mean territory sizes varied from 1.02 km^2 at Nqutsheni, where both population was

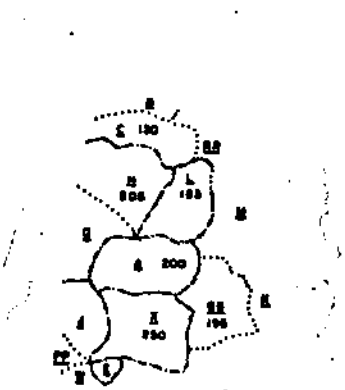
FIGURE 28. The territory mosaic at Madlozi at three different times

Territory limits were determined by mapping locations of individual bulls and by interactions occurring at boundaries.

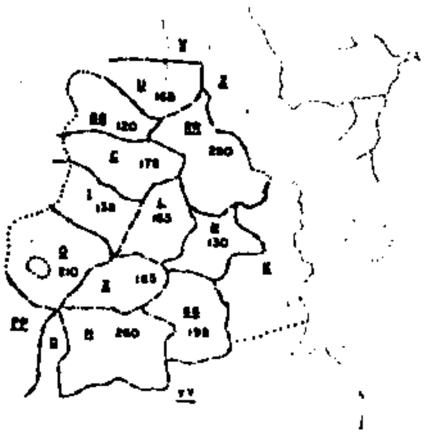
THE TERRITORY MOSAIC
MADLOZI STUDY AREA, JUNE 1966



THE TERRITORY MOSAIC
MADLOZI STUDY AREA, JUNE 1969



THE TERRITORY MOSAIC
MADLOZI STUDY AREA, JUNE 1971



TERRITORY BOUNDARIES
(TENTATIVE)
LETTERS = INDIVIDUAL TERRITORY HOLDERS
FIGURES = TERRITORY EXTENT IN HECTARES

highest, to over 2.00 km^2, closely similar to that prevailing at Madlozi.

Territory boundaries frequently coincided with topographic features, either watercourses or watershed ridge-crests, but never with roads. In other cases, boundaries were not marked by any physical feature. They were revealed simply by a sharp transition in the relative likelihood of encountering one or the other of two neighbouring territorial bulls (Fig. 29). Boundaries were narrow zones of 50-100 m width that were visited by both neighbouring territorial bulls, and in the absence of the neighbour, bulls occasionally wandered as far as 100 m across the boundary "line" before turning back. Other behavioural patterns assisted determination of the location of boundaries. Territorial bulls spray-urinated repeatedly while moving along a boundary region; and when in consort with an oestrus cow, a territorial bull moved ahead to block the movements of the cow in the vicinity of boundaries (Fig. 30). Occasional border confrontations between neighbours confirmed exact boundary locations. Boundary locations remained stable with time, altering only in some cases where territory ownership changed.

TABLE 18: Mean territory sizes in the various study areas

Study area	pop. dens /km²	total extent km²	no. of territ. included	Mean territ. size (km²)
Madlozi, 1966	5.3	6.50	4	1.62
Madlozi, 1971	5.3	19.70	11	1.79
Mqutsheni	7.0	5.10	5	1.02
Gqoyini	5.1	7.50	4	1.88
Dengezi	(3.7)	(6.10+)	3	(2.03+)
All		44.90	27	1.65

FIGURE 29. Relative frequency of occurrence of neighbouring territorial bulls across a border zone

Based on 191 points from either single sightings or half-hourly locations during periods of continuous observation for the territorial bulls I, C and L at the eastern and northern boundaries of I's territory; data obtained over the two year period October 1969 to September 1971. Location points were counted within successive 35 m wide strips parallel to the putative boundary lines.

RELATIVE FREQUENCY OF OCCURRENCE OF TERRITORIAL BULL VERSUS NEIGHBOURING TERRITORIAL BULLS ACROSS BOUNDARY REGION

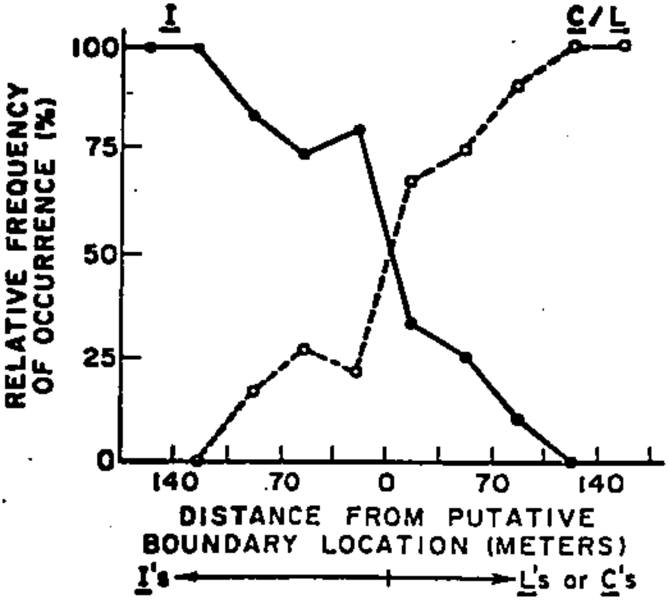
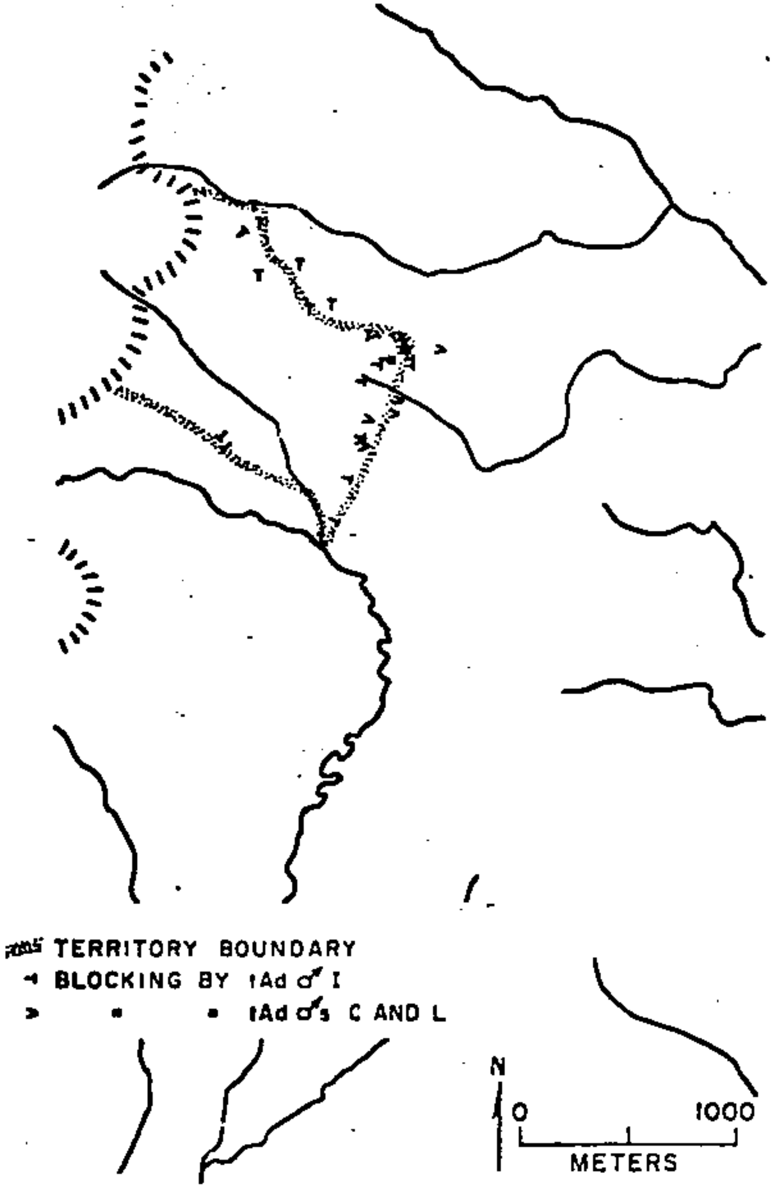


FIGURE 30. Locations of territory boundary blocking interactions with cows by tADm.I and neighbouring territorial bulls L and C.


TERRITORY BOUNDARY
BLOCKING BY tAd ♂ I
" " tAd ♂s C AND L
N
0
1000
METERS

Territorial bulls displayed a high degree of fidelity to their own territories. On only five occasions was a territorial bull seen more than 100 m beyond his own territory while water was available within the territory. The total number of encounters with all territorial bulls in all areas under wet season conditions was 870; indicating a frequency of wandering beyond the home territory of only 0.6%. Such wanderings seemed to be merely exploratory sallies a short way across the border. The frequency of wandering out of the home territory during the dry season, when water supplies were restricted, was 6.9% (N = 370), and all excursions could be related to movements to and from the nearest water source.

The boundaries of several territories commonly adjoined at major waterholes. For example, in 1966 five territories met at the upper Madlozi Spring (those of _H_, _L_, _A_, _P_ and _R_), some having narrow corridor extensions leading to the spring. A similar arrangement persisted from 1968 through to 1971, though the spring no longer provided any significant water. No important waterhole lay entirely within the territory of any one bull.

(b) Duration of territory occupancy

In Table 19 is presented the number of changes in territory ownership that occurred during the study period, in relation to the total duration for which all territories were observed. An average duration of occupation of the same territory by the same bull of 5.4 years is indicated. However, this estimate is based mainly on Madlozi, and changes in territory ownership were less frequent in other areas.

The study period was too short for me to observe the total duration of territorial reign of any individual bull except in one case. This bull Q had been a subordinate bull in 1966, but had become a territory holder by November 1968. In July 1971 he was displaced by another bull, and thus held the territory for between 2.7 and 5.0 years. Only one of the 10 bulls known in 1966, tADo.L, was still territory holder in the same territory when the study ended in September 1971, having had thus an unbroken reign of at least 5.3 years. Two further bulls, H and X, still remained as territory holders, but occupied different territories to those held in 1966, and G of 1966 might have been the same individual as K of 1971.

TABLE 19. Changes in territory ownership occurring during the study period

Study area	no. of territ. observed	no. of changes	sum of observ. durations* (yrs)
Madlozi	15	11	49.5
Mqutsheni	6	0	9.3
Gqoyini	4	0	3.2
Dengezi	4	1	3.3
All	29	12	65.3

* = sum of the periods between the first and the last sightings of the territorial bull in each territory

(c) Utilization of the territory

The territory occupied by tADm.I from late October 1969 onwards provided favourable conditions for mapping detailed spatial utilization. It lay wholly within the bush-cleared zone, allowing excellent long range visibility, while the adjacent slopes of the Zintunzini range offered a good overlook vantage point. It will therefore be used as a detailed example, and comparative reference will be made to patterns prevailing in other territories.

The territory of I was relatively small, covering about 135 ha. It included sections of all three major grassland types, and four temporary rainwater-holding pans (Fig. 31). The nearest permanent water was 3 km away at the Nyonikazane Spring.

The spatial distribution of different activities performed within the territory will be considered (Fig. 32).

(i) Grazing. (Fig. 32a) tADo.I concentrated his activities particularly in the eastern section of the territory, where the favoured grazing areas of short grass grassland lay. The western and southern parts of the territory which had a long grass cover, were visited less frequently. More

FIGURE 31. The territory of t4Dm.I, showing habitat features

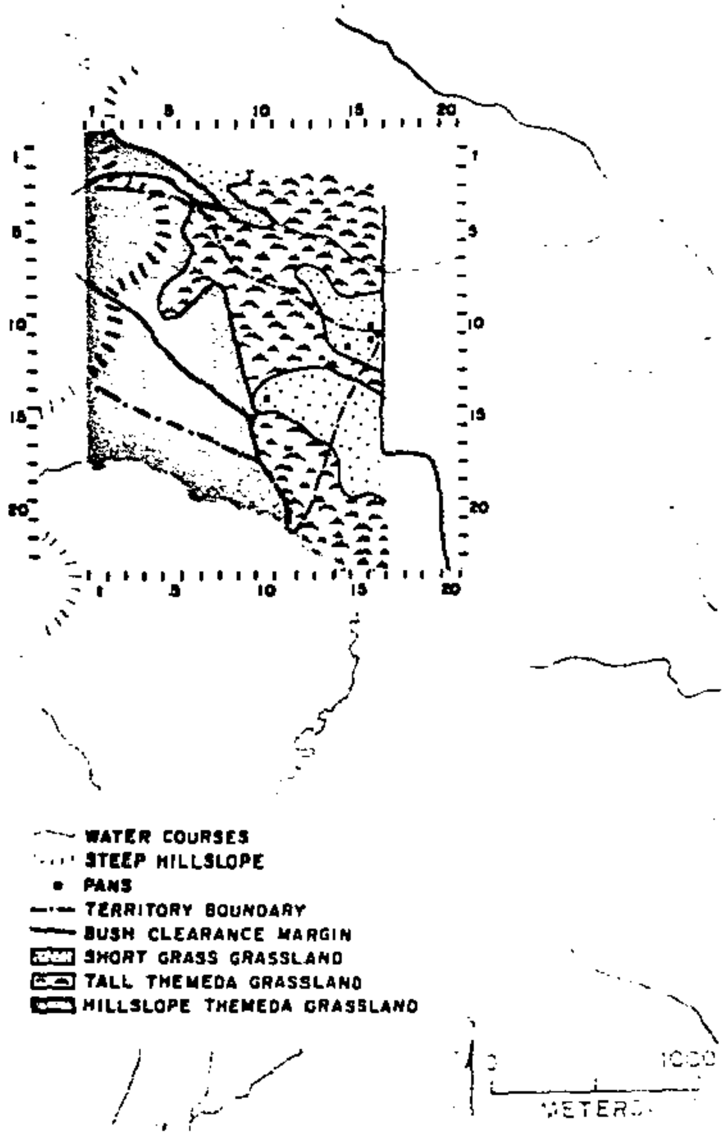

1
5
10
15
20
WATER COURSES
STEEP HILLSLOPE
PANS
TERRITORY BOUNDARY
BUSH CLEARANCE MARGIN
SHORT GRASS GRASSLAND
TALL THEMEDA GRASSLAND
HILLSLOPE THEMEDA GRASSLAND
0
1000
METERS

FIGURE 32. <u>Distribution of activities within the territory of territorial bull tMDs.I</u>

Based on single sightings plus movement paths during continuous observation sessions over the two year period Oct. 1969-Sept. 1971 (but relating mostly to wet season conditions).

Shading indicates relative frequency of occurrence within 100 m square sectors; grid key is related to habitat features in Fig. 31.

a. Grazing, grass green

N = 247 points

b. Walking

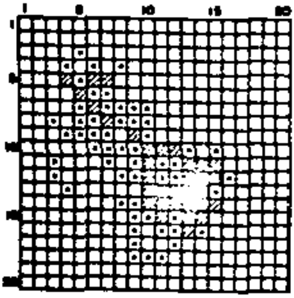
N = 188 points

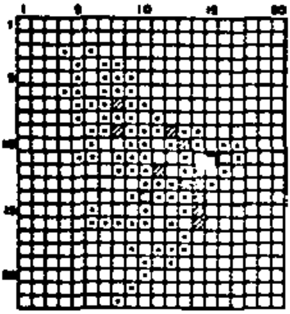
c. All activities

N = 507 points

d. Resting

N = 52 points


1
5
10
15
20
1
5
10
15
20


1
5
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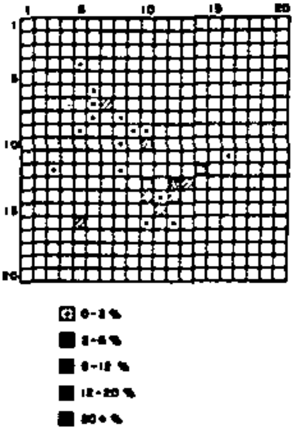
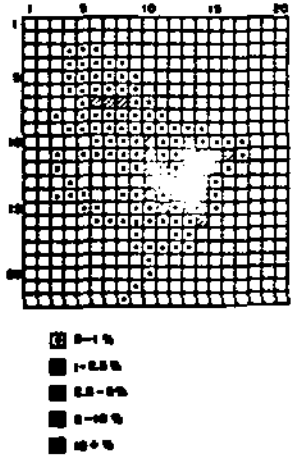
20


1
5
10
15
20
1
5
10
15
20
0-2 %
2-6 %
6-12 %
12-20 %
20+ %


1
5
10
15
20
1
5
10
15
20
0-1 %
1-2.5 %
2.5-5%
5-10 %
10+ %

use of these sections was made during the dry season, for which data are more limited.

As a result of the close interspersion of grassland types, all territories at Madlozi included sections of both tall themeda grassland and short grass grassland. That of tADo.I̲ had a smaller extent of short grass than most others. At Nqutsheni, the extent of tall grass was limited within study area territories. Only a few territories included hillslope themeda grassland, favoured by cows during the late dry season. However, despite these variations, all bulls seemed well able to obtain all their year-round food requirements from within the territory limits. No bull was observed to leave his territory for grazing needs at any season.

I was not able to observe the effects of a fire burning through a territory, which could force a bull to seek food elsewhere. Because of the mosaic of short and tall grass, it is possible that sufficient foliage might still be left in localised areas to supply a bull's needs for a short period at least.

(ii) Resting. (Fig. 32d) The territory of tADo.I̲ contained one particularly favoured midday resting site, and an alternative resting site a short way to the north-east that was less frequently used. The other notable resting sites evident in Fig. 32d are those that were favoured during the dawn rest period.

