of "space claim". However, there seems to me good reason to distinguish those displays which leave enduring olfactory signals, and I will apply the term "space claim" only to these. Such olfactory marks persist after the departure of their producer, and can potentially assist in delineating and maintaining the exclusiveness of particular fixed pieces of space or territories. Variability in the chemical composition of such marks could indicate not only the sex and age status of the originator, but also his individual identity.

Schenkel (1966) has emphasised the manifold functions that scent marks can have, indicating the limits of the home area and facilitating orientation within it (see also Eisenberg and Kleiman 1972). However, Schenkel used the black rhino as his example of a species which displayed elaborate scent marking without being territorial, a species which has since been found to be territorial at least in Zululand (Hitchins 1971). His main thesis, that scent marking is not necessarily equivalent to territory marking, is nevertheless valid. Olfactory signals may serve many functions in non-territorial species (see Müller-Schwarze 1973). However, the formation of dungheaps and development of glands for scent marking seem particularly striking among territorial species. Many Bovids have pre-orbital glands which territorial males use to deposit scent marks on bushes or other objects within the territory; (and in Thomson's gazelle, at least, such scent marks are concentrated along boundaries, (Walther 1972). Large dungheaps occur for example in the vicuna (Franklin 1973), topi (Gosling 1973), Thomson's gazelle (Walther 1964), dikdik (Hendrichs 1971) and Grevy's zebra (Klingel, 1972); all these species are territorial. In the dikdik and Grevy's zebra, dungheaps are concentrated particularly along territory boundaries. Hendrichs demonstrated that dikdik males could differentiate a neighbour's dung from that of a stranger, returning repeatedly to place their own marks over the dung of the stranger. The vicuna, topi and dikdik make pawing motions scattering the dung in association with defecation. Conspicuous display-urination is performed at the dungheaps for example by dikdik and Thomson's gazelle males. Spray-urination has not been reported in any ungulates besides the rhinoceroses, but occurs in several Felids (though less strikingly). Among these it is notable that it is performed by the lion, which displays territorial intolerance (Schaller 1972); by the tiger, in most territory boundaries remained unaltered; and where boundary locations shifted, they became fixed in their new locations within a few days of the takeover (see Section E). New territory holders seemed to have no difficulty in recognising the location of territory limits, orientated appropriately to block cows, and turned back after exploring a short way over boundary regions. Territorial bulls patrolled along boundary regions, spray-urinating repeatedly while doing so. A traverse across a boundary region would reveal an increase in the density of the urination sites of one bull, followed by a sharp transition to a similar density of urination sites mainly of the other bull. Bulls evidently noted these scent-marks. The urine scent marks thus seem able to provide adequate information defining the location of territory boundaries. Bulls observably showed hesitancy to move far across a boundary zone. It seems likely that the sudden transition from being surrounded primarily by their own scent marks, to primarily by those of a rival neighbour, strongly influenced their relative assurance. The effects of this inhibition on movement patterns seemed primarily responsible for the sharpness and fixed location of territory boundaries. It seemed that direct encounters between neighbouring territory holders were too infrequent, in relation to the extent of boundary lines, to account for the stability of boundaries (see next section).

It was also shown that certain subordinate bulls generally orientated towards the same boundary locations, though they themselves displayed no special scent marking techniques, and did not engage in boundary confrontations. They must therefore have recognised the locations of these boundaries on the basis of the scent marks of the territorial bulls. Wandering strange bulls also frequently orientated to follow territory boundary regions while passing through the unfamiliar area. The scent marks of the territorial bulls can be discerned by other rhinos, and may influence their movements. Though cows showed no observable responses to the scent marking system, they performed no special scent marking actions of their own, and it is possible that they also recognised the extents of their home ranges on the basis of the scent marks of the territorial bulls over whose territories they ranged.

Dungheaps are more localised in distribution than spray-urination sites. However, as Goddard suggested for the black rhino, the kicking action can transfer the scent of the dung to the feet of the bull and thereby distribute it more widely. Goddard demonstrated that black rhinos would follow the scent of a dung trail over a considerable distance, and could distinguish their own dung scent from that of strangers. Dungheaps provide focal points for investigation by rhinos, and the conspicuous presence of the scent of territorial bulls on the heap can indicate occupation of the locality by a particular bull. The border dungheaps may be of particular significance to neighbouring territorial bulls, since they could thus readily confirm the continued presence of the neighbour without the need for a direct encounter. It was observed that territorial bulls occasionally check all such across border dungheaps. However this information is perhaps superfluous, since it would already be evident from the fresh scrapemarks likely to be encountered sooner. Though territorial bulls normally made use of these border dung-heaps while patrolling boundaries, there was no indication that they did so particularly before beginning a patrol, and thus delineation of boundaries seems based on the urine scent marks rather than on transfer of dung odour from the feet.

Dungheaps also provide other information. The dung of cows is of particular interest to bulls, and could reveal the presence of a potentially oestrous cow within the territory. Assuming that rhinos can recognise individually distinctive odours in the dung, they may also facilitate group cohesion. I observed that companions that had become separated, commonly during capture and marking operations, had no difficulty rejoining again within a day or two. Thus, the suggestion by Ripley (1958) that the dungheaps serve as "bulletin boards" has some validity. It seems particularly important for a territorial bull to ensure that his "message" is also present in such locations.

A tendency to defecate on other dung may have originated as a method for avoiding excessive contamination of grazing areas. It is exhibited also by such non-territorial species as the plains zebra (Klingel 1967), and the horse (Taylor 1954). Individuals do not feed on grass growing among faeces. It therefore seems advantageous for any species relying on the ground layer of the vegetation for food to restrict defecation to particular sites; particularly if it is to live within a limited area for an extended period of time, as is the case with species showing territoriality. This may explain evolutionary origin of dungheaps; but once formed, dungheaps may serve several additional functions in social coordination.

Thus, the motivational and evolutionary origins of scent marking with dung and urine may be complex, and the resultant olfactory signals may perform several different functions. They can indicate the occupation of an area by a particular individual, reveal his sex and age status, and potentially even his androgen levels. The odours emanating from them may be equally as intimidating to a potential rival as visual displays of attributes of body size (see Geist 1966); and may enable him to gauge potential fighting ability before engaging in combat, or even meeting the rival. Where territories are large and cannot be surveyed visually, as in the case in the white rhino, scent marking seems to provide the only information system that can account for the observed exclusiveness and temporal stability of the territories.

2. <u>Interactions in encounters</u>

An encounter was held to have taken place when two independently moving rhinos reacted to the discovery of one another's presence; or when they came sufficiently close together for me to be certain, on the basis of previous experience, that they must be aware of one another's presence, even though they showed no overt response.

Special note was taken of all encounters occurring between rhinos during observation sessions. The actions of both individuals were described, by notebook and pencil, in as much detail as this method allowed. This technique generally proved adequate to record the relatively slow moving sequence of actions typical of rhinoceroses, though some individual movements may have been overlooked. Sometimes, though, I was too far from the scene to detect more than the gross features of actions and sounds other than loud snarls. Encounters may be considered to proceed through three stages: (i) the initiating stage of awareness; either no overt response was given, or one or both animals approached, or other actions were made; (ii) an approach was likely to lead to a meeting in which one or both individuals stood or moved at close quarters attentive to one another's actions; (iii) meetings were terminated by further actions leading to withdrawal. In some more prolonged encounters, I did not observe all of these stages;

several times my attention was drawn to the interactants only after a meeting had commenced.

The nature of the actions displayed during encounters varied, depending firstly upon the social status of the animals involved. Secondly, in the case of bulls, the spatial location of the encounter within the system of territories strongly influenced its nature.

2.1. Encounters involving bulls

(a) Encounters between territorial bulls.

Since territorial bulls rarely intruded across territory boundaries, most observed encounters were between neighbouring territory holders at a mutual border. However, even such encounters were infrequent. About 1500-1600 hours was spent in direct observation of territorial bulls; during this time 29 encounters between neighbouring territorial bulls at or near a mutual border were seen and only 22 of these led to meetings. Six of these were detected at long range when the bulls were not under close observation, leaving only 16 meetings detected during observation periods. Hence, it is estimated that each bull experiences a meeting with one of his neighbours on the average only once every four days; and, assuming the average territory to be surrounded by four neighbouring territories, each individual neighbour is met on the average once every two weeks. Observations were limited mostly to daylight conditions, but it seems likely that encounters occur significantly more frequently at night. For the months March to June the overall activity level during the night was estimated to be 65.5% (see Figure 10). The average daylight activity level for the season April-June was 64.2%. Thus, overall activity levels then were not significantly higher at night. During the hot season daytime movements were restricted more to the vicinity of midday resting sites. Nevertheless, during 1966 my camp was situated only 100 m from the boundary between two territories; and though one of the neighbouring territorial bulls was frequently detected moving by at night, I was never aware of any meetings. I also spent 47 hours following territorial bulls at night, during which time four encounters with neighbouring territorial bulls were seen, but all observed encounters took place in the vicinity of the Madlozi spring during the dry season where the various bulls were drawn together by the water supply.

During the dry season, when many bulls were forced to cross other territories to journey to one of the few remaining waterholes, encounters undoubtedly occurred more frequently than was observed; since such trips were normally made at night. However, I was able to follow either territorial bulls or subordinate bulls for most or all of the journey to or from water or both on 14 occasions during the day, and once at night. These represent a total of 9 trips (one trip = completed journey to and from water), and 45 territories crossed. Only 6 encounters with resident territorial bulls were observed, and only 2 of these led to meetings. In the remaining cases the trespassing bull noticed the other bull ahead and took evasive action. Thus meetings occurred on the average only once every 4.5 trips or once every 22 territory crossings. The bull BB whose territory lay on the northern edge of the study area probably had about as far to travel to water as any bull in Umfolozi Game Reserve; he crossed four other territories on his way to the Nyonikazane Spring. Even tAD♂.BB would thus probably meet a resident territorial bull in such circumstances only once every 2.7 trips, or about once every 10 days, assuming that drinking excursions are made once every 3-4 days (see Section IV.B.1). A bull with only three territories to cross (e.g. tAD♂.C, see Figure 27) would meet a resident territory holder about once every 12 days, and one with two territories to cross (tAD♂s I and L) would do so only once every 2.5 weeks.

Territorial bulls are also likely to encounter one another at the waterholes. At a distance of about 75 m from a drinking pool, the usual patterns of border encounters took place. However, the immediate vicinity of a drinking pool seemed to be "neutral territory".

(i) Border encounters between neighbouring territory holders

Twenty-five border encounters between territorial bulls were seen; the initiating stage was witnessed in 19 cases.

In 7/19 cases, the bulls declined to meet though at least one of the bulls showed awareness of the other's presence, looking towards it and making slow hesitant movements. In 5 cases, the second bull also stared back hesitantly. One or both bulls horn wiped, scraped and urinated sprays in 3 cases, and horn wiping alone by one bull was recorded twice. In 5 cases the separation distance between the two bulls was 70-120 m. Twice, the spacing between the two bulls was only 25-30 m; but once they were separated by a watercourse, and once one of the bulls was accompanying a cow and seemed reluctant to leave her vicinity (Example 5).

In 2 cases the two bulls walked forwards to meet; in the other 10 cases, a short charge was made by one of the bulls. An approach was preceeded by initial hesitation. The bulls stared towards one another sometimes horn wiping or urinating sprays, or sometimes withdrew several metres. In one filmed instance, exaggeratedly slow movements are clearly evident as one bull moved forwards just prior to charging. The charge was made as a sudden trotting rush over the last 10-15 metres, but the rush was almost always checked just before the other bull was met. A cloud of dust was commonly raised suggesting that dragging of the feet occurred during the rush. Three times a charge ended in a momentary clash of horns. The other bull met a charge standing calmly and lowering its head to block the rush. Once, one of the bulls yielded 50 m before the rush of the other, suggesting that the initial location of the meeting had been across the boundary. A rush was never made by both bulls simultaneously. In the six instances in which one of the bulls was accompanying a cow, the charge was

EXAMPLE 5. <u>Two territorial bulls decline to meet at a border</u> <u>(Nadlosi, 23 Dec. '69).</u>

<u>1533</u> tADm.<u>A</u> grazes 30 m NNW of a cow and calf in the proximity of his W border/ <u>1542</u> neighbouring tADm.<u>Q</u> appears from the north and stands looking towards <u>A</u> from 23 m; <u>Q</u> takes several slow steps backwards, then advances a few paces, stands staring at A, takes a few paces backwards stands, scrapes and urinates sprays, stands attentively facing <u>A</u>, turns to look away, watches <u>A</u> again, backs 3-4 paces, stands; <u>A</u> grazes around, then slowly towards <u>Q</u>, without appearing to notice the other bull's presence/ <u>1547</u> <u>A</u> now stares head up, attentive towards <u>Q</u> who stands 25m away WSW; <u>Q</u> half turns away, stands facing N; turns facing NW, pauses, walks off W, pauses at a dungheap, gives 4 kicks, defecates, gives 12 more kicks, moves on NE, commences grazing; <u>A</u> stands attentively listening to his movements/ <u>1550</u> <u>A</u> half turns away, pauses, shifts on S, scrapes and urinates sprays; <u>Q</u> grazes about 30m away NW of him; <u>A</u> moves on S after the cow and calf, scrapes and urinates again, resumes grazing near the cow; he grazes around in her vicinity, scraping and urinating three more times in the next 18 minutes.

always made by the bull that was with the cow.

In all, 18 border meetings were observed. Meetings typically followed the following repetitive sequence: (i) the bulls stared at each other with raised heads horn against horn with ear pinnae forwards for several seconds; (ii) one, or both bulls simultaneously, backed away 10-15 metres; (iii) one bull horn wiped vigorously over the ground or a bush while the other bull stood looking on or both horn wiped simultaneously; (iv) one or both advanced at a walk to meet horn against horn again (Example 6, Plate 14).

In 5/17 cases there was a single brief horn clash either terminating a charge or occurring shortly after an initial horn to horn confrontation. Once there were two brief horn clashes with several blows being struck each time; but it is clearly evident in film taken that blows were directed sideways against the opponent's horn in at least the second instance. In one prolonged and tense confrontation lasting at least 88 minutes in the presence of an oestrous cow, there were perhaps ten or more brief horn clashes (Example 7). Several of these had a forward thrust component, though sometimes the bull clearly pulled back as he made the horn jabbing movement. Both bulls

EXAMPLE 6. Border confrontation between two neighbouring territorial bulls (Nadlozi, 12 Dec'60)

0922 two bulls are seen confronting at long range; they are tADm.A and tADm.Q who have met at a border; A's territory is on the east, Q's is on the west; initially Q backs away; then Q confronts A and drives A back several metres with an apparent clash of horns; Q turns away side-on repeatedly, A keeps facing towards him, there is much horn-wiping, particularly by A/ 0935 Q backs away several metres, turns aside and horns a bush, turns to face A 10 m away as A horn wipes, Q shuffles, horns a bush, approaches a few metres, looks at A, approaches slowly, A advances head high, Q advances and they meet horn to horn, withdraw to wipe horns, advance to meet again, repeatedly; once they meet heads low, but there is no horn clash/ 0950 Q advances, A backs, A pauses, horn wipes vigorously, backs further to a total distance of retreat of 40 m; A stops, the two bulls suddenly lunge together to clash horns, then stare at each other horn to horn with raised heads; both horn wipe vigorously while turning away simultaneously until standing anti-parallel 8 m separate, both look back, Q shuffles turning to face A, A remains side-on, Q approaches a few steps, stops, both horn wipe, A faces Q but Q has now turned away side-on, A grazes moving 2 paces towards Q, Q grazes side-on to A, both graze in parallel gradually moving apart from 10 m separation to 25 m; Q moves away SW grazing, A turns away grazing SE, and the two bulls separate.

PLATE 14. A typical border confrontation between neighbouring territorial bulls

a. Two territorial bulls confront horn to horn.

b. One bull horn wipes vigorously while the other looks on.

c. The first bull looks on while the other horn wipes.

d. The two bulls meet horn against horn again.

EXAMPLE 7. Prolonged tense confrontation between neighbouring territorial bulls at a border in the presence of an oestrous cow (Madlozi, 19 Feb '70)

1727 A confrontation is glimpsed several 100m away in the region of the three way corner between territories of I, L, and C./ 1743 tADm.C and tADm.L stand making slow fencing movements with horns touching or close together with heads lowered or raised; each has about 4 small bloody gashes on the head; C is on the E, L on the W, a cow and calf stand looking on from the N about 1.5 m away; the two bulls fence, knocking, pressing and touching their horns together with slow, checked movements; twice they suddenly drop their heads and clash horns hard; each time the cow springs forwards with a roar and the bulls check; this pattern continues, with L the more active in sparring with his horn pressed against that of C; C is mainly blocking; both bulls keep in the same place; there are several more horn clashes, each time the cow steps forward with a roar and the bulls avoid her without breaking off their confrontation/ 1800 L backs away, circles round and approaches C from the N, curls his tail briefly as he comes forward to engage C again, the cow turns to keep watching, slow horn fencing is resumed with several more sudden feints to clash horns with lowered heads occurring/ 1827 both bulls now back away a few paces then advance to meet again, repeatedly, C wipes his horn over the ground, twice briefly, then more vigorously/ 1845 C grazes a few mouthfuls, resumes the horn to horn confrontation, there is a horn clash; C backs away a few paces, grazes facing 60° away from L, L looks on, advances with short steps, the horn to horn engagement is resumed/ 1855 the confrontation still continues, but it is now too dark to see and I depart.

incurred a few gashes around the eye region. Most of the time, however, even this engagement consisted simply of slow fencing movements with lowered heads and horn pressed against horn. During this encounter and in two other cases one of the bulls grazed briefly in front of the other. Three meetings lasted less than one minute, four lasted 2-5 minutes, seven lasted 7-20 minutes, one lasted 36 minutes, one lasted 65 minutes, and one was still in progress 88 minutes after my arrival when darkness fell. No sounds were made by either bull during such confrontations apart from sniffing noises. Termination was accomplished by either one bull or both bulls simultaneously turning away side-on in front of the other, hesitantly looking back attentive to the other's actions, then finally turning and moving slowly away. In 7/12 cases one of the bulls scraped and urinated sprays while moving away, but in only one case was the other bull seen also to do likewise. In one filmed instance, one of the bulls scraped stiffleggedly over the ground while moving away while the other simulated grazing facing him a few metres away. In another encounter when one of the bulls remained grazing without moving away, the second bull returned to resume the engagement. This happened three times, and the confrontation in consequence was prolonged for 65 minutes.

One observed encounter is particularly interesting in illustrating the shift in relative dominance between two bulls across a boundary region (Example 8). One of the bulls was with a cow. The neighbouring territory holder (F) initially approached, clashed horns briefly, then moved away. Meanwhile the cow moved on 115 metres. The bull F then returned, drove the other bull back, and moved off after the cow. Two other similar interactions were observed near drinking pools. The bull that had initially been with the cow did not follow across the boundary. Example 9 illustrates a hesitant turning back at the apparent territory boundary.

(ii) Encounters in which one territorial bull had intruded into a neighbouring territory.

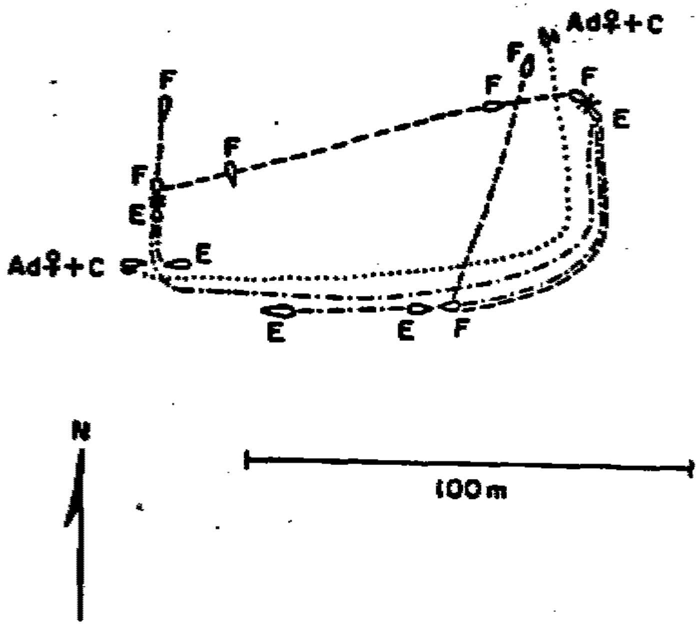
Seven encounters were observed in circumstances in which one bull was intruding into a neighbour's territory. In at least four of these one of the bulls was crossing on the way to or from water and only one instance was clearly an exploratory sally across the border.

In four cases, the trespasser had penetrated only a

EXAMPLE 8. Confrontation showing transfer of possession of a cow across a territory boundary region (Nqutsheni 15 Feb '69)

(see accompanying sketch map)

1715 tADm.E2 stands in front of a cow and calf blocking their movements eastwards; 2 mins later tADm.F2 appears from the east, circles and approaches them from the north i.e. downwind); at 35 m E notices F's approach, turns to face him, curls his tail, shifts NW, then turns N to face F again; F approaches steadily horns the ground when 20 m away, E moves towards F head down feeding, while F has his head up; E suddenly rushes at F but checks just before their horns meet, then F drives E back with a clash of horns; F backs away 6m and E half turns towards the cow and calf which snort at him from behind; F backs away, horns a tree, urinates with backward kicking movements of his hindlegs, E grazes slowly towards him several times inclining his head to look towards the cow which snorts behind him; the cow and calf walk on E, E hastens after them following the cow closely on the S flank curling his tail, F stands 25 m away to the N looking on; the cow grazes E 80m, then veers N, snorts at E who is now 15 m away on her right flank, on opposite side to F; F starts moving away, then stands looking on from 20m range; cow and calf graze N for 35 m, E lags behind slightly, turns to look towards F who stands facing him from 20m; F suddenly rushes at E, the two bulls meet 100m ENE of their first encounter, F drives E back 10m with his rush though no horn clash is heard, E then backs steadily as F advances in an arc S then W for about 70m; F then turns and walks away N, E walks off W; F returns to the spot where the cow and calf had last been, sets off N following their scent trail; E walks W then N, lies down in the vicinity of the first encounter; F is later found with the cow and calf.



Ad♀+C
F
E
Ad♀+C
F
E
F
E
E
F
N
100m

EXAMPLE 9. Border confrontation between two neighbouring territorial bulls, with one bull declining to follow a cow across his territory boundary (Nqutshoni, 25 Jan'69)

1627 tADn.G2 is encountered together with a cow near the northern edge of his territory/ 0933 the cow is disturbed by scent and runs north-eastwards, G hastens ahead and stands blocking N of the cow midway between two water-courses /1650 the neighbouring territorial bull E2 appears walking up from the east, G immediately walks towards him 30 m then rushes at E in a cloud of dust; E stands silently blocking G's advance; E backs a few meters; G rushes again, there is another silent meeting; E backs away 10 m, shuffles around side-on to G, swings his head in a low arc; G moves slowly towards him, scrapes and urinates sprays; E walks slowly away NW, G remains standing; G walks off SW, sniffs around where the cow had been standing earlier, moves off S with his nose to the ground then E; rhino snorts are audible from the north; G looks up, moves a few paces W, then sniffs around, scrapes and urinates sprays; more snorts are heard from 200-3— m to the north; G sniffs around, moves on N more rapidly, nose to the ground with his tail curled; he enters a woodland patch following a trail, pauses then backs several paces, shuffles, stands head up staring northwards; drops his head, rubs his anterior horn sideways over the ground, turns and walks back S, scrapes and urinates sprays, sniffs around where the cow had been, scrapes and urinates, looks around (probably encountering my scent trail), then wanders away southwards /1705 I locate the cow grazing about 150 m north of the location of the meeting between the two bulls.

short distance, between 90 and 300 metres. Three of these meetings followed a course similar to that typical of territory border confrontations except that the intruding bull steadily yielded ground (Examples 10 and 11, Plate 15). In one of the meetings there were several horn clashes and both bulls incurred a few gashes on the head; in the second, only a few momentary horn clashes occurred; in the third, no attacking gestures were made by the resident bull. The raised heads, horn against horn stare was recorded in only one of the three meetings; in the other two, the bulls met horn against horn with lowered heads (Plate 16). In two of the three cases, the trespasser scraped and urinated sprays immediately after crossing back over the watercourse demarcating the territory boundary; the other bull stopped on the bank looking on. The two bulls then separated.

In one case the intruding bull gallopped 100 m back to his own territory with the other bull in pursuit. This behaviour was highly unusual, and it may be significant that the fleeing bull was deposed as territory holder several days later.

In one case, a territorial bull returning from water

EXAMPLE 10. Confrontation between neighbouring territorial bulls in which one has intruded 150 m into the territory of the other (Madlozi, 18 Mar '66)

0835 two bulls are seen confronting /0840 tADm.J confronts tADm.F about 150 m W of the Madlozi stream; J advances steadily, F retreats, whenever J stops advancing F comes forwards a few steps; in between they wipe horns vigorously over the ground; there are several brief clashes of horns; when F stops retreating; two small gashes are visible on J's face, there are no sounds other than heavy breathing F retreats in a semicircle then backs towards the Madlozi stream; he descends into the dry stream hollow, urinates several sprays with scraping movements of the hindlegs; J remains watching on the bank; F retreats across the stream, and J backs away on the opposite bank then turns and walks off; the Madlozi stream was later confirmed to be the location of the boundary between the territories.

EXAMPLE 11. <u>Confrontation between two neighbouring territorial bulls in which one has intruded 300 m into the territory of the other.</u> (Madlozi, 28 Aug '71)

<u>2155</u> tADm.<u>X</u> and tADm.<u>N</u> are discovered engaged in a silent horn to horn confrontation about 60m E of my campsite, at the E boundary of <u>X</u>'s territory and about 300m S of the SW corner of <u>N</u>'s territory. The two bulls shuffle about, forwards then backwards, sometimes turning half aside, with heads in 45° down posture; <u>N</u> slowly yields ground nortwards; <u>N</u> then walks backwards steadily for about 30 m with <u>X</u> advancing on him 1-2m away; <u>X</u> pauses, turning away facing W, while <u>N</u> stands quietly 17m away N of him, for 2 min; <u>X</u> moves away NW, scrapes and presumably urinates, then circles round approaching <u>N</u> again from the W, <u>N</u> starts backing when <u>X</u> is still 15m away, then there is a backward walk by <u>N</u> and advance by <u>X</u> for 60m, with horn wiping by <u>X</u> and a few less vigorous horn wipes by <u>N</u>; <u>N</u> backs against the fence of the horse paddock, there is a momentary feint at a clash of horns, the two bulls shuffle about, <u>X</u> turns away then advances on <u>N</u> again, horn wiping and scraping hard without urinating when 5m away, slow horn against horn fencing is resumed; <u>X</u> somehow gets N of <u>N</u> then the two bulls adjust orienation so that <u>N</u> is on the N, then <u>N</u> backs away again /<u>2207</u> just W of the guard camp huts <u>X</u> turns aside and moves away W, scraping and urinating after 30m, moves on W and commences feeding about 100m W of the huts; <u>N</u> remains standing quietly about 35 m NW of the huts for 10 min, then commences grazing here.

PLATE 15. Confrontation between two neighbouring territorial bulls in which one has intruded into the territory of the other (Madlozi, 14 Jan '70)

a.
X retreats scraping his hindlegs as D advances on him in head low posture

b.
X continues backing away steadily throwing up much dust by dragging his feet; D advances on him in head raised posture

c.
X stops retreating, D advances to stare horn against horn

d.
X resumes backing away, while D is about to horn wipe

e.
D advances on X again

f.
X backs away across the watercourse dividing the two territories; D pauses on the bank, horns a bush and makes backwards scraping kicking motions over the site

PLATE 16. Confrontations between bulls

a. A trespassing territorial bull backs away while the resident bull advances in head low posture.

b. The two bulls clash horns momentarily when the intruding bull stops retreating.

c. A subordinate bull (formerly the neighbouring territory holder) gives a snarl display as a territorial bull approaches.

d. A lone adolescent male gives a snarl directed towards an advancing territorial bull.

met a neighbouring bull in the region of the latter's boundary with a third bull while still 500 m away from his own boundary. There was a brief horn against horn confrontation with the trespasser swinging round to be on the side nearest his own territory. The trespasser then backed away before the resident bull dragging his anterior horn along the ground for about 70 m. When the resident bull turned away, the trespasser resumed walking back towards his own territory.

In one case, a trespassing bull on his way to water noticed the resident bull lying sleeping about 50 m ahead. He circles round him passing downwind and continued on his way. The other bull remained unaware of his passing.

In one case, the territorial bull B, whose territory adjoined that of tADσ.C on the north, met C at the southern boundary of the latter's territory. Presumably B was on his way back from water. In this case a prolonged and violent fight took place (Example 12). The bulls spent long periods fencing horn against horn, then fighting suddenly erupted with heavy horn to body blows being struck. After a bout, the bulls faced breathing heavily for several minutes before resuming slow fencing movements. One bull (the "loser") sweated profusely. The fight continued for

EXAMPLE 12. Fight involving neighbouring territorial bulls
(Madlozi, 1 Oct '69)

1740 tAdm.C and tAdm.B are discovered confronting each other silently at the S border of C's territory (while B's territory lies N of C's); several heavy horn to body blows are struck, then slow horn against horn fencing takes place; C takes the initiative while B blocks breathing heavily, sweat covered /1743 fighting suddenly erupts with resounding horn against body blows being struck, B drives C against a bank and digs his horn repeatedly against C's side, C breaks away and runs with B chasing behind, after 20m C suddenly plants his forefeet and spins round to face B again and the two bulls confront each other standing horn against horn breathing heavily, both now covered in sweat /1748 slow horn sparring is resumed, C being the more active, at times shuffling back 2-3 paces then forwards to touch horn against horn/ 1755 the heavy breathing is subsiding, horn fencing movements become more active, B makes a sudden feint to lowered head with an air expulsive grunt and C counters with lowered head, there is no clash of horns; B makes 2 more dropped head movements which C blocks by hitting his horn against B's; C backs away a few paces, advances to horns close, B backs away a few paces in front of him; B is still sweat covered, C is now dry; both bulls horn wipe and shuffle forwards to touch horns, repeatedly; B twice initiates a momentary clash of horns /1815 this same pattern continues, then B backs away before C in a semicircle, W then S then E, with several more brief horn clashes occurring; it is now too dark to see, and I depart.

