

The Social System of the White Rhinoceros

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ABSTRACT

Results of behavioural study carried out on the white rhinoceros in Zululand, South Africa, between 1966 and 1971 are summarized. Cohesive social groups included cow-calf pairs, adolescent groups, cow-adolescent groups, cow-cow groups and adult male singletons; the largest group numbered six. Adult males occupy territories of about 2 km² for periods of several years. Olfactory marking is carried out by dung-scattering and urine spraying. There are subordinate adult bulls which coinhabit certain territories, but do not perform territory marking. Cows have overlapping basic home ranges covering about 10-12 km² but at times they may wander further afield. Some adolescents are resident, others semi-nomadic. There are ritualised encounters between neighbouring territorial bulls, while subordinate bulls adopt a defensive threat posture when approached. A deposed territorial bull is not driven out of his territory but becomes a subordinate bull. Territoriality is characterised as a spatially localised dominance. Reproduction is year-round with seasonal peaks. A consort period of 5-20 days precedes mating. A bull manoeuvres to confine the oestrous cow to his territory. Courtship approaches last 15-20 hours and copulation 20-30 mins. Subordinate bulls do not mate with cows. Gestation is 16 months.

The new-born calf remains shaky for 2-3 days. When alarmed it runs off ahead of the cow. Weaning commences at 2 months, but nursing continues to well over a year. The older calf is driven away upon the birth of a new calf. It then bonds onto another adolescent or a cow without a calf. Females have their first calf at 6½-7 years, but a male is probably over 12 years before he can claim a territory and mate.

The well-ordered social system has probably contributed to the success of the species. Large bulk with consequent low predation and year-round reproduction have favoured a territorial organisation. Territoriality regulates reproductive competition but not population growth. For management purposes it is recommended that population expansion be controlled without major social disruption by confining removals to certain 'vacuum' zones.

INTRODUCTION

The white or square-lipped rhinoceros *Ceratotherium simum* holds special interest in relation to the evolution of ungulate social systems. It is a species which has persisted with little anatomic modification since at least the early Pleistocene, and might therefore also retain 'primitive' features in its behavioural patterns. With adult male weights of about 2300 kgms, it is perhaps the largest entirely grass-feeding animal ever to have evolved. However, apart from the short term observations of Backhaus (1964) on the northern subspecies *C. s. cottoni*, no previous behavioural study has been carried out.

My own investigation was aimed at elucidating the basic features of the ecology and behaviour of the southern subspecies *C. s. simum* in the Umfolozi-Corridor-Hluhluwe game reserve complex in Zululand, South Africa. Because of the unusually favourable conditions for a study of this nature, particular emphasis was placed on social behaviour. Field observations were commenced in January 1966, for a six month period, and were then resumed in November 1968 and continued without further interruption to September 1971. The main study area of about 20 km² was located in the western section of the Umfolozi Game Reserve, where relatively high white rhino population densities (about 5/km²) occur. Comparative observations were made in four supplementary study

areas. The basic technique was to maintain a watch on the activities and interactions of particular individuals or groups for periods of up to twelve hours. Observations were carried out on foot, which method was facilitated by the relatively poor eyesight of the species. Notebook and pencil recording were supplemented by photographic documentation on still and movie film. Individual recognition of all adults was possible using particularly variations in horn shape. Thirty ear-tags were inserted to assist identification mainly of subadults, and ten radio transmitters were placed to follow the movements of cows and subadults.

The background history of this population has been described by Player and Feely (1960) and its continuing rapid growth was reviewed by Vincent (1969). The 1971 helicopter census figure was 2002 white rhinos in the 900 km² of the Umfolozi-Corridor Hluhluwe unit. The reserve supports large numbers of a wide variety of other large herbivores, and habitat deterioration is causing serious concern.

At the time of writing, field work has only just been concluded and a detailed analysis of data has yet to be undertaken. This contribution will thus merely summarise the essential features of social structure and dynamics; a full treatment of results will be published at a later date. A brief consideration of white rhino territoriality has already appeared elsewhere (Owen-Smith, 1971; also in press).