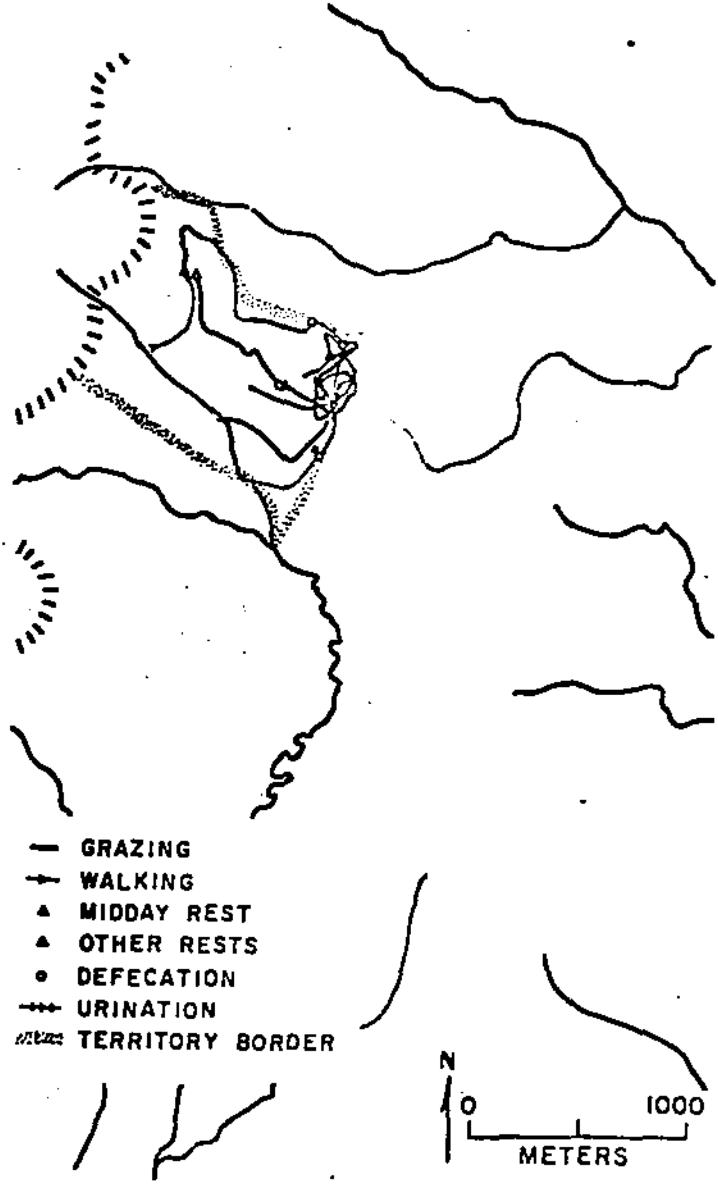
All territories contained at least one, more usually two, such particularly favoured resting areas, commonly situated on low ridgecrests under shady trees. These were shared with other rhinos, and no particular tree was monopolised by the territorial bull. Most of the bush-cleared zone territories were longitudinally arranged, including a segment of undisturbed woodland and extending westwards to the Zintunzini range slopes. The territory of tADo.I was unusual in not including any particularly large shady trees. The boundaries maintained by the previous occupant, tADo.H, had taken in a section of shady woodland to the north-east which was used as the midday resting area. However, at the time of I's takeover, some of the trees regenerating in the bush-cleared zone had grown sufficiently to provide at least adequate shade.

(iii) Drinking and wallowing. The four pans within I's territory (Fig. 31) provided him with adequate water and mud for wallowing for about 8 months of the year. After this he had to drink either at the Lily Pan (2km to the south-east) while it still held water, or at the Nyonikazane Spring (3 km to the south).

All territories included at least one temporary pan. Only the few bulls occupying territories adjoining Nyonikazane Spring, the Mphafa Pools, Gqoyini Pans or the two rivers had access to water supplies within the territory for most or all of the year. Other bulls had to leave their territories every 3-4 days during the late dry season in order to drink.

(iv) Walking and patrolling. (Fig. 32b) Walking by the bull I tended to be concentrated in the vicinity of the pans lying in the north-east corner of the territory, and along border zones. The latter is related to patrolling movements made along sections of the boundaries. These are more strikingly depicted in Fig. 33, which shows the movements of the bull over three consecutive days. However, the daily repeated patrols made by tADo.I along part of the eastern border of his territory over this period was unusual, and seems to have been the result of a confrontation with the neighbouring bull L that had taken place there the day preceeding the commencement

FIGURE 33. Daylight movements of the territorial bull I over three consecutive days, 30 Mar - 1 Apr. 1971.


GRAZING
WALKING
MIDDAY REST
OTHER RESTS
DEFECATION
URINATION
TERRITORY BORDER
N
0
1000
METERS

of observations. Neither of the neighbouring territorial bulls L or C was seen patrolling along their adjoining borders during daylight hours over this period.

Sometimes a bull grazed while moving along the border, but more usually he walked slowly, nose to the ground, investigating scents encountered (Examples 1 and 2). Parts of the eastern and northern boundaries of I's territory coincided with trails that were sometimes used by tAD.I and also by the neighbouring bulls C and L, while patrolling the boundary. However, routes followed were not consistent. These trails were commonly used also by other rhinos moving in towards the resting area situated to the north-east of I's territory. tADo.I less frequently patrolled the southern border of his territory and the western part of his northern border. These lay within long grass regions where both neighbouring bulls spent less time.

(v) Urinating. Territorial bulls spray-urinated in all parts of their territories, but they spray-urinated more frequently while moving along a border region than elsewhere within the territory (Fig. 34). Usually only 1-2

EXAMPLE 1. Border patrol by tADm. I (Madlozi, 30 Mar'71)

1717 tADm.I grazes shifting on NNE towards his E border with L; he scrapes and urinates sprays, repeats this at 1719 and again at 1722; at 1723 I walks on N (now on the boundary line), pauses to rub his horn on a tree, continues, urinates sprays, walks 150 m to the S bank of a watercourse hollow just east of a bushy tree (this was the site of a confrontation with tAD.m.L the previous day), turns and moves W under the tree, pauses sniffing, stands; sniffs, walks on NW crossing the watercourse then continues N, horns, scrapes and urinates 70 m on, pauses briefly to look around 70 m further, turns W, pauses sniffing, walks on N, steadily and purposefully, reaches the territory corner dungheap, sniffs, digs his horn into the dung pile, kicks, dungs, kicks 13 times, walks on NE, urinates sprays, reaches a small pan at the corner of his territory, pauses there presumably drinking at 1736

EXAMPLE 2. Border patrol by tADm. I (Madlozi, 1 Apr'71)

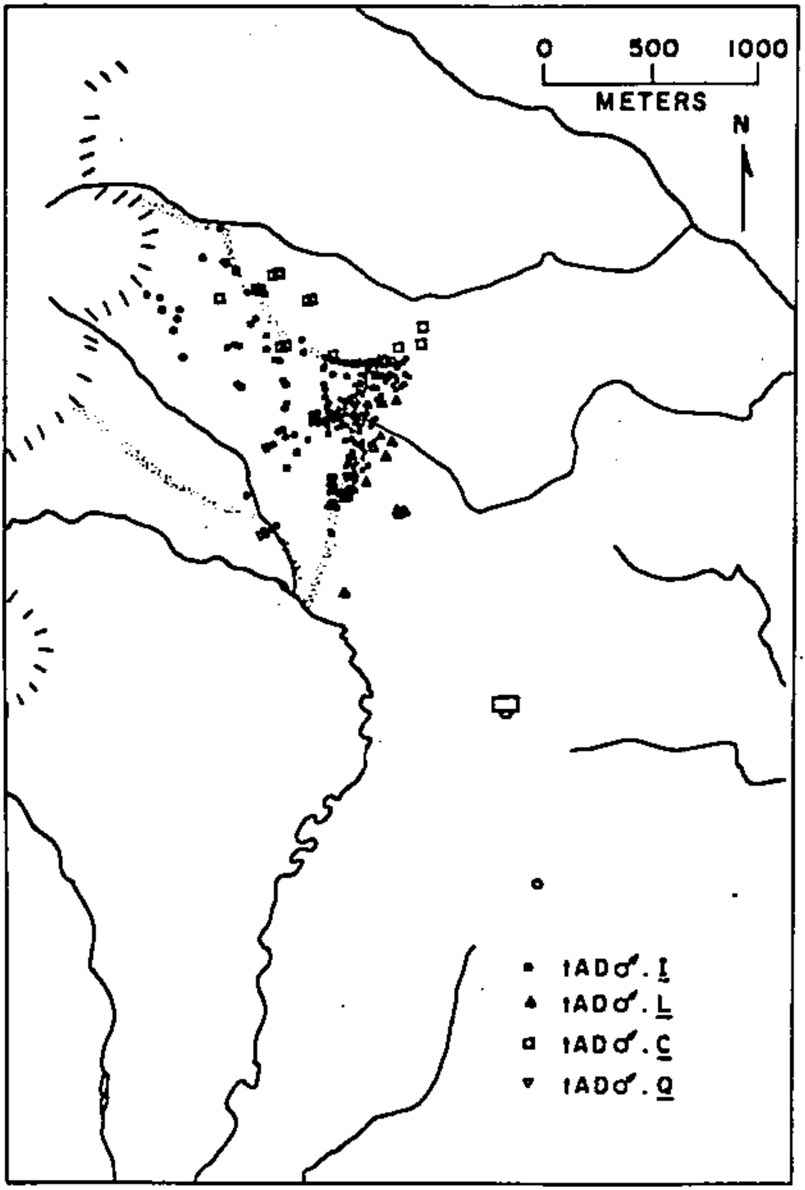
0807 tADm.I grazes N passing just E of the bushy tree on the S bank of a watercourse hollow which marks the E territory boundary location; he walks on N crossing the watercourse, horns, scrapes and urinates sprays 33 m on, walks NE then NNE, then N; about 100 m N of the watercourse he looks about, turns W, urinates sprays, walks NW, continues NNW, reaches the territory corner dungheap, sniffs about at its edge then at its center, digs his horn in the dung with a sideways movement, positions himself, kicks, dungs, kicks, walks on W, turns NW, urinates sprays/0820 I horns, scrapes and urinates 150 m NW of the dungheap, turns W along the trail at the N border between his territory and C's, horns, scrapes and urinates, sniffs around at bush, stands pushing his horn into the bush, stands munching; weaves his horn in the bush; finally turns away S past it, scrapes and urinates sprays over the bush/0826 I walks S, pauses; continues S, commences grazing.

FIGURE 34. Dispersion of spray-urination sites by tADm.I and neighbouring territorial bulls

Period covered is 28 October 1969 - 4 September 1971.

Locations show all observed instances of spray-urination.

DISPERSION OF SPRAY-URINATION SITES
BY tAD♂. I AND NEIGHBOURING tAD♂s
28 OCT. 1969 – 4 SEPT. 1971



spray urinations per hour were recorded while a bull was grazing quietly well away from the periphery of his territory. A few repeated spray-urinations were likely to be made by a bull if he moved on shifting location. Away from border regions, a mean rate of 2.0 spray-urinations per hour was recorded (N = 40 hours). In contrast, while grazing or walking along a territory border territorial bulls spray-urinated an average of 10.0 times per hour (N = 12 hours). In one instance, 12 spray urinations were recorded in 40 minutes, in another 20 in 2 hours. In a case in which a bull was blocking the movements of a cow at a territory boundary, 29 spray urinations were recorded in 122 minutes.

Variations in the density of urination sites were investigated by counting scrapemarks in strip transects orientated both perpendicular and parallel to the boundaries between the territories of I, C and L. Urination sites unaccompanied by the usual scraping action could not be detected. Four days had elapsed since rain, which had obliterated all older scrapemarks. Peak urination scrapemark densities of 5-8 per 1000 m^2 were recorded on either side of the apparent boundary line, while densities were less than 1 per 1000 m^2 within the central part of the territories (Fig. 35). This suggests that the neighbouring bulls tended to orientate their patrols a short distance on their own side of the boundary. However, neighbouring territorial bulls were seen patrolling along the same border trail on some occasions, so this may have been merely a chance effect that had occurred during the sample period. The increase in the density of urination sites along a boundary region was however clearly evident.

To investigate further the relationship of urination sites to trails, in late May 1971 I counted urination scrapemarks visible within 3 metres of certain trails, some located in border areas and some centrally situated within a territory, and also along straight line transects through the same areas away from trails. Twelve days had elapsed since the last rain. Highest densities were recorded alongside border trails, on the average one scrapemark being encountered every 25-30 metres (Table 20). A high density of urination sites was also present alongside the trails passing through the centre of X's territory, beside the Madlozi stream. These were some

FIGURE 35. Variation in urination scrapemark density across a territory border region

Based on counting scrapemarks along 5 east-west transects cutting across the border between the territories of tAD♂s I and L and 4 north-south transects across the border between the territories of tAD♂s I and C, plus 3 further transects parallel to the I-L border, one following a border trail, one 5 m east of this trail, and one 15 m west of this trail; four days had elapsed since the last rain obliterated all previous scrapemarks.

Figures indicate sample sizes = total number of scrapemarks recorded.

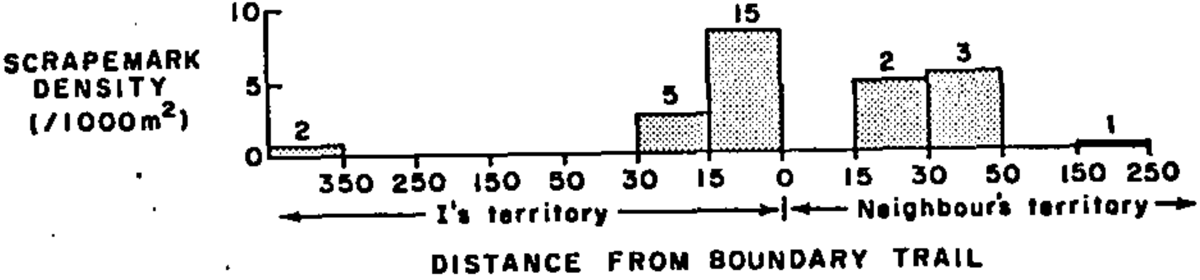


TABLE 20: Urination scrapemark densities alongside trails

Scrapemarks were counted within 3 m of trails both along border regions and away from borders; scrapemarks were also counted along similar transects away from trails. A 12 day interval had elapsed since the last rain obliterated older scrapemarks.

Territory	I-L	I-C	X	I	I	X
Location	border trail	border trail	central trail	centr. trail	border 20m W of trail	central, no trail
Distance traversed (metres)	400	400	1780	300	420	720
No. of scrapemarks found	14	16	47	0	2	3
Density of scr-marks	1/29	1/25	1/38	0/300	1/210	1/240

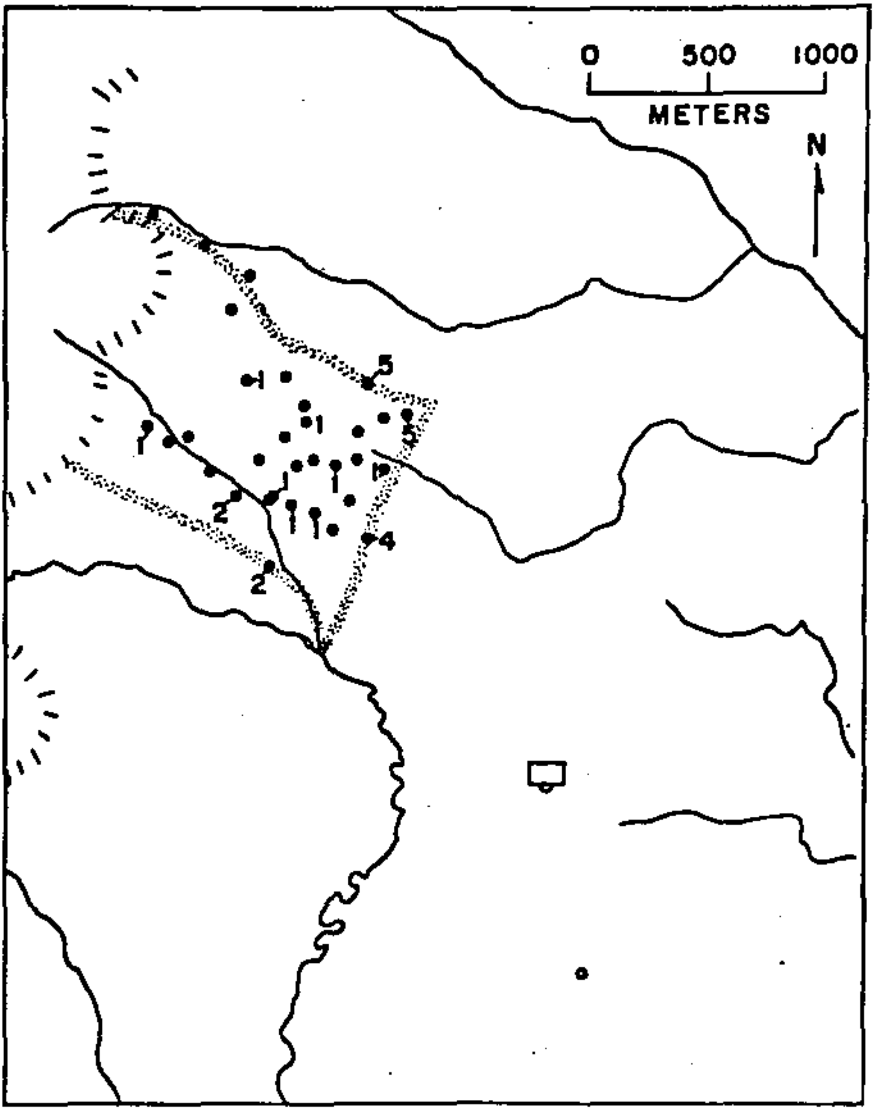
of the main trails followed by rhinos travelling southwards towards the Nyonikazane Spring. Alongside another trail passing through the central part of I's territory, no scrapemarks were found; but this trail bore few signs of recent use. Away from trails, only a few scrapemarks were found. This indicates that territorial bulls concentrate marking not only in border areas, but also beside trails that are being frequently used by other rhinos.

In only one instance was a territorial bull seen urinating while out of his territory travelling to water; this bull urinated in a stream in the manner of subordinate bulls and cows. On crossing the home boundary after returning from water, territorial bulls invariably spray-urinated several times in quick succession. Spray-urination thus occurs only within the home territory and along its borders.

(vi) Defecation. With rare exceptions, territorial bulls always defecated at one of the numerous dungheaps present within the territory. The territory of tAD♂.I contained 30 such dungheaps of varying size, scattered throughout the extent of the territory (Fig. 36). Large dungheaps were present around resting areas, drinking pools and alongside trails, and other such frequently visited locations. They were used not only by territorial bulls, but also by other rhinos in the area. However, only territorial bulls scattered their dung by kicking movements after defecation. Located along boundaries were certain large, well hollowed out dungheaps which attested to frequent visitations by territorial bulls.

In conjunction with monitoring the movements of tAD♂.I, I also monitored daily the use of the various dungheaps within his territory over a five day period. The surfaces of the dungheaps were raked smooth each afternoon, and then examined the following afternoon for signs of a hollow kicked out by a territorial bull. Three of the four major border dungheaps were marked almost daily over this period by the bull while that on the southern border was marked twice (see Fig. 36). Only one other dungheap was used more than once during the five days. In all, 15 out of the 28 dungheaps monitored were marked over the five day period (two dungheaps were not discovered until later).