35 minutes until it became too dark to see, and from signs the next morning it evidently continued into the night for some time. The trespassing bull _B_ was located the next morning two kilometres to the east still out of his own territory. His right eye was a swollen bloody mass and there were numerous bloody gashes on his head and shoulders. It was at least several days before he returned to his own territory again. The resident bull _C_, in contrast, showed only a few not very striking bruises and gashes. This was one of only two fights that I observed during the study.

(iii) One territorial bull intruding on a more distant territory.

Five encounters were observed in which one bull was intruding on the territory of a bull that was not a neighbour of his.

In two of these the intruding bull noticed the resident bull ahead, and altered course to avoid him and continue on his way to water.

Three encounters led to confrontations. In each case, the intruder faced the resident ears back uttering loud snarls or shrieks. Two confrontations were brief lasting only a few minutes (Example 13). One lasted over 25 minutes, with the resident bull advancing repeatedly to confront the intruder horn against horn, while the latter stood defensively (Example 14). In all three cases, the resident bull turned away leaving the other. In two cases, the intruding bull then continued on his way back towards his home territory. In the third case, the intruder remained standing in the shade near the Nyonikazane Spring where he had drunk a short while earlier.

(iv) Encounters between territorial bulls taking place in the immediate vicinity of drinking pools.

Six encounters were witnessed at drinking pools in which I knew the social status of both bulls.

In three cases, one bull noticed the other drinking or standing near the pool, horn wiped, and stood declining to approach (Example 15). In two cases, one bull started approaching, then turned and moved away before meeting. In one of these, the approached bull horn wiped, in the other the approaching bull horn wiped then backed away (Example 16). In the sixth case, one bull continued past at 25 m range ignoring the other, and the latter snorted as he passed. Several other encounters between bulls were

EXAMPLE 13. Brief confrontation between a territorial bull and an intruding territorial bull who is not a neighbour of his (Nadlozi, 26 Aug '71)

1608 tADm.BB walks N steadily crossing the territory of L. tADm.L sees him at 50m, stands watching intently, BB continues, then stops at 30m range looking towards L; L advances, BB stands facing him shuffling his feet uneasily, then flattens his ears and gives a loud roar; L comes at him at a trot and they meet with lowered heads without a clash of horns, L checking upon meeting BB; BB backs away before L with ears flat making repeated roars and shrieks, L advances on him horn to horn, they stop and stand facing each other /1612 L backs away, stands half turned away at 5m separation, walks on, scrapes and urinates sprays, commences grazing, BB stands watching; L grazes away SSW ignoring BB /1620 L is 35 m away from BB, BB now turns and continues on his way N back towards his own territory.

EXAMPLE 14. <u>Prolonged confrontation between a territorial bull and an intruding territorial bull who is not a neighbour</u> (Madlozi, 8 Jan '70)

<u>0700</u> tADm.<u>PP</u> and tADm.<u>A</u> are discovered in confrontation at the N border of <u>PP</u>'s territory: <u>PP</u> stands facing <u>A</u> with head raised, <u>A</u> stands with his head thrust forwards and ears laid back uttering repeated loud roars which rise in pitch to a shrill shriek at each slight movement by <u>PP</u> /<u>0705</u> <u>PP</u> turns side on, then faces <u>A</u>, <u>A</u> shrieks loudly with ears back, <u>PP</u> stands, lets his head sag/ <u>0708</u> <u>PP</u> backs away, <u>A</u> remains standing, <u>PP</u> advances again, <u>A</u> shrieks, <u>PP</u> advances to horns touching, makes 2 brief drop head moves which <u>A</u> fends, <u>A</u>'s tail is curled; <u>PP</u> backs away, moves round and confronts <u>A</u> from the S/ <u>0713</u> <u>PP</u> stands head low facing 45° away from <u>A</u> (his shoulder exposed); <u>PP</u> backs a few paces, turns side on, stands head low in front of <u>A</u>; turns to face <u>A</u>, <u>A</u> stands with roars and shrieks waving his head from side to side, <u>PP</u> turns away again and stands side on a few m in front of <u>A</u>; <u>PP</u> walks away, then turns and approaches <u>A</u> again, <u>A</u> stands tail curled with loud shrieks, <u>PP</u> makes one drop head gesture (cannot tell whether horns clashed) / <u>0725</u> <u>PP</u> turns and walks away S, scrapes and urinates sprays, <u>A</u> remains standing facing S, <u>PP</u> dungs with kicks, wanders on /<u>0727</u> <u>PP</u> is 60m away, <u>A</u> now turns and walks slowly N, then more steadily; about 100 m SW of his border he pauses to graze briefly, walks on, grazes a few mouthfuls, walks on; on crossing his own territory border he scrapes and urinates, then commences steady grazing.

EXAMPLE 15. Encounters between neighbouring territorial bulls at a drinking pool (Madlozi, 21 Aug '71)

1723 tADm.X stands drinking at the Lily Pan (X's territory adjoins the Lily Pan on the northwest) / 725 tADm.WW approaches from the SW, walking slowly (WW is a new bull and I am not sure of his territory location); X turns to face towards the other bull, backs a pace and nudges the ground with his horn, advances, WW does a backwards walk when X is 25 m away, X stops 18 m separate, then turns and moves back to the pool, resumes drinking, WW stands looking on 35 m away /1732 X moves away WNW, horns and scrapes but there is no urine spray; X moves away disappearing WNW /1738 WW moves towards the pool and commences drinking on its south edge /1742 tADm.H (whose territory adjoins the Lily Pan on the southwest) approaches from SW, pauses to defecate with kicks, explores around sniffing, urinates sprays, slowly approaches the pool; WW turns to face towards H at 50 m range, stands staring, H approaches sniffing the ground, then stops looking ahead towards the other bull; H steps backwards 3 paces, stands; walks backwards 10 m, then stands looking towards the other bull; WW stands quietly observing him; H moves away N, WW resumes drinking; H explores around sniffing where X departed earlier /1757 WW wallows on the pool edge, H stands quietly about 50 m WNW of the pool/ 1802 WW walks off SW /1805 H advances, approaches the water slowly, reaches it at 1808 and commences drinking.

EXAMPLE 16. Two territorial bulls avoid meeting at a drinking pool (Madlozi, 28 Aug '71)

1925 tADm.X drinks at the Mphafa Pool (which is about 3 km E of X's territory) /1940 X leaves the pool, slowly approaches another bull who stands quietly nearby, stares intently towards him from 3 m range, makes 2 backwards flicking movements with his ears and gives a soft rumble, the other bull makes 2-3 horn wiping gestures but stares back calmly at X; the strange bull then wanders away S and X moves off W.

EXAMPLE 17. <u>A territorial bull ignores his resident subordinate bull</u> (Madlozi 19 June '66)

<u>1230</u> sADmQ stands up in his shady resting place as tADm.P approaches, walks forwards a few m towards P, P hesitates momentarily looking ahead towards Q then advances, Q snorts twice with flattened ears as P approaches then gives a loud snarl as P passes by 5m in front of him; P continues on his way without seeming to notice the presence of the other bull, stops in the shade of a tree 8m away, turns so that his rear is towards Q; Q stands watching him, then moves away about 10m; P shuffles, then lies down in the shade; Q stands facing him for a further 8 min., then also lies down in shade about 20m away from P.

seen at drinking pools in which the bulls were strangers to me. Bulls usually hesitated in the shadows before moving down to water, avoided meetings when other bulls were noticed, and sometimes drank on opposite sides of the same pool paying little attention to one another.

(b) <u>Encounters between territorial bulls and subordinate bulls</u>

(i) Subordinate bull resident in the same territory.

Encounters between a territorial bull and a subordinate bull sharing the same territory were frequent; in all, 117 such encounters were observed.

Three-quarters of these did not lead to meetings. In 50 cases, the territorial bull did not approach (Example 17). In 31 cases, the territorial bull started approaching (8 times with a sudden charge), but veered away before meeting; or the subordinate bull moved away at the territorial bull's approach (8 cases). In another 5 cases, the subordinate bull fled at the territorial bull's approach, and the latter pursued for a distance of 30-70 m. Subordinate bulls responded to the approach or nearby movements of a territorial bull with snorts (20), snarls (24) or shrieks (6).

Twenty-four observed approaches led to meetings: the territorial bull advanced (7 times with a charge) to confront the subordinate bull horn against horn. Subordinate bulls faced such approaches standing their ground with tail curled giving repeated loud snarls or shrieks (Plate 16).

In all 31 confrontations were witnessed. Momentary horn clashes were initiated by the territorial bull in 10 cases, which were fended off by the subordinate bull to the accompaniment of loud shrieks. In 3 cases the subordinate bull advanced a few quick paces towards the territorial bull with a horn prodding gesture and a shriek. Twenty-three confrontations were brief, lasting less than a minute, and another 6 lasted 2-5 minutes (Example 18). One confrontation lasted at least 10 minutes; in this case the subordinate bull was the deposed former territory holder. Another lasted 30 minutes, in provocative circumstances in which the subordinate bull courted the cow that the territoria. bull had mated with two hours earlier (Example 19). In this case the territorial bull clashed horns vigorously several times but finally wandered off leaving the subordinate bull with the cow. In another case in which a subordinate bull made a hiccing approach towards

EXAMPLE 18. Brief confrontation between a territorial bull and a resident subordinate bull (Nqutsheni, 10 Feb'69)

0557 an aggregation of 5 rhinos lies resting in a sand patche; they include tADm.L2, sADm.K2, an adolescent female and an adolescent male; the two subordinate bulls lie 30 m and 27 m respectively away from the territorial bull; all three bulls are fully mature; /0617 sADm.H stands and commences grazing, moving slowly away /0723 the two adolescents rise, commence grazing E; sADm.K rises with a grunt as they move across behind him, and half turns; tADm.L remains lying, about 25m from K /0728 L stands 18 m away to the side /0732 L moves his head slightly, K immediately inclines his head towards L and gives several more snorts and low grunts; L commences grazing, then suddenly runs at K, K snarls and shrieks backing a few paces, they meet horn to horn, then L turns and wanders off E resuming grazing; K remains standing giving a few more soft snorts; L grazes, K remains standing in the same place.

EXAMPLE 19. Prolonged and tense confrontation between a territorial bull and his resident subordinate bull after the latter had courted an oestrous cow. (Madlozi 30 Nov '70)

0940 sADm.B starts courting the cow which tADm.C had mated with earlier in the day then left; B approaches with hics and the cow counters with a snarl; from 250m away C evidently hears this noise and hastens towards them, veering round to approach from downwind; at 35m separation B suddenly becomes aware of C's approach and swings round advancing several paces towards with ears flattened giving loud shrieks; C advances to meet B horn to horn without clashing, there is horn to horn fencing with B in a defensive snarl posture giving shrieks; the cow advances at C with a snarl, C retreats from her and stands 10m from B; C then circles round, rushes to meet B, B jumps back with a shriek but C also pulls back checking just before meeting; C confronts B horn against horn moving backwards and forwards a few paces at a time repeatedly, B stands defensively giving shrieks each time C approaches/ 0955 C jumps forwards to clash horns, B fends waving his horn vigorously and C jumps back again in the same movement, the cow snarls, fencing then continues; C moves away then circles round and comes in to meet B again; there are a few quick thrusts to clash horns but both bulls pull back; C steps backwards then forwards 1-2 paces at a time repeatedly, prodding his horn against B's; B faces C giving continual breathing roars, there is one more horn clash/ 1012 C backs away, and turns and walks off leaving B with the cow.

an oestrous cow, the territorial bull did no more than clash horns briefly with the subordinate bull several times and the subordinate bull several times and the subordinate bull stayed in the vicinity (Example 20).

In 29/31 encounters, the territorial bull terminated the meeting by backing then turning and moving away paying no further attention to the subordinate bull, even when it remained nearby. The subordinate bull remained standing until the territorial bull had moved away 25-30 m, then either resumed previous activities in the same vicinity (23 times), or wandered away (5 times). In two cases, the subordinate bull backed then moved away, while the territorial bull remained standing taking little notice.

There were variations in the relationships between particular territorial bull-subordinate bull pairs, related to the age status of the subordinate bull. Young adult bulls (aged probably 10-12 years) were more likely to be approached (Table 44; $\chi^2 = 10.1$, df = 1, $p < 0.005$), and frequently retreated from the territorial bull; fully mature subordinate bulls always stood their ground. One supplanting interaction was

EXAMPLE 20. Territorial bull clashes horns briefly with a resident subordinate bull when the latter courts an oestrous cow (Madlozi, 25 June'66)

1033 tADm.A and a cow and calf lie down close together; the cow had displayed full oestrous receptivity and been mounted by A the previous day/ 1035 subordinate bull O, who has been nearby for the past hour and a half, now walks forwards approaching, stands looking hesitantly towards the other 3 rhinos from 30 m range (sniffing?)/ 1039 O turns away/ 1050 O moves slowly forwards towards A and the cow and calf, pauses 25 m away, there is a soft rumble from one of them; O circles round behind A approaches the cow very slowly; the cow gives snort without rising, the calf stands/ 1055 O edges forwards, the cow gives a soft grunt; tADm.A then rises to his feet and walks across, comes at O driving him backwards with a clash of horns, O roars repeatedly with ears back; there is another brief clash of horns, then the two bulls stand again; the cow and calf stand looking on 5 m away/ 1103 O turns away from A, stands near the cow and calf/ 1107 A lies down again; O remains standing 10 m away in front of him. (O stayed in the vicinity of the territorial bull and cow for most of the day).

TABLE 44. <u>Variations in interaction patterns among individual territorial bull-subordinate bull pairs.</u>

Figures represent number of times recorded

ident. of tADm	ident. of sADm	background of sADm	N	TYPE OF ENCOUNTER: no meeting, sADm stands	brief mtg < 1 min	confr. 2+ mins	sADm retreats
I	HH	just post-adolescent young bull	21	6	4	0	11
I	SH	newly settled, just post-adol. young bull	5	2	0	2	1
A	O	young adult bull	14	8	3	0	3
		other young sADms	8	5	2	0	1
		ALL YOUNG sADms	48	21 44%	9 19%	2 4%	16 33%
H	N	elderly bull of long standing as sADm	8	7	1	0	0
I	N	ditto	13	12	1	0	0
I	H	deposed former tADm	11	9	1	1	0
C	B	formerly neighbouring tADm'	12	5	5	2	0
		other fully mature sADms	20	14	6	0	0
		ALL MATURE sADms	64	47 73%	14 22%	3 5%	0

observed: the young subordinate bull HH moved from the shady restplace he was occupying at the approach of the territorial bull I, and I lay down at this restplace while the subordinate bull selected another site 40 m away. In another observation in similar circumstances, a fully mature subordinate bull lay with snorts and snarls when the territorial bull approached, and the territorial bull selected another shady tree 12 m away.

There was an interesting change in the relationship between the young subordinate bull HH and the territorial bull I following the latter's takeover of HH's home territory. For the first few months, the young bull usually fled or walked away tail curled whenever the territorial bull appeared nearby, and the territorial bull chased after him for a short distance on several occasions. A year later, the territorial bull usually paid little attention to HH, and the two bulls were frequently seen in close proximity. Eighteen months after the territory takeover, the two bulls were watched engaging in a playful horn wrestling match that lasted forty minutes. This was initiated by the territorial bull and readily accepted by the subordinate bull. The movements of both bulls were relaxed and their actions were similar to those observed in play wrestling between adolescents. Only twice the territorial bull seemingly became too vigorous, and the subordinate bull responded with a brief advancing horn gesture and a shriek before resuming wrestling.

(ii) Subordinate bull intruding from another territory.

Subordinate bulls sometimes wandered beyond their home territory limits, and this sometimes brought them into contact with one of the surrounding territory holders. I saw 41 encounters in such circumstances, but 15 times my attention had been attracted to the scene by the loud roars and shrieks of the subordinate bull only after a meeting had commenced.

In 5/26 case in which initiation was observed the territorial bull did not approach. In two cases, the territorial bull started approaching, but desisted when the subordinate bull moved away. In 4 cases, the territorial bull advanced and chased after the other bull a short way when it fled. In the remaining 15 cases, the territorial bull advanced to confront the subordinate bull horn to horn. In 5 of these, a short charge was made by the territorial bull; in the remainder the territorial bull aproached at a walk, twice accompanying the approach with a few hics. Subordinate bulls met such approaches by standing with loud snarls or shrieks.

Thirty meetings were observed, of which 12 lasted less than one minute. The territorial bull simply stared briefly then moved away (Example 21). Momentary horn clashes took place in 6 of these. Sixteen meetings were prolonged and tense confrontations with the territorial bull backing away a few metres then readvancing to stare horn against horn again, repreatedly (Example 22, Plate 17). The subordinate bull faced the confronting territorial bull uttering loud snarls and shrieks with every breath. The territorial bull initiated one or more horn clashes in 11 cases, horn wiped in 4, displayed head flings in 3, and scraped and urinated sprays in 2. The subordinate bull snarled in 14 cases, shrieked in 15, advanced several steps towards the territorial bull in 4, and 3 times made a horn prodding gesture at the end of an advance. Three confrontations lasted 2-5 minutes, 8 lasted 5-20 minutes, 4 lasted 20-40 minutes, and one lasted for 80 minutes.

In one case, the territorial bull violently attacked

EXAMPLE 21. Brief confrontation between a territorial bull and an intruding subordinate bull (Nadlozi, 31 Dec'69)

0547 tADm.L approaches from the SW to meet sADm.B near the western border of L's territory (sADm.B is normally resident in the territory of tADm.C which adjoins L's territory to the northwest); B stands with snarls; L turns away, stands side-on; L approaches again, B snarls, L comes forwards head down to clash horns briefly, then stands looking at B, B faces L with repeated snarls waving his head from side to side; L turns and moves away B, resumes grazing; B stands watching him/ 0555 L is 50 m away from B, B now turns and resumes walking northwards.

EXAMPLE 22. Prolonged tense confrontation between a territorial and an intruding subordinate bull (Nadlozi, 21 Dec'70)

1605 sADm.B grazes while moving on steadily northwards passing through the territory of tADm.I; evidently he is returning from water (his home territory is that of tADm.C, which adjoins I's territory on the north); 250 m N of B tADm.I grazes/ 1018 B now stands 130 m S of I/ 1622 I walks S, pauses listening, walks on S /1625 I notices B standing 35 m W of him and pauses inclining his head to look towards B; B snorts; I suddenly rushes uphill towards B, B snarls then shrieks as I meets him, there is no horn clash; I circles round N of B getting downwind, approaches slowly to horns crossed position, there are snarls from B; I stands staring, drops his head then stares against horn to horn; I makes a dropped head feint, there is an immediate loud shriek from B, I checks his action, stares again with his horn 0.3 m from that of B, there are hoarse gasping snarls from B/ 1629 I backs, wipes his horn, stands 1.5 m separate; I horn wipes again, starts turning away, hesitates, slowly approaches B stands staring; B makes a horn prodding gesture with a shriek, I stands without yielding;/ 1632 I backs, wipes his horn several times, approaches slowly then more rapidly, B snarls, I stands staring horns close; I jumps forwards a pace with a dropped head feint, B fends with a shriek; I backs, turns aside and horn wipes, approaches, stares from close, backs a step, stands, advances a step, B snorts, I advances another pace, B drops his head with a shriek three times, each time I blocks with his horn but remains staring at B horn to horn, edging forwards; B has backed 3-4 paces, they stand close, then relax slightly/ 1637 B snorts, I backs,

(contd. - Example 22) from page 429

turns aside, horn wipes several times, moves W, horns a 1 m high bush, turns and advances again, B snarls, I stands with his horn almost touching that of B, B gives gasping grunts with ears laid back but his head has sagged: I relaxes, backs, horn wipes, suddenly advances, there are snarls from B, I stands staring horns crossed; B shrieks and makes a dropped head feint, I backs 1 pace at this but then readvances a pace again; I turns aside, horn wipes, looks back towards B from 4 m, advances again, stops with his horn almost touching that of B as B snorts; B waves his head from side to side giving gasping grunts; I backs, horn wipes, turns away, B backs a step, I advances a step, B makes a dropped head feint with a shriek, I responds by clashing horns momentarily, there is a loud shriek from B, I stands staring, horns touching /1642 I backs, makes a cursory horn wipe, advances, stares from 0.5 m range, makes a suppressed head flinging gesture, then circles round E of B; B turns to keep facing him/ 1644 I turns and wanders away S/ 1648 B walks on N.

the subordinate bull, directing repeated horn blows against its head and shoulders and chasing it jabbing it in the groin when it ran (Example 23). The subordinate bull was completely on the defensive, but was unsuccessful in warding of the fierce attack of the territorial bull. The encounter took place at a territory border.

There was one other strange meeting in which the territorial bull moved in parallel with the subordinate bull, then moved ahead to block its movements when it reached the territory border, as if blocking the movements of a cow.

In 26/27 cases, termination was achieved by the territorial bull turning and moving away. Once the territorial bull remained standing while the subordinate bull moved away.

Subsequent to an encounter, the subordinate bull remained in the same vicinity in 7 cases. In 16 cases, the subordinate bull left the territory on which it was trespassing, and in 5 cases it departed from the vicinity of the encounter, though not from the territory.

(iii) Trespassing territorial bull with resident subordinate bull.

EXAMPLE 23. Attack by a territorial bull on an intruding subordinate bull (Hadlozi, 25 May '66)

0900 My attention is attracted by loud roars and shrieks; sADm.O appears running with tADm.G chasing at his heels; O stops and turns to face G and there is a violent battle; G attacks with repeated blows of his horn at O's head then shoulders which O is unsuccessful in parrying, O roars and shrieks loudly; the two bulls rest breathing heavily with G's head against O's shoulder for 2-3 minutes, then G resumes attacking O; O breaks away and flees and G pursues him digging his horn into O's groin several times, then O turns to face G again and there is another fierce and noisy battle with many blows struck; the two bulls separate and standing facing about 0.5m apart breathing heavily; O gives bellowing roars with every breath, his ears laid back; G shuffles backwards and forwards 2-3 paces at a time, coming forwards to touch his horn against that of O; after several minutes of this G backs away then turns and walks off S; 16 mins have passed since my arrival; O remains standing breathing heavily for a further 12 min, then wanders away N; O has incurred many bloody gashes around his head and shoulders; G shows only a few cuts around his head; the meeting took place at the N boundary of G's territory.

Two encounters were seen in which the territorial bull was intruding on the home territory of the subordinate bull. On one occasion, neither bull noticed the other at a range of about 75 m though the subordinate bull later followed along the scent tracks of the territorial bull a short way. In the other, the territorial bull stared from about 35 m away, then trotted hastily back towards its own territory which was only a short distance away. The subordinate bull merely paused briefly, then continued on its way.

(iv) Encounters in the immediate vicinity of waterholes.

I observed three encounters between subordinate bulls and territorial bulls at waterholes in which I knew the status of both bulls. In each case both bulls had come from distinct territories. The territorial bull faced the subordinate bull, giving snorts in 3 cases, snarls in 2 cases, and shrieks in 1 case. The subordinate bull watched, replying with snorts in 2 cases.

(c) <u>Encounters between territorial bulls and adolescent Males</u>

(i) Adolescents of age class S_2 (age 6-9 years)

Thirty four encounters were observed between a resident territorial bull and such older adolescent males. In 9 of these the territorial bull did not approach; in 13, the territorial bull started approaching, then turned away (in 4 cases because the adolescent retreated at its approach); there was one approach in which the adolescent male fled with the territorial bull chasing after a short way; 11 approaches led to meetings. Adolescents faced approaches with snorts (6), snarls (14), or shrieks (1), and once with an advancing snarl. Ten meetings were brief, lasting less than one minute, then the territorial bull moved away (Example 24), and only one included a momentary horn clash. One meeting lasted 42 minutes judging by sound, but I observed only its termination; the territorial bull had been confronting two adolescent males at a territory boundary. Adolescent males were commonly tolerated in the vicinity of oestrous females; the single recorded instance of a horn clash occurred when the adolescent approached a cow hiccing.

Because I distinguished adolescents from adults by behaviour some males classed as adolescent (because they were paired up with a companion) were of similar age to other single young males regarded as subordinate bulls.

EXAMPLE 24. Meeting between a territorial and an adolescent male aged about 7 yrs (Nadlozi, 10 May'66)

1635 tADm.X wanders into a woodland patch and there encounters the adolescent male b together with an adolescent female c; b and c snort as X approaches to stand in front of them; b snorts at X, then gives two advancing snarl-shrieks coming forwards 2-3 short paces each time; X watches calmly from 5m range; the rhinos stand, X takes a step towards b, b snorts, X turns away and moves on past.

EXAMPLE 25. Brief confrontation between a territorial bull and two young adult males that are still paired up as adolescents (Nadlozi, 8 June '70)

1703 tADm.X notices the two young adult males VV and VI (ages 11-12 yrs) grazing about 40 m from him; X approaches, VV snorts and curls his tail, X approaches hiccing from ESE, the two young males stand side by side with grunts, X swings his head in a low arc as if to wipe his horn over the ground but does not do so, turns away, circles round, approaches the young males from downwind, stands with his head extended towards the two young males staring intently, his horn almost touching that of VV; the two young males snarled as X moved round and approached; X stands thus about 1/2 minute, then suddenly swings round to face away from the young males/ 1706 X can be heard scraping and presumably urinating sprays, but is hidden from my view by a bush/ 1708 X is visible again standing quietly facing 135° away from the two young males at 6 m range/ 1709 X walks slowly away WSW sniffing around, presumably at the tracks of the two young males, then turns and commences grazing S/ 1712 the two young males resume grazing E; X grazes on S.

Prolonged tense confrontations were usual with the latter, but were never observed with the former. For example, a wandering young adult male VV, aged 11-12 years, was confronted for 32 minutes when encountered alone by a territorial bull (see Plate 17). Five months earlier, when VV was together with another young adult male of similar age and thus considered to be an adolescent, the two were confronted only briefly by another territorial bull X (Example 25). A year later, tense confrontation lasting 10 minutes was observed between this territorial bull X and the young male VV who was now alone.

(ii) Younger adolescent males of age class S_1 (age 2.5-6 years)

Thirty-six encounters between territorial bulls and young adolescent males were witnessed. In 12, the territorial bull did not approach. In 15, the territorial bull started approaching but turned away, 12 times because the adolescents retreated at his approach. Seven approaches led to short chases. Only one approach led to a brief meeting in which the two adolescent males faced the territorial bull with snarls and one advancing horn gesture. Once a territorial bull violently attacked the young adolescent male that was with a cow and chased around after it for 2-3 minutes before it escaped.

(d) Territorial bull-male calf encounters

In two observed cases territorial bulls suddenly attacked male calves briefly before the mother intruded. In all other cases, territorial bulls paid little attention to calves accompanying cows. On several occasions territorial bulls passively allowed the calf to sniff at their nose or nudge horns.

(e) Encounters between subordinate bulls

Fifteen encounters were observed between subordinate bulls sharing the same home territory. In 5 cases, both bulls paid little or no attention to each other. In 6 cases one bull, or once both bulls, made separation maintaining threats, either snorts or snarls. Two approaches led to nasonasal meetings, on both occasions one of the bulls was a young male that had only recently settled in the territory and the other individual was the young adult male, HH. On another occasion when these two bulls met, HH approached to look at the other with a closer approach being inhibited by snorts and snarls from the other male. On a fourth occasion, these two bulls engaged in prolonged and fairly vigorous playful wrestling (Example 26).

Five encounters were observed in which one of the bulls was trespassing on the home territory of the other. In two of these, there was no approach. In two others, the resident bull advanced to meet the intruder who stood defensively with snarls. In one of these cases the resident subordinate bull made a short charge over the last few metres, then turned away with head flings when the other bull blocked him with a loud snarl. In the fifth encounter, which took place in the region of a border between the territories occupied by the two bulls, both stood tensely about 10 m apart for 33 minutes without approaching nearer.

Another 5 observed encounters took place at drinking pools. In each case, either one or both bulls directed snorts or snarls at the other.

(f) Subordinate bull-Adolescent male encounters

Ten observed encounters involved subordinate bulls and adolescent males of age class S_2. In 8 there was either no approach or a checked approach. In 4 of these cases, separation maintaining threats were made by the subordinate

EXAMPLE 26. Play wrestling between two sADm's sharing same territory (both are young males, sADm.SH has newly settled in the territory) (Madlozi, 20 Jan '71)

0732 sADm's HH and SH stand confronting each other about 1m apart, HH with head low seemingly grazing, SH watching him with ears flicking back and forth attentatively; they meet heads close with HH in grazing attitude and slow, relaxed horn fencing develops; HH shakes his head and prances his forequarters up and down, stands staring at SH with flicking tail, SH pushes his horn gently against the side of HH's head; HH turns away, flings his head up and down with exaggerated movements and approaches SH again, they stand horn to horn; HH pushes SH back horn against horn, SH breaks away giving an ears flat gesture and a grunt, HH prances away, approaches, prances away, approaches again; SH advances, relaxed with head low, to push horns, stands, then pushes HH back; HH makes a slow head down gesture, SH stands head low with ears back, wrestling is resumed.... wrestling in this fashion continues for 20 minutes, becoming fairly vigorous with both males taking turns to push each other backwards and more vigorous prancing up and down by HH.

EXAMPLE 27. Nasonasal meeting between a subordinate bull and two adolescent males aged 7-8 years. (Madlozi, 25 June '66)

0923 sADm.O stands sleepily under a tree; adolescent males m and n appear grazing about 100 m E of him; m and n look up alert, possibly seeing O; they move hesitantly towards O, looking up then resuming grazing; at about 35 m separation they stop looking towards O; O strolls over towards them; m and n stand looking at him with snorts, O stops about 2 m in front of them; n moves forwards a few steps to make contact and the pair stand with horns crossed; O then turns and walks away, either m or n grunts behind him, O hastens on a few paces then resumes walking more slowly.

bull, and in 2 similar threats were made by the adolescent males. Once the subordinate bull approached and remained in the vicinity of two adolescent males and was tolerated by them apart from one brief grunt. One approach led to a nasonasal meeting, reciprocated by the adolescents after their initial snorts and snarls (Example 27).