A. BASIC ECOLOGY

The white rhinoceros is entirely a grass-feeder, with a preference for short grass. Grazing and resting occur in alternate spells of a few hours throughout the night and during the cooler part of the day. This pattern is broken by a longer rest period through the heat of midday, particularly during summer. For this the animals tend to aggregate under shady trees at certain favoured rest places, usually on the crests of low ridges. Mud wallowing is performed more frequently during summer, but may occur at any time of the day or night. Drinking can occur twice daily while water is abundant. Towards the end of the dry season, when water availability becomes restricted to a few sources, journeys to water are made at 2-4 day intervals. Though lions, leopards, cheetahs and hyenas occur in the area, predation has not been recorded.

B. SOCIAL STRUCTURE

1. Groupings

Cohesive social groups consist mostly of twos, with a few larger groups which may number up to six individuals. The following basic units occur:-

(a) *Cow-calf pairs.* Most adult females are accompanied only by their most recent offspring. In rare instances the previous calf may remain, associated with its mother after the birth of a new calf.

(b) *Adolescent groups.* Animals which have separated from their mothers, but which have not yet reached social maturity, usually team up with one or more companions of similar age. Though groupings of this type numbering up to five and occasionally more animals have been encountered, persistent individual bonds are apparently not formed between more than two adolescents. Both homosexual and heterosexual groups occur, with the former more prevalent.

(c) *Cow adolescent groups.* A cow which has lost her calf through mortality or, more commonly, as a result of rhino capture operations, will readily accept the company of one or more adolescents. Stable groups numbering between two and six individuals have been observed, each adolescent apparently bonding independently to the cow. Transient attachments between adolescents and cow-calf units also occur.

(d) *Cow-cow groups.* Two adult cows, both lacking calves, may also join together. They are likely to be accompanied additionally by one or more adolescents. In some cases one of the two cows is clearly a younger animal, and the possibility of a mother-offspring relationship exists. Because of the readiness with which they will accept the company of others, solitary females are not commonly observed.

(e) *Adult male singletons.* All mature males are basically solitary. They do however attach themselves for short periods to female groups. A bull-cow association persisting over several days is indication that the female is coming into oestrus.

2. Spatial patterns

(a) *Adult male territories.* Space utilisation patterns are based on the division of all suitable habitat into a mosaic of adult male territories, typically each about 2 km² in area. The territories are occupied by individual bulls for periods of several years, and a territorial bull normally restricts all his activities to within his territory, which is thus also equivalent to the home range. The only exception occurs during the dry season, when many bulls are forced to make an excursion to water every few days. Borders are narrow zones which are patrolled and marked by both neighbouring bulls.

Defecation and urination have become ritualised in territorial bulls, and apparently function in olfactory marking of the territories. Defecation is almost always carried out at one of the numerous (20-30) dungheaps which are scattered throughout a territory. Backwardly directed kicking movements are made both before and after defecation, so that the dung is broken up and scattered over the heap. Elements in the urination ritual include wiping the anterior horn over a low bush or the ground, scraping the legs along the ground past this site, then ejecting the urine in the form of a fine spray in 3-5 spasmodic bursts (Plate I). Urination in this manner may occur anywhere in the territory. It is, however, carried out repeatedly whenever the bull patrols a boundary, so that the density of urination sites is highest in a border region. There are also certain large, well hollowed-out dungheaps in the border region attesting to frequent visitation by the territorial bull.

About one third of the adult males are not territory owners. Each of these subordinate (or subsidiary) bulls coinhabits the territory of one of the territorial bulls. In some territories only the territorial bull is resident, in others two or three other bulls may share the territory with the territory owner. Unlike the territorial bulls, these subordinate bulls may occasionally wander outside their home territory. They use the same dungheaps as the territorial bull, but neither scatter their dung nor spray their urine, defecating and urinating without embellishment like females and subadults.