DISPERSION OF DUNGHEAPS WITHIN TERRITORY OF tAD♂. I



Figures indicate number of times dungheap was marked over 5-day period, 29 Mar. – 2 Apr. 1971.

░ TERRITORY BOUNDARY

However, the daily marking of border dungheaps by tAD♂*I* over this period was unusual, and as in the case of his regular border tours, was probably related to a confrontation with the neighbouring bull *L* that had taken place on the day preceeding the commencement of observations. In late July, I carried out a further survey of border dungheaps, including six other such dungheaps in addition to the four situated along the borders of tAD♂*I*. Much variability in marking frequency was found (Table 21). Some were marked twice in one 24 hour interval, at others 3-4 days passed between successive visits. Three were marked only once in the 4-5 day period covered; while for the remaining seven, a sum total of 18 visits was recorded; suggesting marking at an average rate of about every second day.

A few instances were observed in which a bull defecated at a dungheap just across his own border in the neighbouring bull's territory, indicating that use of the dungheaps was not strictly exclusive. However, bulls seldom explored far enough beyond their own borders to come into contact with a neighbour's dungheap. On one occasion a bull exploring outside his own territory

TABLE 21. Frequency of marking of ten border dungheaps by territorial bulls

Dungheaps were examined daily for signs of the kicking movements characteristic of territorial bulls over the five day period 27-31 July 1971.

X = freshly marked - = not marked

	Dungheap									
Date	I-Q	I-L	I-L-C	I-C	L-X	L-C	C-L	B-U	U-B	N-L
27 July	-	X	X	-	X	X	-	X	-	
28 July	X	-	-	-	-	-	-	-	-	X
29 July	-	-	-	X	X	_	X	-	-	
30 July	-	XX	-	-	X	X		XX	-	-
31 July	X	X	X	-	-	-	X	-	X	-
Sum total	2	4	2	1	3	2	2	3	1	1

limits stood tail curled at a neighbour's dungheap, but no dung was produced. During journeys to water, territorial bulls sometimes defecated at trailside dungheaps passed on the way with the usual kicking movements.

Territorial bulls were observed walking directly towards dungheaps for distances of up to 100 m before defecating there. Apparently they knew the location of the dungheaps. At least some of the hollowed out border dungheaps were maintained mainly by the territorial bull concerned. For example, in 1966 there was a prominent dungheap used by tAD♂.*A* where his territory adjoined that of tAD♂.*L*. In 1968, when the border between these two territorial bulls lay further south, this dungheap was overgrown and evidently little used. Other abandoned overgrown dungheaps could similarly be related to changing patterns of utilization by different territorial bulls.

(vii) *Orientation at borders*. Usually a bull displayed no overt response on coming into a boundary region; he merely turned quietly aside while continuing grazing. Sometimes a bull paused to stare ahead across the boundary, and such actions typically accompanied occasional explorations a short way across a boundary. In two instances, new territory holders displayed more positive response at boundaries. One bull was watched as he explored carefully investigating scents encountered a short way over his own border, then veered back into his own territory (Example 3). In another instance, a new territory holder of only two days standing stared hesitantly ahead across the border, then turned and moved somewhat hastily back into his newly acquired territory (Example 4).

Though the area of short grass favoured for grazing by tAD♂.I extended unbroken across the border into the territory of L, both I and L spent more time grazing 100-200 m on their own sides of the border than in the boundary zone; indicating some degree of avoidance of boundaries. Since this region was also grazed by many other rhinos, there was no noticeable vegetational difference at boundaries. When tAD♂.H had occupied the territory adjoining that of L, both bulls regularly rested only about 200 m apart on the same ridgecrest.

(viii) Excursions to water. Journeys to water were most usually undertaken during the early evening. But drinking times were not consistent, even for particular

EXAMPLE 3. Exploration across a border region by a new territorial bull of 10 days standing (Madlozi, 29 Oct'69)

1035 tADm.I emerges from a wallow at the NE corner of his newly acquired territory and stands rubbing/ 1040 I walks E, at bush clearance margin (just across his territory boundary); he horns a bush, scrapes over it and stands tail curled, but no urine spray is seen; he turns S, scrapes bare soil and urinates sprays, stands rubbing his horn on a tree, then his head, then his side/ 1045 I wanders on E. (over the border), a cow snorts at him 25 m away, I pauses, then grazes E, then stands rubbing again/ 1050 I wanders on E, rubs, walks on E then S, pauses to sniff around, nibbles at either scent or grass, wanders on SSE then E, wipes his horn on the ground at two successive sites 1 m apart, scrapes hard with both front and hind hooves over the spot, but no urine spray appears; I walks S, turns W, pauses at a pan to drink (about 130 m E of his border)/ 1100 I turns S away from the pool, stands listening uncertainly at the sound of my footsteps, walks W, commences grazing about 60 m W of the pan/ 1103 I walks N (now 40 m E of his border) turns towards a cow plus adolescent, the cow gives a few snorts without rising, I pauses 12 m S of them; then turns away W, horns, scrapes and urinates, turns N in the vicinity of the border, rubs his horn vigorously over a log several times, scrapes past it and urinates 3 powerful sprays; walks NE then E (crossing the border in corner region), pauses to sniff at a dungheap about 30 m on, digs his horn vigorously into it twice, throwing up dung as he lifts his head, pauses sniffing, wanders on S, then W; turns S about 45 m E of the border/ 1120 turns SW, urinates on crossing over the border region, walks on SW (back into his own territory).

EXAMPLE 4. Nervous turning back at territory border by a new territory holder about 2 days standing (Madlozi, 6 Jun'70)

1702 tADm. X moves on NE towards N border of his new territory, horns, scrapes and urinates sprays, walks on E, sniffs at the ground, stands with head lifted, nibbles, walks on E(this was at the old dry urine site of cow)/ 1705 X horns, scrapes and urinates, walks NE, pauses at the W edge of a pan, inclines his head to listen to noises from the nearby guard camp (this pan lies at the N border of the territory)/ 1707 X shifts E, horns, scrapes and urinates, stands/ 1710 X moves to the pan, stands head down presumably drinking/ 1713 X turns away from the pool, walks NW, (which is just over the border); X looks up, continues walking NE, horns, scrapes and urinates, stands looking N, swings his head in a low arc as if to turn away, then walks on NW, head up attentive ahead, then stands; turns away, walks WSW, recrosses the track; pauses to sniff at dung, continues walking S, pauses to sniff at the ground briefly (there were fairly fresh scrapemarks here), walks on S and disappears down the slope back in his territory; I investigate to see if there are any other rhinos ahead where he turned back, but find only two steenbok).

individuals, and occasionally the journey to water was made during daylight hours (see Section IV.B.1). On 15 occasions I was able to take advantage of such instances to follow a territorial bull for part or all of the way to and from water, and once I followed a bull back from water at night.

While thus away from their own territories travelling to water, territorial bulls walked steadily pausing only momentarily to investigate scents along the way, until the drinking pool was reached. Usually a major trail was followed for most or all of the way, but bulls were also seen proceeding to water without following any established trail. Bulls sometimes paused for several minutes in the vicinity of a pool before moving down to water. Usually about 20-30 minutes was then spent at the water, drinking and standing around and occasionally wallowing. In most cases, the return journey was likewise made without pause until a bull regained his home territory. Immediately on crossing the border region, a bull spray-urinated several times in quick succession and commenced feeding. On two observed occasions only, a territorial bull grazed during the return journey though continuing to move in the direction of home.

In October 1969, I followed tAD♂.C all the way to the Nyonikazane Spring and back. The outward journey of 4.2 km took him 75 minutes; he then spent 121 minutes drinking, wallowing and standing quietly in the vicinity of the spring, until 1115 hours. He then walked back through the heat of midday in 72 minutes. He was thus away from his territory for a total of 4 1/2 hours, but the extended time spent at water was unusual. In January 1970, I similarly followed tAD♂.A to the Mphafa Pool and back, a distance of 4.1 km outwards, but only 2.9 km by the shorter return route he followed. Travelling time was 93 minutes outwards and 65 minutes return. He spent 24 minutes wallowing and standing around, but was not able to drink as the pool had evaporated down to mud a few days earlier. He tried drinking at pits that had been dug in the sandy margins by warthogs, but only pushed in the sides. He regained his territory at 1120 hours, on a day during which the temperature rose to 41.7°C, having been away from his territory for a total of 3 hours. In January 1971, tAD♂.BB took 100 minutes to accomplish the 4.9 km distance back to his territory from Nyonikazane.

This is probably as far as any bull needed to travel to water in Umfolozi Game Reserve. The adjoining territorial bull to the north, U, was only once seen crossing the study area to water, and apparently more usually travelled northwards either to the Black Umfolozi River or the Gqoyini Pans.

These water excursions thus keep some territorial bulls away from their home territories for periods of up to 4-5 hours every 3-4 days.

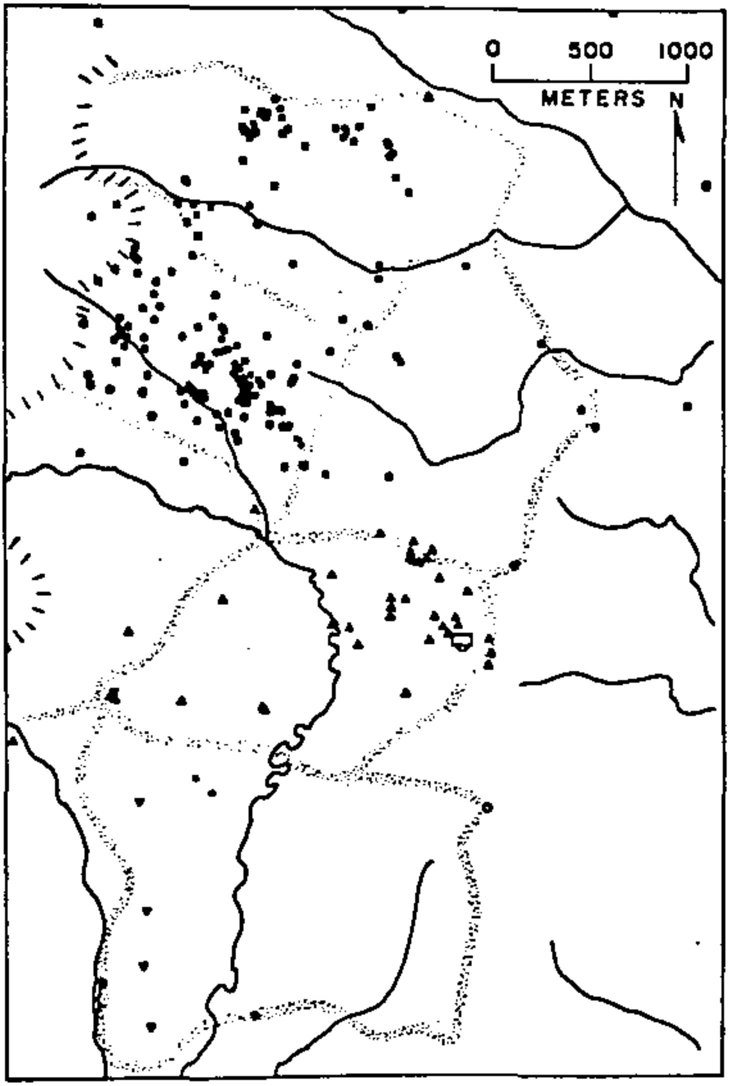
3.2. Subordinate bulls

The distribution of points of location for subordinate bulls shows that each subordinate bull tended to localise his movements within the territory of a single territorial bull (Fig. 37). However, wandering further afield occurred more frequently than was the case for territorial bulls. The best known subordinate bull, a young adult male HM, was recorded within the territory of tADo.I on 89% of 253 records over a two year period, including radio-telemetric locations. For other subordinate bulls, the frequency of location within the home territory varied from 56% to 100%, but some of this variability is undoubtedly due to inadequate sampling. For all sightings

FIGURE 37. Home ranges of four subordinate bulls at Madlozi, June 1970-Sept. 1971.

All single sightings of each bull have been plotted; when bulls were maintained under continuous observation, the first and last locations for the day have been plotted; additional locations have been included where they are of significance in relation to boundaries; territory boundaries shown are those of the territorial bull ranges based on Fig. 27.

HOME RANGE DISPERSIONS OF
SUBORDINATE BULLS
MADLOZI STUDY AREA, 1 JUNE 1970 – 4 SEPT. 1971



INDIVIDUAL	■	●	▲	▼
NO. LOCATION RECORDS	56	112	37	6

⁓⁓⁓ TERRITORIAL BOUNDARIES

of all subordinate bulls, the average frequency of location within the home territory was 87% (N = 553), and there was no significant seasonal variation.

Some territories were shared by both a territorial bull and a subordinate bull (Table 22). Omitted for simplification from Fig. 37 are the locations of a second subordinate bull that settled within the territory of tAD♂.I in January 1971. One of the Nqutsheni territories contained three subordinate bulls in addition to the territorial bull, and for a short period after his takeover of the territory in October 1969, there were also three subordinate bulls in the territory of tAD♂.I. In all study area samples combined (Table 22), there were 25 subordinate bulls in 48 territories, indicating that about one third of all adult males were not territory holders.

It seemed that subordinate bulls spent most of their time within their home territories, but made occasional exploratory sallies which sometimes took them some distance away (see Fig. 37). Some of these were terminated after a confrontation with one of the surrounding territorial bulls. After one such meeting, the subordinate bull concerned was followed as he walked steadily 2.5 km

TABLE 22. The incidence of subordinate bulls in territories

Study area	No. of territories	tADm alone	tADm +sADm	tADm +2sADms	tADm +3sADms	total no. of sADms
Madlozi, 1966	8	4	4	0	0	4
Madlozi, 1969	11	8	2	1	0	4
Madlozi, 1971	15	10	4	1	0	6
Nqutsheni	6	3	1	1	1	6
Gqoyini	4	2	1	1	0	3
Dengezi	4	3	0	1	0	2
All	48	30	12	5	1	25

back towards his home territory. He did not pause until he crossed over the home boundary, then stopped to rest for several minutes in the shade of a tree before continuing on more slowly. After another similar confrontation, the subordinate bull grazed in short spells only while working his way back, then paused grazing steadily immediately after crossing the boundary back into his home territory.

Subordinate bulls were followed while travelling to water or from on six occasions. In a like manner to territorial bulls, they walked steadily until water was reached; but unlike territorial bulls, they commonly grazed while making their way back home.

Subordinate bulls utilized the area of their territory in a manner similar to that of territorial bulls. They favoured grazing in the same localities, rested at the same rest-places, and used the same wallows and dungheaps. Except in one special case to be discussed in another context, no avoidance of the territorial bull was evident. However, subordinate bulls neither patrolled borders nor spray-urinated.

3.3 Cows

Unlike the ordered array of exclusive home ranges occupied by bulls, even the home range core areas of cows present a rather confusing overlay, with multiple overlapping existing (Fig. 38).

Another way of considering the home ranges of cows is in relation to the territorial system of the males, using the "territory occupancy index" (see section II.A.5) to estimate the frequency of occurrence of each cow in each of the study area territories (Table 23). Only wet season conditions are considered, but this includes wandering movements made beyond the core area during periods while the grass was drying out, but water was plentifully available. The majority of cows spent over 50% of their time in one or the other of two adjacent territories. In most cases four territories encompassed 75% or more of the estimated frequency of occurrence, and seven territories over 95%)(average territory size = 1.65 km^2). However, no individual relationship was evident between cows and the territorial bulls whose territories they shared.

The lack of spatial intolerance among cows is also evident in Table 23. For example, seven different cows shared the territory of tAD♂.C as their most favoured territory, while 26 of the 30 study area cows were

FIGURE 38. Overlay of the home range core areas of 25 cows frequenting the Madlozi study area

Shown are the apparent boundaries of the various home range core areas, determined as in Fig. 20. Total home ranges are larger than these core areas and overlap more extensively.

OVERLAY OF HOME RANGE CORE AREAS OF 25 COWS

MADLOZI STUDY AREA

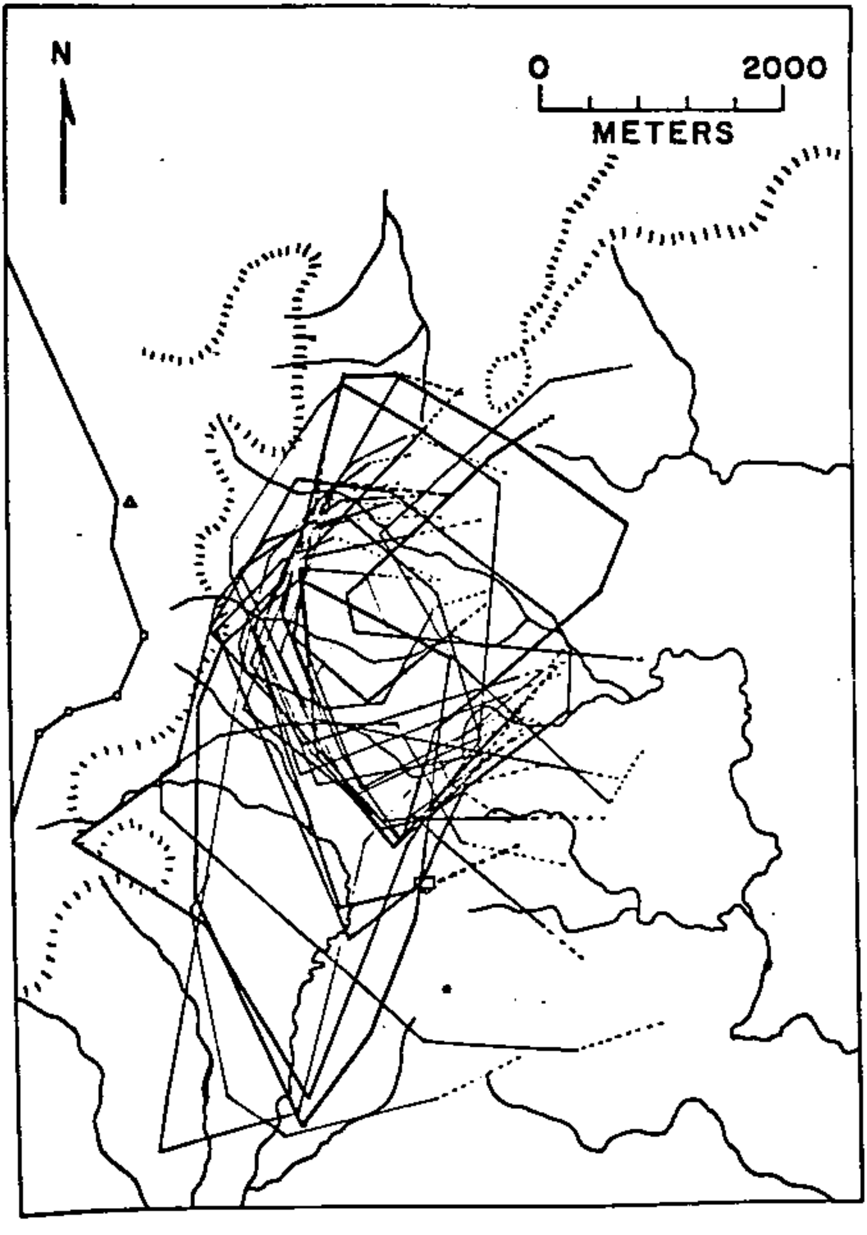


TABLE 23. Frequency of occurrence of individual cows in various adult male territories at Hadlozi

Individual frequencies of occurrence have been calculated by "territory occupancy index" (based on ratio of sightings relative to each territorial bull), under conditions of ready water availibility between Nov.'68 and Sep'71. Total frequencies under 100% indicate that time was also spent outside study area. Territories are listed in circular order from south to north then east; reference should be made to Fig. 27 for locations of individual territories.