Twenty-seven encounters were observed between subordinate bulls and adolescent males of age class S_1. In 11 of these there was either no approach or a checked approach initiated by either the subordinate bull (5 times) or the adolescent males (3 times); in 4 of these the adolescent males retreated. Three approaches led to brief nasonasal meetings, and on another 7 occasions nasonasal contact developed into playful horn wrestling, despite the size discrepancy between the two bulls (Plate 21).

In one encounter, the adolescent male approached to rest its head on the flank of the recumbent subordinate bull. The subordinate bull sprang up and chased after the adolescent male a short way and the latter fled at a gallop.

Summary and comparisons

Two differing basic responses are displayed by bulls bull, and in 2 similar threats were made by the adolescent males. Once the subordinate bull approached and remained in the vicinity of two adolescent males and was tolerated by them apart from one brief grunt. One approach led to a nasonasal meeting, reciprocated by the adolescents after their initial snorts and snarls (Example 27).

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In one encounter, the adolescent male approached to rest its head on the flank of the recumbent subordinate bull. The subordinate bull sprang up and chased after the adolescent male a short way and the latter fled at a gallop.

Summary and comparisons

Two differing basic responses are displayed by bulls in confrontations: (i) one bull confronts the other horn to horn silently; (ii) one bull stands defensively making repeated loud snarls and shrieks.

Territorial bulls on their home territories usually approached other bulls they encountered and always confronted them silently (Table 45). Neighbouring or intruding territorial bulls or intruding subordinate bulls were approached more frequently than subordinate bulls resident in the same territory (77% vs 55%, $X^2 = 10.0$, df = 1, $p \angle 0.005$); and fewer approaches begun towards the latter led to meetings (41% vs 83%; $X^2 = 23.8$, df = 1, $p \angle 0.001$). Once a territorial bull moved past a resident subordinate bull without paying it any attention to accost an intruding subordinate bull that was standing 100 m away downwind at night. Charges were made commonly against other territorial bulls, less frequently against subordinate bulls. Horn clashes were recorded in about 50% of the meetings but were rarely more than momentary. Meetings with resident subordinate bulls were usually very brief, lasting less than one minute, while meetings with other bulls were commonly more prolonged. However, even in the case of intruding subordinate bulls, 43% of observed meetings were merely

TABLE 45. Interaction patterns in encounters between territorial bulls and other males

Figures represent frequencies (in percent) of different actions observed; sub-sample size are usually less than total N.

Type of encounter	N	Initiating actions of tADm: no approach	checked approach	chase	meeting	type of approach: with hic...	charge	Duration of meeting (min): 1	2-5	6-30	30+	Actions during meeting: by tADm: horn wiping	horn clash	attack	fight	by sADm: snort	snarl	shriek	retreat	term.: tADm moves away
1. tADm-tADm	43																			
(a) border meeting	25	28	0	0	72	0	83	18	24	41	18	100	41	0	0	0	0	0	0	100
b. neighbour tresp.	7	14	0	14	72	0	100	0	40	41	10	100	60	-	20	0	0	0	0	100
c. distant tADm tr.	5	40	0	0	60	0	100	0	67	33	0	0	33	0	0	.0	100	33	0	100
d. waterhole mtg	6	67	33	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-
2. tADm-sADm	163															no appr. by tADm:				
a. resident sADm	117	45	28	5	22	0	29	72	19	6	3	6	31	0	0	30	20	4	12	94
																checked appr.				
																16	45	13		
																meeting				
																16	84	74		
b. tresp. sADm	41	19	8	15	58	8	19	43	10	37	10	17	57	3	0	7	100	70	23	96
3. tADm-adolm	69																			
a. adolm 6-9 yrs	33	27	39	3	30	10	20	100	0	0	0	2	10	0	0	10	70	10	15	100
b. adol 21/2-6 yrs	36	33	42	19	3	6	12						.50			0	100	0	52	

brief confrontations. In almost all cases the resident territorial bull terminated the meeting by turning and moving away paying no further attention to the other bull. In most cases the intruding bull departed from the territory after the territorial bull had left, though such departure was not necessarily immediate.

One fight was witnessed directed against a neighbouring territory holder; and two attacks, one directed against an intruding subordinate bull, the other against an adolescent male (another brief fight was observed in association with a territory takeover and will be discussed in this context). Two of the attacks occurred at territory borders. In other cases, meetings with an intruding bull taking place at or near territory borders were more commonly prolonged tense confrontations than those centred within a territory. Thus, territorial bulls seemed more excitable in meeting with other bulls in border regions. Though few attacks or fights were seen, territorial bulls not uncommonly showed fresh gashes and abrasions on their heads or occasionally on their shoulders, particularly during the dry season. Thus, fights or attacks evidently occurred more frequently than was observed, presumably developing in circumstances in which one bull was crossing a neighbouring territory on the way to or from water. However, while some bulls frequently exhibited wounds others never showed scars, indicating individual temperamental differences.

Territorial bulls were generally quite tolerant of adolescent males and calves, but three sudden attacks were recorded. Rangers report occasional cases of adolescent males killed by horn wounds presumably inflicted by territorial bulls.

Territorial bulls reciprocated confrontations by neighbouring territory holders in border regions in like fashion. At a mutual boundary, both bulls wavered between advance and retreat. Actions were highly ritualised, with aggression restricted to momentary horn clashes which however occurred in fewer than half of the observed meetings.

If one bull had intruded a short way into the territory of a neighbour, the trespassing bull displayed similar actions to those occurring in border meetings, except that he backed away steadily during the confrontation until he regained his own territory. A wandering territorial bull accosted by another bull on a more distant territory instead responded with snarls and shrieks; that is, he behaved as did a subordinate bull. Only two observations are available to indicate the behaviour of a territorial bull accosted by a neighbour some distance from his own territory: (i) once, 500 m from his own boundary, a territorial bull faced the neighbouring bull silently but retreated; (ii) once, accosted by the neighbouring territory holder at the opposite boundary to his own, a bull fought. The prolonged, tense, silent confrontations between bulls sometimes reported by other observers presumably originated when one of the bulls had been accosted by a neighbour still some distance from his own territory.

Subordinate bulls always gave separation maintaining threats at any move by a nearby territorial bull suggestive of approach. If confronted, subordinate bulls made repeated loud snarls and shrieks but usually stood their ground. This display contrasts strongly with the silent ears forwards orientation displayed by resident territorial bulls. Young adult males sometimes retreated from a territorial bull. Subordinate bulls sometimes made symbollic attacking gestures such as advancing steps or a horn prodding action; but such "attacks" were never carried through and were accompanied by loud shrieks. Subordinate bulls remained in place until the territorial bull eventually moved away. Some of the subordinate bulls sometimes appeared with fresh wounds, suggesting skirmishes with surrounding territorial bulls. Again, there were individual differences in incidence.

Adolescent males sometimes behaved towards territorial bulls as did subordinate bulls, but younger adolescents in particular were likely to retreat from an approach by a territorial bull.

Subordinate bulls sometimes directed separation maintaining threats against other subordinate bulls or adolescent males (Table 46) but such cases seemed usually due to uncertainty of the identity of the other individual. If downwind a bull was more relaxed. At other times, subordinate bulls sharing the same territory took little notice of one another, and playful horn wrestling was observed between two young adult males. Once intolerance was displayed by a resident subordinate bull towards an intruding subordinate bull, though this was ineffectually carried out. Towards adolescent males, subordinate bulls appear friendly and sometimes moved to stay nearby. Close

TABLE 46. Interaction patterns in encounters between subordinate bulls and other males

Figures represent observed frequencies in percent of different actions; sub-sample size are usually less than total N.

Type of encounter	N	Initiating actions: no approach	checked approach	chase	approach to meet	appr. by	charge	Actions during meeting: head flings	nasonasal contact	nn develops into wrestl	snort	snarl	shriek	horn gesture	retreat
1. sADm-sADm	25														
a. both resident in territ.	15	53	20	0	27		0	10	75	33	50	30	10	0	0
b. one sADm trespassing	5	40	20	0	40		33	33	0	-	0	67	33	0	0
c. at waterhole	5	100	0	0	0		-	-	-	-	100	40	0	0	0
2. sADm-adolm	32														
a. adolm 6-9 years	10	50	30	0	20	sADm 83	0	0	50	0	22	44	0	0	0
						adolm17					22	33	0	11	10
b. adolm ? 1/2-6 yrs	22	27	23	5	45	sADm 69	0	0	100	70	5	5	0	0	0
						adolm31					16	11	0	5	26

approaches were usually prevented by threats from the adolescents.

2.2 <u>Encounters between bulls and cows or adolescent females</u>

(a) <u>Encounters between territorial bulls and cows</u>

(i) Territorial bull on home territory

A total of 142 encounters were observed between resident territorial bulls and cows.

In 16 cases, no approach was made by the bull. In 52 cases, the territorial bull started approaching but veered away; the average separation distance at which this occurred was 15 m (range 4-50 m); 7 of the approaches were charges. In 66 cases, the bull approached making a few hics as he drew close to stand facing attentively towards the cow from close range, almost always downwind; the average separation distance was 7 m (range 1-15 m); two of the approaches were charges. The territorial bull then turned and walked away, after perhaps a minute, in 56 cases. In 12 cases he remained near the cow, commencing grazing or some other activity (Example 28). Cows met such approaches standing facing the bull with separation maintaining threats (see Plate 11): either snorts (58), EXAMPLE 28. Territorial bull meets and joins a cow (Ngutshoni, 14 Feb'69)

The territorial bull grazes moving eastwards, scraping and urinating repeatedly; / 1738 the bull encounters a cow and calf grazing southwards ahead of him and walks towards them; the cow snorts with ears back, the bull continues approaching and stops 5 m from the cow, backs away a little, stands facing the cow; the cow snorts but continues grazing, the bull stands 12 m away as they graze past, the cow turns her head with a snort then resumes grazing again; the bull resumes grazing, parallel to the cow; he lifts his head from grazing, the cow swings round with a snort; the bull approaches head high to within 6 m of the cow and stands looking at her; the cow snorts, but resumes grazing, snorting once more; the bull backs, stands facing 45° away from the cow; the cow snorts again, the bull backs several paces, stands; the cow gives a short snarl, the bull backs then resumes grazing 7 m away from the cow; several more times he pauses from grazing to stare at the cow (the next day the bull was still with this cow).

snarls (54), advancing snarls (13), shrieks (1) or a horn clash (2). However, unlike subordinate bulls, they did not make snarls repeatedly. A single short or more prolonged snarl was given and perhaps repeated a short while later if the territorial bull persisted in remaining near.

Four times territorial bulls approached, suddenly attacked a cow with horn to body blows. The cow attempted to fend off the bull making loud snarls or fled. All attacks were brief and no obvious damage was inflicted. In one case, the bull seemingly attacked the cow in mistake for an adolescent male; he sniffed at the urination site of the young male, then suddenly attacked the cow, who happened to be the nearest animal to him (Example 29). In one other case of attack, an adolescent male was similarly present with the cow concerned.

In one encounter, a territorial bull moved hesitantly out of the way of a cow when she approached with a snarl. In another case, a cow reacted to a territorial bull's approach by advancing to stand in nasonasal contact briefly.

(ii) Territorial bull out of home territory

Five cases were observed in which territorial bulls that were out of their home territories on their way to

EXAMPLE 29. <u>tADm attacks cow, seemingly in error for adsm</u>
(Madlozi, 23 Dec '70)

<u>1002</u> tADm.<u>C</u> approaches a group consisting of four rhinos: the two cows P and PP, the adolescent male <u>p</u> (age 5yr) and an adolescent female (age 3yr); <u>C</u> approaches hiccing, stares from 5m range, then moves to stand a short distance away; the other four rhinos move towards a dungheap, one cow and one adolescent defecate there, then the adolescent male stands urinating in a stream, then all move and stand a short way on; tADm.<u>C</u> goes up to the dungheap, defecates with kicks, then stands sniffing carefully at the edge of the dungheap for 1-2 min, sniffing then lifting his head to stand with parted lips; the other four rhinos start moving on; <u>C</u> suddenly charges the cow P ignoring her threats and directing blows with his horn against her head and the side; the cow runs and is chased round by <u>C</u> for 1/2 min, then she turns to face him with a loud snarl; the bull confronts her briefly then turns away and moves up to the other three rhinos; they stand together facing him with snorts; the bull stands looking at them and the attacked cow joins them; the bull moves to lie down 10m away; I check the site where the bull sniffed, and confirm that this was at the urination site of the adolescent male.

water encountered cows. In 4 cases, the territorial bull circled around avoiding the cow at a range of 25-50 m. In one case, the territorial bull approached, stared at the cow from 8 m range, then moved on.

(iii) In the vicinity of a drinking pool

Nine cases were recorded in which territorial bulls encountered cows in the vicinity of drinking pools. In 3, the territorial bull did not approach. In 2, the cow advanced with threats and the territorial bull moved out of her way. In 2, the territorial bull circled downwind then approached, stared briefly at the cow, then moved away. In one, the territorial bull started approaching, but turned away when the cow gave an advancing snarl. In one case, the territorial bull snorted when a cow approached; the cow then advanced to clash horns with him with a snarl.

(b) <u>Territorial bull-adolescent female encounters</u>

Twenty encounters were recorded between a territorial bulls and an adolescent female. In 7, the territorial bull started approaching, then turned away when the adolescent female hastened away. In 6, the territorial bull approached to stand looking from close quarters. The adolescent female(s) faced him with threats: a snort (1), snarls (6), or advancing snarls (2). In 3 cases, the territorial bull did not approach. In 2, a territorial bull chased after two adolescent females a short way when they fled. In 2, the territorial bull suddenly attacked an adolescent female, and in one of these chased round after the adolescent female for 1-2 minutes. In both cases, the bull afterwards resumed grazing near the adolescent female paying little further attention to her.

(c) Encounters between subordinate bulls and cows

(i) Subordinate bull on home territory

Resident subordinate bulls were observed to encounter cows on 54 occasions.

In 13 encounters, the subordinate bull did not approach. In 21, the subordinate bull started approaching, somewhat hesitantly, then turned away (average separation distance = 13 m, range 4-20 m). At least 3 of the approaches were accompanied by hics, in one the subordinate bull panted, and in another a snort was made by the subordinate bull. In 16 cases, the subordinate bull approached, sometimes hesitantly, stood looking at the cow briefly from close range (average separation distance = 6 m, range 1-12 m), then either moved away (12 cases) or stayed near the cow (4 cases). Cows responded to such approaches as they did to an approaching territorial bull by giving separation maintaining threats: snorts (20), snarls (15), or advancing snarls (5).

Two approaches led to brief nasonasal contact, one initiated by the subordinate bull, the other by the cow. After one approach, a subordinate bull rested his chin on the rump of the cow in a courting gesture. In one peculiar incident, a subordinate bull ran around a cow, approached her repeatedly to stare horn against horn, made head flings on turning away and suppressed squeals, and in general displayed great agitation. This lasted for five minutes, then the territorial bull arrived on the scene, confronted the subordinate bull briefly, then approached the cow but showed no great excitement.

(ii) Subordinate bull out of home territory

Thirteen meetings between subordinate bulls and cows were observed in which the subordinate bull was out of his home territory. In 3, the subordinate bull paid no attention to the cow, or circled round avoiding her. In 2, the subordinate bull started approaching then turned away. In subordinate bull approached to stare from close range, and the adolescent female faced him with threats. Once a subordinate bull approached to stand briefly in nasonasal contact with an adolescent female.

Summary and comparisons

Territorial bulls usually approached all unfamiliar cows encountered on their territories. Where an approach was not made, it seemed likely that the territorial bull had already investigated the cow a short while earlier. Approaches were frontal and were usually made from downwind. Nasogenital investigation was never seen, cows being highly intolerant of any approaches from the rear. Charges seemed related to mistaken identification, and the bull usually checked his rush or moved away at the snarls of the cow. Two attacks on cows may be related to mistaken identification, while for two others there was no ready explanation.

Subordinate bulls also approached cows, but did so less frequently (Table 47; $X^2 = 3.24$, df = 1, $0.05 < p < 0.10$) and more hesitantly. Whereas territorial bulls walked confidently up to cows making a few hics when they drew near, subordinate bulls usually edged forwards, a few steps at a time, and hicced less commonly.

TABLE 47. Interaction patterns in encounters between bulls and cows

Figures represent frequencies in percent of different actions: sub-samples sizes are usually less than total N.

		Initiating actions of tADm					Actions of tADm during meeting						Actions of ADf				
Type of encounter	N	no approach	checked approach	approach to meet	with hics	with charge	stares close	attacks	nasonasal contact	nn develops int wrestling	horn wiping	head flings	snorts	snarls	shrieks	advancing snarl	horn gesture
1. tADm-ADf	156																
a. resident tADm	142	12	37	51	25	7	93	5	2	0	3	8	41	42	1	10	3
b. tADm out of territ.	5	80	0	20	-	-	100	-	-	-	-	-	-	-	-	-	-
c. at waterhole	9	67	33	0	33	0	-	-	-	-	-	-	62	37	0	37	25
2. sADm-ADf	74																
a. resident sADm	54	24	39	37	20	0	89	0	11	0	0	25	37	31	0	13	4
b. sADm out of home ter.	13	31	15	53	0	0	85	-	-	-	-	28	40	40	0	20	0
c. at waterhole	7	57	14	29	0	0	100	-	-	-	-	0	33	67	0	67	17

2.3 Encounters among cows, adolescents and calves

(a) Encounters between cows

Seventy-nine encounters between cows were recorded.

In 22 of these, the two cows concerned took no notice of one another even though moving past at close range. In another 23 cases, there was no approach, and in 13 cases a checked approach with soft snorts or brief snarls being made by one or both individuals (Example 30). Sixteen approaches led to nasonasal meetings (Example 31) and 4 of these developed into playful horn wrestling. In another 5 cases, a brief clash of horns occurred; two of these happened at drinking pools, and in another 2 cases, the cow that initiated the horn clash was accompanied by a very young calf. Other horn clashes were seen between cows coming into close contact at drinking pools on several occasions when I was not making detailed behavioural records.

(b) Encounters between adolescents

Thirty-four encounters between adolescents belonging to different groups were observed. In 18 of these, there was no approach or only a checked approach. The other adolescent responded by retreating in 3 cases, and stood

EXAMPLE 30. Encounter between two cows, one with a small calf (Madlozi, 4 June 71)

0940 the cow LL with 6 week old calf has grazed to within 4 m downwind of another cow K with a yearling calf; LL gives an ears back gesture, probably snorts (not audible at my observation range) as the other cow grazes across in front of her, stares at her for several seconds, then resumes grazing; the other cow grazes on past; both cows then graze 5 m apart ignoring one another.

EXAMPLE 31. Meeting between several cows and adolescents (Madlozi, 28 Nov. '69)

0703 A cow O with adol.f companion graze; suddenly both turn and look northwards; another cow K plus adol.m companion approach, both pairs stand facing at close quarters; the two adolescents advance to press horns together and this gradually develops into very slow horn wrestling; O then resumes grazing in front of K, K stands observing her; after a minute O suddenly turns towards K, K backs away a few paces, stands; O then continues grazing; /0706 the two adolescents separate, the adolescent female passes close by K, the adolescent male stands close by O; K then walks forwards passing between O and the adolescent male moving in the direction of the nearby resting area, the adolescent male and the other cow turn and follow her; another cow VV with yearling calf approaches the restplace, O suddenly turns as VV approaches behind her, the two cows stand heads up facing about a metre apart, turn their heads away slightly; both relax their heads, VV then advances to engage horns, the two cows stand briefly with heads pressed together; VV then moves on towards the restplace, her calf investigates the cow O briefly then follows.

with separation maintaining threats in 12. Fifteen approaches led to nasonasal meetings, and 6 of these developed into playful horn wrestling (see Section E.1.4 for further discussion). Once, an adolescent male attacked an adolescent female and chased her around for several minutes until she sought refuge near a cow.

(c) <u>Encounters between cows and adolescents</u>

(i) Adolescent males

Fifty-six encounters were observed between adolescent males and cows belonging to different groups. No approach was made by either in 7 cases. In 20 cases the adolescent male started approaching but was checked by threats from the cow. Once a cow approached, looked at the adolescent, then resumed grazing. Eight times, a cow advanced on an adolescent with threats causing it to retreat. Nineteen encounters led to nasonasal meetings, and 8 of these developed into playful horn wrestling; in 15/19 cases, the approach was initiated by the adolescent. In one encounter, reciprocal snorts were exchanged.

(ii) Adolescent females

Twenty encounters between cows and adolescent females

(f) Encounters between calves

Fifty-one encounters between calves were observed, but in 29 of these both calves remained near their mothers without approaching. In the remaining 22 cases, the two calves approached to meet nose to nose, and 14 of these meetings developed into play wrestling matches.

Summary and comparisons

Two cows commonly paid little attention to one another both while grazing past at close range and when coming together at restplaces. Snorts and snarls were given mostly when one animal approached directly, and cows with small infants were likely to direct snorts or snarls at nearby rhinos than other cows. Snorts and snarls were commonly exchanged among cows coming into close contact at drinking pools, though afterwards the cows frequently drank close together. Sometimes friendly nasonasal meetings or horn wrestling matches occurred among cows. Adolescents and calves commonly approached other rhinos to make nasonasal contact (Table 48), and horn wrestling matches frequently developed, particularly among adolescents and calves. Adolescents only rarely snorted at an approaching cow; they were more commonly approached by calves than the reverse.

TABLE 48. Interaction patterns in encounters among cows and adolescents

Figures represent frequencies in percent of different actions.
Subsample sizes are generally less than total N.

Type of encounter	N	Initiating actions: no approach	checked approach	chase	meet nasonasally	approach by	run develops into wrestl.	Actions during approach or meeting: snort	snarl	advancing snarl	horn prod	horn clash	attack	retreat
1. ADf-ADf	79	57	16	6	20		25	46	14	0	1	8	0	0
2. adol-adol	34	20	32	0	44		40	20	18	9	3	0	0	9
3. calf-calf	51	57	0	0	43		64	0	0	0	0	0	0	0
4. adol-ADf	76	18	37	14	33	adol 53	44	4	1	0	0	0		10
						ADf 13		30	15	1	5	3		0
5. adol-calf	58	59	0	0	33	adol 7	53	2	0	0	0	0		0
						calf 17		0	0	0	3	2		0
6. ADf-calf	60	68	20	0	12	ADf 2	14	8	0	0	5	0		0
						calf 18		0	0	0	0	0		0

Discussion

Territorial bulls within their home territories generally respond to any other rhino encountered by approaching.

If the other rhino is a cow, the approach brings the bull close enough presumably for him to be able to detect olfactorally whether the cow is potentially about to enter oestrus. Bulls sometimes remained near a cow after an approach, and at least one observed instance of this initiated a consort relationship (see Section D.2.1).

Approaches directed towards other bulls can be interpreted as challenges. Strange bulls encountered on the territory are invariably thus challenged when detected while subordinate bulls sharing the same home territory are usually ignored. Thus, territorial bulls are evidently able to distinguish their resident subordinate bulls from other bulls, presumably by familiarity with some features of their behaviour (since this seemed independent of wind direction). The presence on the territory of such individuals is thus tolerated, and it was not uncommon to find the territorial bull and subordinate bull grazing or resting only a few metres apart.

A resident territorial bull never emphasises an approach vocally. His unhesitant direct approach is evidently sufficient indication of his status. Sometimes, however, he makes a sudden charge, particularly against another territorial bull. Cows, adolescents and subordinate bulls always respond to charges with loud snarls, while neighbouring territorial bulls meet charges silently--and, presumably, so also would a challenger for territory ownership. Thus, by this display a territorial bull is able to confirm the status of the other individual and modify his actions accordingly. Charges were never made by both bulls simultaneously, since the approaching bull had already made his status clear.

The horn against horn stare can be interpreted as an intimidatory or superiority display. The impression conveyed seems based on the physical presence of the dominance claiming bull at such close quarters, virtually breathing into the other's nostrils; it emphasises the assurance of the displayer and may potentially also reveal attributes of relative size, though much of the effect is probably based on olfactory stimuli. Since an attack cannot be carried out directly from the head high posture, it does not represent readiness for immediate aggression and is thus not a threat (see Walther (1973) for a discussion of distinctions between superiority displays and threats). An attack is initiated by dropping the head so that the anterior horn is parallel to the ground (see Plate 17) then the horn is driven forwards with an upwards swing of the head. Confrontations with the head held lower and the horn pressed against that of the opponent incorporated a strong threatening element. Such a posture was observed on two occasions against intruding territorial bulls, once between neighbouring territory holders when possession of an estrous cow was probably being decided, and once against an intruding subordinate bull in a territory boundary region.

A striking feature of meetings between rival bulls is the strong inhibition of attack. Attacking gestures are restricted to brief feints to clash horns, and even these occurred in only about half of observed meetings. The vigorous horn wiping action directed against the ground or a bush is strongly suggestive of a harmless redirection of aggression. The horns of rhinoceroses are directly functional sabres (in contrast to the elaborately shaped antlers of deer and curved horns of many Bovids). Thus, there is a high injury risk associated with fighting, and it is advantageous to both opponents to avoid this (see Geist 1966).

Another bull may respond to a challenge in three ways: (i) he may reciprocate with a similar challenging posture; (ii) he may maintain the challenging posture, but retreat; (iii) he may give separation maintaining threats.

At a mutual boundary, two neighbouring territory holders reciprocated challenges, wavering equally between approach and withdrawal. This has become ritualised into a peculiar display of repetitive advancing then retreating by each bull in turn. Having thus demonstrated their relative spatial dominance, the two bulls then separate. In the white rhino, neighbouring territory holders do not actively seek meetings with one another, as occurs for example in the wildebeest (Estes, 1969). Encounters seem to be merely accidental, occurring when two bulls happen to "collide" while patrolling the same border from opposite directions. Both bulls appear "embarrassed" when they detect one another, staring or veering away hesitantly, and if separated by more than 50 m declining to meet. Border patrols are evidently directed towards reinforcing scent marks, not confronting neighbours.

If one bull is confronted while intruding on a neighbour's territory, he maintains dominant face but yields ground steadily in the face of the resident's advance until he regains his own border. High tension is present in such meetings, evidenced by a lower more threatening head posture and by more frequent horn clashes. In a situation in which an intruding neighbour could not readily retreat towards his own territory, a serious fight developed. Evidence, limited though it is, suggests that a territorial bull must always present a dominant face to a neighbouring territory holder wherever the meeting might take place on their respective territories. Upon crossing onto a territory once removed from his own, a bull adopts instead the subordinate defensive stance if challenged. Thus, territorial bulls must be able to detect also the opposite boundaries of the various neighbouring territories.

Subordinate bulls, wherever they might be, respond to challenges by standing their ground, giving a repetitive high intensity display of the sounds used by rhinos of all social classes to inhibit intrusions on personal space. Such a display by a bull is usually ineffective in stopping an approach by a territorial bull; but where the territorial bull recognises the other as merely the coinhabitant of his own territory, he may not "bother" to confront him. The snarl display indicates clearly that the performer is not challenging. The volume of sound contrasts strikingly with the silence of a resident territorial bull, and the posture with the head thrust forwards, thus raised (see Plate 16) is the opposite of attack readiness. However, to a casual observer, the loud roars and fierce-looking posture of the subordinate bull, coupled sometimes with advancing steps or horn prodding gestures, can appear strongly threatening or intimidatory leading to a misinterpretation of the relative status of the two bulls (see for example Player and Feely 1960). As discussed earlier, threat implications are of a purely defensive nature. Close observation reveals subtle demonstrations of fear by the subordinate: a curling of the tail; a tendency to step backwards away from the territorial bull, or show intention movements to do so; and tense, hesitant movements.

For a white rhino, this defensive stance is the most suitable display of submission. Subtle visual gestures of appeasement are likely to be overlooked by animals endowed with such poor eyesight. Running is highly expensive energetically, particularly so for an animal as large as an adult white rhino. It is furthermore likely to be ineffective, simply exposing the fleeing individual to an attack from the rear (see Example 22). Only adolescent or young adult bulls, lighter on their feet and thus capable of outdistancing a territorial bull, run away. Subordinate bulls have no safe refuge to which they can retreat; even within their home territories, they may be challenged by the resident territory holder (there is no unclaimed ground). A subordinate bull's best strategy is thus to stand his ground ready to deflect attacking moves by the territorial bull, repeatedly assert non-challenge, and wait it out until the territorial bull eventually tires and leaves him alone.

That it is the territorial bull who moves away may seem confusing, in view of the commonly applied assessment of relative dominance on the basis of supplanting interactions. However, this is the only possible termination of such meetings since the subordinate bull refuses to retreat. An attack would only draw forth defensive responses from the subordinate bull, expose the territorial bull to the risk of receiving injuries himself, and drain his energy. Having asserted his superiority and had this accepted by the other bull, he has achieved a "psychological dominance" and need waste no further time and energy.

Subordinate bulls coinhabiting the same territory are challenged by the territorial bull in about one quarter of encounters. However, these intermittent brief confrontations are probably highly significant in reinforcing the dominance relationship between the two bulls. The subordinate bull is thereby forced, at short intervals as long as he remains resident within the territory to reassert his acceptance of the territorial bull's superiority. Though several subordinate bulls subsequently became territory holders (see Section F), no case is known in which a subordinate bull took over dominance in the territory in which he had formerly resided as a subordinate. Seemingly, territorial bulls eventually become partially habituated to the continued presence within their territories of particular subordinate bulls who readily demonstrate submission whenever challenged.

The operational expression of the dominance of a territory holder is that all other rhinos respond to him either by retreating or by giving separation maintaining displays. Resident territorial bulls themselves never use separation maintaining threats. However, this dominance is effective only within the spatially localised confines of the bull's own territory. Once a bull leaves his territory he loses his dominant status and his demeanour of confident assertiveness towards other rhinos changes to one of nervous apprehension. He chooses to avoid meetings; if challenged by a neighbour, he retreats, while if challenged further afield, he reacts as does a subordinate bull with separation maintaining threats.