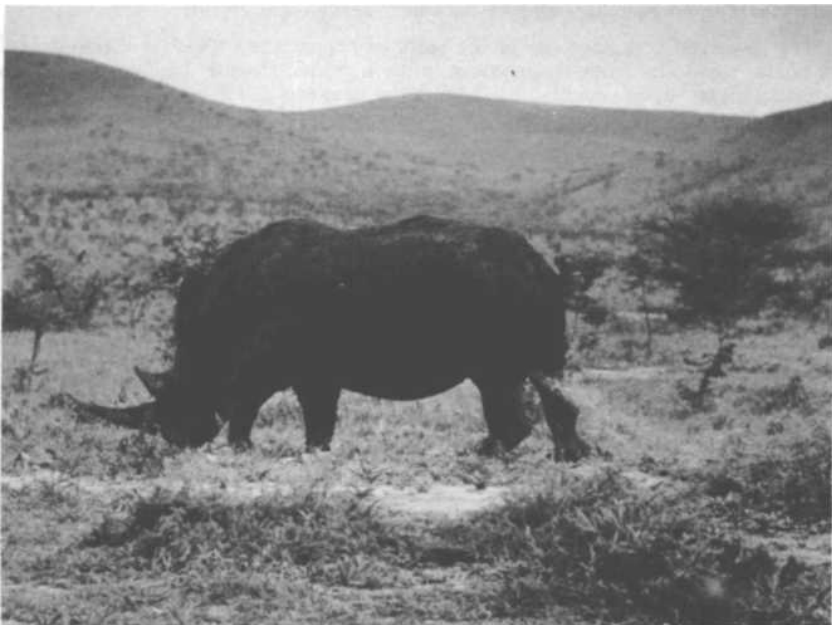


Plate I. Spray urination by a territorial bull

(b) *Home ranges of cows and adolescents.* Adult cows have a basic home range covering about 10-12 km² and encompassing 6-7 male territories, to which they restrict their movements while good quality food and water are plentifully available. Wandering movements outside their basic range may occur during drying periods or after rains, apparently in search of the best grazing; while drinking excursions become forced during the dry season. The basic home range then becomes extended by corridors leading to long-lasting water supplies, so that the total annual range traversed may encompass 25 km² or more. However, the cows tend to return to the basic home range in between such journeys. There are no core areas within the basic home range, different sections being favoured during different periods.

The home ranges of individual cows are independent, but overlap extensively with the ranges of other cows. Implications of exclusiveness are thus absent.

Some adolescent groups remain within home ranges of 4-10 km². Others appear to be semi-nomadic, appearing in a study area, remaining for several months, then disappearing again.

C. SOCIAL DYNAMICS

1. Interactions between bulls

Interactions between males are ordered within the framework of the territorial structure. The course of an encounter is dependent both on the status of the bulls concerned and on the location of their meeting.

Meetings between neighbouring territorial bulls are usually restricted to a border region, and are of infrequent occurrence. One bull may make a lowered head rush at the other, but this is usually checked just before contact. The two bulls come together to stare at each other horn against horn with raised heads (Plate II), then back apart to wipe the anterior horn vigorously over the ground. A sequence of repeated advances to touch horns, then retreats to rub the horn on the ground, usually lasts for only a few minutes, but may occasionally continue for over an hour. There may be momentary clashes of horns with lowered heads, but attack is not driven through further than this. Both males remain silent. Eventually the two bulls back, turn away hesitantly, then move apart. One or both may scrape and urinate.

In three observed instances one of the bulls has penetrated 100-200 m into the territory of the other. In these circumstances the intruder steadily backed away during the engagement. Upon reaching his border, he scraped and urinated sprays, and the two animals then separated.