Territory		G	X-H	A-X	Q	H-I	L	C	B	U	R	M-K+N	Tot.%
No. of sightings of tADm		11	25	80	35	167	114	98	47	24	17	37	
Ident. of ADf	No. of sightings												
Z	18	40*		2									42
Y	13	25*	8	1									34
B	40	36*	12	25	6	1	5					14	99
N	44	9	41*	14	3	1	11	3				2	84
AA	65		28	32*	11	4	12	1			6		94
U	128			14	24	14	27*	6	3		2	6	96
LL	78				6	6	33*	24			12	16	97
VV	95		9	1		8	32	37*	2		7	3	99
DD	70					5	37*	16	2		12		72
K	54					6	12	23*	6		5	16	69
V	72			3	9	8	20	27*	3	14	8	7	99
HH	62			1		5	19	28*	4		12		69
H	53			3		2	19	20			29*		73
A	53					2	9	32*	2		23	12	80
JJ	24					6	9	26			38*	9	88
J	64		4	5		4	16	21	17	6	24*		97
T	65					5	4	46*	2	8	21	8	94
TT	48					4	6	25	4	4	29*	6	78
MM	47					4	9	16	12		44*	10	95
O	113					6	12	26*	23		21		88
P	78					1	13	14	4	22	39*	5	98
PP	49					1	8	16	4	26	36*	6	97
RR	22						3	12	2	20*	6		43
E	25					1	3	4	9	18*	12		47
ZZ	40						1	4			10*		15
NN	62					1	40	3			12	44*	100
II	41			4		5	17	2	4		6	22*	60
SS	9			1		1	2				18*	16	37
FF	11					1	2	2				27*	32
D	25						2					98*	100
av. Adf pop. in territ.			2,7	1,5	0,6	2,8	3.6	4,2	1,1				

*most favoured territory

recorded within the territory of tAD♂.L. However, individually distinctive patterns were shown by different cows in their occupation of the various territories.

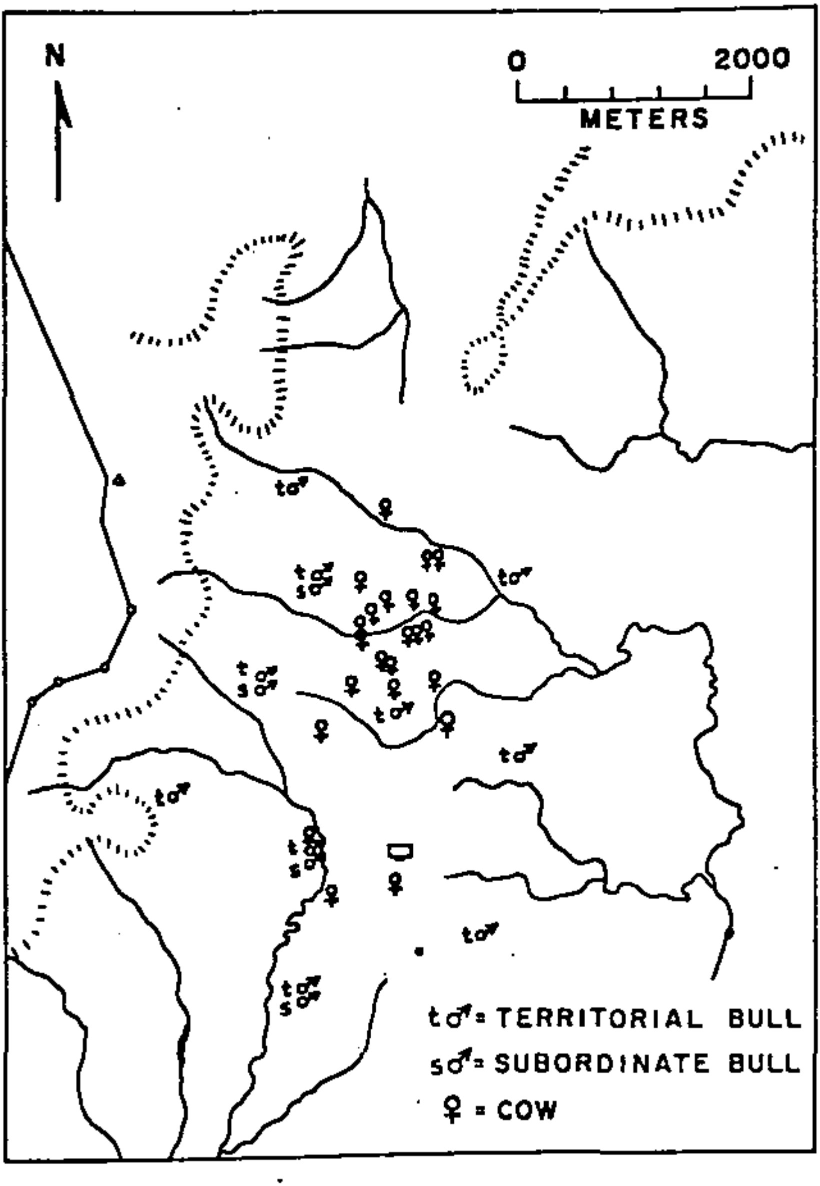
These estimates of the frequency of occurrence of different cows in different territories allows calculation of the centres of gravity of the individual home range dispersions, plotted relative to the geographic centres of the male territories (Fig. 39). Study area cows may be divided into two groups, one consisting of three females favouring the Madlozi valley and another including the remaining 20 cows favouring the northern part of the study area. However, apart from this topographic separation related to a habitat feature, there was no clustering of individual ranges suggesting the existence of distinct home range groups (Grubb and Jewell, 1966) or 'clans.'

Striking differences are also evident in the average populations of cows present in each of the study area territories (Table 23). These vary from a mean of 0.6 cows in the territory of tAD♂.Q and 1.5 cows in the territory held at different times by tAD♂s A and X, to 3.8 in the territory of tAD♂.L and 4.2 in that of tAD♂.C. These are of significance in relation to the potential

IGURE 39. <u>Dispersion of the centres of gravity of the home range distributions of bulls and cows at Kadlozi</u>

Centres of gravity of ranges were determined by the vector sum of the distributions of cows among individual territories (Table 22), weighted relative to the frequency of occurrence in each territory and plotted spatially relative to the geographic centres of these territories. Only females that were regular visitors to the central study area are included.

DISPERSION OF CENTRES OF GRAVITY
OF HOME RANGE DISTRIBUTIONS
OF BULLS AND COWS
MADLOZI STUDY AREA



reproductive contribution made by different bulls. The territories of C and L, covering areas that were highly favoured by cows for grazing during the wet season, are probably among the most favourable in the whole reserve in this regard.

3.4. Adolescents

Comparable data on the distribution among various territories are available for four adolescent groups only (Table 24), and for three of these the total number of sightings was limited. A pair of adolescent males spent most of their time within a single territory, while groups consisting of an adolescent female-adolescent male pair, or two adolescent females, moved over a wider area.

Discussion

Different social castes in the white rhino population exhibit differing forms of spatial dispersion. Territorial bulls are distributed in a regular cellular array of sharply bounded, mutually exclusive areas occupied by particular individuals. Some of these cells are shared, less strictly, by individual subordinate bulls. Adult females range widely over an area including

TABLE 24. <u>Frequency of occurrence of individual adolescents among the territories, Madlozi SA.</u>

calculations as in Table 23.

<u>Territory</u> <u>Ident. of adol.</u>	<u>% of sightings</u>	<u>X-H</u>	<u>A-X</u>	<u>Q</u>	<u>H-I</u>	<u>L</u>	<u>C</u>	<u>H-K+N</u>	<u>Tot. %</u>
adolm.<u>b</u> (with var. adolms)	42	71	5	4	1		2		83
adolm<u>c</u> (with var. adols)	28	43	11	3	3		3		63
adol.m.<u>r</u>+adolf.d	71	15	20	57	2	4	1		99.
adolf.s (with adolf)	25	12	9	14	4	18	3	8	68
av. adol. population		5.8	2.3		1.9	2.5	2.5		

up to seven male territories. Adolescent males show an intermediate pattern (see Table 25, Fig. 40).

This underlying territorial spatial structure strongly influences the behavioural actions of adult males. It circumscribes their ranging, influences accessibility to food and water, promotes special patrols related to boundaries, and modifies defecation and urination patterns. As will be shown on the next section, spatial position in relation to the territorial structure strongly modifies the nature of interactions occurring between adult males. There is evidence that subordinate bulls heed and orientate their movements to the same boundaries as those observed by the territorial bulls. In contrast, the ranging patterns of females are apparently not restricted by the territorial system of the males (except for the short period of oestrus), nor are they influenced to any striking degree by the ranges of other females.

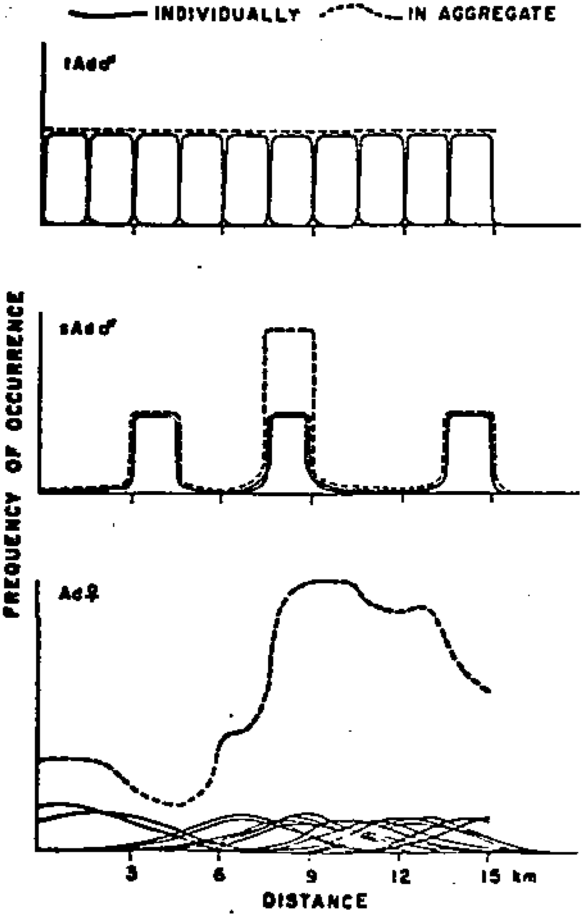
A similar pattern of adult male territories and overlapping female home ranges exists in many African bovids (Estes, 1973), and adult male territories are also reported for Grevy's zebra and the African wild ass (Klingel, 1972), the pronghorn (Kitchen and Bromley 1973),

TABLE 25. Comparative spatial dispersions of different social castes among the territories

Figures represent averaged frequencies of occurrence within territories arranged in order of preference. Reference should be made to Tables 23 and 25 for calculations of individual frequencies of occurrence.

social caste	no. of indiv.	frequencies of occurrence within particular territories, arranged in order of preference								
		1	2	3	4	5	6	7	8	9
territorial bulls	19	99.4	0.6	0.4	0	0	0	0	0	0
subordinate bulls	3	87	6	4	2	1	0	0	0	0
adolescent males	3	70	22	4	2	1	1	0	0	0
adol.m + adol.f	1	57	20	15	4	2	1	0	0	0
cows	10	34	25	14.5	11.5	6	5	2.5	1	0.5

FIGURE 40. Schematic representation of cross-sections through the spatial distributions of individuals of differing social castes



roe deer (Kurt, 1968) and vicuna (Franklin, 1973). Exclusive territories do not exist in the highly social bovids of the tribe Bovini, in Caprines except possibly the chamois (Krämer, 1969), in cervids except for the roe deer, or in elephants (Laws, 1970; Eisenberg and Lockhart, 1971).

Goddard (1967) reported overlapping home ranges for the black rhino in Ngorongoro Crater; and Schenkel denied the existence of territoriality in the black rhino populations occurring in Tsavo and Amboseli Parks in Kenya (Schenkel, 1966; Schenkel and Schenkel-Hulliger, 1969), but presented no detailed information on home range relationships. However, Hitchins (1972), using radio telemetry, found that in Hluhluwe Game Reserve the ranges of three black rhino males overlapped only marginally along one border, while a fourth male shared one of the ranges. This pattern closely resembles that existing in the Umfolozi white rhinos.

In most ungulates, non-territorial males aggregate into so-called bachelor herds; and are thus readily distinguishable from territorial males, which are either solitary or associated with a female herd. In the white rhinoceros, in which all adult males are basically solitary, it is necessary to use other behavioural criteria to demonstrate the coexistence of two classes of adult male in order for the territorial pattern to become apparent. If all adult males are considered together without this distinction, a system of partially overlapping ranges is suggested. Since neither Goddard nor Schenkel considered the possible coexistence of different classes of adult males, the reported absence of territoriality in East African black rhinoceroses remains questionable.

The territories held by white rhino males (0.8-2.6 km^2) are larger than those existing in most other ungulates, but are exceeded in size by those of Hluhluwe black rhinos (3.9-4.7 km^2, Hitchins 1972), the African wild ass (10+ km^2) and Grevy's zebra (2.7-10.5 km^2 (Klingel, 1972). Lichtenstein's hartebeest (1.5-5 km^2) (Dowsett, 1966) and sable antelope (2.5+ km^2, Estes 1973).

In most territorial antelopes, bachelor males are excluded from the territories, though the actions of the territory holder may be ineffective in preventing intrusions by larger bachelor herds, particularly where territories are large (e.g. in bontebok, David 1971, and in Grant's gazelle, Walther 1972). Impala territorial males show a varying degree of tolerance for the presence of bachelor herds (Leuthold, 1970); sable bulls accept satellite males within their territories (Estes, 1973), and Grevy's zebra territorial males readily accept the presence of bachelor stallions (Klingel, 1972). However, the white rhinoceros is apparently unique, among species so far investigated, in that the subordinate males (which are equivalent to the bachelor males of other species) restrict their activities almost entirely to the territory of individual territorial males.

While some wildebeest males have been known to occupy the same territories for over two years (Estes, 1969), the average durations of territory occupancy of individual white rhino bulls are longer than those so far reported for any other species.

C. INTERACTIONAL DYNAMICS

1. Communication

Introduction and methods

In order to interpret interactions occurring between animals, it is necessary first to understand the significance of certain displays which are of communicatory valence. An action performed by one animal, the actor, can be regarded as communicatory if it modifies the subsequent behaviour of another, the recipient. Any movement, posture, sound or odour displayed by one animal is of potential communicatory significance if it can be perceived by other animals. However, consideration will be restricted here to the more overt and conspicuous displays which appeared frequently in social interactions and which seemed to have special communicatory functions.

Sounds were frequently made by white rhinos in interactions, and many times they drew my attention to an incident. Auditory displays were often coupled with certain actions, but ritualised movements and postures alone were less conspicuous. Special actions accompanied urination and defecation by territorial bulls, but these were performed independently of the presence of other rhinos. They may be related to the placing of scent marks which potentially function in indirect communication.

During observation sessions, all sounds heard to be made by rhinos were noted, and a similar procedure was followed for certain action patterns, once these had been distinguished. The performer and recipient were identified.

and the prior and subsequent behaviour of both recorded, wherever possible. In quantifying results, all discrete occurrences of each sound or gesture, recorded separately in my field notebook, were enumerated. Thus, a series of ten sound utterances each separated by only a few seconds would be tallied as one occurrence, but if spaced by say two minutes or longer would yield ten occurrences. Comparisons of recorded frequencies of occurrence are qualified as certain sounds were soft and audible only at close quarters, while actions demanded closer and more intensive watching to be detected. Furthermore, action patterns were distinguished for a shorter part of the study period.

Results will be expressed quantitatively in terms of the number of times (N) that a particular auditory or visual display was observed, and of the frequency of occurrence of particular contexts and responses. The response of a recipient (R) to a display varies depending not only on the immediate context, but also on preceeding events, and on the social and individual identity of the actor (A). The treatment followed here will be somewhat simplified.

1.1. Auditory displays

I distinguished ten distinct sounds, though some of these were somewhat variable in patterning and in intensity between different performances and in rendition by different individuals. Of these, four were aspiratory, either nasal or thoracic-oral, and six were vocal. Vocalizations were further made in two distinct registers: low-pitched roars or grunts, and shrill squeals of variable tonal quality.

a. Snort (N = 870)

Form: A nasal exhalation, or inhalation, or series of these (Fig. ~~60~~41a). The actor sometimes turned its head to look towards the recipient, while at other times snorts were given without lifting the head from grazing or making any discernible movement.