Territoriality is usually defined in terms of actions which defend a fixed piece of space against intrusions by rivals. The usefulness of such a definition derived from ornothological studies, has been challenged recently by several workers familiar with mammalian behaviour (e.g. Schenkel 1966; Walther 1972). In the case of the white rhino, it seems clear that a territorial bull does not defend the spatial area of the territory in meetings with potential rivals, but rather demonstrates his dominance within that area. Another bull may be tolerated within the territory if he demonstrates acceptance of this dominance. Intruding territory holders retreat if challenged on a neighbouring territory and in such meetings the actions of the resident bull may be interpreted as "defence of the territory." However, the challenging actions of the resident do not differ greatly from those shown to other bulls and this outcome is based on the type of response chosen by the intruder. If the intruder were not to retreat, he would be contesting the dominance of the territory holder, and then a fight would be likely to ensue. Even if such incidents are accepted as demonstrations of defence, it may be noted that only four instances were observed during 3 1/2 years of concentrated study; they thus occur too infrequently to be used as a practical criterion of territoriality. Border meetings do not demonstrate spatial defenses, since the neighbour would not have intruded even if there had been no confrontation. The significance of such meetings in confirming the location of boundaries is not denied. However, the location of the boundary and the continued presence of a dominance claiming rival somewhere on the other side of it can be detected through scent marks. Territorial bulls evidently prefer not to intrude across boundaries where there is the risk of being challenged by a rival.

Consideration of the functional advantages of such spatially localised dominance will be delayed until reproductive behaviour has been covered (Section E).

Apart from the two-tier rank relationship between a territory holder and all other males within that territory, no dominance hierarchies were evident among subordinate bulls sharing the same territory, or between cows.

Cows and adolescents respond to the close proximity of a territorial bull with separation maintaining threats. Almost always, territorial bulls act non-aggressively towards cows and adolescents. However, the occasional occurrence of sudden unprovoked attacks demonstrates the aggressive potential which is always latent in a territorial bull. It is thus safest for other rhinos to avoid the close proximity of territorial bulls.

Relationships among rhinos apart from territorial bulls may be characterised as neutral to friendly. Separation maintaining threats are sometimes used to maintain a small individual distance but this may be reduced to permit nasonasal investigation. Approaches by subordinate bulls are usually inhibited by other rhinos but occasionally cows allow nasonasal meetings with a subordinate bull, and sometimes adolescents even wrestle playfully with subordinate bulls. Except for one nasonasal investigation, such familiarity was never permitted of a territorial bull.

Thus other rhinos are evidently able to distinguish the status of subordinate bulls presumably on the basis of their hesitant actions.

Nasonasal meetings seem designed to facilitate individual identification of other individuals. Cows engage in nasonasal contacts less frequently than immature animals, presumably because cows are already familiar with one another. Adolescents seem particularly interested in meeting cows, and calves display curiousity towards all other rhinos. Thus, though white rhinos commonly move in small independent units, the individuals in a local population are potentially individually familiar with one another on the basis of numerous contacts over a period of years. Conspicuously more intolerance among cows is exhibited at waterholes where many strangers are forced into close proximity.

In the black rhinoceros, nasonasal contact and horn wrestling also commonly occur in encounters between cows and adolescents (Schenkel and Schenkel 1969). Between bulls, a variety of interactions are described. Sometimes bulls stared at one another, but declined to meet. Sometimes complex displays were performed, including stiff-legged scraping, "imposing postures", circling, and rushing forwards to a sudden stop with a scream. These actions seem closely similar to those displayed in meetings between white rhino males. However, Schenkel did not consider the possible existence of different social classes of adult males. There is evidence that at least in Zululand, dominant and subordinate classes of male exist as in the white rhinoceros (Hitchins 1971). Without recognition of this distinction, patterns are confusing and a direct comparison with the white rhinoceros cannot be made.

3. Intra-group relationships

Introduction and methods

To be considered are the interactions occurring between white rhinos associated together in the same groups particularly actions which influence the cohesion of such groups. The term group, as here used, refers to a cluster of two or more individuals that exhibits some degree of cohesion; that is, the individuals orientate their movements so as to remain together for at least a few hours (see Section B.1). The following group types occur:- (i) cow-calf; (ii) cow-adolescent(s); (iii) cow-cow (+adolescent(s); (iv) adolescents; (v) bull-cow (+ calf or adolescents).

Most white rhino groups consisted of two individuals only (see Section B.1.). Within larger groups, two individuals could usually be distinguished that tended to keep closer together and were more responsive to one another's movements. Such closely bonded companions included cows and calves, cows and adolescents, and pairs of adolescents, and had usually been associated together for a period of several months or longer. Additional more peripheral individuals were mostly either temporarily attached adolescents or bulls.

To obtain more detailed information on the actions influencing cohesion, special intensive observation sessions were devoted to particular groups. During such sessions, interindividual distances, orientation and activity of all animals in the groups were recorded at five minute intervals. Interindividual distances were estimated in terms of body length, which for an adult white rhino is about 4 metres from horn tip to tail. All sounds and other social interactions occurring were noted as well as actions initiating changes in location or new activities. Additional records of interindividual distances were obtained when other opportunities presented themselves.

3.1. Close companions

Interindividual distances changed constantly while one or both animals moved around grazing. Spacings under 5 metres, that is about one body length or less, were maintained 58-90% of the time by close companions of all categories (Table 49). Companions rarely moved further apart than 25 m or 5-6 body lengths. Greater separations distances were tolerated with increasing age of the companion associated with a cow; thus, calves maintained average spacings from a cow of 1.4-3.7 m, for an adolescent the average distance was 5.7 m, and for two cows 8.1 m (see also Figure 42). Calves 2-4 months old seemingly maintain greater separation distances than calves 4-12 months, but wandering by the older calves was probably inhibited by the usual additional presence of a territorial bull with most such groups observed. Two adolescent companions maintained smaller interindividual distances than were maintained between an adolescent and a cow.

Separation distances were reduced when individuals settled down to rest. Close companions usually lay within a metre or less of one another (Table 50) though always, when I was able to see, not quite touching.

TABLE 49. Intra-group spacing during feeding

Interindividual distances were recorded at 5 minute intervals.

Group type	Interindividual distances (m)						
			distribution (%)				
	mean	range*	0-4	5-9	10-19	20+	N
Cow + calf:							
a. calf ∠ 2 mo	1.4	0-15	100	0	0	0	21
b. calf 2-4 mo	2.5	0-15	83	13	4	0	52
c. calf 4-12 mo	2.2	0-15	91	7	2	0	84
d. calf 12-24 mo	3.7	0-25	81	11	4	4	47
Cow + adolescent	5.7	0-45	58	23	16	3	131
Cow + cow	8.1	0-35	36	33	25	6	64
Adol. + adol.	2.9	0-11	77	18	5	0	40
Cow + sev. adols.:							
i. indiv. adols. from cow	11.2	0-40	33	18	33	18	61
ii. cow from nearest neighbour	2.3	0-6	92	8	0	0	13
iii. adol. from nearest neighbour	3.7	0-14	77	16	7	0	61
Additional adol (esc.) with other gps:							
i. from cow	10.5	0-150	25	30	29	15	264
ii. from nearest neighbour	6.2	0-40	44	32	20	0	257
Cow + bull	15.0	3-sev. 100	2	19	60	19	118

* includes additional observations outside sampling regime

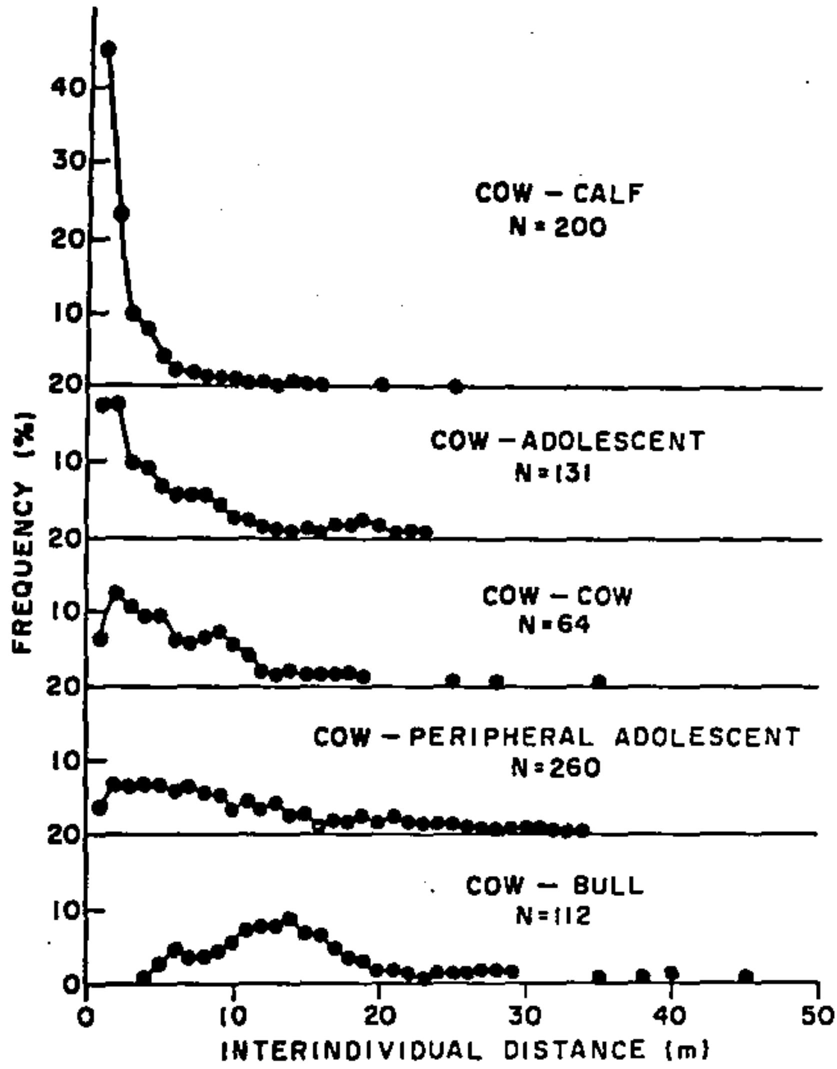
TABLE 50. Intra-group spacing during resting

Group type	Interindividual distances (m)		
	mean	range	N
Cow + calf	0.5	0–1	6
Cow + adolescent	0.7	0.2–2	12
Cow + cow	0.8	0.5–2	4
Adol. + adol.	2.2	0.5–4	8
Additional adolescent, from nearest neighbour	3.6	0.5–15	10
Cow + bull	9.7	2–20	13

FIGURE 42. Frequency distribution of interindividual distances in various groupings

Interindividual distances recorded at 5 min. intervals

3-point running averages used for distances over 5 m.



Close companions were sensitive to one another's movements, commonly choosing grazing orientations that kept them in close proximity and responding almost simultaneously to changes in direction or location by the other. Frequently, both individuals grazed side by side in parallel for periods of several minutes. But with time, they tended to drift apart as they followed their own meandering grazing pathways. Close spacing was restored when one individual turned and moved closer to the other before resuming grazing.

Calves and adolescents were more active in moving nearer to a cow than vice versa (Table 51). Small calves commonly moved nearer when spacing exceeded 6-9 m or occasionally as much as 25 m, were recorded when calves actively explored away from the mother briefly before returning. I had the impression that calves tolerated greater separation distances when downwind of the cow than when upwind, but data are insufficient to confirm this. Adolescent companions were more tolerant than calves of separation distances over 10 m, and occasionally ranged as far as 30-45 m from an accompanying cow. At such distances they apparently lost touch with the cow, and made

TABLE 51. <u>Intra-group interaction frequencies</u>

Group type	total hrs. intensive observ.	threats (/hr) cow	threats (/hr) other indiv.	tactile contact (times recorded) cow	tactile contact (times recorded) other indiv.	moving nearer (times recorded) cow	moving nearer (times recorded) other indiv.	initiation of moves cow	initiation of moves other indiv.
Cow + calf	37	0	0	2	6	4	13	7	1
Cow + adolescent	32	.3	.07	2	3	2	6	12	1
Cow + cow	19	.08	-	3	1	3	4	5	4
Adolescent + adolescent	7	-	.4	1	3	0	0	2	2
Cow + several adolescents	3	0	.6	-	-	0	2	1	1
Additional adolescent with group	30	.3	.9* .06+	0	3	0	20	15	0
Cow + bull	47	2.3	0	0	0	0	n	n	-

* by adolescent companion of cow against additional adolescent
\+ by additional adolescent against cow or her adolescent companion
n = numerous

EXAMPLE 32. Moving nearer by an infant calf (Madlozi, 18 May '70)

1605 the cow TT commences grazing, her 2 1/2 month old calf wanders about beside her then lies down / 1607 calf rises and moves to catch up to the cow who grazes 9 m away, rubs against the side of the cow, wanders around, sits down beside her/ 1610 the calf rises from 6 m away, hastens to catch up to the cow, walks past beside her; it nibbles at grass for several seconds, then wanders away to rub on a tree, then grazes some more/ 1622 the calf wanders about near the cow, investigates some low shrubbery, romps a few paces with up and down head movements/ 1633 the cow walks on, the calf follows behind then moves ahead; the cow resumes grazing, the calf stands head up alert/ 1653 the calf lies down, the cow grazes around it in circles/ 1700 the cow grazes moving on, the calf rises and moves up beside her/ 1710 the calf lies down, the cow grazes back past it.

EXAMPLE 33. Moving nearer by an adolescent female companion (Madlozi, 15 May'70)

0853 pants are heard presumably from the adolescent female V who is out of sight; the cow V suddenly shift ESE ca.20 m, stands head low but exhibits restlessness /0900 more pants are heard, the adolescent female appears 30 m N of the cow, gives a pant, the cow inclines her head to look towards her then stands head low at right angles; the adolescent female approaches to stand beside the cow/ 0902 the adolescent female grazes around near the cow, who remains standing;/ 0907 the cow lies down.

EXAMPLE 34. Reciprocal moving nearer by two companion cows (Madlozi, 5 Mar.'71)

0915 the two cows P and PP graze about 35 m apart/ 0918 P stands, urinates, wanders towards PP, gives a soft pant, resumes grazing 4 m downwind of PP/ 0948 from 35 m away the cow PP turns to graze towards P, walks towards P, grazes briefly 23 m away, moves on, resumes grazing at 12 m separation/ 1643 PP wanders nearer from 20 m to 2 m, resumes grazing 1652 P stands; PP wanders up, stands near her; the two cows move on together, then stand drowsily.

pants while wandering back towards her (Example 33). Cows, less frequently, also maintained close spacing by moving nearer to a calf or adolescent companion. At other times, they merely waited for it to catch up before moving on. Commonly while a small calf lay sleeping the mother grazed around it in circles without moving further away than 7-8 m. Two cows that were close companions (both were adults of similar age that had lost their calves) maintained close spacing by reciprocally moving nearer when interindividual distance exceeded about 15 m (Example 34). Detailed data on adolescent groups are limited mostly to two groups, both of which were peculiar in some way. One consisted of three individuals, and will be discussed later. The other consisted of two young adult males aged about 11-12 years, thus nearing maturity. These two individuals had been seen together intermittently over the preceeding year; on other occasions, they had been seen alone. Both coordinated their movements and activities as did younger adolescent pairs, but seemed to maintain slightly greater interindividual distances (mean = 5.6 m, N = 5, vs average of 2.6 m, N = 33 for all other adolescent groups; but difference not significant in view of the limited sample size).

In the young adult male pair referred to above, 3 brief grunt-snarls were made during a 3.2 hour observation session. Between other close companions, separation maintaining threats were heard more rarely, and were usually soft snorts, or occasionally a horn prodding gesture (see Table 51). During the entire study period, only twice was a cow heard to snort at her calf. One instance occurred when the calf sought to nurse while the cow was standing distracted by the noise of a passing heavy vehicle; the calf desisted from sucking. The other occurred when a calf rubbed its horn on the cow's shoulder; the calf remained beside the cow, and was thereafter ignored. Calves rubbed against their mothers on numerous other occasions without eliciting snorts. Most of the cow-adolescent data are based on one particular cow accompanied by a six-year-old subadult female that had been her companion for at least nine months. Occasionally this cow snorted or made a gentle horn prodding gesture when the adolescent female moved at close quarters behind or beside her; in some of these instances, she may have mistaken her companion for one of the temporarily attached adolescents that were also with the group. The companion ignored such threats, or backed 1-2 paces only. More rarely, the adolescent directed snorts or horn gestures towards the cow. On some days the two individuals exchanged no threats, on others they seemed more "edgy" and several threats were exchanged. Similarly, threatening snorts were only rarely made between adolescents that were close companions.

Close companions of all types frequently rubbed sides together while grazing or moving past one another, or rubbed the head or horn against some part of the body of the other. Such action was usually ignored by the companion.

A change in location or activity was commonly initiated in the following manner: one individual walked steadily in the chosen direction; if the companion did not simultaneously follow, the initiator paused waiting after 10-15 m; when the companion moved up beside, the two individuals moved on together (Example 35). Sometimes the initiator returned to walk close past the other, thereby drawing it to follow (Example 36), or rubbed against the companion in passing (Example 37), or drew its attention with pants (Example 38).

In cow-calf and cow-adolescent groups, most moves were initiated by the cow, though sometimes a cow took up a

EXAMPLE 35. An adolescent female stands waiting for a companion cow to join her before moving on (Madlozi, 20 Apr.'70)

1707 a group consisting of the cow U, her adolescent female companion v (aged ca. 6 yrs) and an additional adolescent male rr stand drinking at a pool/ 1712 the adolescent female finishes drinking, moves away E, pauses after 10 m; the cow remains standing at the pool edge, facing E; the adolescent male wallows/ 1713 the adolescent female moves on 3 m, stops when the cow does not follow/ 1715 the adolescent male leaves the pool, walks E past the cow, she ignores him/ 1717 the cow and the adolescent female shift on E simultaneously, the adolescent female walking 8 m ahead of the cow, the cow pauses to defecate at a dungheap and the adolescent female stands waiting a few metres on; both then walk on E together and commence grazing.

EXAMPLE 36. A cow initiates a move by walking close past a companion cow (Madlozi, 22 Dec'70)

(the group consists of the two cows P and PP, together with an adolescent male and an adolescent female) 1205 the cow P continues grazing, the other 3 rhinos stand from 8 to 15 m away/ 1207 PP wanders towards P, stands facing her laterally about 1 m away head low, P continues grazing; PP then turns and walks away SE, P follows her; they move to a pan and wallow there.

EXAMPLE 37. An adolescent initiates a move by rubbing against a companion (Madlozi, 13 Dec.'70)

0457 a group consisting of the adolescent male r (ca. 6-7 yrs) adolescent female d (ca. 4-5 yrs) and adolescent female t (ca. 3-4 yrs) stand drowsily close together/ 0450 adolescent female d walks 5 m N, stops; the other two remain standing/ 0500 d shifts 3 m to a tree, stands rubbing slowly against it/ 0502 d wanders back passing between r and t, nudges against t's flank very gently in passing, stands/ 0505 d walks on S, pauses, t moves alongside her, r shuffles forwards a few paces after them; all three then walk on S together, pause, then commence grazing.

EXAMPLE 38. Two adolescents rejoin and move on together with pants (Madlozi, 24 Mar.'71)

1640 an adolescent female (ca. 3 yrs) lies in a pool, her adolescent male companion (ca. 3 yrs) stands several metres away; there is a loud thinderclap; the adolescent female moves quickly away from the pool several metres; the adolescent male stands up in the pool and pants, there are answering pants from the adolescent female; the adolescent female shifts on 3 paces giving soft pants, stands; the adolescent female moves on, the adolescent male pants and moves to follow, the adolescent female answers with pants, both stand 10 m apart; the adolescent walks towards the adolescent female with pants, the adolescent female stands waiting until the adolescent male is 3 m away then walks on giving a few pants; the adolescent male moves up beside her as the two walk off together.

directed movement started by a younger individual. In the group in which two similar aged cows were companions, one cow was seen to initiate a move on 5 occasions, the other on 4 occasions. In a group consisting of a 6.7 year old adolescent male, a 4.7 year old adolescent female and a 3.7 year old adolescent female, control was exerted mainly by the older female; moves initiated by the other two individuals were less likely to be followed (Example 39). Observations on other heterosexual adolescent groups suggested that control of movements was generally by the female unless the male was considerably older. In even-aged homosexual adolescent groups, either individual seemed able to initiate moves and activity changes.

While walking, companions moved within a few metres of each other in single file or side by side. The initiator of a move seldom led the move; calves and adolescents tended more often to walk ahead of a cow than behind her.

Resting was initiated by one of the individuals standing drowsily, then perhaps lying down. The other usually joined it within a few minutes to lie down beside it. After a rest period when one individual rose and started moving on, the other usually quickly joined it. If the

EXAMPLE 39. Control of movements exerted by older adolescent female (Madlozi, 26 Nov,'70)

(Group consists of adolescent male r aged 6-7 years; adolescent female d aged 4-5 years; and adolescent female t aged 3-4 years) 0740 the two adolescent females lie side by side, the adolescent male wanders sound restlessly nearby; r approaches, rubs his shoulder on d's rump but is ignored; he walks away 7 m, stands rubbing on a tree/ 0809 the adolescent male moves to stand beside the two adolescent females; adolescent female t rises/ 0828 r wanders away, stands rubbing, then wanders around restlessly; d remains lying, t stands beside her/ 0850 t walks SSW 5 m, stands/ 0852 t shifts on SE a few metres, stands, r moves to follow her, stands close behind her/ 0853 d rises, shifts E, stands rubbing/ 0855 r shifts S a few paces; t shifts E a few metres; d moves on E, the others follow her, all commence grazing.

companion did not immediately follow, the first individual to rise stood waiting, or sometimes returned to rouse the other by rubbing against it (Example 40).

At an alarm, occasioned by detection of the presence of the observer or other humans, an individual's first response was to rush towards its companions, usually making pants. The two individuals then stood agitatedly rump to rump facing in different directions, or stampeded off together exchanging loud pants. Small calves commonly gallopped to keep in front of the mother while running off, hastening to get ahead again if she changed direction, and stopping instantly when she stopped. Frequently, however, the cow simply followed the line of movement taken by the calf. Older calves and adolescents also usually ran off ahead of a cow, though this tendency decreased with increasing age.

When approached by a territorial bull, calves and adolescents stood close beside the cow, looking on attentively while the cow threatened the bull. Older adolescents, for example the six-year-old adolescent female V sometimes threatened bulls with snorts or snarls along with the cow.

EXAMPLE 40. Initiation and termination of a rest period in a two-cow group (Madlozi, 23 Dec.'70)

(The two cows P and PP are accompanied by an adolescent male and an adolescent female) 0740 all graze; PP shifts on N 8 m, stands rubbing, the adolescents follow her, P turns to look towards them but does not move; all resume grazing/ 0822 PP and the two adolescents stand rumps touching, P stands slightly to one side, they have just been confronted by a territorial bull/ 0825 the adolescent male lies down; PP lies down, in shade; P shifts 2 paces, stands in light shade/ 0829 P shifts 2 paces, PP rises, turns to watch her/ 0831 PP approaches, rubs against P's rear, stands/ 0832 PP rubs past P's posterior, stands/ 0838 P shifts position, shuffles, lies down/ 0840 PP backs in between P and the adolescent female, lies down..../ 0955 Adolescent male rises, PP rises/ 1000 PP walks E 12 m, stands, adolescent male follows; P rises, followed by the adolescent female; PP and the adolescent male walk on E, adolescent female moves to follow, P remains standing; the other three pause 30 m away; PP turns, stands looking back towards P; P then moves towards her, PP pants and walks forwards 10 m, pauses, stands watching P's approach; P moves past and stops a short way S of the others/ 1007 P approaches nearer to the others, the two cows stand facing close together, then P turns aside/ 1009 PP walks back WNW followed by the adolescents then P.

Close companions were almost never seen separated. Occasionally an adolescent temporarily lost touch with the cow while engaged in a wrestling match with another adolescent, but the cow waited and the two rejoined afterwards, occasionally with initial hesitation (Example 41). Companions parted during marking operations had always rejoined when next located a day or two later, except in one instance. In the exceptional instance, a yearling calf never rejoined its mother. It attached itself to an adolescent female whose home range did not overlap with that of the cow, and probably mother and calf never crossed each other's path again. Bonds between cows and calves, adolescents or other cows persisted until the birth of a new infant to the cow. Cows with small calves did not tolerate additional companions. Close bonds formed between adolescent companions probably persist for several years barring accidents (see Section E).

3.2. Multi-adolescent groups

An intensive observation session of 4.7 hours was devoted to a group consisting of a 6-7 year old adolescent male, a 4-5 year old adolescent female, and a 3-4 year old adolescent female. The older female and the male had

EXAMPLE 41. Adolescent rejoins a companion cow after a temporary separation (Madlozi, 24 Nov.'70)

0733 an adolescent male j meets and wrestles with another adolescent male while his companion cow VV stands nearby; the cow walks on N, j turns away from the other adolescent and moves after her; the cow turns to face him, advances a couple of steps, the j jumps away and stands looking hesitantly towards the cow from 9 m away upwind, apparently uncertain of her identity; the cow stands looking at him passively; j turns and walks S, the cow walks S passing the j and j follows her.

EXAMPLE 42. Interactions within a group of three adolescents (Madlozi, 26 Nov.'70)

(The group consists of the adolescent male r aged 607 years; the adolescent female d aged 4-5 years; and the adolescent female t age 3-4 years) 0917 all graze; r suddenly turns with a snort, advances 2 paces towards t, t hastens away several paces, resumes grazing/ 0929 d snorts, turns to face r who grazes beside her at 1 m range, r turns away slightly, both continue grazing, t is also 1 m away from d but is ignored/ 0931 t grazes close behind d, possibly rubs her side against d's rump/ 0933 d suddenly swings round with a snort to face r grazing beside her, r turns away, continues grazing/ 0941 d lifts her head, r turns away.

been companions for 11 months, while the younger female had joined the group only a month previously. Observations indicated a transference of the allegiance of the older female from the male to the younger female. The two females keep smaller interindividual distances, were usually reciprocally nearest neighbours, made mutual tactile contact several times, and never exchanged snorts while under observation. In contrast, the older female directed several threats at the adolescent male while the adolescent male threatened the younger female on several occasions (Example 42). The younger female tended to avoid the close proximity of the adolescent male, and these two individuals lay down to rest on opposite sides of the older female. About four months later the adolescent male had broken away from the group alone, subsequently rejoining the two females for brief spells only.

Another 3.2 hours of intensive observation on two separate days was devoted to a group consisting of a cow together with six adolescent companions aged 3-4 years. Four of these were probably the same individuals that had been with this cow for at least nine months, a fifth had joined five months previously, and the sixth had attached himself to the group only a few days earlier. Nearest neighbour analysis revealed no preferential associations between any of the adolescents, but one of the young males (d) spent more time close beside the cow than any of the others did (mean spacing from the cow 5.7 m, vs 12.7 m for the other four adolescents; N = 13; difference not significant in view of the limited sample). The sixth adolescent was clearly an outsider maintaining an average spacing of 23.4 m from the cow and 6.7 m from his nearest neighbour (vs. 12.7 m and 3.7 m respectively for all the other adolescents except d). This seemed due more to lack of confidence on his part than to active intolerance by other group members. No threatening gestures directed against him were noticed, and once he wrestled playfully with one of the adolescent males. Threatening snorts or horn prodding gestures were recorded several times between other adolescents in the group, but the cow was not seen to threaten any adolescent. The cow seemed to be the focus of the group. Though one of the adolescents could initiate a move by walking ahead, if the cow did not follow the move was abortive. Any move made by the cow was quickly taken up by all the adolescents. When resting, the adolescents clustered around the cow.

Another group comprising an aged cow with a ca.10 year old adolescent male, a 7-8 year old adolescent male and a ca.5 year old adolescent female was seen on several days over a period of several months. In this group the cow and the older adolescent male were clearly close companions while the other two individuals were more peripheral and later left the group.

One or two additional adolescents were also usually associated during observation sessions with the cow U and her 6-year-old adolescent female companion v, and with the two companion cows P and PP. With the former group, these were young adolescents aged 2.5-3 years that had evidently only recently been rejected by their mothers. A 5-year-old adolescent male was commonly with the two cow group, and on some days a 2.5-year-old adolescent female was also with them. Other observations were made on adolescents that were associated with other cow-adolescent or cow-calf groups.

Additional adolescents maintained significantly greater average spacings from a cow than did adolescents that were close companions (Table 49, $N = 260 + 129$, $z = 3.69$, $p \angle 0.001$). Close companions were more frequently within 1-2 m of each other than at any other distance; additional adolescents exhibited a fairly even spread of interindividual distances from a cow (Figure 42). They seemed to orientate more to the group than to the cow or any other particular individual. They moved to keep with the cow and her companion, but the reverse never occurred. Additional adolescents were less attentive to the movements of the cow, and sometimes got left behind when she suddenly moved on. In two cases, an additional adolescent rejoined the group by following their scent trail. Sometimes such adolescents moved away from the group they had been with to investigate other rhinos, and sometimes this resulted in their transferring their attachment to the other group.