A subordinate bull responds to the approach of a territorial bull by standing his ground, uttering loud roars or snarls with head thrust forward, ears laid back and tail curled upwards (Plate III). He may make a few quick paces towards the territorial bull. Despite their seemingly intimidatory nature, these gestures are interpreted as defensive threats. The same *snarl-threat* is employed by cows and adolescents against an approach by a bull, among subadults usually by the smaller animal. The territorial bull may approach to stare silently horn to horn, or may clash horns briefly. Such a horn clash is fended off by the subordinate bull to the accompaniment of trumpeting shrieks. Engagements between a territorial bull and a subordinate bull which is resident within his territory, however, are usually very brief, and the territorial bull soon walks away, leaving the other bull standing. Quite often the territorial bull simply wanders on past as if oblivious of the other bull's presence, despite nervous snorts and grunts from the latter. The two bulls can be observed grazing or resting together peacefully only 20-30 m apart.

Should a territorial bull encounter a subordinate bull which is a trespasser from another territory, the basic actions of both animals are the same, but the engagement is likely to be more prolonged (sometimes over an hour), with more frequent horn clashes. The territorial bull may circle away, then approach again, several times. Again the engagement is terminated by the territorial bull wandering off. In one observed instance a fight developed, with the territory owner attacking the trespasser with horn to body blows which the latter was unable to fend off.

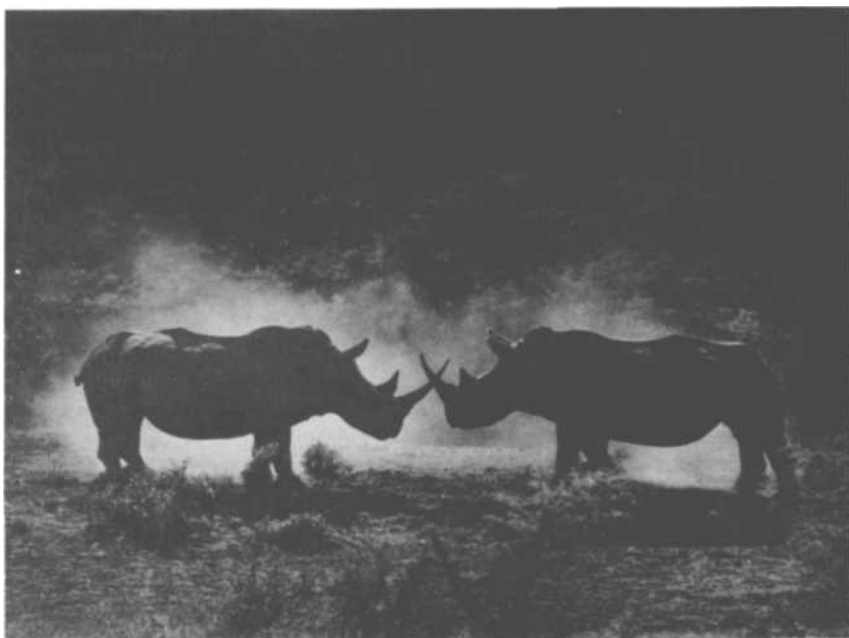


Plate II. Two territorial bulls stare at each other horn against horn during a border confrontation



Plate III. A subordinate bull (on right) stands defensively giving the snarl-threat at the approach of a territorial bull

If confronted by a resident territorial bull while off his own territory during a journey to water, a territorial bull will also adopt the defensive snarl-threat stance with roars and shrieks. In one case a serious fight developed when a territorial bull returning from water attempted to cross the territory of a neighbouring bull, but was accosted by the neighbour at the boundary. There were long periods of slow horn against horn fencing with raised heads, with occasional sudden lowered head feints. These were interrupted by bouts in which one bull was able to strike through the defences of the other and deliver blows to the head, shoulders, and sometimes the body, with upward jabbing movements of the head and horn. Both bulls remained silent, apart from heavy breathing. The fight was still in progress after 35 minutes when darkness fell. The next day the wandering bull was still off his territory, and had a badly bloodied eye and numerous bruises and gashes. The resident bull showed only a few cuts. It seems significant that in this instance the trespassing bull did not demonstrate submission.