Social distribution: Snorts were commonly made by cows, adolescents and subordinate bulls, but only in rare instances by territorial bulls (Table 26). Adult males and to a lesser extent adolescents were commonly the targets of snorts. Among adolescents, snorts were directed by a smaller individual towards a larger one on 26 occasions, and by a larger animal towards a smaller one on 25 occasions; in 13 instances, the sizes of the two individuals

TABLE 26. Actor-recipient matrix for the SNORT

Upper figure represents number of times recorded
Lower figure indicates relative frequency, in percent

ACTOR

RECIPIENT	tADm	sADm	ADF	adol	calf	Total
tADm	2 0.2	71 8.1	381 43.7	82 9.4	0 0	537 61.6
sADm	6 0.7	21 2.4	75 8.6	8 0.9	0 0	111 12.7
ADF	1 0.1	3 0.3	33 3.8	7 0.8	0 0	45 5.2
adol	1 0.1	6 0.7	79 9.1	64 7.3	0 0	150 17.2
calf	0 0	2 0.2	16 1.8	2 0.2	0 0	20 2.3
Total	14 1.7	106 12.4	585 67.1	163 18.7	0 0	871

TABLE 27. Actor-recipient matrix for the SNARL

Legend as above

ACTOR

RECIPIENT	tADm	sADm	ADF	adol	calf	Total
tADm	4 0.6	83 13.5	198 32.1	134 21.7	1 0.2	420 68.1
sADm	2 0.3	13 2.1	48 7.8	9 1.5	8 1.3	80 13.0
ADF	3 0.5	4 0.6	14 2.3	4 0.6	0 0	25 4.1
adol	2 0.3	5 0.8	29 4.7	39 6.3	0 0	75 12.2
calf	0	0	0	0	0	0
Total	15 2.4	111 18.0	295 47.8	186 30.2	9 1.5	616

were similar.

Contexts:

(i) (f=394/870) R was standing near A, or made a move near A (average separation distance = 12.7 m, range 1-5 m, N = 231). This was most commonly related to a territorial bull being in the close vicinity of another rhino (the territorial bull being the recipient), but also arose within groups when one individual moved near another; it also occurred when animals came into close proximity at waterholes.

(ii) (f=355/870) R turned towards, or started approaching A (average separation distance = 14.4 m, range 1-40 m, N = 67). Cows and adolescents quickly responded with snorts to any direct approach by a territorial bull.

(iii) (f=48/870) R stood confronting A at close quarters, only a few metres away. This most commonly arose when a territorial bull investigated another rhino, or when a territorial bull blocked the movements of a cow at a territorial boundary (the territorial bull was the recipient.

(iv) (f=40/870) A found R in front in its intended path of movement. Such situations arose when a territorial bull was accompanying a cow, the cow being the actor, and within multiple adolescent groups.

(v) (f=10/870) R either snorted, grunted or squealed in close proximity to A. Reciprocal exchanges of snorts sometimes developed between animals coming close together at waterholes.

(vi) (f=10/870) R touched A. This arose either where an adolescent rubbed against the side of a companion, or when a bull nuzzled the rump of an oestrous cow.

(vii) (f=9/870) R moved close by, or otherwise interacted with a calf, and the mother of the calf snorted.

(viii) (f=4/870) Miscellaneous cases: once, one animal snorted during playful wrestling which had become over-vigorous; once, a cow snorted at zebras that were drinking close beside her; twice, seemingly "vacuum" snorts were made when there were no other animals in the vicinity.

Responses:-

(i) (f=264/752) R displayed no overt response, continuing with its previous activities or direction of movement. A then either ignored the other animal, or gave several more snorts.

(ii) (f=253/752) R checked its approach and stood looking at A without moving nearer, or turned aside and moved past keeping the same distance.

(iii) (f=136/752) R backed away several steps or turned aside and moved further away.

(iv) (f=30/752) R remained at the same distance, but turned to present its side towards A.

(v) (f=29/752) R continued approaching ignoring the snorts of A (R in such cases was a territorial bull approaching a cow or another bull).

(vi) (f=27/870) R remained confronting A from close quarters ignoring its snorts; this occurred where a territorial bull was confronting a subordinate bull or, less commonly, a cow.

(vii) (f=13/752) R responded with snorts.

Interpretation: the snort is generally elicited when another animal either moves nearby or approaches. Such situations most commonly arise when territorial bulls approach to investigate other rhinos, or when a territorial bull is accompanying a cow. Snorts sometimes caused the recipient to stop approaching or move further away, and they may be characterised as mild "keep-away warnings" that are not always heeded. Snorts were liberally employed to control spacings between strangers and within groups.

b. <u>Snarl</u> (N = 621)

Form: When fully expressed, a gruff vocal roar lasting 1-2 seconds; (Fig. 41b) at lower intensities, either a brief grunt (Fig. 41c), or a soft rumble (Fig. 41d). The vocalization was always coupled with a laying back of the ear pinnae against the side of the head, the head was thrust forwards, and the mouth opened to let out the full volume of the sound (Plate 11).

Social distribution: Similar to that of the snort, but adolescents and subordinate bulls were relatively more likely to use the snarl instead of snorts against a territorial bull than were cows (Table 27). Against group companions, a soft rumble or grunt was commonly given instead of a full roar. Among adolescents, snarls were directed by a smaller individual against a larger on 13 occasions, by a larger against a smaller on 9 occasions, and against a similar sized adolescent 17 times.

Contexts:-

(i) (f = 261/621) R approached A; frequently A snorted

PLATE 11. Separation maintaining displays

a. A cow snorts and lays her ears back facing a territorial bull; the bull backs away.

b. A cow faces a confronting territorial bull giving a snarl display.

c. A subordinate bull couples a snarl with advancing steps against an approaching territorial bull.

d. A cow advances to clash horns with a bull.

first, then snarled when R continued approaching (average separation distance = 15.1 m, range 2-37 m, N = 24). The snarl was relatively more commonly elicited from adolescents and subordinate bulls; accordingly the average separation distance was greater than that recorded for the snort.

(ii) (f = 181/621) R stood or moved near A, perhaps ignoring earlier snorts. Subordinate bulls were particularly prone to snarl if a territorial bull made any sudden move nearby. Cows also snarled loudly if an accompanying territorial bull moved in close proximity (average separation distance = 11.8 m, range 0.5-45 m, N = 47).

(iii) (f = 126/621) R stood confronting A at close quarters (Plate 11). A subordinate bull confronted horn to horn by a territorial bull made snarls with every breath.

(iv) (f = 25/621) A found R ahead blocking its intended path of movement; this most usually occurred when a cow found an accompanying bull in her way.

(v) (f = 11/621) Another animal species moved nearby, or there was nothing there. In one instance a cow gave a rumble at zebras drinking beside her. All other cases can be ascribed to territorial bulls or subordinate bulls moving outside their home territories. The bull seemed to "imagine" that another rhino was approaching, and relaxed when it found no rhino there.

(vi) (f = 7/621) A cow stood watching two bulls sparring horn to horn in front of her; whenever they clashed horns the cow stepped forwards with a grunt. The seven recorded utterances of the snarl in such a situation derive from three separate incidents of this nature.

(vii) (f = 5/621) R touched A, either a territorial bull resting chin on rump in a precopulatory advance, or an animal rubbing against a companion.

(viii) Miscellaneous instances: twice, when a nearby rhino at a waterhole made snorts or grunts; once, when her calf ran away from near a bull, the mother advanced with a snarl, and similarly on another occasion when another cow confronted a calf; once during a playful wrestling march when one animal seemingly become overvigorous.

Responses:-

(i) (f = 135/476) R halted its approach, or turned aside and moved past keeping its distance. This and the next were most commonly the responses of a territorial bull to a snarl by a cow that it had attempted to approach.

(ii) (f = 134/476) R retreated, either backing away a few paces, or turning and walking away, or changing its direction hastily to move away from A.

(iii) (f = 90/476) R remained confronting A despite its snarls. This commonly occurred when a territorial bull was confronting a subordinate bull, or blocking the movements of a cow at a territory boundary.

(iv) (f = 88/476) R paid no attention, continuing with its ongoing activity at the same spacing. Territorial bulls usually appeared not to notice the snarl of nearby subordinate bulls, and sometimes also ignored snarls from companion cows or adolescents.

(v) (f = 19/476) R turned side on to A without retreating.

(vi) (f = 7/476) The sparring bulls jumped back at the snarl of the cow, then resumed their contest.

(vii) (f = 2/476) R responded with a snort or snarl.

Interpretation: The snarl is given in similar contexts to the snort, but is more likely to be performed in situations of more extreme provocation, and has a more powerful approach inhibiting or distance increasing effect. It may be regarded as a stronger keep-away threat than the snort.

c. Pant (N = 246)

Form: a chesty exhalation, or inhalation, or series of these, most commonly three syllabled (Fig. 41e). It can be imitated by breathing hoarsely, open-mouthed, "out-in-out," with a long accent on the exhaled breaths. An animal usually had its head up while making pants, but no special accompanying movements were made.

Social distribution: in contrast to the previous two sounds, pants were most frequently directed by adolescents towards cows or other adolescents, or by territorial bulls towards consort cows (Table 28).

Contexts:-

(i) (f = 93/246) an individual separated from companions made pants at intervals either when alone, or while moving towards other rhinos. Most commonly the sound was given by lone adolescents recently separated from their mothers, that had not yet formed a stable attachment with another individual. Cows that had lost their calves, and also calves that had become separated from their mothers, made repeated pants. In one instance, a territorial bull

TABLE 28. Actor-recipient matrix for the PANT

Upper figure represents number of times recorded
Lower figure indicates relative frequency, in percent

	ACTOR					
RECIPIENT	tADm	sADm	ADf	adol	calf	Total
tADm	0	0	0	0	0	0
	0	0	0	0	0	0
sADm	0	1	0	1	0	2
	0	0.4	0	0.4	0	0.8
ADf	33	4	11	69	5	122
	13.2	1.6	4.4	27.8	2.0	49.0
adol	5	0	11	42	0	58
	2.0	0	4.4	16.9	0	23.3
calf	0	0	14	0	0	14
	0	0	5.6	0	0	5.6
none	1	0	22	27	3	53
	0.4	0	8.8	10.9	1.2	21.3
Total	39	5	58	139	8	249
	15.7	2.0	23.3	55.8	3.2	

TABLE 29. Actor-recipient matrix for the HIC

Legend as above

	ACTOR					
RECIPIENT	tADm	sADm	ADf	adol	calf	Total
tADm	0	0	0	0	0	0
	0	0	0	0	0	0
sADm	2	0	0	0	0	2
	0.7	0	0	0	0	0.7
ADf	139	20	0	4	0	163
	49.1	7.1	0	1.4	0	57.5
adol	83	0	0	33	0	116
	29.3	0	0	11.6	0	41.0
calf	0	2	0	0	0	2
	0	0.7	0	0	0	0.7
Total	224	22	0	37	0	283
	79.1	7.8	0	13.1	0	

panted while tracking down a cow that he had earlier left in order to drink.

(ii) (f = 40/246) One or several members of a group exchanged pants while running off from a disturbance. Territorial bulls made loud repeated pants while running off behind a cow.

(iii) (f = 40/246) One member of a group initiated a move, making a pant as it did so; or two companions exchanged pants as they moved off together.

(iv) (f = 36/246) One individual in a group had become separated by a short distance from its companions, or had lagged when they moved on; it panted as it moved nearer to them.

(v) (f = 24/246) One individual in a group detected something alarming, such as the presence of a human intruder; it hastened towards it companions giving pants.

(vi) (f = 10/246) The actor heard another rhino pant nearby; it replied with pants.

Responses: In 10 cases, the recipient responded with pants. In 4 cases, a companion responded by approaching or moving after the actor. In other cases, no overt responses were shown to pants, unless they were accompanied by specific actions. For example, if one rhino ran towards others while making pants, the latter looked up or ran to join it.

Interpretation: In some contexts the pant appears to function as a contact seeking or maintaining call, in others it served to emphasise a friendly approach, and at times it is used when communicating alarm. It assists in maintaining or restoring contact between companions. It seems that the pant carries no specific message, but rather draws attention to the performer, who may then convey further information by his actions.

d. Hic (N = 283)

Form: Repetitive wheezy exhalations, with a throb produced at the initiation of each inhalation; breaths are short and erratic as if the animal were choking (Fig. 41f). The sound produced varies in individual renditions: usually the hiccing throb is clearly audible, but in some bulls merely a squeaky wheezing is produced. A throb is sometimes produced in the pant between exhalation and inhalation, and the hic is distinguished by the choking pattern of breathing. However, intermediate sounds that were difficult to classify were sometimes heard. Hics were heard less commonly than pants, but were made repeatedly in the context of courtship, and so were recorded more times than pants. Hics usually accompanied an approach and were made with the head held high.

Social distribution: hics were made only by males; most usually by territorial bulls, but in a few cases also by subordinate bulls or adolescent males that were nearing maturity. Except in a few seemingly accidental cases, they were directed only towards females (Table 29).

Contexts:-

(i) (f = 164/283) Most cases were associated with courtship advances made by a bull towards an oestrous cow. All such approaches, which may lead to a chin-on-rump precopulatory posture by the bull, were accompanied by a continual hiccing.

(ii) (f = 66/283) While approaching to investigate strange cows, bulls frequently made a few hics when they drew close. A few such approaches were, apparently mistakenly, directed towards young males.

(iii) (f = 58/233) A bull made a few hics while moving nearer to a cow that he was accompanying.

Responses: Cows usually responded to hiccing approaches by a bull with snorts, snarls or other distance maintaining displays. Only oestrous cows that were ready to accept pre-copulatory contact tolerated such approaches.

Interpretation: hiccing signifies that the approach by the bull is in the context of courtship testing, and this context is simulated in other situations in which bulls need to move nearer to a cow. Since all close quarter approaches were accompanied by hiccing, it was not possible to observe whether a cow would react more antagonistically in the absence of the hiccing sound.

e. Squeal (N = 219)

Form: A high-pitched vocal sound rising then falling in tone, sometimes breaking into a soft rumble at the end (Fig. 41g). Under greater excitement it may become a loud singing wail rising and falling in pitch several times before termination (Fig. 41h). There were no special associated gestures, and sometimes squeals were made without lifing the head from grazing.

Social distribution: squeals were made by territorial bulls (206 cases), only rarely by subordinate bulls (13 occurrences).

Context: the sound was made only when a bull was interacting with a cow at a territory boundary. Bulls squealed repeatedly while standing in front of the cow blocking her progress, while moving round to get between her and the boundary, and also while merely grazing in her vicinity while near the territory limits.

Responses: in most cases a confrontation ensued with snorts or snarls by the cow, and further squeals by the bull. In a few instances, submissive cows appeared to change direction to move away from the bull when he circled round squealing.

Interpretation: the squeal signifies that the actions of the bull are in the context of territory boundary blocking.

f. Shriek (N = 75)

Form: An intense shrill vocal sound, with a tonal quality reminiscent of the trumpeting of an elephant, usually rising from a gruff roar; or sometimes a falsetto groaning sound in place of the roar (Fig. 41i). The ears back, head thrust forwards posture of the snarl is maintained, or the shriek may accompany a horn prodding gesture.

Social distribution: the sound was made only by subordinate bulls or by territorial bulls out of their home territories or occasionally, by an adolescent male, and was directed almost exclusively against territorial bulls (Table 30).

Contexts: the sound was virtually restricted to situations in which a resident territorial bull was confronting another bull. At any move by the resident territorial bull suggestive of attack, such as an advancing step, or a feint towards lowered head, or a horn clash, the repeated snarling of the subordinate bull erupted into a loud shriek. A few individuals made groaning shrieks instead of snarls in such situations, this appearing to be mainly an individual voice aberration. Similarly in two cases adolescent males directed groaning shrieks in place of snarls against a nearby larger adolescent male, and once a cow made groaning shrieks instead of snarls against a confronting bull.

Responses: the shrieks appeared to inhibit the confronting

TABLE 30. Actor-recipient matrix for the SHRIEK

Upper figure represents number of times recorded
Lower figure indicates relative frequency, in percent

		ACTOR					
		tADm	sADm	ADf	adol	calf	Total
RECIPIENT	tADm	5	58	0	6	0	69
		7	77	0	8	0	92
	sADm	0	3	1	2	0	6
		0	4	1	3	0	8
	ADf	0	0	0	0	0	0
	adol	0	0	0	0	0	0
	calf	0	0	0	0	- 0	0
	Total	5	61	1	8	0	75
		7	81	1	11	0	

TABLE 31. Actor-recipient matrix for ADVANCING STEPS

Legend as above

		ACTOR					
		tADm	sADm	ADf	adol	calf	Total
RECIPIENT	tADm	0	14	34	47	1	96
		0	10	25	34	1	70
	sADm	0	0	21	4	1	26
				15	3	1	19
	ADf	0	0	1	1	0	2
				1	1		2
	adol	0	0	7	6	0	13
				5	4		10
	calf	0	0	0	0	0	0
	Total	0	14	63	58	2	137
			10	46	42	2	

territorial bull from carrying through the threatened attack.

Interpretation: shrieks seemed to be elicited by a fear provoking element, and appeared to have an attack inhibiting function.

g. Whine (N = 41)

Form: a thin mewing tone, rising then falling in pitch, usually of short duration (Fig. 41j). It may sometimes become a more prolonged sound rising then falling in pitch several times (Fig. 41k). It thus has resemblances to the squeal of a territorial bull, though I was readily able to distinguish the two sounds in the field.

Contexts:-

(i) (f = 30/41) the sound was made by a calf prior to seeking the udder to nurse. A calf invariably made a few whines before suckling, and the whines became more insistent in tone if the cow did not immediately allow it to nurse.

(ii) (f = 11/41) whines were also heard from young adolescents while they were moving near other rhinos to which they were only temporarily attached.

h. <u>Squeak</u> (N = 17)

Form: A short duration, high-pitched note, abruptly cut off, which may be repeated at intervals (Fig. 41.1).

Contexts: the sound was mostly made by calves separated from their mothers. In three instances, calves or adolescents attacked by a territorial bull made continuous squeaks. Once a lone calf squeaked while hastening away from a threatening gesture made by a cow. In another instance, when several adolescent males made repeated courtship advances directed towards an adolescent female, the females squeaked each time she rose to chase them away.

Responses: when a separated calf squeaked, its mother either moved towards it, or panted, and the calf then moved towards the cow. When an attacked calf squeaked, its mother advanced on the bull with snarls, causing it to break off the attack.

Interpretation: the squeak is a protection-eliciting distress signal used by calves.

i. <u>Gruff squeal</u> (N = 15)

Form: a throaty, rumbling squeal rising in pitch to a tensed cut-off, usually repeated in a series (Fig. 41m).

Contexts: the sound was made by territorial bulls while chasing after other rhinos, usually adolescents, or while swinging round to initiate a chase. Once a territorial bull made a brief gruff squeal while clashing horns with a subordinate bull, but otherwise the sound did not occur during fights or confrontations with other adult males. Once peculiar suppressed squeals were heard from a bull while attacking an adolescent, and similar suppressed squeals were heard from bulls accompanying head flings in other situations of excitement.

Responses: No specific responses could be discerned.