Cows occasionally snorted at additional adolescents when they got in her way or rubbed against her, but in general took little notice of them. The six-year-old adolescent female <u>v</u> directed more threats against such additional companions than did the cow <u>U</u> (Example 43) but threats were generally of low intensity. Young adolescents panted frequently or made soft whines while moving around near a group to which they had temporarily attached themselves. Additional adolescents occasionally rubbed

EXAMPLE 43. Threats directed by a cow and her adolescent female companion against additional adolescent companions (Madlozi, 27 Apr.'70)

(Group consists of the cow U, her 6 year old adolescent female companion v, and two temporarily attached adolescents, a male and a female both aged 2.5-3 years) 0905 the rhinos graze; the cow moves on, v follows, the adolescent male is in front , v snorts, adolescent male turns away 90°, the cow turns round, the adolescent male moves quickly a few paces from between her and v and resumes grazing, the cow turns away resuming grazing/ 0910 the young adolescent female looks up, pants, moves to catch up to U and v, whines, stops 6 m from U, there is a soft snort from the cow/ 0924 v lifts her head with a snort, the adolescent male is 6 m away/ 0927 v turns to snort at the adolescent female grazing 7 m away behind her/ 0932 the cow snorts at the adolescent male who stands in front of her, the adolescent shifts 2 paces only/ 0935 adolescent female approaches and moves close past v, v lifts her head but does not snort/ 0937 there is a loud snort, adolescent male moves on from in front of U and v/ 0940 U turns to look at the adolescent female standing 2.5 m away, then ignores it/ 0941 U gives a soft snort, adolescent female moves on 4 paces from 1.5 m away in front of her, the cow resumes grazing.

themselves against the cow they had joined, but such action usually drew a snort or soft rumble from the cow. When the cow and her companion lay down to rest, additional adolescents moved to lie down close beside them and were tolerated; but they maintained slightly greater spacings than did close companions (Table 50, Example 44). Additional adolescents also rushed to join other rhinos at an alarm and stood rump to rump with them. If a general stampede did not occur, this resulted in a formation in which the group of three or four individuals stood with their rear ends together facing outwards in different directions.

Usually additional adolescents remained with a particular group for only a few days. However, some groups of three or four individuals remained stable for several weeks or months. In most groups larger than two, additional adolescents could be distinguished from a close companion by the greater separation distances they maintained, by their one-sided moving nearer, and by their being the recipients of more snorts or horn gestures from the other two individuals.

EXAMPLE 44. <u>Additional adolescents settle to rest near the cow and adolescent to which they have attached themselves</u> (Madlozi, 28 Apr.'70)

(Same group as in Example 43)/ <u>0742</u> adolescent female <u>v</u> lies resting, the cow <u>U</u> stands drowsily 9 m away; the adolescent male wanders up, sniffs at the head of <u>v</u> near her anterior horn base, <u>v</u> turns away slightly with a sigh, otherwise ignores him/ <u>0744</u> adolescent male turns away, lies down 3 m from <u>v</u>; the young adolescent female grazes 10 m away/ <u>0746</u> <u>U</u> moves up beside the adolescent male, turns towards <u>v</u>, stands, nudges <u>v</u>'s horn, stands facing away from her/ <u>0755</u> <u>U</u> lies down 2 m from <u>v</u>; the adolescent female sits down 10 m away/ <u>0757</u> <u>v</u> stands, turns facing <u>U</u>, stands, shift 1 pace closer, pauses, shifts 2 paces nearer; adolescent male rises, turns towards <u>v</u>, <u>v</u> turns towards him with a soft rumble and a checked horn gesture, adolescent male hastens away several paces, stands 4 m away / <u>0801</u> adolescent male turns facing the cow, lies down 5 m away from her; <u>v</u> moves towards <u>U</u>, there is a soft snort from the cow, <u>v</u> circles round behind her and lies down beside her 1/2 m away; the young adolescent female lies down 4 m away from <u>v</u>.

3.3. Bull-cow groups

The attachment of a bull to a particular cow or adolescent female containing group rarely lasted longer than 2-3 weeks. All associations lasting longer than a day seemed related to an oestrus period by the cow concerned. However, for the first 5-20 days of such consort associations, there was no indication of oestrus behaviour on the part of the cow, and no courtship actions were exhibited by the bull. Numerous days were spent watching bull-cow associations, aimed at elucidating reproductive behaviour and at delineating territory limits. In addition, 47 hours of observation was devoted to intensive recording of inter-individual distances and other interactions.

Cows generally followed their own activities and directions of movement independently of the presence of the bull, and the bull merely moved with them to stay in the vicinity. Bulls usually maintained spatial separations of between 10 and 18 m (Figure 42), but occasionally became separated by 30-45 m or more. Approaches closer than about 10 m were inhibited by separation maintaining threats from the cow, such threats being elicited at an average separation distance of 10-11 m (refer to Table 43b).

Bulls usually responded by turning or moving away, or at least by not approaching any nearer. An average rate of 2.3 threats per hour by the cow was recorded (N = 38 hours). Bulls sometimes made hics or hic-pants while moving back towards the cow from some distance away. When the cow lay down, the bull edged in closer, frequently backing in cautiously a few steps at a time to reduce interindividual distance, before lying down to rest himself. Bulls rested at an average separation of 9.7 m from a companion cow (range 2-20 m, N = 13; Table 50).

Bulls usually rested while a companion cow rested, and grazed when she grazed. Sometimes bulls continued grazing for a while longer but did not move far away. Sometimes the bull seemed still sleepy when the cow rose and resumed grazing. He shifted on periodically to keep near the cow, but in between merely stood drowsily head low. On two observed occasions, a bull left the cow and wandered off to drink at the nearest water source; in one case, this was almost 2 km away at the opposite corner of the territory. An hour and a half later the bull returned to the spot where he had left the cow and tracked her down by scent over a distance of 700 m. Cows were unresponsive to activity changes by accompanying bulls.

Bulls were usually readily able to relocate cows that had run off by following their scent tracks; but sometimes they seemed confused, probably by the scent tracks of other rhinos. A bull that had temporarily lost contact with a companion cow displayed great agitation. He hastened around tail curled with his nose to the ground until he found the cow again.

When a cow walked off, the bull followed behind her. Cows never waited for bulls. At an alarm, a bull sometimes hastened towards a cow with pants, never nice versa. If the cow ran off, the bull hurried after her making repeated loud pants. When the cow stopped, so did the bull's pants.

If the cow found the bull blocking her chosen path of movement, she advanced with snorts or a snarl causing the bull to move hastily out of her way, except at territory boundaries. Once a cow displaced a bull from the shady restplace at which he was lying in this manner; the bull sought an alternative site.

Territory boundary blocking

While the cow was within the central part of a territory, the bull "obediently" kept his distance. However, if the cow wandered towards a territory boundary region the actions of the bull changed.

While the cow was still 100 m or more from the boundary, the bull moved round to place himself between the cow and the boundary making soft squeals as he did so. Sometimes cows changed direction appropriately when the bull did this (Example 45). If the cow grazed or walked parallel to the border, the bull kept in a flanking position between her and the border. If the cow turned or moved towards the border, the bull immediately shifted in front of her squealing louder. He horned, scraped and urinated sprays at short intervals while moving round to block the cow, and horn wiped without urination while standing in front of her. If the cow tried to turn and move past him, the bull circled round squealing and positioned himself between the cow and the boundary again. Cows responded to such actions with snorts, snarls or advancing snarls, but at a boundary a bull did not yield; he stood his ground squealing loudly. A confrontation frequently ensued, the two rhinos standing facing each other at close quarters with snorts and snarls from the cow and squeals from the bull. Territorial bulls in this way persistently blocked all

EXAMPLE 45. Territory boundary blocking: quiet interaction with cow readily changing direction (Mputshoni, 14 Feb'69)

0717 the bull, cow and calf graze near the SE corner of the bull's territory; the cow snorts at the bull who grazes 10 m in front (S) of her at right angles; the bull raises his head, gives a hoarse squeal, remains standing; the cow turns and grazes W, the bull grazes E then N then back W/ 0723 the cow turns facing S, the bull (facing away) half turns, the cow gives a low rumble, the bull gives a hoarse squeal, grazes past eastwards in front of the cow; the cow resumes grazing facing E, then turns NW; the bull grazes in parallel on S flank.

EXAMPLE 46. Territory boundary blocking: vigorous blocking by bull (Madlozi 21 Nov.'69)

1310 the cow and calf walk SE near the NE corner of the bull's territory; the bull hastens after them on the N flank, horns a low acacia bush vigorously, scrapes and urinates sprays, gives a gruff squeal, the cow pauses 20 m S of him, they stand/ 1315 the cow turns, walks N, the bull walks N 20 m away NE of them horns, scrapes and urinates sprays; cow plus calf pause, the bull stops N of them; the cow snorts, the bull squeals, rubs his horn on ground, repeats this, shifts a few m SE with a squeal, the cow gives 2 soft snarls, the bull stands squealing/ 1318 the bull turns facing N, scrapes and urinates/ 1320 the cow turns and walks S, the bull gives a squeal, shifts round E of her, the cow stands: the cow faces NW, the bull horns, scrapes and urinates; the cow takes a few paces NE, the bull horns hard, scrapes and urinates, squeals; cow plus calf stand, the bull walks N to get E of them, cow plus calf walk on N, the bull shifts with them squealing, the cow gives a prolonged snort, the bull gets ahead NE of cow with squeals: they pause at a pool to drink... 1342 the cow turns away from pool facing SSE, the bull gives a rumbling squeal, stands side on 15 m NNE of them/ 1346 the calf shifts NW, the bull squeals, moves W, stands NE of the cow and calf, gives a long grumbling squeal; the cow walks W, the calf follows, the bull follows.

attempts by companion cows to move across territory boun- deries (see Examples 46 and 47). If the cow ran off, as sometimes happened when I disturbed the animals, the bull raced round at a trot making loud wailing squeals to head her off. In some instances when hard pressed by a cow, the bull advanced to clash horns with her. In one case, the bull faced the cow displaying the ears back, head ex- tended action of the snarl threat, giving soft rumbles (Plate 18); this was the only time that I saw a defensive threat used by a bull on his own territory. The extreme persistence of territorial bulls in such situations is well illustrated in Example 48. This bull blocked all moves by the cow to cross his territory boundary from 0730 hours in the morning to 1700 hours in the late afternoon, though the rhinos remained out in open sunshine the whole time. The cow finally escaped over the boundary when I disturbed the group.

I never saw a bull pursue a cow more than 100-200 m beyond his own territory limits. Cows were sometimes able to transfer from one territory to another while the accompanying bull was engaged in a confrontation with a neighbouring territory holder. Since bulls normally

PLATE 18. Territory boundary blocking

a. A territorial bull walks to get ahead of a cow and calf who are grazing towards his territory

b. A territorial bull horns a bush while blocking the progress of a cow and calf at a boundary.

c. The bull drives the cow back with his horn when she attempts to advance.

d. The bull remains persistently in front while the cow snarls at him.

EXAMPLE 47. Territory boundary blocking: persistent blocking by bull (Madlozi, 7 Aug'69)

1433 The cow, adolescent female companion and the bull move out from their shade rest place near the SE corner of the bull's territory; the cow and adolescent walk SW, stand, the bull moves S of them 20 m away, stands in shade/ 1440 the cow turns facing S, snorts, the bull squeals loudly standing facing her, gives whining squeals as he turns side on in front of her, all stand/ 1450 cow plus adolescent move E a few m, the bull shifts with them on S flank squealing; cow plus adolescent commence grazing ENE, the bull shifts round to 25 m SE of them, scrapes and urinates sprays, commences grazing facing NNE/ 1457 the bull squeals facing the cow and adolescent female from 20 m away SE, the adolescent backs away from him, the cow and adolescent turn and graze back WSW, the bull then grazes in parallel 20 m away SW of them...
/1522 the bull stands watching as the cow and adolescent graze E passing 7 m N of him, the cow gives one snort at him; the bull turns, squeals, scrapes and urinates as he moves round in front of the cow and adolescent 15 m away, stands across their path facing S; the cow and adolescent stand staring at him, the bull backs a few paces; cow plus adolescent resume grazing, turn S, pause looking up, the bull squeals loudly as he advances SE of them, the cow and adolescent remain standing watching him/ 1532 the bull moves round to 28 m E of the cow and adolescent, they then walk on S, the bull runs round quickly with loud squeals, stands 20 m away SE of them, horns the ground and squeals loudly facing towards the females; they stand/ 1540 the cow takes 2 paces E, the bull turns, squeals, stands facing her, the cow snorts, remains standing head low/ 1543 the females walk NE, stand, the bull moves round squealing to stand facing them from 18 m away SE; the females resume grazing NNE/ 1547 cow plus adolescent graze E, the bull squeals, stands facing them from 20 m away SE, cow plus adolescent look up, resume grazing E; they graze past 8 m N of the bull; the bull squeals, turns towards them, the cow snarls, the bull stands, females resume grazing E; the bull squeals, turns and circles round squealing loudly to stand facing them from 20 m SE; the females look up, graze on E/ 1555 cow plus adolescent turn, graze NNE, the bull watches, squeals, shifts NE, horns ground, scrapes and urinates sprays, stands facing them from 20 m SE; cow plus adolescent graze NW away from him / 1558 cow and adolescent turn and walk NE, the bull looks up, squeals loudly, horns a fallen branch, scrapes over it, urinates, 20 m SE of them; shifts to stand 20 m ESE of the females; they stand, facing him/ 1603 cow and adolescent female shift NE, the bull squeals, advances to stand 10 m S of them, they face him/ 1619 the females at last turn and graze back W, the bull squeals 10 m S of them.........................

EXAMPLE 40. Extreme persistence by a bull in blocking a cow at a territory boundary (Hadlozi, 10 June'66); abridged)

0730 I hear squeals and roars, and discover a bull and cow confronting one another on the north bank of a watercourse; the bull blocks all attempts by the cow to continue northwards. Twice the cow advances on the bull snarling driving him back several metres with her horn, but he refuses to give way....../1320 the cow has gained 30 m from her early morning position; all the time the rhinos have been out in full sunshine, the air temperature is 30° c, and I am sweating where I am sitting in the sun / 1337 the calf runs off northwards followed by the cow and the bull chases after them; they gain 65 m before the bull gets in front again/ 1405 the bull lies down, followed 8 mins later by the cow/ 1620 the sun dips behind the hills, all three rhinos commence grazing; the cow moves N past the bull; he ignores her, and moves off S; when 200 m away he suddenly turns and hurries back to get in front of the cow again, and the confrontation is resumed;/ 1658 I approach the rhinos to ascertain their identities before departing; the cow takes fright and runs off N; the bull follows a short way only, stops to look towards me, then walks away southwards; the bull abandoned the cow about 200 m north of the watercourse that evidently marked the northern limit of his territory.

blocked the movements of a cow before the territory limits were reached and since other bulls did not cross territory boundaries, such incidents were rare, except at waterholes where several territories adjoined. Except in such unusual circumstances or when I disturbed the animals, bulls were always successful in turning back cows.

Territory boundary blocking actions were observed on the average once every 3.5 hours (N = 110 hours) while the rhinos were actively moving, either grazing or walking. This rate varied with the size of the bull's territory, and the attractiveness of the grazing conditions for the cow.

Discussion

White rhino groups are based on an amicable relationship between two individuals, evidenced by a close coordination of activities and movements. Such companions fed, rested and wallowed side by side, did not move far without the support of the other, and rushed to the other's side at any hint of danger.

A close attachment is typically shown by a mother and her offspring. In the absence of one of the partners, either a cow or an immature animal forms a similar bond with another individual. It was suspected in a few cases that the adolescent companion of the cow might be an older offspring that had rejoined her following the loss of her subsequent offspring. However, in many cases it was known from the past history of the two individuals that the adolescent was definitely not her offspring. In all cases I could detect no behavioural differences to distinguish the relationships. In one instance, when the yearling calf of a cow died, it was replaced by another juvenile of similar age (of unknown origin). If I had not had photographic evidence of this, I would have doubted that any change had occurred. In the two cow group observed closely, both cows were young adults of similar age. They had shared largely overlapping home ranges, but had never associated while both had calves, though they must have encountered one another frequently. When observed a month after they had joined together, they cooperated quite amicably. It is possible that a filial relationship between them may have existed, or they may previously have been adolescent companions; but any such relationship must have dated back several years. The attachment between two adolescents that were companions was particularly close;

since both individuals were usually of similar age, no filial relationship could have existed in most cases. The relationship is best described as one of close "friendship".

Evidently, a close friendship can be formed with only one other individual, and additional companions are clearly peripheral. The attachment between close friends is dualistic, whereas with peripheral individuals it is unreciprocated. Cows without calves, and also adolescents, exhibit a general tolerance towards the close presence of other cows and adolescents, except for mild threats when such individuals get in the way of their movements. It is thus relatively easy for additional adolescents to attach themselves to such individuals. Initially, at least, a temporarily attached adolescent seems to orientate merely to the group of other rhinos, rather than to any specific individual. More persistent attachments seem directed towards a cow rather than to any other adolescents accompanying her. In the cow-multi-adolescent group observed, each adolescent seemed bonded independently to the cow, and no individual friendships between any of the adolescents could be discerned. The cow in turn seemed merely to tolerate the presence of all the adolescents, though there was tentative evidence that a closer relationship may have existed with one of them. Following the disappearance of the cow, two of the adolescents remained together as companions. In adolescent pairs, individual compatibility seems to be a factor in bond formation. Some adolescents did not stay together for long. However, once a close attachment was formed, the two individuals were always seen close together thereafter. Allegiances may however change as described in the three adolescent group.

Cohesiveness is achieved largely by attentiveness to the other's movements, though this need not be overt. Spacing between companions is compact, probably on account of the poor vision of the animals and resultant difficulty in maintaining contact at greater distances. A contrasting situation exists in the horse, in which even young foals not infrequently move away more than 50 m from the mother (Tyler, 1972). Tactile contact is made frequently between close companions, and the acceptance of such action probably reinforces the amicable relationship. Temporary companions may also make tactile contact, but such gestures are less likely to be tolerated.

Changes in activity and location are signalled by directly demonstrative actions, with tactile contact or pants sometimes used to draw the companion's attention. An individual does not proceed far without the close support of the friend. Where a cow is present, she is clearly the control animal in the group. Her support is needed for any change in activity to be effective, though she may respond to move initiated by a calf or adolescent. Leadership is expressed in this way rather than by walking ahead of the companion. When two companions are of similar age/sex status, neither exerts clear leadership. In adolescent groups young females are more assertative in directing movements than similar aged males, anticipating the similar relationship that exists in adulthood between cows and bulls.

The concept of dominance has little meaning for characterising relationships within white rhino groups. Competitive situations with regard to food or other requisites do not arise. No displacement interactions were observed between close companions. Peripheral companions may be supplanted, but this has little functional significance.

The relationship between a bull and a companion cow operates as a one-sided attraction, balanced by close quarter repulsion by the cow. The cow is the control animal, the bull merely a follower. Dominance is exerted by the cow in the form of displacement of the bull from her chosen pathway, and the bull submissively gives way without contest. However a relationship changes at a territory boundary. Here the bull exerts dominance by forcing the cow to yield and change direction. Again dominance-subordinance terminology seems of little utility. Functionally, the concilliatory actions of the bull can be viewed as the best strategy for ensuring that the cow stay within his territory limits until ready for mating.

The frequency distributions of interindividual distances in different bond types (see Figure 42) are reminiscent of those resulting from physical force fields, though based on considerably more complex behavioural relationships of attraction and repulsion (see McBride 1964).

Functionally, the formation of close friendship bonds between young white rhinos seems advantageous as an anti-predation strategy. Though adults are almost invulnerable to non-human predators, this is not the case for immatures. A benefit of companions is suggested by rump to rump formation adopted when alarmed. Individuals are thereby protected against an attack from the rear and confront a predator with outwardly directed horns. Potentially, a companion may also divert a predator attack. Immature individuals never run off alone if other rhinos are nearby. Adolescents attaching themselves to cows may also derive benefits in terms of familiarisation with new sections of the environment. Adult cows, in turn, could also gain predator protection from associated adolescents or another cow. Few, if any detrimental results accrue to the cow in accepting their company. As a non-selective grazer, food availability for the cow is little influenced by the close presence of other individuals (see Jarman, 1973). The close friendship bonds formed between white rhinos are mutualistic rather than altruistic.

It is commonly suggested that herd formation is based on the persistence into adulthood of mother-offspring bonds. There is evidence that this is true for the African elephant (Laws 1973). However, it is demonstrated by the white rhino that pseudo-mother-offspring bonds can be transferred to other individuals with whom there is no genetic relationship. Similarly, in the plains zebra stallions abduct young females out of their maternal groups at the time of their first oestrus (Klingel 1967). Accordingly, mares belonging to the same groups are probably not closely related.

The attachment formed between white rhino adolescent males is analagous to the formation of bachelor herds by the more highly social bovids and equids. However, bachelor herds are generally characterised as loose associations with no close bonds between individuals. The close and persistent friendships formed between white rhino young males thus seems unusual.

D. REPRODUCTION

1. Reproductive physiology

Information of reproductive physiology is limited to that obtainable from behavioral observations on living animals in the study population. No specimens were available for examination of reproductive tracts.

1.1 Oestrus

Persistent accompaniment of a cow by a bull over a period of several days was a reliable indication that the cow was either entering or in oestrus. Several such associations which were followed eventually led to courtship and mating. All observed copulations, except one in unusual circumstances, were preceeded by such consort relationships. Bulls attached themselves preferentially to cows that were likely to be in oestrus condition, and only rarely to pregnant cows or cows with very young calves. Cows known (from subsequent parturition) to have been pregnant were being accompanied by a bull on only 2.5% of days seen (N = 728), and cows with calves under six months of age were seen together with a bull on only 1.6% of all sightings (N = 186). In contrast, for all cows combined this proportion was 13.0% (N = 2499). Since roughly three quarters of all cows were likely to be either pregnant or had calves under six months old at any given time, about half of the potentially oestrus cows were being accompanied by bulls when seen on a year-round average basis. Associations of bulls with non-oestrous cows were brief, lasting for less than a day.

The period of attachment of a bull to an oestrous cow will be referred to as the consort period. For the first part of the consort period, the cow showed no behavioural or physical indications of oestrous, and the bull made no courtship advances. The bull merely followed the cow in her movements, and blocked her from leaving his territory as described in Section C.3. It was difficult to establish the precise duration of these pre-oestrous consort periods since to do so would require that the cow be seen daily over several successive days in order to know when she had first been joined by the bull. Observations suggest that the duration may vary widely between extremes of 4 and 20 days (Table 53).

Onset of full oestrous was taken to be when the

TABLE 53. <u>Data on oestrus and mating</u>

Date	ident. ADm	ident. f	duration of (days)* pre-oest.	duration of (days)* post-oest.	consort period total	court-ship dura-tion (hrs)	no. of mounts before copul.	duration of copul (min) mounted	duration of copul (min) intromis.	no. of ejac.	time of day
1. Mar. '66	A	dd	11+	3	15+	10+	-	-	-	-	-
2. May '66	X	dd	10-24	4	15+	-	-	-	-	-	-
3. June'66	A	I'	20	5	26	25+	7+	-	-	-	-
4. Dec. '68	H	U	13-14	5	18-19	16+	2+	24	20	5+	0847
5. Feb. '69	L2	r2	-	3	-	-	1	28	21	9	1525
6. No. '69	L	NN	4	5-16	10-21	(17)	2+	23	15	10	0725
7. Nov. '69	N	LL	0	0	< 1	-	-	14+	14+	5+	1248
8. Apr. '70	L	HA	8-10	3	12-14	< 17	-	(22)	(10)	(3)	1000
9. Oct. '70	RR	ZZ	-	-	-	-	1+	30	28	12	0628
								(12)	(10)	(9)	1006
10. Nov. '70	L	DD	-	-	16-20	-	-	-	-	-	-
11. Nov. '70	C	BA	-	-	-	24	-	26	24	-	0617
12. Jan. '71	Q	d	3+	2	6+	-	5+	-	-	-	-
13. Jan. '71	I	mm	6+	2	8+	-	-	-	-	-	-
14. Jan. '71	C	TT	6-9	6	13-16	-	-	-	-	-	-
15. Jan. '71	X	AA	17+	12+	29+	-	-	-	-	-	-

* ranges shown are between minimum and maximum estimates

bull began making regular advances towards the cow accompanied by hiccing. This commenced about 24 hours prior to copulation (Table 53), and the frequency of such approaches increased with time until mating occurred. The cow then began emitting repeated little squirts of urine. There seemed to be some vulvar oedema, but this was not conspicuous enough to be a reliable indicator under field conditions. Initially the cow warded off such advances, but later contact by the bull was tolerated, and this led to mounting attempts and eventually to copulation (see sub-section 2).

Oestrous is apparently terminated by a successful copulation, and consequently lasts about one day. Only a single copulation was observed in each case, except in one case in which copulation was repeated after an interval of three hours. Generally bulls ceased making hiccing approaches after a successful copulation. Once when a subordinate bull attempted to mount a cow six hours after she had been copulated by the territorial bull, the cow threw him off violently.

One observation suggests the occurrence of a "silent heat" (Fraser 1968) in which full signs of oestrous were not exhibited. A cow was copulated by a subordinate bull with no preseeding or subsequent consort period (case 7 in Table 53). This cow was accompanied by a calf only five months old at the time of the first mating, so that this was probably her first post-artum oestrous. The mating was not fertile since the cow came into oestrous again a month later and was then joined by a territorial bull.

Some cows were accompanied by a bull for a single consort period only, while others were rejoined by bulls several times over a period of months. Evidence suggests that oestrous may recur at intervals of about a month until fertilization is achieved, but that it can be suppressed if dry conditions prevail during a particular month. The length of the oestrous cycle is apparently close to 30 days. One adolescent female was seen being mounted by a bull, and was being courted by another bull 72 days later. Another adolescent female was seen being mounted once, then again after an interval of 162 days; she was consorted with by other bulls during the interval.

The earliest recorded post-partum oestrous was when the previous calf was six months old (3 records).

There were 3 records of a first recorded post-partum oestrous after seven months, 2 after eight months, 2 after nine months, and other records at longer intervals.

No data on oestrus are yet available from captive white rhinos. For black rhinos, records of oestrous cycle length vary from 17 to 60 days, with 25-30 days seeming usual. Oestrus duration varies between 1 and 6 days, and a first post-partum oestrus was once recorded 20 days after parturition (Jarvis 1967, Goddard 1967).

1.2. Gestation period

Estimates of the gestation period are obtained by measuring the interval between the last known occurrence of oestrus (as shown by a consort relationship with a bull) and the birthdate of the subsequent calf (based on estimating the age of the calf when first seen). Six records indicated a gestation period of about 16 months, two showed 17 months, and one was 18 months. In the last instance copulation was observed on 23 December, 1968, and the newborn calf was discovered on 30 June, 1970 and estimated to be 4 days old. In the case of all records suggesting gestations longer than 16 months, the cow was not seen by me 16 months prior to the birth of the calf, may well have come into oestrus again and been fertilized then. The true gestation period is thus probably 16 months. This accords with two published records of gestation period obtained from captive animals: 484 days, for a calf born in the Krugersdorp Game Rexerve, Transvaal (Schaurte 1969); and 476 days, for a calf born in the Pretoriuskop enclosure in the Kruger National Park (Pienaar, 1970).

For the black rhinoceros the gestation period is apparently about 15 months, though records show some variability (Jarvis, 1967; Goddard, 1967).

1.3. Lactation

Nursing continued until calves were well over a year old in most cases, but the frequency of suckling declined after 15-18 months. There were three records of nursing by calves over 18 months of age, in one instance by a 24 month old calf (Table 54). Records suggest that lactation is normally terminated at about the third or fourth month of the ensuing pregnancy. Apparently lactation is continued for a longer period if pregnancy is delayed.

TABLE 54. Records of extended lactation: calf over 18 months of age, or cow pregnant

Based on last observed record of suckling by the calf

Date	ident. of cow	age of calf (months)	period before parturition (mo)
May'70	N	24±2	18*
Apr'70	T	20±1	13 1/2
Jan'70	JJ	19±2	-
Dec'69	JJ	18±2	-
May'70	HH	18	10 1/2
Jan'70	H	17±2	14 1/2
Jan'70	HH	14	14 1/2
Mar'70	LL	9	13

* estimated on basis of last recorded oestrus period by the cow.

Lactation is not suppressed by oestrus; calves were observed being suckled even on the day of mating.

1.4. Seasonality in reproduction

Cows being accompanied by bulls and cows with newborn calves were encountered in all months of the year, indicating that there was clearly no narrowly restricted breeding season. However seasonal variations in the incidence of both oestrus and parturition were evident.

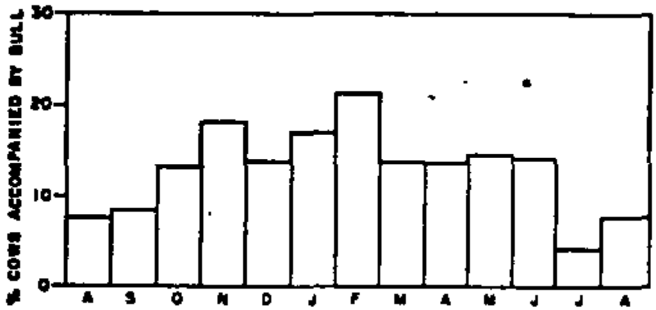
If data for all study years are combined, two peaks in oestrus levels are evident occurring in November and February, that is early spring and late summer, and a high proportion of cows were in oestrus throughout the wet season (Figure 43). In contrast, few cows were being accompanied by bulls during the winter dry season months of July, August and September.