2. Changes in territory ownership

Because of the long duration of territory occupancy, changes in territory ownership are rare events. I observed in detail three such changes, which resulted from the ingress of a new bull and subsequent chain displacement of two further bulls. In one case the defeated bull had numerous bruises and gashes around the head, shoulders and sides; and I was able to glimpse a brief second fight in which the new territory holder laid into the former owner with repeated horn head to body blows, until the latter broke and fled after a few minutes. But in two of the cases, there were only a few superficial cuts on the deposed bull, so that the mechanism of the dominance shift was not clear.

In all of these transitions the deposed bull was not driven out of his territory, but remained there taking on subordinate bull status. In the first case this situation persisted for a few months, then the bull shifted a few kilometres and claimed another territory. The bull he displaced stayed on only a week, then took over the next-door territory. The third bull to be deposed was still present over a year later as a subordinate bull in the territory he had formerly held.

That violent fights do occur is evident from rangers' reports of bulls killed by fighting, and by the presence of subordinate bulls with numerous scars around the head, shoulders and belly regions. The horns of the rhinoceros are directly functional weapons, and social constraints are necessary to reduce the incidence of violent conflict.

A defeated territorial bull immediately ceased spray urination, and more gradually eliminated dung scattering, with an initial decrease in the number and intensity of kicks.

The reverse transition can also occur. Two of the four males which I knew as subordinate bulls in 1966 had by 1968 become territory holders, though not in the same territory they had formerly inhabited.

3. Territoriality and dominance

The approach adopted by a resident territorial bull on encountering another bull is essentially the same in all cases. The horn against horn stare is obviously a powerful intimidatory gesture. The course of the encounter depends on the response of the other bull. If the latter consistently adopts subordinate stance and vocalisations, attack is unlikely to be carried out. If submission is not shown, a fight can only be avoided by the intruder back-peddalling. In a border region, both bulls waver between attack and withdrawal, and a sequence of ritualised advances and retreats results.

All intruding bulls are potential territorial rivals, but an intruder is not driven out of the territory if he demonstrates submission when confronted. It appears that a territorial bull eventually becomes habituated to the presence of particular subordinate bulls on his territory. Regular testing serves to ensure that the dominance-subordination relationship between them is maintained.

Spray urination is partly an assertion of dominance, and is not performed once a male leaves his territory, or loses his dominance within that territory. That dung

scattering still occurs in these circumstances is probably a result of force of habit. While off his territory during a journey to water a territorial bull shows hesitancy and avoidance when he encounters other rhinos, whether bull, cow or adolescent.

Thus territoriality as shown by the white rhinoceros may be characterised as a spatially localised dominance by adult males.

4. Relationships with adolescent males

Adolescent males show nervousness of the close proximity of a territorial bull, and are occasionally chased. There are recorded instances in which young males have apparently been killed by horn wounds. However, most of the time the territorial bulls pay little attention to adolescent males, even when the latter are accompanying an oestrous female. Adolescents thus move relatively freely across the territories.

5. Relationships among cows and adolescents

Cows appear indifferent to the presence of other cows and adolescents in their vicinity. A cow may give snorts when another approaches to within a few metres, but on occasions two cows may come together to stand quietly with lowered heads in contact. This may develop into slow, gentle horn wrestling. Adolescents show interest in other rhinos, and more frequently approach for such naso-nasal contacts. These meetings can develop into prolonged and vigorous playful wrestling and chasing. Rather than avoidance, there seems to be a slight aggregative tendency among cows and subadults. In addition to the congregations at resting areas, there is also a noticeable clustering tendency in grazing distribution. At waterholes, where strangers are forced into close contact, repeated snorts and grunts are exchanged between cows, and one may sometimes drive another back with a clash of horns.

D. COURTSHIP AND MATING

Reproduction in the white rhinoceros is not seasonally restricted, and births have been recorded in every month of the year. However, oestrus is apparently stimulated by a flush of green grass following a dry period. There is thus a mating activity peak through October-November-December, following the onset of spring rains, and subsequent calving peak through March-April-May. The gestation period is sixteen months. Oestrus can recur at intervals of about 30 days until fertilisation is achieved. The first post-partum oestrus may occur after six months, and inter-calving intervals vary between two and three years.