Interpretation: in chasing interactions, the sound may serve to emphasise the presence of the bull and thus keep the other animal running. In other situations, it appeared to be merely an expression of the state of excitement of the bull.

j. Gasp-puff (N = 12)

Form: a sudden nasal or chesty inhalation or exhalation of breath, like a curt snort or pant.

Contexts: a gasp-puff was elicited in situations in which the actor was startled as a result of the action of some other rhino, or upon discovering the close presence of a human, or at some other cause; it was emitted as the animal jumped away from the cause of alarm.

Responses: I observed no specific responses from nearby rhinos.

Interpretation: the gasp-puff seemed to be a direct response to a sudden fright, and had no obvious signal function, except possibly that of drawing attention to the actor. It resembles in its eliciting contexts the elaborated "steam engine" puffs made by black rhinos while running off or charging towards the source of a disturbance.

Other sounds

During mating, a bull commonly made repeated soft rumbles while mounted on the cow, and suppressed squeaks accompanied ejaculations. However, these seemed to have no signal valence, appearing rather to be simply the consequence of abdominal pressure. Sounds were also produced by actions such as scraping and horn wiping, and may emphasise the effect of the action (v.l.).

1.2. Visual displays

Special action patterns were less strikingly displayed in social interactions than were sounds. I recognised fifteen particular movements or gestures that seemed of potential communicatory significance, though some of these are better interpreted as directly functional actions rather than as ritualised displays, and some are of dubious signal value. Auditory and tactile elements are frequently coupled with movements. More elaborate movement sequences occurring in special types of interaction will be considered in later sections.

a. Ears back action

Form: The ear pinnae were laid back simultaneously against the sides of the neck, with the orifices directed postero-laterally (see Plate 11). This posture was held momentarily or for several seconds. Usually the action was coupled with a forwards thrust posture of the head and a loud roar was simultaneously emitted, but occasionally the ears were merely held back briefly without adoption of the full snarl action or a snort was made instead of the snarl. The actor faced directly towards the recipient while doing so.

Contexts: The ears back action alone appeared in identical contexts to those eliciting the full snarl.

Responses: Responses of recipients were similar to those given to the snarl.

Interpretation: The ears back action seems an intention movement towards adoption of the full snarl, appearing in situations of lower provocation, or when the provocative situation was dissipated before adoption of the full snarl. It may thus function similarly to the snarl as a distance-increasing display, with less energy expenditure. Since the displaying animal always faced towards the recipient, the flicking back of the two ears would be conspicuous to the latter, and the action could thus serve to give directivity to the threat. Companions standing beside the actor did not respond. However, this was also the case with snorts which were unaccompanied by any special actions. At night the snarl was still coupled with the ears back action, and recipients responded appropriately, though it was doubtful that they could discern the movements (observations aided by Starlite Scope).

b. Advancing steps (N = 136)

Form: The actor took several quick steps in the direction of the recipient, always coupling the advance with a snarl, or, in a few instances, a shriek or snort.

Social distribution: Similar to that of the snarl alone, but advancing steps were relatively more commonly made by adolescents than by other rhinos (Table 31).

Contexts: Similar to those of the snarl alone: (i) R approached A (f = 59/136); (ii) R moved near A (f = 46/136); (iii) R confronted A (f = 17/136); (iv) R blocked A's intended advance (f = 9/136); (v) R made tactile contact with A (f = 3/136); (vi) R snorted near A (f = 1/136); (vii) two bulls clashed horns in front of a cow (f = 136).

Responses: Again, similar to those given to the snarl alone: (i) R retreated (f = 74/124); (ii) R ignored A (f = 28/124); (iii) R stopped approaching, or desisted from touching (f = 20/124); (iv) R turned side-on to A (f = 2/124).

Interpretation: Advancing steps coupled with a snarl exert a more powerful distance increasing effect than the snarl alone.

c. Horn prod (N = 44)

Form: the head was lowered and an upward jabbing movement with the horn made in the direction of the recipient. Occasionally the body of the recipient was struck but more usually the action was checked before contact was made, or the recipient was pushed away gently with the horn. A horn prodding gesture was sometimes made at the end of an advancing snarl, at other times it was coupled with a grunt, rumble or snort, and sometimes it was delivered silently.

Social distribution: Horn prodding gestures were most commonly made by cows or adolescents against adolescent companions (Table 32).

Contexts:-

(i) (f = 23/44) R moved close by A, usually at a range of only 2-3 m. (ii) (f = 8/44) R was in front blocking A's intended path of movement. (iii) (f = 6/44) R approached A. (iv) (f = 6/44) R stood confronting A at close quarters. (v) (f = 1/44) R rested its head against the blank of A.

Responses:-

(i) (f = 29/41) R retreated moving away from A; (ii)

TABLE 32. Actor-recipient matrix for the HORN PROD

Upper figure represents number of times recorded
Lower figure indicates relative frequency, in percent

ACTOR

		tADm	sADm	ADf	adol	calf	Total
RECIPIENT	tADm	3	4	2	3	0	12
		6	8	4	6		24
	sADm	0	0	0	0	0	0
	ADf	0	0	2	3	0	5
				4	6		10
	adol	0	0	17	9	2	28
				34	18	4	56
	calf	0	0	3	1	1	5
				6	2	2	10
	Total	3	4	24	16	3	50
		6	8	48	32	6	

TABLE 33. Actor-recipient matrix for the HORN CLASH

Legend as above

ACTOR

		tADm	sADm	ADf	adol	calf	Total
RECIPIENT	tADm	20	0	2	2	0	24
		30		3	3		36
	sADm	21	0	3	1	0	25
		32	0	5	2		38
	ADf	1	0	6	1	0	8
		2		9	2		12
	adol	0	0	3	6	0	9
				5	9		14
	calf	0	0	0	0	0	0
	Total	42	0	14	10	0	66
		64		21	15		

(f = 9/41) R ignored A's action--this was usually the case of a territorial bull confronting another rhino; (iii) (f = 2/41) R threatened back; (iv) (f = 1/41) R turned to face away from A.

Interpretation: the horn prod is a ritualised attacking movement serving to drive another rhino away from the close proximity of the actor.

d. Horn clash (N = 72)

Form: The head was lowered so that the anterior horn was almost parallel to the ground, and the horn was hit sideways once or several times against the horn of the recipient. This action usually appeared at the end of an advancing snarl by a cow or adolescent when the opponent did not yield. Horn clashes by bulls differed in that they were usually made without accompanying vocalizations, and sometimes a forward thrust was made rather than a sideways hitting together of horns.

Social distribution: Similar to that of the advancing snarl, except for its occurrence also in male-male interactions (Table 33).

Contexts: (f = 44/72) in confrontations between territorial bulls, or between a territorial bull and a subordinate bull; (ii) (f = 12/72) when R was close beside or near A; (iii) (f = 9/72) R approached A; (iv) (f = 3/72) by a cow confronted by a bull; (v) (f = 3/72) when R snorted or snarled close beside A; (vi) when R was in front blocking A's path of movement.

Responses: (i) (f = 54/68) R blocked the horn clash with its own horn, but did not yield ground; (ii) (f = 12/68) R was driven back, or retreated; (iii) (f = 2/68) R also clashed horns back with snarls.

Interpretation: the horn clash is a more extreme gesture than the advancing snarl alone, used to repel encroachment. Similarly to the horn prod, the attacking motion is ritualised, in that the blow is usually delivered merely against the opponent's horn. However, in some instances when used by bulls it seemed to be more a checked attacking move.

e. Charge

Form: The charge was distinguished from advancing steps in that the actor advanced at a rapid trot for a distance of at least several metres, and in that charges were made silently.

Context: Charges were made only by territorial bulls, and were usually directed against other bulls encountered within the territory. Occasionally territorial bulls charged cows, but these instances seemed due to mistaken identification.

Response: Neighbouring territorial bulls met charges silently, while subordinate bulls and cows stood giving loud snarls. Charges led either to a brief clash or horns, or to a horn to horn confrontation.

Interpretation: The charge is an intimidatory display used by bulls.

f. Head flings

Form: The head was swung up and down rapidly with a tossing movement, frequently with sufficient vigour to produce a prancing action of the forequarters.

Contexts: Head flings were commonly made by young animals either preceeding or during a play interaction. On 10 occasions, head flings were also displayed by bulls, both territorial bulls and subordinate bulls. On 9 occasions, they were made by a bull while turning away from a confrontation with a cow under conditions of excitement; for example, twice when the meeting had taken place at a territory border, and once when an oestrous adolescent female had blocked an attempted approach yet again. Once, a young subordinate bull made head flings while turning away after a playful horn wrestling interaction with another young subordinate bull. Once a cow made head flings while turning away from a nasonasal meeting with another cow.

Responses: except in play, no specific responses were shown by the recipient.

Interpretation: Head flings seemed to function as a play invitation among young animals. When given by bulls they indicated a state of excitement but had no apparent signal value occurring at the termination of encounters.

g. Presenting the side

Form: The actor shifted orientation from facing towards the recipient to stand side-on.

Context: This gesture was made by bulls sometimes in response to snorts or snarls from companion cows.

Response: The cow then tolerated the bull's presence the same distance away when he was in lateral orientation.

Interpretation: Since an approach could not be initiated by the bull from the lateral orientation, the action appeases the cow.

h. <u>Horn against horn stare</u>

Form: A bull stared head up with his horn pressed against that of the other bull. The ear pinnae tended to be held directed forwards, though this orientation was not rigidly sustained (see Frontpiece).

Contexts: The display appeared in meetings between bulls. Towards cows, a territorial bull in contrast usually maintained a spacing of a few metres, though the alert posture of the confronting bull was similar.

Responses: Such displays were reciprocated by neighbouring territorial bulls during border confrontations. Subordinate bulls faced the territorial bull uttering repeated snarls

Interpretation: The physical presence of the dominant bull at such close quarters seems to serve as an intimidatory display.

1. Horn wiping

Form: The anterior surface of the front horn was wiped over the ground or a bush with a sideways twisting movement of the head.

Contexts: Horn wiping was most commonly observed as the initial element in the urination ritual of territorial bulls. Without urination, it appeared during confrontations between neighbouring territorial bulls, and bulls also horn wiped while blocking the movements of cows at territory boundaries. It was also made by bulls discerning or being approached by another bull at waterholes. Twice, subordinate bulls were seen to horn wipe after sniffing at the urination site of a territorial bull. On several occasions, territorial bulls dug their horn vigorously into a dung-heap. Once, a subordinate bull horn wiped when approached by my car.

Responses: In waterhole interactions, the horn wiping action seemed to cause the other bull to stand back avoiding a meeting.

Interpretation: The horn wiping action appears to function as an assertion of presence and status. The audible sound of the wiping movement draws attention to the presence of the actor. It was exhibited mostly by territorial bulls and never by cows.

j. Scraping

Form: The hindlegs, and sometimes the forelegs as well, were dragged forwards with the medial hoof nail pressed against the ground, leaving a scour mark 0.5-2 m long (Plate 13). Usually each leg was dragged no more than twice.

Contexts: Scraping was most commonly seen as an element in the urination ritual of territorial bulls. In cases in which urination did not follow, contexts were similar to those eliciting spray-urination, and it seemed that the final step had merely been omitted. Territorial bulls also sometimes dragged their legs along the ground while shuffling backwards or forwards during confrontations, and once a territorial bull scraped stiff-leggedly several times while moving away terminating a confrontation.

Interpretation: The sound produced by the scraping action could serve to emphasise the presence of the bull during interactions. There was no indication that rhinos responded visually to the scrapemarks produced, and in the urination ritual its function seems related to deposition of the scent mark (v.i.).

k. <u>Tail curled</u>

Form: The tail was curled upwards in a spiral. This posture was held, or the tail was curled and uncurled in response to changing stimuli.

Contexts: (i) during urination and defecation; (ii) upon becoming alarmed, or while running off from a human intruder; or upon smelling human scent tracks; (iii) while being chased by another rhino (usually the case of adolescents being chased by a territorial bull); or while walking on after being chased; (iv) in conjunction with the snarl display; (v) by a territorial bull, while manoeuvreing to block the movements of a cow at a territory boundary;

(vi) by a territorial bull, after losing contact with a cow that he was accompanying; (vii) by one particular young subordinate bull, whenever the territorial bull appeared nearby; (viii) by a lone adolescent, while approaching or moving near strange rhinos; (ix) while walking on yielding sand beside a river; (x) at a sudden thunder crash. Numbers (i)-(iv) were the general and most commonly observed contexts, (v)-(viii) represent less frequently observed contexts, and (ix) and (x) were single instances.

Responses: No specific responses were observed. The tail curling action was inconspicuous and was given independently of the presence of other rhinos, and other rhinos when present paid no apparent visual attention to the displayer, except in circumstances such as chasing. When given with a snarl display, the tail curling would not be visible to the recipient.

Interpretation: Tail curling appears associated with situations of general autonomic stimulation; that is, with elimination, and with situations where nervousness or fear on the part of the displayer might be suspected. It was particularly useful to the observer in indicating elements of fear where this might not otherwise have been apparent --as with a bull blocking a cow at a boundary. However, there was no indication that it had any such signal value to other rhinos.

1. <u>Nasonasal meeting</u>

Form: One, or both, animals advanced to meet. Sometimes they sniffed with raised heads or, more commonly, they stood with heads low in relaxed posture, frequently with their anterior horns pressed together (Plate 21). Movements were slow and relaxed, seemingly to overcome the antagonistic reaction likely on the part of the respondent to a direct approach. The initiator commonly advanced to a few metres separation, then stood quietly, head low, as if dozing. The respondent then approached to make horn nudging contact, or sometimes this was achieved after several such moves. Nasonasal meetings commonly lasted about a minute or less, and longer meetings were likely to develop into horn wrestling.

Contexts: Nasonasal meetings commonly developed out of encounters involving adolescents, calves or cows, and were rare among bulls (Table 34).

TABLE 34. <u>Interactant matrix for NASONASAL MEETING</u>
Upper figure represent number of times recorded
Lower figure indicate relative frequency, in percent

		RESPONDENT - I					
		tADm	sADm	ADf	adol	calf	Total
R	tADm	0	1	1	0	4	6
E			1	1		3	5
S	sADm		3	2	12	0	17
P			2	2	9		13
O	ADf			16	25	7	64
N				13	20	6	38
D	adol				15	19	34
E					12	15	28
N	calf					22	22
T						17	17
II	Total						127

TABLE 35. <u>Interactant matrix for HORN WRESTLING</u>

Legend as above

		RESPONDENT - I					
		tADm	sADm	ADf	adol	calf	Total
R	tADm	0	1	0	0	0	1
E			2				2
S	sADm		1	0	7	0	8
P			2		13		15
O	ADf			4	11	1	16
N				7	20	2	29
D	adol				6	10	16
E					11	18	29
N	calf					14	14
T						25	26
II	Total						55

Responses: Sometimes the approach to meet was mutual, in other instances the respondent merely stood quietly permitting the actor to advance. In some cases the other rhino responded with snorts or snarls to an attempted approach, causing the actor to desist.

Interpretation: Though visual and tactile elements are included, the significant feature seems to be the close olfactory contact allowing potential individual identification. I have distinguished these nasonasal meetings from other cases of olfactory investigation by the slow relaxed movements which commonly lead to a gentle horn nudging contact. However, many encounters between bulls and cows can be interpreted as one-sided nasonasal investigations, in which an approach closer than within a few metres was prevented by the antagonistic response of the cow. Similarly, territorial bulls come into close olfactory contact during the horn against horn stare. Nasogenital investigation was never seen, except during precopulatory contact.

m. <u>Horn wrestling</u>

Form: Horn wrestling commonly developed out of a nasonasal encounter. Weaving movements were made rubbing the two horns together, and these led to more active pushing and prodding movements. Adolescents and calves were most active in initiating horn wrestling, but adult cows, and in one instance two adult bulls, also wrestled horns (Table 35). The actions are those of playful fighting, and will be treated more fully in Section E.

n. Attack

Form: Attacks were distinguished from horn clashes in that several successive horn jabbing movements were made, which were clearly directed towards the body of the opponent. Cases of attack were rare and will be considered in more detail in the next section.

o. Fight

Form: In a fight, attacking gestures were reciprocated by both opponents. Only two fights were observed, both between territorial bulls. Further consideration will be deferred to the following section.

1.3. Tactile displays

Tactile elements are incorporated within several of the visual displays described above, as when two animals rubbed horns together. There was only one primarily tactile display.

Rubbing sides

Form: One animal rubbed its side against that of another in moving past; or less commonly one animal rubbed its head or another part of its body against that of a companion.

Contexts: Rubbing sides mostly occurred simply when one animal was moving close past the other. In two instances, when one animal was up and apparently ready to move on while its companion still lay sleeping, the active individual rubbed its head on the rump of the other. Rubbing was restricted mostly to companions of long standing, though on a few occasions it occurred between temporary companions.

Responses: In the two instances described above, the sleeping companion did not immediately respond, but a few minutes later roused itself and moved off with the other. Rubbing sides was tolerated by a close companion without overt response, but in several cases a rhino responded with snorts when tactile contact was made by a more temporary group associate.

Interpretation: Acceptance of such tactile contact was seemingly an expression of a close bond between two individuals, probably serving to develop and strengthen such bonds.

1.4. Olfactory displays

The only scent glands reported to occur in the white rhino are preputial glands (Section II.A.4). Olfactory signals thus seem limited to the odours of dung and urine and general bodily odour. Special actions were associated with defecation and urination by territorial bulls. These defecation and urination rituals seem related particularly to the placing of persistent scent marks in the environment. While defecation and urination by cows, subordinate bulls and immature animals was performed in a directly functional manner (Section II.C.3), odours attached to the dung and urine may carry significant information.

In ten cases I was able to follow sufficiently closely behind bulls to investigate all sites where they paused to sniff. Three of the bulls were territorial bulls exploring within their home territories; three were deposed ex-territorial bulls exploring around the borders of formerly held territories; two were territorial bulls travelling to water, and two were subordinate bulls travelling to water. Some 54 sites of evident olfactory interest were recorded. Small dung piles, the products of cows, subordinate bulls or immature rhinos, were present at 16. Scrape-marks indicating a territorial bull urination site were found at 14. At 10 there were damp puddles, marking the urination site of a cow, subordinate bull or immature animal. Large permanent dungheaps were present in 8 cases. At 6 sites, nothing was discernible; these could potentially also have been the urination sites of territorial bulls, where the scraping action had been omitted, or some other scent may have been present. Territorial bull urination sites and scattered dung piles are more abundant in the environment than puddle urination sites and dungheaps. All are evidently of significance to bulls.

a. <u>Defecation</u>

Form:

(i) Defecation ritual of territorial bulls (Plate 12). Territorial bulls always made kicking movements before and after defecation (Table 36). Typically a bull first

PLATE 12. Defecation ritual of territorial bulls

a. A territorial bull sniffs at a dungheap prior to defecation.

b. A territorial bull scatters his dung with backwardly directed kicks following defecation.

c. A dungheap showing marks of utilization by a territorial bull; in the centre, two bare patches indicate the placement of the hindlegs.

d. A large border dungheap with a prominent central hollow; scattered around the perimeter are single dung piles.