Corresponding variations are shown in the monthly distribution of newborn calves (Figure 43b). Peak calving months are March and July, that is in autumn and winter, and few calves were born during the early wet season months of October to January. The two calving peaks are displaced 16 and 17 months respectively from oestrus peaks, providing further support for a gestation length of 16 months

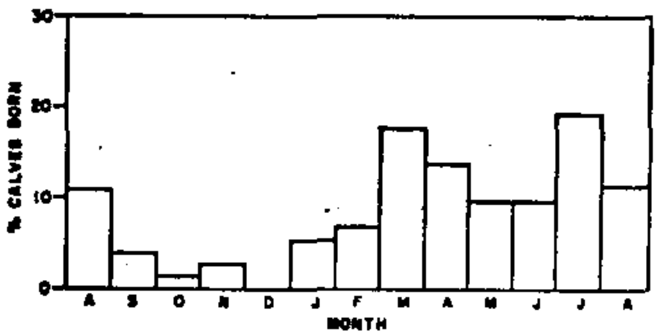
FIGURE 41. <u>Seasonal variations in reproduction</u>

Averaged data for the study years 1966, 1968-71.

a. <u>Oestrus</u>



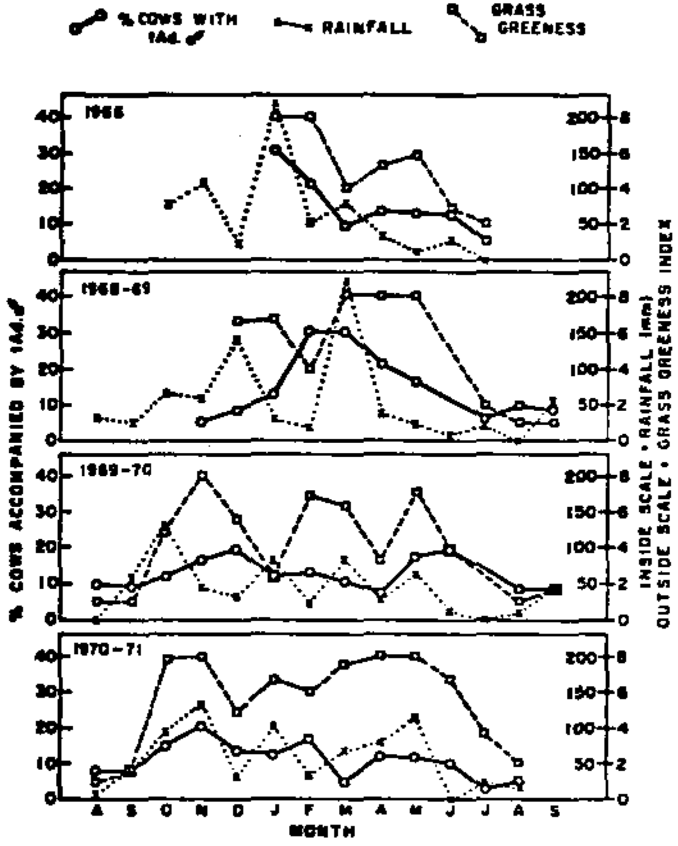
b. <u>Calving</u>



(considering that a particular oestrus may not be fertile). Exact correspondence between the oestrus and calving monthly distributions is not to be expected since they are derived from different combinations of years.

Variations occurred in the timing of peak oestrus levels in different years, and these may be correlated with differences in rainfall patterns and corresponding grass condition trends (Figure 44). In 1966 generous rains fell through January followed by a dry period, then further light rain in late March and April brought on a flush of green grass through April-May. The main oestrus peak occurred in January-February, while several more cows came into oestrus through April-June. In 1968-69 little rain fell until early December, then there was a midsummer drought which was broken by generous rains in March, tapering off thereafter. In 1969-70 rainfall patterns were erratic, with a severe midsummer drought that was broken only at the end of January. Peak oestrus months were November-December and May-June. In 1970-71 there were good spring rains, then a summer drought that was less prolonged than in previous years, then good rainfalls occurred through April and May. Oestrus peaks occurred in November,

FIGURE 44. Seasonal variations in oestrus levels correlated with monthly rainfall and grass greeness



February and May. The general pattern was for a good fall of rain to produce within a week or two a flush of freshly sprouting green grass, followed within another week or two by an increase in the number of oestrous cows. Conversely, a drying period evidently inhibited oestrus. After a more prolonged drought, such as occurred particularly in 1968, there seemed to be a greater time lag before oestrus levels rose.

Discussion

The white rhinoceros is evidently polyoestrus and shows no regular seasonal cycle. Nevertheless, there are month to month fluctuations in the incidence of oestrus which seem correlated directly with prevailing forage conditions. Oestrus is apparently stimulated by a diet of freshly growing green grass and inhibited when food is restricted to dry grass.

All study years were to some extent atypical in their summer droughts and late rains. Under average conditions, the major oestrus peak would probably be that occurring in November, with the main calving months being March-May. But variability in rainfall patterns can result in calves being born in any month.

A similar situation evidently prevails in the African elephant which is also perennially polyoestrus (Laws 1969). In several areas of East Africa there are two conception peaks associated with the two annual peaks in rainfall (Laws et al., 1970). In Luangwa Valley, Zambia, where there is a single rainy season, a peak in conceptions occurs one month after the rainfall maximum (Hanks 1969) and few calves are born during the dry months of July to September. Laws et al. postulate that the seasonality in reproduction is influenced proximally by rainfall through its effects in improving the nutritional regime and hence influencing ovarian activity. In the elephant, the gestation period is 22 months so that peak births occur two months before the rains, this apparently results in most calves being born during the optimum conditions for their survival.

In the hippopotamus in Queen Elizabeth Park, Uganda, conception peaks occur in February and August, immediately preceeding the ends of the dry seasons (Law and Clough, 1966). Births peaks therefore occur at the beginning of the subsequent rainy seasons following the gestation period of 8 months. Among most African ungulates, calving peaks similarly occur early in the rainy season.

The white rhinoceros is thus unusual in that the two calving peaks coincide with the beginning and middle of the dry season. This may be related to the drawn out nature of the different stages of reproduction, so that the different critical stages for the survival of the young are passed during different times of the year, and no one period is clearly more advantageous than any other. Hence there is apparently no photoperiodic regulation of oestrus season, and this seems influenced simply by the proximal effects of nutrition on ovarian activity.

The white rhinoceros is also unusual in that the male is able to detect an impending oestrus period as much as 20 days in advance. Presumably this is dependent on olfactory stimuli present in the urine of the female during dioestrus or early proestrus. Obviously, there are strong selective advantages for a male to detect a potentially oestrus female far in advance, so she can then be confined to his territory until ready for mating. It is possible, however, that an effect similar to the Whitten effect in mice (Parks 1960) may be operative, with the presence of the male inducing onset of oestrus. This phenomenon is known to occur in the sheep and goat among domestic ungulates, and may be more widespread in other species (Fraser 1968).

2. Courtship and mating behaviour

2.1. Pre-oestrus consort period

During the first part of the consort period, the only indication of oestrus in the cow was the bull's interest in staying with her. The cow actively inhibited any approach by the bull nearer than about 10 metres, and the bull readily responded by keeping his distance. This pre-oestrus consort period lasted from 4 to 20 days and the only noticeable behavioural change was that some cows seemed to become more tolerant of the bull's proximity.

If the cow defecated or urinated, the bull stood waiting until she had moved on, then moved up to sniff carefully at the dung or urine. Flehmen was exhibited after smelling at urine, but not at dung.

The territory boundary blocking manoeuvres of the bull confined within his territory not only the cow, but also her companions. The bull did not distinguish between individuals in his blocking; all attempts by any individual to move out of the territory were headed off. Where an adolescent female was with one or more adult females, I could not tell from the behaviour of the bull which of the females was entering oestrus. Probably the bull could not readily distinguish the females visually. Since rhinos in a group tended to keep close together, the bull's best strategy was to block egress by all individuals.

Bulls displayed tolerance towards accompanying calves and adolescents. On several occasions, when a small calf approached to press its horn against that of the territorial bull, the bull merely stood passively. Usually, however, calves avoided the close proximity of territorial bulls and territorial bulls paid little attention to them.

Adolescent male companions aged three to six years accompanying cows or adolescent females were mostly ignored by territorial bulls, even when they directed vehement snarls towards the bull. In one case, the territorial bull advanced to clash horns briefly several times with the 6-7 year old male companion of an adolescent female. This action was resisted by the adolescent male with loud snarls and horn shaking gestures, and he remained with the group through oestrus and mating. In another case, a 10 year old male, in the transitional phase between adolescent and subordinate bull status, stayed with the cow and territorial bull through most of the consort period, and the territorial bull displayed no antagonism to his presence.

Likewise the relationship between a territorial bull and his subordinate bull(s) remained unchanged.

2.2. Oestrus and courtship

Territorial bulls occasionally made brief hiccing approaches towards cows during the pre-oestrus consort period. Such action was recorded on the average once per five hours of observation, and occurred while the bull was moving nearer to the cow after having become separated by some distance.

The onset of oestrus was indicated by the commencement of regularly repeated hiccing advances by the bull. The bull approached the cow from behind with head held high, moving cautiously with short steps and accompanying the approach with a continuous wheezy hic-throbbing sound (Plate 19). Such advances commenced about 24 hours prior to copulation. Between 24 and 16 hours before copulation, these hiccing approaches occurred at a rate of 2-4 times per hour (N = 3 hours). Their frequency increased with

PLATE 19. Courtship and mating.

a. A bull approaches hiccing.

b. A bull rests his chin on a cow's rump.

c. Mounting without intromission

d. Copulation.

time, so that over the last few hours before copulation during which initial mounting attempts were made, they occurred every few minutes; an average rate of 9.7 times per hour was recorded (N = 33.5 hours), with a range between 5 and 21 times per hour.

Initially the cow reacted each time to the approach of the bull with snorts or snarls. The bull then desisted from his approach, only to start another approach a few minutes later. After a time, the cow responded to approaches by curling her tail and emitting a little squirt of urine. This response seemed to be an automatic reflex; it was made by cows even when they were still actively resisting approaches, or, in the case of adolescents, avoiding the bull. As time progressed, cows reacted less strongly to the advances of the bull; they more commonly made simply a soft snort, or merely turned their head to look at the bull.

The bull made first contact with the cow by ignoring her threats and continuing his approach, edging forwards very slowly over the last few metres hiccing continually to place his head on the rump of the cow (Plate 19). The cow responded by snorting or snarling, and the bull then moved away hastily. With decreasing resistance by the cow, an increasing proportion of approaches led to this chin-on-rump posture. After having achieved this posture several times, the bull made initial mounting attempts. He leaned the weight of his head more heavily on the cow and made a few pawing motions with one or both forelegs. A penile erection sometimes occurred at this stage. The first few mounting attempts were usually abortive as the cow shifted position and the bull lost his balance.

After several attempts, a successful mount was achieved. The bull leaned his head on the rump of the cow, and using his head as a brace raised his forequarters to place his forelegs on the back of the cow. He then pulled himself forwards over the cow to stand with his chin resting on her nape, and his forelegs on either side of her neck (Plate 19c). The cow merely stood passively accepting such action. In the first few mounts, the pair simply stood quietly and the bull gradually lost erection. After a few minutes dismounting was activated by the cow shifting position, or the bull slid off without prompting.

As should be clear from the above description, courtship is a slow moving, long drawn out affair. The detailed sequence of behavioural interactions during courtship in

EXAMPLE 49. Courtship sequence; no copulation, bull's interest wanes (Madlozi 23-24 June'66; tADm.A, ADf.U+c; extracted)

23 June, 1355-1500: no hiccing approaches observed; /1500-1600, the bull makes 2 hiccing approaches, but stops each time when the cow snorts; / 1630-1730 the bull makes 12 hiccing approaches; each time he is stopped by a snort or snarl from the cow; no squirt of urination or any other stimulus from the cow is observed.
24 June - (first observed contact):
0650 rhinos located resting lying down/ 0655 rhinos rise;/ 0700 the bull approaches cow hiccing, she snorts at 8 m, the bull shakes his head, lies down again;/ 0711 the bull rises, approaches the cow hiccing, cow snorts, the bull shakes his head, lies down again, digging his horn into the ground as he does so;/ 0715 the cow lies down, the bull gives a hic, the cow responds with a snort, the bull rises, moves round hiccing, continues hiccing as he slowly comes up behind the cow, the cow snorts but does not rise, the bull achieves contact by placing his chin on her rump, and is ignored; the bull stops hiccing, stands, then lies down close behind the cow.
(first observed urine squirt):
/0805 the bull rises, the cow snorts, the bull gives a few hics, calf snorts blocking his path; the bull circles round the calf to approach hiccing from the opposite side, the cow gives a grunt then a snort, the bull drops his head, then raises it, resumes hiccing approaching; the cow then rises and springs at the bull with a snarl driving him back several m; they stand facing; the bull walks away to a dungheap and defecates there/ 0815 the cow turns round, the bull approaches hiccing, moves very slowly as he nears over the last metre, sniffs at cow's perinneal region with his nostrils almost touching her, the cow gives a soft snort, the bull steps back a pace; the cow curls her tail, urinates 1-2 little squirts only;/ 0820 the cow turns her head towards the bull with a soft grunt, the bull steps back, is now 8 m away; he then lies down. ....0908 the bull rises, approaches cow hiccing, the cow gives a short snort, the bull continues approaching, places his head on cow's rump, then more anteriorly on the crest of her back; the bull then slides his head down, the cow's tail is curled, the bull holds his head close, appears to sniff at urine squirt from the cow; the bull lifts his head, as he touches the cow's rump, she gives a snort and jumps slightly, the bull walks away and lies down about 4 m behind the cow.................................
(first mounting attempt):
1013 the bull rises, starts to approach cow hiccing, she turns to face him with a snort, the bull lies down again/ 1017 the bull rises, approaches cow hiccing, she ignores him, the bull comes up to place his chin on cow's rump, moves his head off appearing to sniff at urine trickle, places his head on cow's rump again, leans

his weight heavily on her, makes two pawing motions with his forelegs, stands; after a minute the cow shifts forwards, the bull remains standing...
(first mounting):
1119 the bull approaches hiccing, the cow turns with a grunt and he backs away/ 1121 the bull approaches hiccing, is ignored by cow, the bull places his chin just anterior to cow's caudal base, the pair stand thus; the bull then raises himself taking his weight on his chin to lift his forelegs onto the cow's rump, slides further forwards over her; there is no penile erection; the bull then slides off laterally, the cow turns with a grunt, they stand, the cow urinates a squirt...
(passive acceptance by cow):
1147 the bull approaches hiccing, the cow stands, the bull places his chin on her rump, the cow urinates a trickle, the bull slides his head down against her flank; the cow remains standing passively, shuffles slightly, stands as if awaiting further action; 1150 the cow shifts forwards a few steps, stops as the bull starts following hiccing, the bull pushes his snout against cow's perineum, stands thus; after a minute the cow turns with a snort, then turns facing away again, stands; the bull turns away to sniff at the ground where she urinated..
(second mounting):
1157 the cow shifts on, stands when the bull starts approaching hiccing, they stand/ 1200 the bull approaches hiccing, rests his chin on cow's rump/ 1202 the bull mounts, stands with his forelegs resting about halfway along her side; his penis extrudes partially; they stand quietly thus (Plate 19c); the cow shuffles slightly, the bull shifts his weight back, then slides off, they stand, the bull's penis now completely retracted.............................
(third mounting):
1242 the cow stands, urinates a few little squirts; the bull approaches hiccing to rest his chin on her rump, then removes his head remaining standing close behind the cow/ 1243 the cow shifts on a few paces, stands again;/ 1245 the bull approaches, stands just behind the cow;/ 1246 the cow walks on, the bull urinates sprays, then follows; the cow stops, the bull approaches hiccing, leans chin-on-rump, paws, then mounts; they stand quietly thus;/ 1249 the cow urinates a tiny squirt/ 1251 the bull slides slowly off; the cow turns to face him, urinates a few little squirts;/ 1253 the cow urinates another little dribble, moves on; the bull walks up to sniff at the urination site, then follows/ 1255 the cow stands, but the bull does not approach; 1256 the cow shifts on a few paces, stands; the bull takes a step after her, the cow turns with a snort.................................
(waning interest by bull)
1355 the bull approaches cow hiccing, touches her flank with his horn, then stands munching behind her, carelessly jabbing her flank with his horn; the cow shifts on a few m, stands, the bull

moves after hiccing, but commences grazing behind her; this is repeated several times; the cow then turns slowly to face the bull, gives a soft snort;/ 1350 the cow shifts on, stands; moves on again, stands; the bull continues grazing/ 1400 the cow walks towards bull, gives a soft snort, the bull backs 2 paces but continues to graze, the cow turns away, commences grazing herself..............

(this pattern continues; the bull mounts again at 1448, but achieves only partial erection; at 1608 he mounts again, achieves full erection, but makes no probing movements, and his penis then subsides again after 2-3 minutes; he dismounts several minutes later; at 1652 he again mounts, achieves penile erection, makes no probing movements, and dismounts after a few minutes; the next day only 4 hiccing approaches were seen in the course of eight hours observation, all were checked by snorts from the cow)

EXAMPLE 50. Courtship sequence leading to copulation
(Nqutsherd, 6-7 Feb'69, tADm.L with adolf and adolm, both aged about 6 yrs)

6 Feb
0642-1132 no hiccing approaches seen; 1652-1805 rhinos watched again...
(first hiccing approaches made):
1743 adolescents lie down; the bull makes a few hics as he moves towards them, they snort, the bull backs, lies down 4 m separate/ 1756 the bull suddenly jumps to his feet with hics, walks a few paces towards the adolescent female, both adolescents rise, the adolescent males faces bull ears flat with a high-pitched grunt; /1800 rhinos graze; the bull approaches head high hiccing, penis partly unsheathed, to within 10 m; the adolescent male turns with a snort, the bull stands head up, the adolescent female turns, snorts, runs a few paces at bull with a grunt; all resume grazing; /1803 the bull approaches hiccing, the adolescent female curls her tail, urinates a squirt, turns with a snort and a snarl, the bull desists, stands head low, all resume grazing.
7 Feb
0742 rhino located; they graze northwards, the bull 30 m behind; he then moves nearer, hiccing; the adolescent female stands, defecates; the bull approaches, rests his chin on her rump; the adolescent female slowly turns with snorts, the bull backs away, they resume grazing/ 0750 the bull approaches hiccing, the adolescent female curls tail, urinates a squirt, half turns her head with a snort, the bull resumes grazing close behind her; the adolescent female snorts again, the bull turns partly away, continues to graze.......
(first mounting attempt):
0801 the bull approaches hiccing, the adolescent female curls tail,

urinates 3 squirts, the bull approaches, stands with his nose just behind her tail, the adolescent female continues grazing ignoring him, the bull rests his chin on her rump, paws, attempts to mount, but the adolescent female shifts as he does so, then turns round slowly with a soft snarl, the bull backs slowly, stands, the adolescent female resumes grazing..............................
0955 all three rhinos are lying down; the bull rises, starts hiccing as he does so, circles round behind the adolescent female hiccing, the adolescent female rises, the bull stops, the adolescent female turns to face him, stands head low;/ 0957 adolescent female lies down; the bull circles round behind her, approaches hiccing, pauses just behind her, then places his chin on her rump;/ 0959 the bull removes his head from the rump of the adolescent female, stands head low/ 1001 the bull hics, places chin on rump, shifts forwards, removes head, stands head low; the adolescent female now rises, swings round with a snarl, the bull jumps away; the adolescent female lies down again, the bull approaches hiccing to chin on rump, the adolescent female snorts, the bull stands head low, gently rubs his head against the adolescent female's flank, she snorts, the bull then lies down just behind her...................
(first mounting)
1157 the adolescent female is lying down; the bull approaches hiccing to stand chin on rump/ 1159 the bull's penis erects, he swings it, still standing chin-on-rump; the adolescent female then rises, turns with a low grunt/ 1203 the bull approaches hiccing, circles round behind the adolescent female, rests chin-on-rump, his penis unsheathes as he paws, he tries to mount breaking off a branch above his head, the adolescent female shifts sideways and he comes off/ 1205 the bull approaches to stand chin-on-rump again/ 1206 the bull attempts to mount, but the adolescent female yields and he comes off/ 1207 the adolescent female walks on, the bull follows hiccing, this time he mounts, the adolescent female shuffles shifting position but bull stays mounted, his penis unsheathes; the adolescent female's tail is curled sideways against bull's belly;/ 1211 the bull's penis subsides;/ 1213 the adolescent female gets restless, shuffles, stands again; shuffles again at 1215, 1220, 1223;/ 1225 the adolescent female pulls forwards from under the bull, trots quickly away, the bull follows..
(second mounting and copulation):
/1510 all rhinos lie in the shade; the bull rises, his penis erects, he swings it, moves closer to adolescent female, the adolescent female rises, turns facing bull, the bull quickly walks away/ 1515 the bull approaches hiccing to chin-on-rump, tries to mount, but the adolescent female shifts forwards, the bull cracks branches off trees overhead as he falls off;/ 1519 the bull approaches hiccing to chin on rump, mounts, shuffles forwards covering the adolescent female, his penis erects, he swings it raises it up, acheives intromission at 1524; copulation lasts 21 min, with 9 ejaculations revealed by

Example 50 - continued

quivering movements of the bull's hindlegs /154/ the bull's penis is now retracted from the vagina; the adolescent female bucks until the bull is shaken off, all stand quietly.

two cases is outlined in Examples 49 and 50. In the first case copulation was not observed and the bull transferred his attention increasingly towards grazing. It was possible that this bull, who was somewhat aged, had become impotent. In this case the cow repeatedly solicited approaches by moving on a few paces in front of the bull, then standing passively waiting, and she emitted repeated urine squirts. The second example shows the sequence through the first mounting attempts to a successful copulation.

2.3. Copulation

Copulations were observed on seven occasions. The bull mounted, and the penis erected to hang pendulously (see Plate 19c). The penis was then raised into horizontal position by muscular effort, and probing movements were made around the perinneal region of the cow. Usually after 1-2 minutes the vulvar opening was contacted and the bull then drew himself further forwards over the cow to achieve intromission (Plate 19).

Copulation duration varied from 15 to 28 minutes (Table 53). Agitated quivering movements of the hindlegs lasting 3-15 seconds were made by the bull every 2-3 minutes; accompanying such action the tail was curled tightly, and sometimes a tensed squeak or gurgle was simultaneously emitted. Such actions probably indicated ejaculations. From 9 to 12 such ejaculations were recorded during copulations (Table 53). Between ejaculations the pair stood quietly, with the bull in some cases making a repeated soft rumbling sigh. This sound resembled that made sometimes by drugged animals while resting on the brisket, and was probably merely a consequence of the abdominal pressure. No sound was made by the cow.

Dismounting was forced by the cow shaking the bull off in four cases; in two cases the bull dismounted after his penis had retracted completely; and in one case the bull was forced off by an overhanging tree as the cow gradually shifted forwards.

Copulations were observed at various times of the day, in one case even during midafternoon on a day in February when the temperature reached 41°C. Consort pairs were watched through the night on several occasions, but no courtship advances were seen. However such cows were apparently not in full oestrus, and there is no reason to suppose that mating does not also take place during the night.

2.4. Post-copulatory behaviour

In one case, mating was repeated after an interval of three hours. In the case in which the bull was forced off by an overhanging tree 10 minutes after commencement of copulation, the bull continued to make advances to the cow, and mounted again briefly twice, during the following two hours. In the five remaining cases, bulls ceased hiccing approaches after completion of copulation. The possibility cannot be excluded that a previous mating had occurred overnight but, judging from the pattern of approaches and responses, this seemed unlikely in several cases at least. Thus, it seems that a single copulation is the rule.

The bull usually remained with the cow for 2-6 days after copulation, but exhibited only an occasional hiccing approach as during the pre-oestrus period. The bull still blocked the progress of the cow at territory boundaries, but tended to lag further behind, and the cow eventually escaped from the territory.

2.5. Behaviour of accompanying calves and adolescents

Accompanying calves and adolescent companions frequently interfered actively with the courtship advances of a bull. In one case, a six month old calf rushed forwards with a croaking snarl each time the bull started approaching, sometimes even banging its miniature horn against the horn of the bull. The bull merely stood passively, then circled round to try approaching the cow again.

Adolescent companions, both males and females repeatedly obstructed courtship approaches by territorial bulls. They snorted or snarled at him, or advanced to clash horns, each time he tried approaching. Bulls patiently circled round them and tried approaching the cow from a different angle. In a few instances only, the bull continued walking straight towards the offending adolescent forcing it to give way. One adolescent male prodded at the flank of the territorial bull while the bull was mounted. The extreme tolerance exhibited by territorial bulls is illustrated in Example 51.

2.6. Behaviour of subordinate bulls

Subordinate bulls were occasionally seen in the company of cows, but except in two cases all such associations were brief lasting a few hours only. While territorial bulls were seen accompanying cows on the average in 39% of all sightings, for subordinate bulls the average was only 8% (Table 55). Excluding 1966 observations (which cover only five months of the year), no territorial bull was seen with

EXAMPLE 51. Tolerance shown by territorial bull towards an adolescent male companion (aged 5 years) of his adolescent female consort (Jhutshord, 7 Feb'69)

1357 the bull circles, approaches the adolescent female hiccing, the adolescent female lets out a shriek-grunt, all stand; the adolescent male advances towards the bull with a shriek-grunt, the bull retreats; /1400 the adolescent male lies down, the bull circles, approaches hiccing to rest chin-on-rump of the adolescent female; the adolescent male shrieks, rises, advances, the bull slides his head off, stands staring at the adolescent male 1 m in front of him;/ 1404 the bull approaches hiccing to chin-on-rump; /1408 the bull tries to mount, but the adolescent female shifts forwards; the adolescent male rises, swings his horn at the bull's flank with a shriek, the bull hastens forwards several steps, turns round to face the adolescent male, all stand heads low/ 1410 the bull approaches, rests chin-on-rump of the adolescent female, tries to mount, but the adolescent male springs up with a shriek causing the adolescent female to jump forwards, and the bull falls off; the 2 adolescents stand side by side facing the bull 1 1/2 m in front/ 1413 the adolescent male lies down, the bull walks away, circles round, starts approaching, but the adolescent male jumps to its feet with a shriek and drives him back about 5 m with its horn...

TABLE 55. Proportionate amounts of time spent in association with cows by individual territorial bulls and subordinate bulls

(a) territorial bulls

study area	Madlozi 1966			Madlozi 1968-1971									Nq	Gq	Do	ALL
identity of bull	A	P	X	A	BB	C	H	I	L	N	Q	X	var	var	var	
total days seen	62	55	22	65	55	135	68	204	170	36	56	97	58	31	36	1150
days with ADf	30	6	13	21	27	54	29	62	70	13	27	40	23	20	13	448
propn. days with ADf	.48	.11	.59	.32	.49	.40	.43	.30	.41	.36	.48	.41	.40	.65	.36	.39
mean no. cows in territ.				1.5	1.1	4.2		2.8	3.8		0.6	2.7				

(b) subordinate bulls

study area	Madlozi 1966			Madlozi 1968-1971						Nq	Gq	Do	ALL
identity of bull	O	Q	V	A	B	D	HH	JJ	N	var	var	var	
total # days seen	34	55	22	57	82	13	166	31	62	47	27		595
# days with ADf	0	2	2	3	9	0	19	6	6	1	1		49
propn. days with ADf	0	.04	.09	.05	.11	0	.11	.19	.10	.02	.04		.08

a cow on fewer than 30% of days seen, and only one subordinate bull was with a cow on more than 11% of sightings. This individual (JJ) was a young adult male who was in all cases associated with the same aged cow and her several adolescent companions. This association seemed merely to reflect the retention of adolescent bonding tendencies. Another young adult male, HH, was recorded with a cow on 11% of sightings, and a similar explanation can be applied. Older subordinate bulls were seen with cows less frequently. Three individuals, A, N and Q, are represented in Table 53 both as subordinate bulls and as territorial bulls; the contrasting proportions of time spent with cows, depending on their status, is clear.

Two cases were observed in which a subordinate bull stayed with the same cow over two successive days. Both involved the same individual bull, B, who had been territorial bull in the adjoining territory a year earlier.

In the first instance, this bull, B, was seen accompanying a cow over two days while the territorial bull consorted with a different cow and calf. No meetings between the two bulls were observed. During this period, B behaved like a territorial bull. He moved round to block the cow at the northern boundary of the territory (which adjoined the territory that he himself had formerly held); he made a few kicks before and after defecation, and horn wiped and scraped his legs several times, though he was not observed to spray-urinate; and on the morning of the second day, he made three hiccing advances towards the cow during an hour and a half of observation. On the morning of the third day, however, he had been displaced with this cow by the territorial bull. The territorial bull proceeded to mate with the cow while the subordinate bull circled round the pair at 20 m range, displaying great agitation. However, the subordinate bull made no attempt to intervene. After copulation, the territorial bull clashed horns with the subordinate bull, then left the cow. The subordinate bull then made repeated courtship advances, all of which were warded off by the cow. Once when the subordinate bull attempted to force a mounting, the cow threw him off violently so that he landed on his side. Several times the subordinate bull directed the motions of mounting against a small tree; he pushed his head against the tree and made pawing motions as if to mount but only broke down the stem.

Seven months later, this same subordinate bull was observed together with a cow over two days, this time wandering with her out of his home territory. Twice he was confronted by a neighbouring territorial bull, but each time the latter showed no interest in the cow.

A subordinate bull was observed copulating with a cow in one instance only. In this case there was no preceeding consort period by the subordinate bull, and no territorial bull had joined the cow. The subordinate bull did not remain with the cow after mating. A month later, the cow was being accompanied by a territorial bull, suggesting that the earlier mating had been related to a "silent heat" in which the full signs of oestrus were not displayed. Evidently, it was also not fertile. Two further unusual features were associated with the mating: (i) it took place in an area which had formed part of the home territory of the subordinate bull, but which three weeks earlier had been incorporated into the neighbouring territory when a new bull took over the former territory; (ii) this subordinate bull became a territory holder himself two and a half months later.

In one instance, a subordinate bull remained 30-50 m away while a territorial bull courted and later mated with an adolescent female. The subordinate bull looked on briefly, but displayed no great interest. In another instance, a subordinate bull directed several hiccing approaches towards a cow on the day following oestrus (though I had not observed copulation). The accompanying territorial bull clashed horns briefly with the subordinate bull several times, but later ignored his continued presence. After a few hours the subordinate bull wandered off. A nine-year-old young male, transitional in status from adolescence, remained with a territorial bull and his cow through most of the consort period, including the day of mating, but made no courtship advances.

In the Hluhluwe North study area, three adolescent males aged 8 to 10 years and one adult male were congregated around an adolescent female that was evidently in oestrus. The adolescents in turn made hiccing approaches toward the female, and in between exchanged threats. These took the form of loud snarls or brief clashes of horns. No mountings were observed during eight hours of observation, and the frequency of approaches decreased with time. The adult male wandered off early on, and it seems likely that he had already mated with the female.

Usually, however, subordinate bulls passed by territorial bulls and their consort cows without displaying any evident interest.

2.7. Masturbation

Bulls commonly had erections after lying down for an extended period, and erections also sometimes occurred at other times. After achieving full erection in such situations, the bull swung the penis to and fro several times, then raised it and held it pressed against the underside of the belly for several seconds. A few times, this was accompanied by a slight quivering action of the hindquarters. I did not observe an ejaculation, but in most cases was too far away to see whether this had occurred. Masturbation in this manner was observed by both territorial bulls and subordinate bulls and in a few instances also by older adolescent males.