A territorial bull will investigate any strange cow encountered on his territory. He makes a frontal approach accompanied by a hic-throbbing sound and stands staring at the cow from a range of a few metres, usually in a downwind position. A cow reacts to such an approach with snorts or the snarl-threat, and may sometimes drive a bull back with a clash of horns. Normally the bull then wanders on, but he may remain grazing in the vicinity of the cow for a few hours. If such an attachment persists for more than a day, it indicates that the cow is coming into oestrus.

The consort period may last for between five and twenty days, the bull simply accompanying the cow everywhere in her movements. The cow gives snorts of varying intensities of the snarl-threat if the bull approaches too close. The bull readily responds by giving way. However, if the cow wanders towards a boundary region, the bull then moves ahead, making soft squeals, to stand in front of her blocking her progress (Plates IV & V). Should the cow run off, he chases after her with loud wails and turns her back. In a few instances he may even drive the cow back with a clash of horns. Most commonly, however, such interactions are more subtle, with the bull quietly moving into a flanking position between the cow and the boundary, and the cow changing direction accordingly. These territory boundary blocking actions are commenced by a bull about 100 m inside the actual limits of his territory.

If the cow urinates, the bull investigates the site, nibbling at the damp soil then standing with raised head and wrinkled, parted lips. The posture, however, is not as exaggerated as *flehmen* in other ungulates. Though dung may also be sniffed, the flehmen response is restricted to urine testing, and may be exhibited also by calves and adolescents.

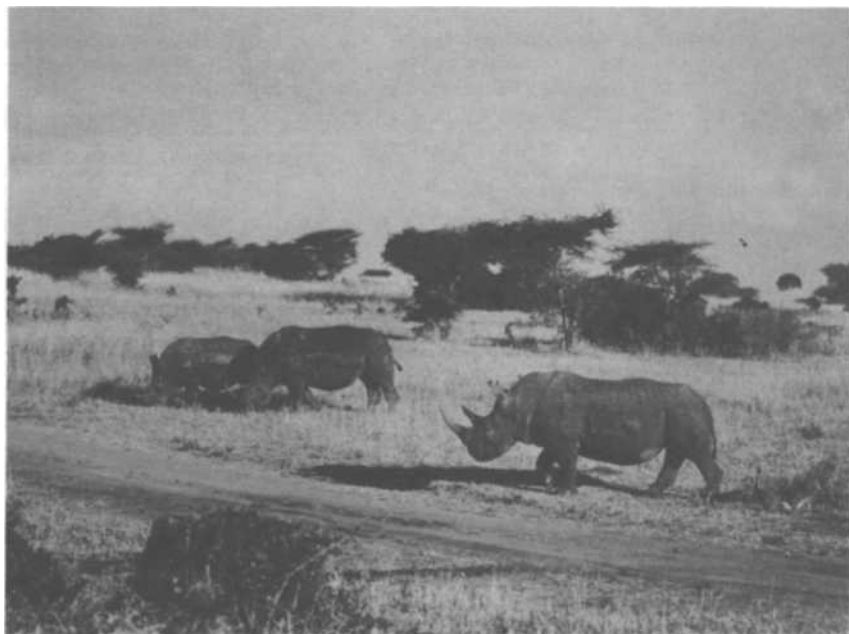


Plate IV. A territorial bull moves round to block the movement of an oestrus cow and her calf towards the territorial boundary



Plate V. A territorial bull (on right) determinedly blocks attempts by a cow and calf to proceed across a territory border. The cow gives the snarl-threat, while the bull counters also with the ears back posture

The onset of oestrus is apparent to the observer by the commencement of repeated hic-throbbing approaches by the bull. These approaches are made posteriorly with the head held high. Initially the cow wards off the bull with snorts, the snarl-threat, or a clash of horns. The bull readily yields, but makes another such testing approach a few minutes later. An accompanying calf or adolescent may block the approach of the bull with threat gestures, and the bull then circles round and tries from a different angle. After several hours the bull rests his chin on the rump of the cow, and after several such positionings, mounting attempts are made. The cow responds to these approaches by curling her tail and ejecting a squirt of urine, which is sniffed by the bull. She offers no other behavioural stimulus, other than by standing to receive the bull. After mounting several times intromission is achieved. Copulation lasts 20-30 minutes, with the multiple ejaculations indicated by quivering movements by the bull. It may take as long as 15-20 hours after the commencement of approaches before intromission is achieved. In only one instance was a repeated copulation observed, after an interval of three hours. The consort relationship is normally broken up 2-5 days after mating, but may continue through another oestrus cycle if fertilisation was not achieved.