TABLE 36. Defecation patterns of territorial bulls

Identity of tAIm	no. of proceeding kicks				no. of following kicks				on dungheap	centrally located
	N	av.	max	min.	N	av.	max.	min.		
I	25	9.1	28	3	30	10.4	15	4		
L	10	5.8	13	1	13	9.5	15	2		
C	3	7.3	8	5	8	9.2	13	4		
X	5	7.8	10	5	5	8.6	12	5		
BB	4	4.0	7	2	5	13.8	19	9		
Others	22	6.1	21	2	38	8.8	18	2		
ALL	69	7.2	28	1	99	9.7	19	2	27/29	19/22

approached a dungheap, and devoted one or several minutes to sniffing around at the dung accumulation. He then positioned himself with his hindlegs near the centre of the heap; if there was a deep central hollow, this meant that his back sloped downwards considerably posteriorly. He then commenced a series of backwardly directed kicks, shifting weight from one hindleg to the other, and pushing the non-supporting leg vigorously backwards, so that the sole of the foot contacted and sent flying any dung in its path. Usually from 3 to 13 preceeding kicks were given. As the fecal boluses emerged, the bull shifted the hindlegs anteriorly, and curled his tail upwards, so that the dung fell clear of the legs. He then delivered usually from 4 to 15 further kicks, then walked off. As a result of the kicking action, his freshly deposited dung was scattered about the surface of the dungheap mixed in with previously accumulated dung. Except in two cases all observed instances of defecation by territorial bulls were on established dungheaps, and almost always in the centre of the dungheap (Table 36). In the two exceptional instances, defecation occurred on the freshly deposited dung of the cow that the bull was accompanying.

(ii) Defecation by other rhinos. Subordinate bulls, cows, adolescent males and even calves occasionally made kicking movements following defecation (Table 37). However, these differed from the kicking movements made by territorial bulls in that in most cases they were merely token gestures performed without any force, and only in rare instances was the freshly deposited dung pile disturbed. Occasional instances of more vigorous kicking by subordinate bulls seemed related to special circumstances. The sADo.N regularly made kicking movements following defecation, and after a few months assumed the status of territorial bull in a nearby territory. While with an oestrous cow, sADo.B preceeded defecation with 1-2 slow kicks, and followed it with 1-7 good kicks; at other times, he was never seen to make more than 1-2 empty kicking gestures after defecation. Male B had been a territorial bull less than a year earlier. Another ex-territorial bull, sADo.A, was once seen to preceed defecation with 11 low intensity kicks, and follow it with 6 good kicks which sent dung flying. This occurred just before he regained his home territory (the same one that he himself had formerly held) after a wandering excursion, during the

TABLE 37. Defecation patterns of other rhinos

Social Class	preceeding kicks occurrences	av.	max.	following kicks occurrences	av.	max.	on dungheap	centrally located
sADms:								
B	2/5	2.0	2	5/9	3.4	7		
HH	0/6	-	-	0/6	-	-		
N	0/4	-	-	7/7	5.0	10		
All	5/39	3.4	11	22/47	3.8	10	10/19	5/9
adolm	1/37	1.0	1	12/42	4.4	10	13/20	1/8
ADf	0/91	-	-	10/91	3.2	25*	28/54	3/13
adolf	0/40	-	-	0/40	-	-	10/25	0/8
calf	0/19	-	-	2/19	6.5	8	5/12	0/4

*excluded in calculating average

course of which he had been challenged by another territorial bull. Six of the ten observed cases of dung kicking by cows can be ascribed to a single individual. In one exceptional instance, this cow delivered a series of 25 kicks post defecation, some of which pushed the top of the dung pile gently backwards. She had a four day old calf with her at that time. Two further observations of kicking movements by cows can be related to individuals with very young calves. Several of the observed instances of kicking movements by adolescent males can be ascribed to conditions of special excitement, for example when agitated by my presence. Two instances of dung-kicking by calves were observed, both by males. One of these was an infant only two months old, which made 5 kicking motions after dunging next to the dung of its mother. Subordinate bulls, cows and immature animals defecated as often away from a dungheap as on an established dungheap, and seldom orientated towards the centre of a dungheap (Table 37).

Contexts: Rhinos were stimulated to defecate by the presence of other rhino dung. It was common for animals, on encountering a dungheap, to pause to add further contributions. Group companions usually defecated almost simultaneously, or within a few minutes of one another. Where defecation occurred away from established dungheaps, there was often a dungheap a few metres away, or at least a few scattered dung piles in the vicinity. Territorial bulls seemed to know the locations of various dungheaps within their territories, and walked distances up to 100 metres to make use of them. However, while some dungheaps had a prominent central hollow, others showed little evidence of kicking movements, and there was variability in the usage of different dungheaps by territorial bulls. The spatial dispersion of dungheaps and their use by territorial bulls was discussed in Section B.3.1.

Responses: Territorial bulls sniffed carefully at dungheaps before defecating there, sometimes spending several minutes in the process. They also sniffed at dungheaps on occasions when they did not pause to defecate. More attention was paid to the scattered dung piles of cows and adolescents around the periphery of the heap than to the central accumulation. Territorial bulls also commonly sniffed at dung piles encountered away from the dungheaps. If the cow that he was accompanying defecated, a territorial bull moved up to sniff at the dung as soon as she had moved on. In one case a territorial bull nibbled at dung on a dungheap, then stood with head lifted in the "flehmen" posture. This response was exceptional, and may have been occasioned by the presence of urine on the dungheap.

Another response occasionally exhibited by territorial bulls was to dig the horn into the dungheap. The bull inserted his anterior horn deep into the dung pile so that his snout was also buried, worked it about vigorously, then lifted his head with a large mass of dung adhering between the two horns. This response which was observed on 9 occasions seemed to be restricted to special circumstances. In two cases, horn digging was exhibited by a territorial bull after sniffing at a border dungheap generally used by the neighbouring territorial bull; in a third instance horn digging also occurred in the region of one of these border dungheaps, though I was too far away to confirm the exact location. In another case horn digging was displayed by the owner of a dungheap, upon arriving there seven hours after the neighbouring territorial bull had defecated there. A fifth case at a border dungheap involved a newcomer bull a few days prior to his taking over one of the territories. Another two cases took place at dungheaps beside waterholes, which were thus likely to be visited by strange bulls. Cases 8 and 9 also took place at border dungheaps, though I had no direct evidence that another bull had previously defecated there.

The horn digging response seemed to be correlated with the presence of the dung of a strange bull on the dungheap. To test this assumption, I transferred territorial bull dung collected in one territory to a dungheap in another territory. However, after several such attempts and many hours of waiting, I secured only one observation. The territory owner gave only a cursory sniff and did not appear to notice the foreign dung. Another negative observation was made at a drinking pool dungheap, where a strange territorial bull had been observed to dung. An hour later the neighbouring territorial bull arrived, sniffed at the dungheap and at various nearby dung piles, but displayed no response to the presence of the dung of the other bull.

In one observation, a territorial bull arrived at a dungheap a few minutes after his resident subordinate bull had defecated there and given ten succeeding kicks.

The territorial bull sniffed but showed no overt response, even though the subordinate bull remained standing only a few metres away.

Territorial bulls on the way to water also paused to sniff at dungheaps encountered in other territories. In one observation, a territorial bull exploring across the border in a neighbour's territory paused looking about tail curled at a hungheap, but did not defecate there.

Cows, calves, adolescents and subordinate bulls also paused to spend periods of 15 seconds to a minute or longer sniffing at dungheaps and dung piles. Once an adolescent female nibbled at freshly deposited territorial bull dung, picking up pieces in her lips then allowing them to fall.

Interpretation:

Dungheaps provide a set of locations which bear a record of the visits of many different rhinos. Though thus not exclusive to territorial bulls, most or all of the dungheaps within a territory are marked with the dung of the resident territorial bull. The dung scattering action would seem to facilitate a more powerful release of scent, by increasing the surface area exposed, and furthermore distributes the scent of the bull over the dungheap. The dung accumulation at the centre of a dungheap is likely to consist mainly of the dung of the territorial bull. Surrounding this are the scattered dung piles contributed by rhinos of other social classes. The odour of the dung may also be transferred to the feet of the territorial bull as a result of the kicking action, and thus transferred some distance away from the immediate vicinity of the dungheap. Airborne distribution of odour from the dungheap may also be significant, the dungheaps perhaps functioning as scent beacons from which any characteristic scent attached to the dung of the territorial bull may be wafted downwind.

Assuming that individually characteristic odours may be associated with the dung of different individuals, the dungheaps provide a record of the identities of the various rhinos that are in the vicinity at the time. By further being marked clearly with the scent of the territorial bull, they also bear a record of the identity of the territory owner, and of his recent presence in the area. The large border dungheaps which seemed to be used mainly by territorial bulls may be of particular significance to neighbouring territorial bulls in this regard.

Dungheaps may thus function as potential territory markers. They also form focal points for the accumulation of the dung of other rhinos, which also clearly bears potential information; perhaps identifying individuals, and indicating oestrous status of females. The olfactory signals emanating from dungheaps and dung piles may thus also have more complex social functions.

b. Urination

Form:

(i) Urination ritual of territorial bulls (Plate 13). Urination by territorial bulls was almost always ffected in the form of a powerful backwardly directed spray. Special actions commonly preceeded spray-urination. First, in 50% or more of observed cases, the bull horn wiped; sometimes this was forcefully expressed, sometimes it was merely a token nudge; sometimes the bull clearly sniffed at the site before horn wiping. In about two thirds of the observed cases, horn wiping was directed against a low bush, usually under 60 cm in height (Table 38), in remaining cases, it was performed against a grass tuft, or over soil that was bare or covered with lawn-like grass.

PLATE 13. <u>Urination ritual of territorial bulls</u>

a. Scraping with the hindleg

b. Spray-urination over a bush

c. Close-up of spray emission

d. Scrapemarks evident on bare
soil, directed against a stump.

However, this frequency varied, depending on the local availability of suitable bushes. For example, beside the Madlozi stream, in the territory of tAD♂.*X*, 46 of 49 recorded scrapemarks were directed against a bush. In the nearby territory of tAD♂.*I*, where the density of shrubs and seedlings was lower, only 29 of 62 recorded scrapemarks included a bush. Plants were commonly seedlings or saplings of *Acacia* species, or bushy clumps of creepers such as *Asparagus* or *Azima*. Occasionally low tree stumps provided the focus. Following horn wiping, a bull scraped over the site, usually once or twice with each hindleg, though sometimes also with the forelegs. Long scour marks were left, directed against the base of the bush if one was present, and occasionally the stem of the bush was broken, or branches torn off, by the action. Finally the bull paused to eject the urine, usually in 3-5, though occasionally up to 8, spasmodic bursts. Each burst lasted 1-2 seconds, and sent a fine "aerosol" spray of urine droplets as far as 3 m backwards. The tail was sometimes curled in an upwards spiral during spray-urination, but more commonly it was curled sideways in contact with the rump. The urine droplets fell over the scrapemarks on ground, or coated the leaves of the bush, evaporating to leave a whitish oily film. Sometimes preceeding steps were omitted, and the bull simply spray-urinated, frequently without pausing from grazing. However, if horn wiping was performed, scraping always followed. In seven observed cases only, a territorial bull urinated in a continuous stream for a minute or longer with hindlegs straddled, in the manner of cows and subordinate bulls.

(ii) Other rhinos. Though stream urination by subordinate bulls was recorded 33 times, on only one occasion was spray urination seen. The subordinate bull N spray-urinated 11 times in 25 minutes, including horn wiping and scraping, while grazing and moving on towards the southern boundary of the territory that he shared with tAD♂.H. He defecated at a ungheap with kicks, sniffed at another dungheap, then veered westwards away from the boundary. I had the impression that he had been about to set out towards water, but had been deflected. This bull became a territory holder in a nearby territory 4 months later.

Adolescent males also usually stream-urinated, but spray-urination was also recorded on 9 occasions. Six of these were performed by one individual aged 2.5-3 years.

This individual emitted 1-2 urine puffs at a time, sometimes repeating this several minutes later, while grazing near or moving after different cows to which he had attached himself. The urine emission was pulsed and in the form of spreading droplets, but lacked the power of territorial bull spray-urination. Once this young male spray-urinated twice while moving tail curled close past a territorial bull at a territory boundary. The territorial bull paid no attention. The three remaining observed cases of spray-urination also occurred in circumstances in which an adolescent male had attached himself temporarily to a cow.

Females always urinated in a continuous stream, except on the day of oestrous receptivity. Then they emitted repeated little squirts of urine. One such squirt-urination was seen from a 3-4 year old female that showed no other indication of being in oestrus.

Contexts:

There were no special urination sites, and urination was generally performed independently of defecation. There was no detectable social facilitation. It was rare to find two successive occurrences of scrape-marks directed against the same bush, though sometimes scrapemarks were only a few metres apart over adjacent bushes. It thus seemed that territorial bulls were stimulated to urinate over bushes that had not been recently marked. Frequency of spray-urination was strongly influenced by the proximity of the bull to a territory boundary; average rates of 2 spray-urinations per hour were recorded near the centre of territories, and 10 per hour near boundaries (Table 39; see also Section B.3.1.) However, sometimes high rates of spray-urination were recorded away from boundaries. Spray-urination tended to occur repeatedly also while a bull was shifting location within his territory or patrolling a well-used trail. It was never seen to be performed outside a bull's home territory. During grazing spells, spray-urination tended to be performed either when a bull paused from grazing prior to moving on a few metres, or just before resuming grazing after moving on, or at an alteration in direction of movement. Sometimes contact with a suitable low bush while grazing seemed to act as a stimulus. While walking on steadily, territorial bulls paused momentarily to spray-urinate at short intervals. Spray-urination was particularly frequent while a bull was blocking a cow at a territory boundary; once 29 spray-urinations in 122 minutes were recorded in such circumstances.

Responses:

Territorial bulls frequently paid olfactory attention to scents encountered while exploring especially in territory boundary regions, but in most cases I was too far away to ascertain whether these represented urination sites. Territorial bulls and subordinate bulls travelling to water were noted pausing briefly to sniff at sites where there were fresh scrapemarks indicating the urination sites of other territorial bulls; but no other reaction was displayed. No notice was taken of other scrapemarks passed on the way. A territorial bull patrolling his border paused only briefly to sniff at a site where I had seen the neighbouring territorial bull spray-urinate an hour and a half earlier. In another instance, a territorial bull showed a stronger response to scrapemarks, probably those of the neighbour, in a boundary region. He rubbed his nose vigorously over the site for 20 seconds with a sideways motion of his head, then repeated this wiping action several more times with pausec to make chewing motions. Finally he scraped vigorously five times over the site and urinated four sprays, then moved on. In three cases, subordinate bulls sniffed at the urination scrapemarks of a territorial bull, then stood with raised heads and lip movements (the flehmen posture). In three other observed cases, cows responded similarly after sniffing at the urination site of a territorial bull.

Territorial bulls also showed considerable interest in the urination sites of cows. If the cow that he was accompanying urinated, a territorial bull approached to sniff carefully at the puddle as soon as she had moved on. At other times upon encountering a damp or even superficially dry stream urination site, territorial bulls paused to sniff for periods up to a minute or longer. Bulls sniffed with their noses close to the ground, sometimes clearly nibbling at the damp earth with the lips, then stood with head raised and lips parted for several seconds. This action is equivalent to the flehmen response given to female urine by a wide variety of ungulates and other mammals (Estes, 1972), though the posture is less exaggerated than that of the black rhinoceros (Goddard, 1966) and most Bovids. The flehmen response by white rhinos was usually but not invariably given after smelling the urination site of a female. In two observed cases, a territorial bull exhibited flehmen after sniffing at the urination site of an adolescent male; one of these was followed by an immediate attack directed against a cow accompanying the adolescent (see Example 29). Subordinate bulls and adolescent males also sniffed at the urination sites of cows and then exhibited the flehmen posture. Twice, a seven month old male calf exhibited flehmen after sniffing at the urination site of his mother. As described earlier, in six cases subordinate bulls and cows exhibited flehmen after sniffing at the spray-urination site of a territorial bull.

Interpretation:

Spray-urination seems to be stimulated by situations that can be characterised as "reassurance needing". This is suggested by its greater prevalence in territory boundary regions, and also by the special circumstances of its occurrence among subordinate and adolescent males. There is possibly a physiological connection between nervous tension and the forceful. expulsion of spurts of urine. Outside a bull's home territory, autonomic nervous tension may perhaps be strong enough to inhibit urination altogether. However, spray-urination as performed by territorial bulls has clearly become elaborated as a special display. Functionally, it serves as an assertion of the presence of the bull within the home territory. In territorial bulls, most urine is apparently diverted for such a purpose, but physiologically directly functional stream urination may occur when a full bladder has been accumulated, as after a rest period.

Though the spray might seem adapted to broadcast scent into the wind, I never saw any rhino respond to the airborne scent of urine spray. Rather, it appears that the spray increases the surface area of the urine deposit and hence the power of the olfactory signal. The inclusion of a bush also increases surface area. The scraping could serve to clear the soil surface of any pre-existing odours before impregnating it with the new scent mark. An analogy can be made with wiping a blackboard clean before writing up another message. The initial horn wiping probably assists orientation of the bull towards a particular site--a set number of paces would then orientate the hindquarters appropriately.

Motivationally, horn wiping is readily incorporated since alone it may also serve as an assertion of presence. The secretion of the preputial glands may add a special odour to the urine; but I had no opportunity to investigate anatomic relationships.

The resultant urine scent marks are dispersed over the extent of a bull's territory, being particularly concentrated along borders and beside trails where they will be encountered frequently by passing rhinos. They thus provide evidence indicating the presence of the territory owner and the limits of his territory. Though little overt response is shown to them by other rhinos, this may be because they serve merely to demonstrate and maintain the *status quo*.