Discussion

Many observers have drawn a relationship between courtship behaviour and displays of dominance or aggression (for example Walther 1973). However, in the white rhinoceros the aggressive tendencies of territorial bulls seem strongly muted throughout the courtship period. Bulls quickly hastened away from cows when they threatened strongly, yielded to their chosen path of movement, and even gave up their chosen restplaces. Even at a territory border, bulls acted in a manner which seemed, to a human observer, somewhat "apologetic". In blocking, they cautiously circled round keeping their distance from the cow, to stand squealing in front of her. Horn clashes were used only in situations of desperation. The whole attitude of the bull during the consort period might be characterised as one of "condescending subordination". Functionally, such tactics seem effective in mollifying the antagonism of the cow to the continued presence of the bull, thereby enhancing the likelihood of her remaining on the territory. Similarly, aggressive acts towards the companions of a female could drive the female from the territory, bearing in mind the tight bonds that exist between close companions. Territorial bulls also seemed less inclined to meet neighboring territorial bulls while with a cow; thereby lessening the risk of the cow slipping across the border while the bull was thus distracted.

Lack of aggression on the part of the bull is exhibited particularly strongly during the active courtship phase. Bulls approached cows cautiously and hastened away quickly if the cow threatened. The patience of bulls in repeatedly circling round obstructing adolescent males and females impressed me. Even against nearby older adolescent males or subordinate bulls, territorial bulls did no more than clash horns briefly in a few instances, and such action was ineffectual in driving away these other males.

The non-aggressive behaviour of the consorting white rhino bull can be seen as the best strategy in the particular circumstances prevailing in the species. In most ungulates, males may potentially have many mating opportunities, frequently concentrated in a restricted rutting season. It is there advantageous for them to overcome the resistance of the female in the shortest possible time. Any delays in achieving this can be ascribed to female strategies of "coyness" ensuring selection of the best male. In the white rhino, only about 40% of the females are mated in any one year, though some may be copulated several times. The average territorial bull probably has only one or two opportunities for copulation per year, and the most active male probably only twice this. Males thus act in such a way as to ensure that they are least likely to miss out on those opportunities that do come their way.

The pre-oestrus consort period serves to accustom the cow to the bull's continued presence. Active courtship is presumably initiated by olfactory stimuli which indicate the onset of full oestrus in the cow. It is performed solely by the bull, and consists of gradually and persistently overcoming the resistance of the cow to a close approach. The cow is passive, demonstrating receptivity behaviourally simply by not chasing the bull away when he makes contact. The most active solicitation observed consisted merely of walking on a few paces, then standing waiting for the bull to approach. However, the frequently emitted urine squirts clearly exert an attractant effect on bulls.

The pattern of courtship is similar to that in the black rhinoceros (Goddard 1966; Guggisberg 1966), except for the greater excitability exhibited by black rhinos. The horn jousting which reportedly takes place between male and female black rhinos does not occur in the white rhino; and in the white rhino attacks by the cow on the bull are limited to the ritualised clash of horns which serves as a distance increasing display.

Copulation is prolonged, as is the case with other rhinoceroses, though repeated ejaculations have not been mentioned by other observers. This lengthy copulation seems peculiar to rhinoceroses. This has advantages in a large-bodied species, in which considerable effort is expended in achieving mounting. Unlike smaller bodied species, increased vulnerability to predation during copulation is of little consequence. However, in contradiction to these arguments, copulation by elephants is brief, with intromission in the Asiatic elephant lasting less than 8 seconds (Eisenberg et al., 1971).

Subordinate bulls are in general excluded from reproduction as long as they hold this status. They seldom attach themselves to cows, and show little interest in oestrous cows that are being accompanied by territorial bulls. However, the single observed copulation and a few other instances in which subordinate bulls exhibited courtship behaviour suggest that they retain sexual potency. The inhibition of their sex drive, or "psychological castration", seems a direct expression of the dominance-subordinance relationship which exists between them and the territorial bull whose territory they share. Any potentially oestrous cow on the territory is likely to be joined immediately by the territorial bull, and the subordinate bull does not contest this priority.

During peak months for oestrus, study area territorial bulls were associated with cows on about two-thirds of days seen, so that there is no saturation of territorial bulls. Potential reproductive opportunities for subordinate bulls could arise should more than one cow happen to be in oestrus on the same territory; this was evidently the case on one observation. However, since a territorial bull can readily displace a subordinate bull it seems unlikely that this leads to more than an occasional mating by subordinate bulls. Subordinate bulls thus cannot be regarded as "satellite males" taking secondary mating opportunities, as this term has been applied in the case of the ruff (Philomachus pugnax) (Hogan-Warburg 1966).

Neighbouring territorial bulls also do not intrude across territory boundaries to contest access to oestrous females. A territorial bull thus has unchallenged rights to associate and mate with any oestrous female present within his own territory limits. The lengthy processes of courtship and copulation can thus proceed with a minimum of interference from other males.

Female white rhinos seem to exert little active choice of mate, but their behaviour is nevertheless likely to achieve this. Cows allow themselves to be joined by males that have already been successful in intra-male competition for territorial rights. They test the physical fitness of such males by persistently attempting to cross over territory boundaries. A male becomes the sire of a cow's next offspring only if he is successful also in keeping the cow within his territory limits until she reaches oestrus. Such a male is likely to possess desirable attributes (in evolutionary genetics terms) of physical vigour.

3. Maternal behaviour

3.1. Parturition

Parturition was not observed. One radio-tagged cow (P) was contacted daily to within two days of giving birth, when her transmitter failed. Another cow (Q) was seen one morning showing signs of impending parturition, then the next afternoon with the newborn infant. Three other cows were seen with calves between one and four days old.

Cows evidently secrete themselves in dense bush or some other secluded habitat to give birth. The cow Q with her newborn infant was tracked down by radio-telemetry in drainage line thicket so dense that I could not discern her until I was within 15 m. Another cow with an estimated day old infant was in more open scrubby _Acacia karoo_ woodland at the foot of the slope of Ntabayamanina hill. Two other cows tracked down by radio-telemetry with calves only a few days old were both in the same locality, on open grassy slopes of the Zintunzini hills above the valley of the upper Madlozi stream. This was an area little frequented by other rhinos. It seems that dense woodland is the usual habitat choice, otherwise newborn calves would have been seen more often than was the case. This accords also with the observations of game rangers.

A cow watched two days prior to parturition showed no unusual behaviour and was still with her usual companions. I could detect no notable swelling of the teats. A cow seen on the day preceeding parturition had noticeably swollen teats. In captivity, swelling of the teats reportedly occurs two to three weeks prior to parturition, but both records refer to primaparous females (Schuarte 1969; Dittrich 1972). In one of these cases, the swelling subsided a week before parturition. In cows that have undergone previous pregnancies, the teats apparently do not become swollen until a day or so before giving birth.

The cow Q when located a day or less preceeding parturition was standing quietly in a watercourse hollow. Respiration, as revealed by flank movements, was rapid, about 35 per minute. She then lay down leaning partly against the sloping bank of the hollow; she restlessly altered the positions of her legs, bracing then flexing again, and also moved her head about. She then heard my movements and ran off, appearing unhandicapped. The time of day was 1108 hours. The next morning was rainy, and I could receive no signal from her transmitter (which was faulty) until that afternoon when the sun came through. When tracked down she had the newborn calf with her. She was about 3 km from where she had been disturbed the previous morning.

The previous calf or other companions are driven away or avoided only a day or less before the birth, and normally do not rejoin the cow again. However, I have very few observations to indicate how the longstanding and close bond is broken. On the day before parturition, the adolescent female companion who had been associated with the cow Q for at least ten months was found already separate from her, though only 100 m away. It ran off independently, and was not in the vicinity the next day when the cow had the newborn infant with her. In another case, the older three year old calf was still with the cow and her day old infant. However, the cow drove it away each time it approached near, using a snort, snarl or horn prodding gesture. The older calf ran around in the vicinity of the cow, panting repeatedly and seeming greatly distressed, but kept returning. Another cow was seen one day with her companions, a cow and two adolescents; two days later, the latter three individuals were found apart from her, and the next day the cow was glimpsed together with her newborn infant. In two other cases, the newborn calf was about four days old when first seen, and the previous companion of the cow was not in the vicinity. Commonly, the first evidence that a birth had occurred to a particular cow was to find her old calf or adolescent companion wandering around alone or in the company of other rhinos.

In a birth that occurred in an enclosure in the Krugersdorp Game Park, the cow separated herself from the other three rhinos in the same enclosure only a few hours before giving birth. The birth itself occurred while the warden was absent for about ten minutes. The cow licked the infant dry, but ate only a small part of the afterbirth (Schuarte 1969). Though several births have now occurred in captivity, parturition is as yet undescribed in the literature.

A cow with a less-than-day-old calf stood quietly in dense thicket while the calf walked around her. She appeared uneasy, apparently getting my scent from wind eddies in the vegetation, as I was downwind of her. Even when I cracked some twigs while moving around, she did not run; she swung her head in a low arc to sniff at the calf, then stood firm. Two other cows with infants only one and four days old respectively likewise lowered their heads to sniff at the calf when disturbed by my approach; they shuffled uneasily, but did not run off as was usual. It seemed that the scent of the new infant blocked the fleeing response. Despite the provocation of my close presence, cows made no move to charge.

One cow seemingly invited nursing as the calf wandered past by lifting and flexing her right foreleg, then extending her hindlegs backwards to expose her teats; another cow also extended her hindlegs backwards when the baby whined softly beside her, and the baby then suckled. However, since cows with newborn infants could not be approached closely without disturbing them, observation sessions were brief, as I did not wish to alarm the cows unduly.

On the second day following parturition, the cow O was still within the same patch of drainage line woodland, but had shifted her position by about 250 m. On the morning of the third day, she was discovered moving southwards through open woodland about 900 m south of her location of the previous afternoon. She ran off with the calf at my approach, and when found again had settled to feed within drainage line woodland once more. The calf, which had been very wobbly on its feet for the first two days, was now much steadier. To reduce disturbance, this cow was not tracked down again until day seven. Then the calf was no longer with her, and her previous adolescent female companion had rejoined. Evidently, the calf had died in the interum. In photographs, this calf looks thin and underweight in comparison with other newborn calves. In another observation, a cow with an estimated four day old calf walked off steadily in the late afternoon, after having remained in the same place all day, and the baby followed at her heels. Cows apparently remain in the same locale for the first few days after parturition. Probably, a move is activated by the need to seek water; in all observed cases, nearest water supplies were several kilometres away from where the cows had given birth. Grazing is also in limited supply in areas of woodland or thicket. Cows evidently confine themselves preferentially to denser vegetation for the first few weeks following parturition. New calves were generally not encountered until they were two to four weeks old.

3.2. Mother-infant relationship

Mother and calf tended to keep close together, usually within a metre or two, as already outlined in a preceeding section on group cohesion (Section C.3). As indicated, both mother and infant maintained cohesion by moving nearer but the calf was more active in doing so.

Cows appeared highly protective of their offspring, not moving far away if the calf did not follow, and watching attentatively when the calf investigated other rhinos. At any sudden move by the other individual, the mother immediately snorted, or advanced beside the calf making a snarl directed at the offender.

At an alarm, a cow immediately rushed to the side of her calf giving loud pants. When making off after a disturbance, a young calf always ran in front of the cow, this position being actively maintained by the calf. Frequently the cow seemed merely to follow the direction chosen by the calf, but sometimes she changed course and the baby had to gallop round to get in front again. However, no case was observed in which mother and calf became separated as a result. When merely walking slowly, calves moved either in front or close behind the mother, though the former position was more usual. No encounters between cows with small calves and predators were witnessed.

A cow found beside a freshly dead approximately two-month-old calf could be driven away only with great difficulty. She persistently returned beside the body. Similar behaviour was observed during marking operations, after a calf had been immobilized with drugs. Notably, however, cows never charged aggressively. Likewise, considerable effort was required to frighten away the accompanying calf of a cow that had been immobilised. In all except one case, the cow and calf were back together again when next seen a day or two later.

PLATE 20. Mother-offspring relations

a. A cow stands protectively over her day old infant.

b. A two month old infant nibbles at tall grass.

c. A 5 month old calf approaches a 7 month old calf while their mothers graze nearby.

d. The calves wrestle horns while the cows graze ignoring one another.

e. A nine month old calf suckles lying down.

f. A year old calf runs off ahead of its mother.

In one case, a sixteen-month-old calf apparently attached itself to an adolescent companion and moved beyond the home range of the cow, as the two did not rejoin after the cow had been fitted with a radio transmitter; the mother had run beyond her usual home range limits before going down. This cow was watched on the morning following the separation as she slowly worked her way back home again. She was clearly restless, grazing for a few minutes then pausing to look in different directions with ears flicking attentively, and she made repeated loud panting calls. Seven such calls were recorded during a 45 minute period. That afternoon she was still panting repeatedly, making six such calls during one spell of eight minutes. The following day she had ceased calling.

Other cows that had become separated from their calves similarly made panting calls at short intervals on the day following the separation. In one case the calf had died, in another two it had probably been captured and in a fourth the calf had somehow become separated from the mother by about 500 m. The ages of the missing calves were 11 months, 15 months, 17 months and about two years respectively. The calf that had become separated from its mother also made several pants, but the two were evidently too far apart to hear one another.

Nursing. In two observations on newborn infants, the mother seemed to invite the calf to nurse by exposing her teats. In all other observations, nursing was initiated by the calf. It made a high pitched whining or whimpering sound while standing next to the mother, and pushed its head towards the udder region. Usually, the cow then stood still allowing the calf to suckle; occasionally a cow continued grazing for a few minutes before standing, and the calf then made louder and more insistent whines until the cow allowed it to nurse.

The usual nursing position was with both animals standing, but larger calves frequently suckled lying down. Nursing also occurred with the cow lying partly on her side exposing the udder while the calf stood beside. The calf sucked at one teat for a while, then shifted to the other, then perhaps back to the first teat again. Calves generally sucked quietly, and pushing or butting movements were seldom seen, and were then relatively gentle. Nursing was almost always terminated by the calf, which dropped its head and turned away from the cow.

Small infants under two months of age nursed frequently, on the average about once every hour (Table 56). Older calves aged between two and twelve months nursed on the average about once every 2.4 hours. After twelve months of age nursing frequencies show an apparent decline. However, this is probably related to the termination of lactation in some of the cows, this apparently occurring when the cow is in the third or fourth month of the next pregnancy (See Table 55). Since the usual intercalving interval is about 27-30 months, lactation normally continues until the calf is about a year old. If pregnancy is delayed, lactation may continue longer, in one recorded instance for 24 months.

Nursing duration shows little variation with the age of the calf, ranging generally between two and four minutes.

Discussion

The thicket and hillslope areas preferred for parturition offer several advantages. They are secluded from the usual haunts of other rhinos, which might possibly interfere with the newborn infant. The availability of a watercourse could also be beneficial, in offering a suitable sloping bank for support during labour. The eddying of the breeze

TABLE 56. Suckling frequency and duration

age (months)	no. of records	Duration of suckling (min)				Suckling frequency (per hour)	
		av.	max.	min.	N	av.	hrs. observ.
0–2	14	3.5	6.0	1.0	12	1/1.0	13
2–6	5	2.9	3.5	2.3	3	1/2.3	7
6–12	30	2.9	5.0	1.3	16	1/2.4	38
12–18	43	3.6	7.0	2.8	18	1/4.8	97
18–24	5	3.8	-	-	1	1/15.0	30

that evidently occurs in thickets ensures that olfactory awareness of an approaching enemy is not limited to the upwind sector. Finally, such habitats are outside the usual hunting areas of hyenas. As discussed later, hyenas are currently responsible for little or no mortality of white rhino calves.

The response of the mother in staying close beside the calf and refusing to be drawn into a charge seems advantageous in not leaving the calf unguarded. The physical invulnerability of the cow, coupled with her potentially dangerous horn would seem sufficient to render fruitless any attempted attack by hyenas or other predators as long as the calf remains close beside her. The habit of the calf of running off ahead of the mother enables the cow to maintain continual surveillance over the calf, and blocks the possibility of any attack from the rear. A similar behaviour is shown also by Indian rhino calves. Notably, however, in the black rhino the calf usually runs behind the mother (noted by many observers, from Selous 1881 onwards), behaviour which seems inadaptive since it renders the calf more vulnerable to hyena attack. It may be that in the more thickly environments commonly favoured by black rhinos, mother and calf would quickly become separated if the calf ran ahead. This argument is however not very satisfactory, since black rhinos may also be encountered in open country in parts of their range, and white rhinos also range through well wooded areas.

Lactation seems prolonged, but not unduly so in comparison with other large mammals. In feral horses, lactation ceases only a few weeks or days before the next foal is born (Tyler 1972). In the African elephant, suckling may continue for as long as 7-8 years in some populations (Laws 1969).

The older calf normally does not rejoin its mother, contrary for example to the case in feral horses (Tyler 1972). However, rejoining may occur should the new infant die, and there may then be no evidence to indicate that the birth had occurred. However, as indicated in Section C.3, the maternal bond may also readily be transferred to another unrelated young white rhino in the absence of the calf.

E. LIFE CYCLE

The life cycle of the white rhino can be divided into two main periods: (i) the period of early ontogeny, leading to the attainment of social maturity; (ii) the period of adulthood, during which the individual functions as an integrated member of the reproductively active population. Both of these periods can be subdivided into several shorter stages, for which the following terminology will be used: (i) infancy: the stage before weaning, during which the individual is completely dependent on the mother for nourishment; (ii) juvenilehood: the subsequent stage of partial dependency on the mother; (iii) adolescence: the stage of independence from the mother, prior to the attainment of social maturity. A distinction could be made between prepubertal and postpubertal stages of adolescence, as was done by Walther (1972) for Grant's gazelle; Walther applied the term adolescent to the former, and subadult to the latter. Though such a distinction is helpful, it will not be made here, since no behavioural changes were evident to me to mark the attainment of puberty in males. As indicated earlier, the term subadult will be used for an age class which is largely equivalent to the socially defined class of adolescent. Lastly (iv) a terminal stage of senescence can be distinguished from the remainder of the adult period.

In this section, the behavioural changes that occur as individuals pass through various stages in the life cycle will be considered. Since the study duration of 5.7 years is short in relation to the potential lifespan of a white rhino (which is probably about 50 years), this is based on piecing together relatively short term changes observed in particular individuals.

1. Ontogeny

1.1. Infancy

One newborn infant was observed briefly over three consecutive days, and another estimated day old infant was watched for an hour. A six hour watch was kept on a cow with an infant estimated to be about four days old. More extensive observations, totalling about 22 hours, were made on other calves aged between 11 days and four months.

The skin of newborn calves appeared wrinkled and a pale grey in colour, with a pale reddish wash noted in one case, and the ears had a sharp medial fold. Calves were rather unsteady on their feet over the first two days, and held the hindlegs somewhat crouched. They wandered shakily around the mother in tight circles, making tactile contact with her limbs in passing, or lay down beside her. One calf was observed suckling for 5 min 45 sec, with two brief interuptions. The second, when the mother extended her hindlegs backwards exposing her teats, probed in various spots around the udder before locating a teat, then nursed for 2 min 25 sec. A short whine was made by the latter calf as it probed for the udder, and by the former when it paused from suckling. Both day old calves suckled once during observation periods totalling 30 min and 20 min respectively, while a two day old calf nursed twice during a 53 min observation session. On the third day, this calf was much steadier on its feet, and was able to run off when the mother made off at my approach. When the cow was next seen on day seven, the calf was no longer with her and had evidently died. An estimated four day old calf was able to follow behind its mother without any difficulty when she walked off slowly, covering a distance of about 1 km before disappearing from view. During a six hour observation spell, this infant spent most of the day lying down beside the cow. It was seen suckling three times, all within an hour and a half spell at midday.

Infant calves kept close beside the mother, usually within a metre or two (Table 49). They rarely allowed themselves to become separated by more than 7-8 m. They alternated their time between lying down near the cow as she grazed, shifting position to keep with her as she moved on, and exploring in her vicinity. Various objects in the environment were investigated by sniffing, mouthing or rubbing including bushes, fallen branches and stones. Infant calves also exhibited spells of galloping back and forth, 5-15 m at a stretch, sometimes kicking and prancing about and coming to sudden stops in head up attitude.

Infant calves displayed great interest when other rhinos were encountered. A month old calf directed short mock charges, head up with puffing sounds, towards a cow and calf standing 10 m away. A three week old calf wandered 15 m away from its mother to investigate an adolescent pair, sniffing at the nasal region of the adolescent female, then moving to stand close in front of the adolescent male with a little prance, then trying to nurse from the adolescent female. Play behaviour may develop in meeting with other calves or adolescents (see later).

A three week old male calf urinated in a squatting posture (Plate 8). At seven weeks of age, the same calf straddled its hindlegs apart in the adult female manner while urinating, and a similar posture was adopted by all other immature animals observed. A month old calf sniffed at its mother's dung, then curled its tail but did not defecate. A two month old calf made five kicking motions after defecating beside the dung of its mother. Generally, calves and older immatures made no kicking movements when defecating.

Weaning. The earliest recorded nibbling at grass was by an eight week old calf. It stood head down making a few plucking movements at the grass, then stood head raised with jaw movements. This action was not repeated, and it seemed to be merely an extension of the tendency to mouth objects. An approximately two month old calf was seen nibbling at clumps of tall grass which were of little nutritive value. The dung of a two month old calf was examined, and was amorphous and dark greenish in colour; it seemed to contain fine hairs, but only a few grass fibres and one leaf were discernible.

Several calves aged 2.2-2.5 months were seen clearly ingesting grass for periods of a minute or so, between other activities. A 2.7 month old calf was filmed giving concentrated attention to grazing for a spell of several minutes. Calves over four months of age grazed for most of the time that their mother grazed (Table 57). Calves however continued to nurse usually until over a year old.

In summary, the newborn infant remains unsteady on its feet for the first two days, but by the third day is capable of moving about with the cow. The infant calf moves about with its mother, keeping close beside her, and spends time investigating features in its environment, or engaging in self-play, which takes the form of running around near the

TABLE 57. Proportinate time spent grazing by calves relative to mother at different ages

(activities recorded at 5 minute intervals during observations sessions)

Age range (months)	no. of records with cow grazing	no. of records calf also grazing	% time spent gr. rel. to cow
0-2	19	0	0
2-4	52	14	27
4-8	43	27	63
8-12	41	37	90
12-24	44	44	100

cow. Weaning onto grass commences at two months of age, and by four months of age a calf is spending much time grazing and can be regarded as weaned, though it continues to nurse much longer.

1.2. Juvenilehood

The stage of juvenilehood will be taken to extend from weaning at four months of age, to separation from the mother following the birth of a new calf which usually takes place between two and three years of age. Three intensive observation sessions totalling 17 hours were devoted to watching juveniles, and these were supplemented by numerous brief observations.

Juveniles generally followed similar activities to the mother, grazing when she grazed, resting when she rested. Younger juveniles still spent less time grazing than the cow did (Table 57), occupying the remainder either sleeping near the cow or standing or walking around in her vicinity. Juveniles still spent most of their time close beside the mother, though they tended to wander further away with increasing age (Table 49). However, they seldom allowed themselves to become separated by more than about 15 m.

Juveniles continued to display great interest in other rhinos, usually approaching them to sniff nasonasally. Particularly with other juveniles or with adolescents, such meeting frequently developed into horn fencing or more vigorous playful wrestling matches (Table 48).

Nursing was terminated during the juvenile period, but this was not marked by any noticeable behavioural changes. It seemed that the milk of the cow merely gradually dried up after the calf was over about a year old, and suckling frequency accordingly diminished. Three instances of nursing by calves over eighteen months old were recorded, the oldest being a calf about two years old.

No striking behavioural changes occur during the juvenile stage, rather there is simply gradually increasing independence from the mother. The most notable behavioural patterns are associated with play, which however is not restricted to juveniles, and will be discussed later. Opportunities for play are however limited to chance encounters with other cows and calves or with adolescents.

1.3. <u>Adolescence</u>

The stage of adolescence, as the term will be used here, is begun following separation from the mother at 2-3 years of age. There is a brief transitional phase, lasting perhaps a few weeks, before a stable bond is formed with another companion, during which time the individual will be referred to as a "lone calf". In females puberty, as indicated by the first oestrus period, occurs between four and five years of age, and adolescence is terminated upon the birth of the first calf at an age of 6.5-7 years. In males there is no behavioural indication of puberty, and males will be regarded as adolescent until they become solitary and settle within a particular territory as a subordinate bull. This does not occur until they are about ten to twelve years old.

Only one of the 1966 adolescents could be recognized again after my return 28 months later; this female had since calved and had thus become an adult. Information on behavioural changes during adolescence is based on about 40 recognisable individuals, whose life histories were followed for periods varying between one and thirty-three months.

<u>Lone calves</u>. The older offspring is driven away at the time of the birth of the next calf, and only rarely rejoins the mother later. Only two or three instances of rejoining were observed, out of 45 births that occurred to well-known cows: (1) A male calf (rr) which was under two years of age when the new offspring was born stayed with his mother for a further 22 months until the birth of the next offspring. He was seen with her on 85% of all sightings (N = 98); on other occasions he was seen in the company of other cows or (twice) alone. The mother drove him away with a snort or horn gesture on several occasions when he approached close to her, but mostly ignored him. However, he maintained a greater spacing

from the cow than did the younger offspring. One instance of rejoining after a temporary separation was observed. The older calf _rr_ walked quietly towards the other two curling his tail when 20 m away, nuzzled the flank of the younger calf briefly in passing, then stood near the cow. The cow ignored him. The bond was clearly one-sided, with the older calf persisting in remaining near the cow despite her rejections.

(ii) A 2.3 year old female was seen accompanying her mother and the new 2-3 month old female calf on three successive occasions, but termination of the study precluded further observations. The cow snorted at the older calf when it followed her down to water, but then ignored it when it drank close beside her.

(iii) A four year old adolescent female rejoined the cow that had been her companion over the preceding year following the death of the new infant born to the cow. No antagonism was shown towards her by the cow and these two individuals were still together sixteen months later. This adolescent may have been an older offspring of the cow, but the only evidence for this was the persistent bond that existed between them.

In all other cases the older offspring was found wandering around either alone, or temporarily in the company of other rhinos. Two encounters between an older calf and its mother, taking place about a month after the birth of the new calf, were observed. In both cases the older offspring started approaching, but moved away when the cow snorted. The behaviour of the two individuals did not differ from that exhibited in encounters between strange cows and calves, and no recognition was evident.

Lone calves panted frequently, both while alone or while moving towards or near other rhinos. They frequently paused after panting, as if listening for a reply, and also curled their tails repeatedly. Upon encountering other rhinos, lone calves usually approached hesitantly to sniff at the other rhinos, either from the side or rear or nasonasally. Usually the investigation was one-sided, with a cow paying little attention to the lone calf or snorting at it. Temporary attachments lasting one or several days were formed with cows or other adolescents. Cows appeared mostly indifferent to the extra company while lone calves remained nervous and uncertain and maintained greater separation distances from cows than did close companions. They continued to investigate other rhinos, and sometimes transferred their attachment from one group to another, or wandered off alone.

Eventually a stable association was formed either with a peer or with a cow lacking a small calf. Some individuals formed a stable companionship very quickly, while with others the process took several months. This may be illustrated by five case histories:

(i) In the case where the older offspring had remained with its mother, the two older siblings separated from her together upon the birth of the subsequent offspring, and were still together four months later; both were males.

(ii) A 2.5 year old male calf had attached itself to a cow and her adolescent female companion within a few days of the birth of a new calf to its mother, and was still with them 4 1/2 months later.

(iii) A three year old female had attached herself to a cow without a calf when seen two months after separation from its mother, and stayed with this cow for 5 1/2 months.

(iv) A three year old male was seen with five different cows over a two month period, then joined a similar aged adolescent male for a 2 1/2 month unbroken spell.

(v) A 2.5 year old male attached itself to at least five different cows over a five month period before forming a stable bond with an adolescent female.

Later adolescence. Stable bonds were formed either with another adolescent, usually of similar age but of either sex, or with a cow lacking a calf (Table 58). However, the main

TABLE 58. Social nature and duration of adolescent bonds

A bond enduring one month or longer is regarded as stable.

Social nature	# of stable bonds recorded	av. min. bond duration* (mo)	max. duration recorded (mo)
adolm-adolm:			
age < 6 yrs	6	8.7	20.5
age 6+ yrs	7	13.6	26
combined	13	11.3	
adolf-adolf:			
age < 6 yrs	7	3.7	9.5
age 6+ yrs	7	3.7	5
combined	14	3.7	
adolm-adolf:			
age < 6 yrs	8	4.1	15.5
age 6+ yrs	5	4.2	8.5
combined	13	4.2	
adolm-ADf:			
age < 6 yrs	7	7.4	22
age 6+ yrs	1	21	21
combined	8	8.1	
adolf-ADf:			
age < 6 yrs	10	10.2	26
age 6+ yrs	2	11.2	12
combined	12	10.3	

* the period between first and last sightings of the same two individuals still together.

Hadlozi study area population was affected by the rhino capture operations, resulting in an atypically high number of calfless cows and relatively fewer adolescents then would otherwise have been the case. Probably, in an undisturbed situation fewer cow-adolescent pairs would have been formed and more adolescents would have joined other adolescents, or alternatively several adolescents might have attached themselves to each of the few cows that did not have accompanying calves. Cows with calves were less tolerant of the company of additional individuals.

The close "friendship" bond that exists between such companions has already been described (Section C.3). Such bonds once formed were likely to endure for many months or years (Table 58).

A bond formed with a cow is usually terminated by the birth of a new infant to the cow. Should the new infant die, the bond may persist longer. One cow and adolescent female stayed together for at least 26 months, broken only by a period of about a week associated with the birth and subsequent death of a calf to the cow. Another cow, which may similarly have lost a calf, had a four year old adolescent female as her constant companion for a ten month period. Four months after the disappearance of this individual, she was joined by another four year old adolescent female, and these two were still together nineteen months later. A rather aged cow had an 8-10 year old male as her constant companion for at least 21 months, until she calved again. Photographs suggest that this male may have been the same individual who had been with her in 1966, in which case the total bond duration would have been over four years.