Subordinate bulls normally do not form such consort relationships with cows and play no part in reproduction. In a single exceptional instance, a subordinate bull attached himself to a cow for several days at a time when the territorial bull was engaged with another pre-oestrus cow. When the first cow was ready for mating, however, it was the territorial bull who served her, while the subordinate bull wandered about agitatedly in the vicinity without interfering.

E. MATERNAL BEHAVIOUR

The actual act of parturition was not witnessed; the cows evidently resort to secluded areas such as dense thicket or, occasionally, little-visited hillslopes at this time. However, some observations on newly-born infants were possible. The calf remains rather shaky on its feet for the first 2-3 days, and spends most of its time walking slowly round and round the cow, maintaining close bodily contact. The cow sniffs repeatedly at the infant, and will not leave its side. Aggressive gestures towards the observer were not made.

The calf is normally 3-4 weeks old before the cow reappears in her usual grazing areas. Both mother and calf keep within a few metres of each other. At any disturbance, the calf gallops off in front, with the cow following at its heels. The calf is attentive to any change in direction by the cow, and responds accordingly. However, it seems that usually the cow merely follows the direction of retreat chosen by the calf.

Nibbling at grass commences at an age of about two months, and by three to four months the calf is directing much time to grazing. Suckling however continues until the calf is well over a year old.

Nursing is initiated by the calf, a thin whining squeal being made before commencing to suck. Suckling lasts 2-4 mins without the active pushing movements typical of many other ungulates, and is terminated by the calf turning away.

A young calf shows great curiosity in other rhinos, and will approach for investigation. The cow watches attentively, and will rush in at the slightest provocation. Cows with small calves show less tolerance of the close proximity of other rhinos than those with larger calves. Playful horn wrestling and chasing often develop between two young calves while their mothers graze nearby.

Mother and offspring maintain a close bond for two to three years until the time comes for the cow to give birth again. The previous calf is then driven away and must seek out a new companion.

F. INTEGRATION OF ADOLESCENTS INTO THE POPULATION

Following separation from its mother, the individual, which I shall now term an adolescent, wanders around forming temporary attachments with cows and other adoles-

cents. Eventually a stable bond is formed, either with a cow lacking a calf, or with another adolescent. Such bonds are persistent, the same two individuals always being found together over periods of a year or longer, and rejoining after an accidental separation. The two animals keep close together while grazing, making occasional bodily contact, and co-ordinate their movements and activities. A hoarse panting sound is made at times and seems to have a proximity-maintaining function. Though adolescent groupings numbering several individuals are sometimes observed, additional animals seems to be treated as outsiders. Their proximity may be tolerated, but they are likely to be driven back if they make too close an approach.

Enduring bonds are most commonly formed with another adolescent of the same sex and of about the same age. In such pairs there is no obviously dominant individual or leader. Heterosexual pairs also occur and, in these, it seems that the female is the more active in directing movements. In cow-adolescent groups, each adolescent apparently bonds independently to the cow, who shows tolerance of their presence. Movements of such groups are controlled by the cow, though the adolescents may walk in front of her.

While some adolescents remained on in the study areas for over two years, others eventually disappeared. There were also strange adolescents which appeared, remained a few months, then vanished again, indicating nomadic tendencies. Adolescents which have been bonded to cows are most likely to stay in the area, even after their separation from the cow. This provides a mechanism by which dispersal movements may be balanced against calf losses. Adolescents, particularly young males nearing maturing, are most prominent in recently colonised areas.