Investigation by bulls of the urine of cows is of potential significance for ascertaining the sexual condition of the female through hormone levels; this is the general function postulated for the flehmen display (Estes, 1972). It is possible that the androgen levels of bulls could also be evident from olfactory cues in the urine, considering the occasional flehmen displays given by cows to male urine; but such information is presumably of lesser importance. Males generally did not exhibit flehmen to the urine of other males. However, it is possible that hormone levels could be revealed by the content of preputial gland secretion in the urine, which could be detected by normal olfactory receptors (rather than by Jacobsen's organ to which flehmen is presumed to be related).

Reactions to other scents

Rhinos also responded to the scent tracks left by other rhinos. A territorial bull was watched following along the tracks of another bull. A subordinate bull sniffed at, and followed for a short way, the scent trail left by a passing strange territorial bull. Territorial bulls on several occasions tracked down apparently by scent cows with which they had temporarily lost contact. In one instance a territorial bull left a cow to go down to water; returning to the site where he had left the cow 75 minutes later, he sniffed noisily, nose to the ground, following a devious course for 800 metres before he relocated the cow 25 minutes later. Probably several cases of sniffing at unidentified scents were related to such scent traces.

Discussion

Twenty-eight different displays performed by white rhinos are listed in Table 40. Visual components are significant in 16, auditory signals in 15, tactile stimuli in 7, and olfactory information in 6 (several signal modalities are combined in many displays).

The most frequently performed displays are those relating to the control of spacing between individuals. The snort, ears back action, snarl with rumble, grunt or full roar, advancing snarl, advancing horn prod and advancing horn clash form a set of actions which are elicited in similar contexts: when one animal threatens intrusion, or has intruded, upon the "personal space" (Marler and Hamilton, 1966, p. 166) of another. They serve to maintain "individual distance" (Hediger, 1950), and may be characterised functionally as "separation maintaining". The order of listing is that in which they are successively likely to be elicited in situations of increasing provocation, and also reflects a gradient towards an increasingly powerful effect on the recipient in maintaining or increasing spacing. However, such relationships are not simple to demonstrate, as both

TABLE 40. Summary of displays performed by white rhinoceroses

Key to text	Display	signal modality	prime displ. classes	no. of times record.	Function
					Controlling spacing:
1a	Snort	a	f,s,m_2	870	approach inhibiting
1b	Snarl (static)	a,v	f,s,m_2	490	approach inhibiting
2b	Advancing snarl	v,a	f,s,m_2	136	distance increasing
2c	Horn prod	v,t,a	f,s	50	distance increasing
2d	Horn clash	t,v,a	f,s	28	distance increasing
1c	Pant	a	all	249	proximity maintaining
1f	Shriek	a(v,t)	m_2	75	attack inhibiting
3	Rubbing sides	t	f,s,c	11	bond reinforcing
				1947	
					Special circumstances:
1d	Hic	a	m_1	283	courtship (dist. reducing)
1e	Squeal	a	m_1	219	territ. bdry. blocking
1g	Whine	a	c	41	nursing
1h	Squeak	a	c	17	distress
1i	Gruff squeal	a	m_1	15	chase
1j	Gasp-puff	a	all	12	fright
				597	
2a	Ears back	v	f,s,m_2	occ.	directivity to threat
2f	Head flings	v	all	10	play invite, excitement
2k	Tail curled	v	all	many	(nervous tension)
					Impressive displays:
2h	Horn to horn stare	v,o,t	m_1	106	intimidation
2e	Charge	v	m_1	43	intimidation
2i	Horn wipe	v,a	m_1	75	assert. presence
2j	Scraping	v,a	m_1	10	assert. presence
2d	Horn clash	t,v	m_1	44	threat
				278	
					Submission:
2g	Presenting side	v	m_1		appeasement of cow
1b	Snarl	a,v	m_2	116	submission
					Indiv. identification
2l	Nasonasal mtg.	o,t,v	s,f,c	127	greeting
2m	Horn wrestling	t,v	c,s,f	55	play
4a	Defec. at dunghp	o	all	many	identity
4b	Stream urin.	o	f	many	reprod. status
					Space claim
4a	Dung scattering	o	m_1	102	marking dungheap
4b	spray-urin.	o	m_1	636	marking territ.

a = auditory, v = visual, t = tactile, o = olfactory
m_1 = territ. bull, m_2 = subord. bull, f = adult female, s = adolescent, c = calf

elicitation and response depend upon many factors. A snarl is relatively more likely to be given than a snort when another individual is approaching, or confronting from close quarters, than when the latter is merely moving nearby (Table 41; $X^2 = 31.6$, df = 1, $p \ll 0.001$). Cows use a snort relatively more often than a snarl towards a nearby territorial bull that is a temporarily attached companion, than to an approaching strange territorial bull (Table 43; $X^2 = 14.5$, df = 1, $p < 0.001$). Adolescents and subordinate bulls direct snarls relatively more often than snorts against territorial bulls than do cows; and adolescents use snorts relatively more commonly than snarls against other adolescents than against bulls (Tables 26 and 27; adolescents vs cows: $X^2 = 49.8$, df = 1, $p \ll 0.001$; sAD♂♂ vs cows: $X^2 = 20.0$, df = 1, $p < 0.001$; by adolescents against adolescents vs bulls, $X^2 = 15.9$, df = 1, $p < 0.001$). Calves display only snarls, and receive only snarls (Tables 26 and 27). Subordinate bulls used snorts and snarls against approaching territorial bulls at greater separation distances than did cows (Table 43; 25.1m vs 15.1 m, t = 3.24, df = 30, $0.0005 < p < 0.005$). However, the functional effects of

TABLE 41. Separation maintaining displays: comparison of eliciting contexts

Central figure = number of times recorded
( ) on right = frequency of context eliciting display (%)
( ) below = frequency of display in given context (%)

		CONTEXTS						
Display	N	R stands or moves nearby	R is in front	R approaches	R confr. from close	other	av. separ. dist. (m)	N
Snort	870	394(45) (65)	40(5) (54)	355(41) (56)	48(6) (27)	33(4)	13.1	298
Snarl (static)	487	135(28) (22)	16(3) (22)	202(42) (32)	107(22) (59)	27(5)	11.4	90
Advancing snarl	136	46(34) (7)	9(7) (12)	59(43) (10)	17(13) (9)	5(4)	8.4	14
Horn prod/ or clash	72	35(49) (6)	9(13) (12)	15(21) (2)	9(13) (5)	4(6)	2-3	
		610	74	631	181	69		

TABLE 43. Varying responses demonstrated towards and by a territorial bull in differing contexts

Figures represent relative frequencies, in percent

(a) A territorial bull approaches (not a companion):-

Display	N	RESPONSE OF tADm contin. appr.	keeps distance	retreats	separ. dist. av. (m)	N
(i) ADf:-						
snort	66	33	58	9	15.0	18
snarl	54	20	72	7	15.2	4
advancing snarl	6	0	33	67	-	-
(ii) sADm:-						
snort	16	37	63	0	28.0	5
snarl	21	43	57	0	22.2	5
advancing snarl	3	67	33	0	-	-

(b) Territorial bull moves near a temporary companion cow:-

ADf:-						
snort	96	3	79	18	10.6	88
snarl	33	0	75	24	11.4	14
advancing snarl	6	0	0	100	-	-

TABLE 42. Separation maintaining displays: comparison of responses given by recipients

I = ignores display; S = stops approaching, or turns away
R = retreats by backing a few steps or by moving away

Upper figure = number of times recorded
Lower figure = relative frequency, in percent

CONTEXTS

Display	R nearby			R in front			R approaches			R confronts			All		
	I	S	R	I	S	R	I	S	R	I	S	R	I	S	R
Snort	209	86	53	11	3	18	64	202	48	38	2	5	332	299	130
	60	25	15	34	10	56	20	65	15	84	4	11	44	39	17
Snarl	64	19	28	6	3	5	40	114	17	79	2	9	192	144	60
(static)	58	17	25	43	21	36	23	67	10	88	2	10	48	36	15
Advancing snarl	14	1	26	1	0	8	2	17	38	11	0	2	28	22	74
	34	3	63	11	0	89	4	28	52	85	0	15	23	18	60
Horn prod	6	1	25	0	2	5	1	2	10	9	0	0	4	20	41
or clash	19	3	78	0	30	70	8	15	77	100	0	0	6	34	63

snorts and snarls on recipients are almost indistinguishable; both are primarily approach inhibiting (Tables 42 and 43). Advancing steps and horn gestures appear in similar eliciting contexts to snarls alone, but at shorter ranges (Table 41). Their effects are more strongly distance increasing, commonly forcing the recipient to back away or otherwise withdraw to a greater separation distance.

In contrast, the functions of the pant and hic may be generalised as proximity maintaining or distance reducing. The pant serves as a call restoring contact between companions draws companions together prior to or during a shift in location, and at other times emphasises friendly approaches. The hic is typically used by a bull approaching a cow in contexts of courtship, and when used in other contexts suggests "pseudo-courtship". Tactile stimuli from rubbing against the side of a companion can also be characterised as proximity maintaining, but in a much stronger sense. Such action is normally tolerated only from a close companion or "friend," and its acceptance by the other probably assists in reinforcing this relationship. I have therefore applied to it the term "bond-reinforcing".

Marler (1968) proposed use of the terms "distance-increasing", "distance-maintaining", "distance reducing" and "proximity maintaining" to characterise the spacing effects of communication signals. This approach has influenced my analysis above. However, difficulties arise in transfering Marler's terms, as he has defined them, to the communicatory system of the white rhinoceros. The signals that I have characterised as separation maintaining would, in Marler's system, be termed distance increasing; yet only the advancing snarl and horn gestures are demonstratedly likely to increase the spacing between interactants. Snorts and snarls primarily merely maintain pre-existing spacings, more or less effectively, by inhibiting closer approaches. The term distance-maintaining is however employed by Marler in a different sense: to cover those signals which, within groups, reveal the locations of members and thus assist in maintaining contact between them (for example, the repetitive grunts given by foraging baboons). It is therefore applicable, in some contexts, to the pant of the white rhino, for which I regard the term proximity maintaining as more appropriate. However, Marler uses the latter for actions such as social grooming in primates, which allow two individuals to remain in close contact for an extended period. I prefer use of the term bond-reinforcing for these (which include rubbing sides as performed by white rhinos). Marler's terminology thus does not seem satisfactory for the white rhinoceros, and I have accordingly deviated from it. More information on a wider variety of species is clearly needed to achieve consistency.

Elements of threat are also incorporated in the separation maintaining displays. If milder signals are ignored, the actor may make a symbolic attack on the other individual by advancing to clash horns. However, actual attack never resulted, and these displays were not performed by territorial bulls in situations in which they were likely to attack. They may thus be characterised as defensive threats, in the sense suggested by Ewer (1968) and Walther (1973).

Separation maintaining threats when directed by subordinate bulls towards territorial bulls may also function as submissive gestures (the term appeasement seems less appropriate), as will be discussed more fully in the next section covering interaction patterns. Despite their seemingly intimidatory nature, they do not lead to attack, and indicate that the performer is not challenging the dominance of the other bull. Walther (1973) likewise suggests a close relationship between defensive threats and inferiority displays. The actions of the subordinate bull resemble those of cows and adolescent males in similar circumstances. However, I could distinguish the snarls of a subordinate bull by the deeper more repeated roars, and presumably a territorial bull could do likewise. Thus the resemblance in the displays probably simply reflects similar motivational origins.

Dominance claiming rhinoceros bulls seldom reinforce their presence vocally. Seemingly their calm relaxed actions, unhesitant approach and physical presence at close quarters (reinforced by scent) are sufficiently intimidating (see next section for a further discussion).

The volume of sound emitted in roars and shrieks frequently attracted by attention from distances of well over one kilometre. But no rhino, other than the interactants involved, was ever seen to react to such sounds. The only sound that I ever saw responded to from a distance was the hic. On several occasions, when a subordinate bull approached a cow hiccing, the territorial bull immediately hastened up and approached the same cow (once from 200 m away). Thus none of the sounds has apparent function in distant communication.

There are relationships between structure and function in auditory signals (Marler, 1967). Soft aspiratory sounds, the snort, pant and hic, are those most frequently used by white rhinos at close quarters to control the spacing between individuals. Less energy is involved in their performance than for example in the snarl. The volume of sound associated with the snarl seems designed simply to have a more powerful effect on the recipient. Squeals may be differentially patterned to function in a variety of contexts. The territory boundary blocking squeal of a bull has strong resemblances to the nursing request whine used by calves, suggesting a derivation from the latter. There are suggestive similarities both in the continuing state of discomfort associated with the corresponding eliciting situations, and in their relief by an appropriate response on the part of the cow. High pitched squeals such as the shriek and squeak suggest a strong fear component in accordance with observed eliciting contexts.

Vocalizations of the black rhinoceros have yet to be described in full. Hitchins (pers. com.) feels that they make an even wider variety of sounds than white rhinoceroses. A snort seems to function in similar contexts in the two species (see Goddard, 1967). The "breathing call" described by Frame and Goddard (1970) seems equivalent to the pant used by white rhinos. The gasping sound "like a man trying to get his breath after a blow on the solar plexus" corresponds in form to the hic, and Ritchie's (1963) original suggestion that it might be a mating call could thus be substantially correct. However, Goddard (1966) does not mention use of the sound during courtship. The "ghastly shriek" described by Goddard (1966, 1967) resembles the white rhino's snarl or shriek, and is likewise performed with the ears laid back; but the contexts he describes are confusing in relation to the relative social status of the performer. In an incident described in the later paper, a resident bull chased away an intruding stranger with ghastly shrieks, while in the earlier paper he reports that an intruding bull gave shrieks while the other bull remained silent. Confirmation is therefore required as to whether usage of this display differs in social significance in the black rhinoceros, as the later observation suggests. The mewing sound made by black rhino cows calling a calf (Goddard, 1967) has no equivalent in the white rhinoceros, though the sound resembles that made by white rhino calves before suckling. To a human observer the loud puffing snorts made by black rhinos either charging towards or away from the source of a disturbance are particularly striking. In the white rhino, snort or pants are not made by solitary individuals in such circumstances, apart from the brief gasp-pant which seems to be a direct response to a sudden fright.

For the Indian rhinoceros, Ullrich (1964) recorded seven sounds: (i) a snort used as a threat against an approaching rhino, and also against human intruders; (ii) a brief grunt made as an alarm warning while fleeing; (iii) long grunts given by males chasing oestrous females and other males, and also by rhinos chasing other individuals from the socalled grazing territories; (iv) a high-pitched neighing squeal given by oestrous cows being pursued by bulls; (v) a long squeal given by bulls being chased by other bulls; (vi) a bleating made by a mother as a call to her calf; (vii) a snoring sound used as a contact call on entering a wallow in which other rhinos were already lying. The snort and grunt seem used similarly in spacing to the snort and snarl of the white rhino, but the other sounds as described have no direct equivalents. For the Sumatran rhinoceros, Hubback (1939) describes snorts, a quacking bark, squeals and gibbon-like cries, but does not indicate social contexts or functions.

Strikingly absent in the white rhino is any specific alarm call; and also lacking are sounds functioning in distant communication. The elaboration of a set of sounds to control spacing between conspecifics is seemingly peculiar to the rhinoceroses and elephants among ungulates, as also is the use of further sounds to signal special contexts such as "territory boundary blocking", "need for nursing" or to inhibit attack.

In accordance with the vocal variety, visual displays are much less distinctive, as was noted also in the Asiatic elephant (Eisenberg et al., 1971). The subtle postures and gestures that are a feature of expressive displays in Bovids (Walther, 1973) are lacking. Most visual displays are based on fairly direct actions, and are frequently coupled with auditory and tactile signals.

The "charge" and "advancing steps" correspond to the "rush-threats" that are widespread among Artiodactyls (Geist, 1964; Walter, 1973). Similarly, horn prods and clashes are basically "weapon-threats", based on symbollic attack or intention movements toward attack. Absent in the white rhino is any broadside presentation displaying attributes of body size to an opponent. Presenting the side functions in different situations, being given towards cows to appease their antagonism by signalling non-approach. The horn against horn stare has strong elements of a "superiority" display (Walther, 1973), and may serve to emphasise the relative size of two potential antagonists; however, olfactory stimuli emanating from the rival are probably at least as intimidating. There are no contrasting displays of "inferiority," this function being served instead by defensive threats.

Stiff-legged scraping actions with the legs occur conspicuously in meetings between black rhino males (Schenkel, 1966; Schenkel and Schenkel-Hulliger, 1969; Goddard, 1967), and seem to be considerably more exaggerated than in white rhino males. In Umfolozi I once noted scrape-marks extending over a distance of 30 m that were attributable to a black rhino, but never observed such extensive scrapemarks produced by white rhinos. The bush-horning performed as part of the "complex bull ceremony" (Schenkel, ibid), and sideways sweeping movements with the head directed towards cows (Goddard, 1967) seem equivalent to the horn wiping displays of the white rhinoceros.

The "complex bull ceremony" described by Schenkel is closely similar to the full urination ritual of a white rhinoceros territorial bull. However in the black rhinoceros the ritual is apparently performed only in special circumstances, at other times spray-urination occuring without preceeding actions. I saw black rhino males spray-urinate on several occasions at Umfolozi, but each time they did so simply by swinging the hindquarters round to direct the spray over a bush; I never saw either scraping or horn-wiping which are usual accompaniements to spray-urination in the white rhinoceros. Also, in the black rhinoceros both males and females usually scatter their dung, whereas in the white rhino such action is performed exclusively by territorial bulls. Indian rhinos also scatter their dung, and Ullrich (1964) indicates no sex distinctions. Large dungheaps are formed except in the

Sumatran rhinoceros (Strickland and other observers quoted in Groves 1972, though this may be related partially to low population density). Spray-urination occurs in the Sumatran rhino (Hubback 1939), but its occurrence in the Indian rhinoceros is described only by Ripley (1952). Several authors have reported that black rhinos frequently scatter dung also with their horns, or drag their hindlegs stiffly through dung piles (Goddard 1967), but Schenkel never observed such behaviour. In Umfolozi I noticed dragmarks in dungheaps attributable to black rhinos on several occasions.

The ritualised ceremonies associated with defecation and urination in the two African rhinoceroses have elicitational and functional similarities to other displays of "assertion of presence." They seem comparable with auditory advertising, and with the self-urinating performed by Caribou males (Lent 1965). The alternate terms "manifestation of presence" (Schenkel 1966) and "advertisement of presence" are equivalent. Horn wiping and scraping alone occur in similar contexts to bush-thrashing and pawing performed by Bovids. Functionally all these displays emphasise the presence and social status of the performer. Walther (1973) regarded all such performances as displays