Adolescence in females may be said to be terminated when the individual breaks away from her companions to give birth to her first calf at an age of 6½-7 years. Among males, adolescent bonds may persist until both individuals are almost full-grown. With time the males become separated and settle within a particular territory with subordinate bull status. There they remain until they reach virtually full weight and are able to challenge for ownership of a territory. By this time they are probably twelve or more years of age.

DISCUSSION

The white rhinoceros is a herbivore which, through its great bulk, is almost invulnerable to non-human predation during its adult life. The pairing up of adolescents probably has a predator-defence as well as possible social-learning function, but the major selection pressure which is believed to favour the aggregation into large herds typical of other open-country grazing herbivores thus exerts minimal influence. With this prime adaptation this slow-moving, relatively slow-witted animal, relying mainly on olfactory cues for orientation, remained abundant and widely distributed through southern Africa, until the arrival of modern man with his weapons. The well ordered social system, which seems to promote a relatively high fecundity for an animal this size, has probably been a strong contributory factor to this success.

The long gestation period and slow growth to adulthood, which are also a consequence of large size, mean that there is no narrowly fixed optimum reproductive season. The resultant year-round mating activity, coupled with low predation pressure and relatively settled range occupancy, have been strong influences shaping social organisation. Thus we find that prime males maintain a fairly stable system of fixed territories, within which there is only a very slow turnover of individuals. Associated with them is a more mobile population of females, all members of which may be individually known to each other and to the males through repeated contacts over a period of many years.

The prime functional significance of territoriality seems here to be to regulate reproductive competition among males, by lowering the frequency of male combats, and allowing courtship and mating to proceed without disruption. Females and sub-adults do not exhibit territorial intolerance and, except for the brief period around oestrus, their movements are not restricted by the territorial behaviour of the males. Though there is pressure on surplus males to emigrate, there is no evidence

that the rate of reproduction by females is limited by the availability of males to serve them. Mortality is currently low. Since marked habitat deterioration is occurring at existing population levels, it seems evident that territoriality cannot serve to regulate population growth within the carrying capacity of the habitat. Apart from a decline in fecundity and infant survival which may come into play at a later stage, the only apparent mechanism of population regulation seems to be the dispersal of adolescents into unfavourable habitat where their chances of survival may be low. This movement is now prevented by the boundary fence surrounding the reserve.

MANAGEMENT IMPLICATIONS

The current natural increase of the white rhino population is nearly 10% per annum. It has become essential to undertake artificial control measures to limit population size to such a level as to ensure maintenance of the habitat and thus the continued survival of the species in this area. This is presently being carried out by a live capture and translocation program, which, in 1970, successfully removed nearly 200 rhinos from the reserve area.

While the aim of a zoological garden is chiefly to exhibit the physical features of different species, that of a game park must be to preserve representative natural communities with their ecologically and behaviourally adapted constituent species. Social behaviour patterns are as much species attributes as more readily visible morphological features, and physiological adaptations. They are of great potential interest, not only to ethologists and evolutionists, but also to a visiting public becoming increasingly well-educated as a result of recent popular literature on the subject.

The relatively stable, slow-changing social organisation of the white rhinoceros could easily be disrupted by the drastic culling measures which may soon become necessary. The problem is how to design management procedures so as to destroy the natural order in the population as little as possible; so as to work in with, rather than against, natural population regulatory mechanisms.

This ideal could perhaps be approached by setting aside certain zones of the reserve to be maintained as white rhino 'vacuums', by the constant removal of all animals which settle within them. The disturbing effects of culling operations could then be confined to these localities so far as is possible, though additional culling may be necessary to achieve population balance. It is, however, to be expected that these 'vacuums' would steadily be filled by surplus animals, mainly adolescents, dispersing out from the bulk of the population. The identity of these expendable individuals would be determined by social interactions among the animals themselves, rather than by the whim of a human management officer. This would permit the natural adjustments of the social order to changing environmental circumstances to have full play.

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