Other adolescents attaching themselves to cows may be forced to form new bonds sooner. A male tagged as a three year old in March 1969 stayed with one cow for 9-12 months. When this cow calved, he was seen either alone or temporarily with a series of other companions for four months, then he joined another cow that had lost her calf, and stayed with her for nine months until she also calved. Over the following 3 1/2 months until termination of the study, he was seen either alone or temporarily attached to several other cows and adolescents, but had formed no stable bond. By then he was 5 1/2 years old.

Bonds formed with other adolescents may endure much longer, up to a potential maximum of five years for females and 8-10 years for males. Observations were limited by the duration of the study period, by difficulties in recognizing adolescents that were not ear-tagged, and by the disruptions due to rhino capture operations. Two adolescent males that were four and five years old respectively when first recognized were still together 26 months later. Three other unbroken bond durations of 24 months, 23 months and 20 1/2 months between adolescent males were recorded.

Most cases of bond disruptions were probably related either to the capture and removal of one or both individuals, or to dispersal movements out of the study area. However, there was one observed case in which a five year old adolescent female transferred her allegiance from the seven year old male who had been her close companion for the preceeding year to a four year old female who had later joined the group.

Dispersal movements. When adolescent disappeared from the study area, I generally did not know whether they had moved out, or been captured and removed. However, clear evidence of dispersal movements was provided by strange adolescents which appeared in the study area, were seen regularly over a period of several weeks or months, then disappeared again. Such strangers were usually within the age range of 6-10 years, and appeared most commonly during the early dry season. Their wanderings may have been prompted by the need to seek out new water sources after familiar ones had dried out. In July 1969, I watched a pair of adolescent females at the Lily Pan, which had dried through to liquid mud during the preceeding twenty-four hours. The adolescents spent over an hour in the vicinity of the pool, returning repeatedly to sniff at the mud. Adults, in contrast, moved away without hesitation upon finding no water there. The impression given was that adults knew the location of alternative water supplies, while the adolescents were at a loss as to what to do.

Those adolescents that remained at Madlozi for the duration of the study were mostly individuals that had home ranges based in the vicinity of the permanent Nyonikazane Spring, or that had attached themselves to cows.

There are two records of extreme dispersal movements based on ear-tagged individuals:

(i) A six year old female was an inhabitant of the Nqutsheni area in February 1969. In August 1970 she was seen once at Madlozi, 5.5 km further south, then in February 1971 she was discovered near Mgqizweni Pan near the extreme south-eastern corner of the Umfolozi Reserve. Her total straight line distance of movement was 25 km.

(ii) A young female estimated to be about 3.5 years old when ear-tagged at Madlozi in December 1969 was still at Madlozi when last seen by me as a 5.5 year old in September 1971. She was then accompanying a cow, with whom she had been associated for the preceeding nineteen months. In August 1972 she was seen, still bearing her ear-tags, by P.M. Hitchins during a helicopter survey. She was located then to the south of the White Umfolozi River opposite Dadethu Pan, which was about 15 km ESE of where I had last seen her.

Dispersal movements seemed to be made equally by young females and young males. Though territorial bulls occasionally chased adolescent males, there was no indication of any social pressures on young females forcing dispersal.

Puberty and social maturity

Females. The earliest recorded incidence of oestrus (as indicated by persistent hiccing approaches by a bull) was in an adolescent female estimated to be 3 years 10 months old (± 2 months). There was another recorded oestrus in a female approximately four years old, and a third in a female of about 4.5 years of age. However, another female had still shown no signs of oestrus by 4.5 years. The adolescent female undergoing first oestrus at 4.5 years came into oestrus again at least three times during the following nine months, the last instance being when she was 5.3 years old.

The sub-four year old female while in oestrus persistently avoided the courtship advances of the accompanying territorial bull. Each time he approached she either turned to face him, sometimes springing forwards with a snarl and horn gesture; or she hastened round behind her companion cow. Despite such actions, she squirt-urinated each time the bull approached hiccing. The same pattern continued the following day, and the bull exhibited frustration by directing the motions of mounting towards a bush. It seems doubtful that any mating occurred.

The most accurate estimation of age at first parturition is based on a female who was estimated to be 4.7 (± 0.5) years old when first seen in December 1968. She bore her first calf in September 1970, at an estimated age of 6.5 (± 0.5) years. Three other females were estimated to be about seven years old (± 1 year) at the time of the birth of their first calves. If the last recorded oestrus at 5.3 years by the previously mentioned adolescent female was fertile, this would lead to an age at first calving of 6.6 years.

In all cases, adolescent bonds remained intact through oestrus, and they probably persist until the birth of the first calf. After calving, females did not rejoin their former companions, and displayed little or no evidence of recognition of them in meetings. They moved around with the calf in the manner of other cows, and were hence forth classed as adults.

Males. Adolescent males exhibited little or no sexual behaviour. Two 7-8 year old males approached a cow on the day following oestrus making a few hics, but moved away after being checked by a threatening approach from the accompanying territorial bull. Another 7-8 year old male twice sniffed behind his five year old female companion when she was in oestrus, but made no hics or other approaches; the accompanying territorial bull did not intervene. On two other occasions, adolescent males aged about six years remained with their female companions through oestrus and mating, but were not seen to give any indication of any sexual interest in her. An 8-9 year old male attached himself to a cow together with her attending territorial bull through most of the consort period, including the day of mating. The only suggestion of a courtship advance was a single checked hiccing approach made on the day following mating. Two years later, aged 10-11 years, this same young male approached an adolescent female that was in oestrus and being accompanied by the territorial bull. He sniffed interestedly from 20 m range, but then moved away curling his tail. The territorial bull made no move to chase him.

However, the lack of courtship behaviour by such adolescent males may have been the result of psychological intimidation by the presence of the territorial bull. As described earlier, fully adult subordinate bulls likewise seldom directed courtship advances to oestrous females in the presence of the territorial bull. Interestingly, at Hluhluwe North in the absence of a territorial bull, three young males aged 8-10 years made courtship advances towards an adolescent female.

Each at different times approached behind her hiccing, and some of these led to the chin-on-rump posture. This pattern continued for most of the day, but mounting was not observed and the female reacted antagonistically to all approaches. It is probable that she had already been mated by the adult male who had been seen in the vicinity earlier in the day.

Adolescent bonds between males persisted in some cases until the individuals were physically indistinguishable from adults except by the relatively smooth appearance of their posterior horns. By this time their age was estimated to be 11-12 years. Other individuals became solitary earlier. One young male became separated from his adolescent female companion when under 8 years of age, but still tended to attach himself temporarily to other rhinos. Numerous observations were made on one young male <u>HH</u> as he passed through the transitional stage from adolescence to subordinate bull status. Between the ages of 8 and 9 years he had no close companion, but tended to attach himself temporarily to various cows and other individuals, being associated with other rhinos in 54% of all sightings ($N = 37$). However he restricted his movements mostly to a single territory. Over the following year he was recorded with companions on only 7.5% of sightings ($N = 92$), and the next year, now aged 10-11 years, he was essentially solitary, being seen with other rhinos on only

3.5% of sightings (N = 83).

Another young male aged about 9 years moved into the study area alone and settled within one of the territories as a subordinate bull. Several other lone males of similar age made appearances in the study area at various times, butdid not remain. They were usually strongly challenged if encountered by a territorial bull. Two young males that were virtually adult in appearance, and must have been about 11-12 years of age, wandered into the study area as a pair, stayed for several weeks, then disappeared again. About six months later one of the individuals reappeared alone and still did not respect territorial boundaries despite some tense confrontations with territorial bulls.

Young males of about twelve years of age can become territory holders. One male was still youthful in appearance, and thus must have been about this age, when he became a territorial bull adjacent to the Nyonikazane Spring. Previously he had been a subordinate bull in a nearby territory. One of the Dengezi territorial bulls was judged to be of similar age.

1.4. Play

Two different types of play need to be distinguished.

Self-play or frolicking was engaged in only by young infants, and consisted of running around in the vicinity of the mother. The individual galloped back and forth, or round in circles, frequently coming to sudden halts. One instance was also observed in which a calf pushed a stone around with its horn.

Social play involved a partner and consisted of horn wrestling matches. It was engaged in most commonly by juveniles and adolescents, but was not restricted to these classes (Table 59). Cows also sometimes wrestled playfully, both with adolescents and with other cows. Playful wrestling was also observed once between two young subordinate bulls (Example 26), once between an old subordinate bull and a young adolescent male, and once between a territorial bull and the young subordinate bull that shared his territory.

Play behaviour only rarely occurred between individuals that were companions in the same group, and was never seen between close close companions. Play generally developed from nasonasal meetings between two individuals from different groups. Calves and adolescents showed particular interest in coming forwards to meet other rhinos (Section V.C.2). Frequently, having achieved nasonasal contact, one animal initiated wrestling by pressing its horn against the horn or head of the other (Plate 21). In other cases, particularly with young calves, one individual tossed its head up and down producing a prancing action, and this seemed to function as

TABLE 59. Frequency of play wrestling matches in encounters

Type of encounter	no. of encount. observed	no. of play wrestl. matches	frequency of play wrestling
ADf-ADf	79	4	5%
adol.-adol.	34	6	18%
calf-calf	51	14	28%
ADf-adol.	76	11	15%
adol.-calf	58	10	18%
ADf-calf	60	1	2%

PLATE 21. Adolescent behaviour patterns

a. An adolescent female approaches a cow to sniff nasonasally.

b. An adolescent male and an adolescent female rub horns gently.

c. Two older adolescents, a younger adolescent and a calf meet naso-nasally.

d. An adolescent rubs its head against that of another.

e. An adolescent male and a subordinate bull wrestle horns playfully.

f. Three adolescents stand in the defensive rump to rump formation.

a play invitation signal.

The following actions occurred during play wrestling matches:

(i) Slow fencing and weaving movements were made in head down attitude with horns in contact (Plate 21). Some play interactions did not develop beyond such slow horn fencing.

(ii) More vigorous fencing and prodding movements were made with horns or heads pressed together.

(iii) Upward jabbing movements were made with the head, pushing the horn against the head or shoulders or under the neck of the other.

(iv) Both individuals pushed head to head or head to shoulder commonly with one individual forcing the other back several metres.

(v) One individual broke away and moved off usually at a slow walk or trot while the other chased behind it, directing horn prodding gestures at its rear or flank.

(vi) One individual galloped about excitedly in the vicinity of the other.

(vii) One individual made head tossing or prancing gestures in front of the other.

The sequences of actions in two play interactions, one between two calves and the other between several adolescents and cows, are presented in Examples 52 and 53.

EXAMPLE 52. Play interaction between two calves
(Gqoyini, 22 Mar'69; both calves aged about one year)

0715 two cows with yearling female calf lie close together in watercourse sand; cow A and calf a rise and stand rubbing; /0743 cow B and calf b rise, calf b approaches calf a, the two calves wrestle heads; b moves away, a follows behind, friskily; b turns, vigorously engages its head under b's neck, they wrestle head to head engaging in a vigorous horn tussle; a backs away against cow A, b breaks away, gallops up to cow B in a frisky manner, gallops on past her and the cow follows, they disappear from view/ 0755 calf b gallops back with a couple of puffs, gallops off again/ 0758 A+a suddenly trot E, then walk slowly; b hastens up to them, cow A turns and sniffs noses with calf b, then turns away and stands; b shuffles around, still frisky, moves back to its mother; calf a moves after it, the two calves engage horns and shuffle backwards and forwards in a vigorous tussle/ 0804 a backs away, b advances, they engage heads briefly, a walks away, b prods its horn at a's rear, a turns, b walks away, a prods b, then they tussle head to head again; b walks up to cow A, cow A gently lowers her head, calf b shakes its head with its horn almost touching that of the cow, then moves away and engages calf a, they gallop around, engaging heads then running off again/ 0807 the two calves engage in a vigorous tussle then gallop off side by side, pants are heard, cow A moves slowly S, the calves gallop around with a few puffs/ 0809 calf b gallops around with puffs; cow A and calf a are now both grazing /0811 calf b gallops up to its mother and commences grazing near her.

EXAMPLE 53. Wrestling matches involving several cows and adolescents (Mdlozi, 28 Nov'69)

(Initial stages of the encounter are described in Example 31; individuals include ADf.O with adol.f companion o ADf.K with adol.m companion j and ADf.VV with year old calf)
0715 ADf.VV and adolm j wrestle heads briefly; j then engages the adolf o horn to horn, they stand; o walks away, j walks behind with his horn almost touching, o stands, j makes two horn jabbing motions at her groin without touching; o moves on then turns round, and the two engage horns fencing slowly; VV walks up, stands head up watching the two adolescents, then breaks in to the wrestling; j then wrestles with VV while the o engages VV's calf; a minute later the j and o wrestle together again/ 0720 j places his forelegs on the rump of his companion cow K, standing at right angles to her, K rises and walks slowly away, j resumes wrestling with o/ 0723 all 6 rhinos stand in a huddle; o wrestles with VV, j stands close behind cow O; a minute later j and o wrestle again; VV wanders up, stands to one side watching attentively, the two adolescents wrestle vigorously ignoring her/ 0728 O and o, K and j meet; j wrestles horns with K, O stands beside him, j then leans his head against O's shoulder from the side, this lead to wrestling; o engages K, wrestles briefly then wanders away and engages the j/ 0733 j and VV wrestle vigorously, j drives the cow back a few paces, then pushes his head at her flank, the cow quickly turns and moves away, j follows, they engage heads and wrestle vigorously again; VV's calf stands watching from the side, o is close by, while 25 m away the two cows O and K stand facing, then commence wrestling slowly/ 0738 j and VV still wrestle vigorously, j drives the cow back a few paces then pushes his head under her neck forcing her head up, VV breaks away; O and K stand close together, no longer wrestling/ 0740 j faces VV, shakes his head up and down, VV comes forwards, j coyfully backs, shakes his head again, and a vigorous neck fight develops; VV moves away, j chases after at her heels; O and K wander up; VV stands near O, then moves away at a slight gesture from O, and approaches j who stands near her calf; VV, her calf and j move side by side crossing a gully, then j turns away and moves towards K, who stand a short distance away near the o, while O stands alone to one side; j joins K, o and O move together, and the aggregation dissolves.

All actions displayed in play are basically those involved in fighting. It was relatively easy in the field to differentiate play fighting from serious fights, but is more difficult to characterize the basis for this subjective impression, as many other observers have noted (see Meyer-Holzapfe 1956). The actions of play seem distinguished by these features:

(i) Actions were relaxed and free-flowing, without the jerkiness indicative of tension; (ii) horn blows were struck gently, and did not seem to hurt the other individual (except in a few instances in which one partner became overvigorous); (iii) individuals readily broke off sequences of action, or switched roles, without any clear relationship to the actions of the partner; (iv) individuals seemed eager to engage in play; sometimes a third individual watched with interest from the side and attempted to join in; (v) play interactions were readily broken off by one individual wandering away and transferring attention to grazing or some other activity; (vi) no direct functional result seemed to be achieved, other than the practice of the movements involved. Absent from play were any elements of mounting or other sexual behaviour, except possibly in two instances when a young animal placed its forefeet briefly on a companion cow that was lying down.

Discussion

The period of ontogeny involves initially familiarization with the environment, later becoming acquainted with other conspecifics besides the mother. Simultaneously there is the practice of particular motor coordinations.

Infancy is associated with development of basic locomotor skills of walking and running. Much attention is directed towards investigating objects such as bushes, stones, water and grass. However, the first object of significance is the mother, and the repeated circling and tactile contacts exhibited during the first two to three days probably assists in impressing her form and odour on the infant. Though interest is shown in other rhinos, coordinated play does not develop.

Through juvenilehood and adolescence, particular interest is displayed in other rhinos. Opportunities for play are restricted to chance encounters with other groups, and both juveniles and adolescents show great interest in approaching to meet other rhinos.

As in many other species, play involves basically the actions of fighting. It is clear that competence in fighting is highly significant to males once they become adult. Adult females were never seen to engage in serious fighting, yet play fighting was exhibited both by immature females and adult cows. Another potential advantage in wrestling matches is the increased opportunity offered for familiarization with other rhinos in the local population.

Immature animals were rarely seen alone. Elsewhere it was suggested that the companion bond, whether with the mother or another cow or adolescent, is adaptive in the protection it may afford in the event of a predator attack. Other potential advantages are also conferred. Young males that were associated with a companion seemed less likely to be challenged by territorial bulls than similar aged males that were alone. Learning of the location of environmental features may also be widened by the experience of the other individual.

Uncertainty of the location of alternative sources of grazing and water, rather than social pressures, seemed primarily responsible for the dispersal movements made by some adolescents. It seemed that individuals simply wandered off and got themselves lost.

As in many other species, the attainment of social maturity, as evidenced by reproductive activity, is delayed considerably longer in males than in females. Females undergo their first oestrous cycles and bear their first calves before growth is completed. Young males are unable to reproduce until they have attained full weight and are successfully able to challenge for a territory.

2. Adulthood

The major changes that occur during adulthood involve transitions by males between territorial bull and subordinate bull status, and vice versa. Females undergo only relatively minor behavioural changes in relation to the age of the accompanying calf, and these have already been discussed.

2.1. Territory changes

Observations indicated an average duration of territory occupation by an individual bull of 5.4 years (Table 19), so that changes in territory ownership are rare events. At Madlozi, 15 territories were observed for periods varying between 1.5 and 5.6 years, and 11 changes occurred (see Table 60 and refer to the maps presented in Figure 28):

During my absence between July 1966 and November 1968, three changes had occurred; (i) the bull A had become territory holder in the neighbouring territory of E, and had yielded part of his former small territory to another adjoining bull L; E had disappeared; (ii) the subordinate bull C in E's territory had become territory holder in the adjoining territory formerly held by R; (iii) a new bull GG had become territory holder in the territory of G.

Between my return in November 1968, and termination of the study in September 1971, a further eight changes occurred: (iv) a new bull I appeared in the study area and took over the territory of H in mid-October 1969; (v) H remained on as subordinate bull until January 1970; he then displaced an old bull E from a small territory adjoining the Nyomikazame Spring 1.5 km to the south; (vi) in late May 1970, H took over the much larger adjoining territory of the bull X; (vii) X stayed as subordinate bull for ten days, then took over the neighbouring territory of A; A was still there as subordinate bull at the conclusion of the study 15 months later; (viii) a bull M disappeared in late 1969 (bones presumed to be his were discovered later), and part of his territory was occupied by the neighbouring territorial bull K; another bull N, who had been subordinate bull in H's territory, claimed a small territory in the remaining part in January 1970; (ix) a young bull D, formerly subordinate bull in the adjoining territory, took over the territory of A in October 1969, while A disappeared; (x) a new comer BB took over the territory of B in late December 1969; B shifted across to become subordinate bull in the neighbouring territory of C; (xi) a newcomer bull OO took over the territory of C in July 1971; C still remained there as subordinate bull when last seen in August 1971.

Thus, changes consisted of a new bull becoming territory holder while the former owner became a subordinate bull either in the same territory or in a nearby territory. However, some bulls remained as subordinates for only a short while before taking over another territory. Five territories were taken over by bulls who had been territory holders in a neighbouring or nearby territory; three bulls were displaced by a bull who had been a subordinate bull in a neighbouring territory; and three territories were occupied by bulls who were newcomers to the study area.

Three of the seven territorial bulls known in 1966 were still territory holders in August 1971, though not necessarily in the same territory (refer to Table 60). Of the fourteen territorial bulls identified in November 1968, eight were still territory holders at the conclusion of the study, three had become subordinate bulls and three had disappeared from the area (one presumed dead). Of the four subordinate bulls known in 1966, two had become territory holders by November 1968, while a third became a territory holder in January 1970; the fourth could not be identified again.

In most cases, I was not aware of these transitions until some time after they had occurred. However, for three territory changes occurring in the central Madlozi study area I was able to make detailed behavioural observations on the bulls concerned shortly after the takeover, and also had some observations on the bulls made shortly preceeding it. The various behavioural changes exhibited by the bulls give some

TABLE 60. Changes in the status of various bulls during the study period

Indicated are the identities of the various territory holders at Madlozi at different times during the study, and of subordinate bulls sharing the same territories.

Territory	1966		November 1968		August 1971	
	tADms	sADms	tADms	sADms	tADms	sADms
1.	A	O	-	-	-	-
2.	P	Q	A	-	X	A
3.	X	V	X	D	H	E
4.	L	-	L	-	L	-
5.	H	N	q	N, HH	I	HH, SH
6.	G	-	GG	-	GG	-
7.	R	-	Q	-	OO	Q
8.	J	-	J	-	-	-
9.			C	-	C	B
10.			M	T	N	-
11.			B	-	HB	-
12.			RR	-	RR	-
13.			K	-	K	JJ
14.			W	-	D	-
15.			PP	-	PP	-
16.			U	-	U	-
17.			V	-		

insight into the relationships between the statuses of territorial bull and subordinate bull, and hence I will discuss them in some detail. The three cases to be considered are these: Case 1 - the displacement of *H* by the new bull *I* between 15 and 23 October 1969: Case 2 - the subsequent takeover of *X*'s territory by *H*, which occurred between 22 and 25 May 1970; Case 3 - the subsequent occupation of *A*'s territory by *X* after 5 June 1970.

a. *Behaviour of the new territorial bull preceeding his takeover*

Case 1. The newcomer bull *I*, in mid or late prime, evidently explored through the study area several times before becoming a territory holder there. In December 1968, he was seen on two occasions moving through the western part of *H*'s territory. He scraped and urinated sprays several times (unusual behaviour for an intruding bull), but appeared ill at ease. On 27 September 1969, he was seen sleeping at the southern border of *A*'s territory. On 15 October, he was discovered grazing at the eastern border of *L*'s territory. Here he dug his horn deeply into *L*'s border dungheap, but did not defecate there or spray-urinate. On 23 October he was glimpsed briefly in *H*'s territory. On 28 October, I observed both *H* and *I*, and confirmed that *I* was now territorial bull in *H*'s territory. Evidently the change had occurred between 15 and 23 October.

Case 2. On 21 May 1970, X was seen in his territory accompanying an oestrous cow. On 20 May, H had been seen with two adolescents still in his own small adjoining territory. On 26 May H was discovered in X's territory accompanying the cow that X had been with, and X behaved subordinately to him.

Case 3. On 5 June, the deposed bull X had shifted across the border into the adjoining territory of A. A short confrontation between X and A was glimpsed at long range. The two bulls faced each other silently horn to horn both in dominant posture; X then turned and moved away southwards through A's territory, scraping and urinating sprays three times on his way; A remained standing. On 6, 7 and 8 June, X was watched exploring through A's territory, scraping and urinating sprays repeatedly. A was seen briefly on 6 and 7 June, and was also still scraping and urinating sprays. When next seen on 9 June, A displayed numerous bloody wounds, and evidently a violent fight had occurred.

Seemingly, bulls preceded a takeover by occupying the territory and commencing spray-urinating there.

b. Mechanism of the transition in status

In no case did I observe the crucial contest that decided the transition, though once I glimpsed the end of a second brief fight. Circumstancial evidence based on wounds shown by the bulls concerned has to be used.

<u>Case 1</u>. The defeated bull <u>H</u> had a fresh cut on the left side of his head, a few other inconspicuous gashes on his head, and a nick on the tip of his prepuce (which later became swollen for 1-2 weeks). There were no marks visible on <u>I</u>.
<u>Case 2</u>. No wounds were evident on the defeated bull <u>X</u>, except that his prepuce looked slightly swollen. <u>H</u> appeared unmarked.
<u>Case 3</u>. The defeated bull <u>A</u> showed prominent gashes and bloody bruises around his head, shoulder and neck region, and he made deep chesty coughs. The victor <u>X</u> showed no wounds, except that the tip of his posterior horn was nicked off.
<u>Other cases</u>. Two other defeated bulls were seen shortly after their deposement. The bull <u>B</u> displayed a large bloody mass in the mid-frontal region (which left a noticeable dent after it cleared up), and several other gashes on his head. The bull <u>O</u> showed several fresh wounds around the facial region, and a few minor gashes on the shoulder and right side. The victorious bulls <u>BB</u> and <u>OO</u> looked clean apart from two minor scratches on <u>OO</u>'s head. In all other cases, new territory holders exhibited no notable wounds.

Evidence suggests that three territory takeovers were accomplished by violent fights, while in remainder some other form of contest took place. The presence of preputial swellings in two cases suggests that a horn jab in this region may have been significant.

c. <u>Relationship between the new territory holder and the deposed bull</u>

<u>Case 1</u>. The first observed meeting between <u>H</u> and <u>I</u> occurred on 28 October, 5-12 days after <u>I</u>'s takeover. <u>I</u> paid little attention to <u>H</u>, while <u>H</u> snorted nervously (Example 54). Seven further encounters between these two bulls were seen during the month following the change. In three <u>I</u> took little notice of <u>H</u>, while <u>H</u> watched <u>I</u> carefully (Example 55). In three, <u>I</u> made a sudden charge, but veered aside when <u>H</u> snarled (Example 56). In one, occurring a month after the transition, there was a tense confrontation lasting about ten minutes with <u>H</u> snarling defensively, then <u>I</u> walked away (Example 57).

<u>Case 2</u>. An encounter between <u>X</u> and <u>H</u> was observed on 26 May between one and four days after <u>H</u>'s occupation of the territory. The deposed bull <u>X</u> watched <u>H</u> intently, making a few snorts and snarls. <u>H</u> remained with the cow, taking no notice of <u>X</u> (Example 58).

<u>Case 3</u>. Judging by the wounds on <u>A</u>, a violent fight had occurred on or about 8 June. <u>A</u> then kept to the border region of the territory, and probably no further meeting between the two bulls occurred until the late afternoon of 11 June. Earlier that afternoon I had watched <u>A</u> as he grazed along the south-eastern border of the territory, scraping and urinating

EXAMPLE 54. First observed encounter between the new territory holder I and the deposed bull H (occurring 5-12 days post-takeover, Madlozi, 28 Oct'69)

1425 I emerges mud-plastered from a pan, walks N alert, approaches another rhino (who turns out to be H), urinates sprays, then turns W and continues on around H; H (who is upwind) stands alert facing I, makes one soft snort; after I has passed H resumes grazing.

EXAMPLE 55. Encounter between the new territory holder I and the deposed bull H; H watches I, while I takes little notice of him (14-21 days post-takeover, 6 Nov'69)

0802 H stands observing I and his cow and calf grazing about 40 m away, they ignore him; H turns away resuming grazing, but looks up towards the other rhinos at intervals; I grazes nearer, H stands head low relaxed watching from 30 m /0813 I grazes facing H and H backs 2 paces, remains standing head low facing I, I grazes around ignoring H/ 0815 I grazes 45° towards H, H backs 2 paces, stands, looks at I first with the left eye then with the right, backs a pace, stands head low but watching I 23 m away/ 0818 I grazes away, H backs a pace, turns slightly to keep facing towards I at 30 m range/ 0820 I grazes away into the shade, H backs 2 paces, stands head low; I rubs on a tree, H backs a pace turning to face directly towards I again; I shifts 2 paces out of the shade, H backs 4 slow steps, I inclines his head to look towards H, H backs a pace; H lies down at 0823, 35 m away from I/ 0835 I lies down in the shade.

EXAMPLE 56. Encounter between the new territory holder I and the deposed bull H; short charge begun by I (12-19 days post-takeover, 4 Nov'69)

0842 H rests standing in the shade of a tree; I moves after his cow and calf, get downwind of H, starts approaching, breaks into a trot, H immediately snarls and I swings aside after only a few steps, stands 40 m away from H.
0915 I rubs on a tree, wanders ESE, passes downwind of the sADm. N at 120 m range, turns and walks towards N, turns slightly aside to get downwind of H at 35 m range, H rises to his feet, I begins trotting at H but turns aside when H snarls; I wanders away towards the cow and calf, pausing to scrape and urinate sprays.

EXAMPLE 57. Encounter between the new territory holder I and the deposed bull H; tense confrontation (24-31 days post-takeover, 16 Nov'69)

1545 the two bulls I and H stand facing, I repeatedly advances a few steps at a time towards H then away again, H blocks each advance by lowering his head, otherwise he stands with head raised and ears flat snarling repeatedly; I advances and H backs away, ears flat snarling repeatedly; I advances, there is a short horn clash with dust, I drives H back several metres/ 1555 I walks off leaving H standing.

EXAMPLE 58. Encounter between the new territory holder H and the deposed bull X only a few days after H's takeover (1-4 days post-takeover, Madlozi, 26 May 70)

0718 X moves southwards exploring sniffing at various sites along the way /0735 X encounters a trail, moves along it; suddenly he notices the bull H together with a cow and calf lying 40 m away in front of him (the breeze is from the side, so neighor bull is downwind); X turns to face towards them head up, turns to stand facing away at right angles, gives a "sigh", remains standing; X shifts 3-4 paces towards the other rhinos, gives one urine spray without scraping, stands staring; the calf stands, the cow rises, yawns, ADm. H rises; they move east, while X stands watching from the north; X makes a deep gruff snarl; the cow and calf shift east, H moves round to block them on the SE with squeals, X stands watching only 15 m away/ 0745 H shifts round E of the cow with squeals, X gives a curt snort, then a checked grunt, from 25 m range /0747 X turns away, walks away NW, turns round to stand facing back towards the other rhinos; H and the cow and calf graze; X moves away W 7 m, stands; then moves on, commences grazing moving away from the other rhinos.

sprays. At 1735 I heard tensed squeals from my caravan, and rushed out in time to glimpse _X_ and _A_ engaged in a pitched battle. _X_ drove _A_ back with a succession of vigorous horn blows, then _A_ broke and galloped off with _X_ in pursuit. The fight lasted no more than 1-2 minutes. No further meeting between _A_ and _X_ was observed until 22 June. Then I heard a loud wailing shriek, and found _X_ walking off while _A_ remained standing.

Thus, the new territory holder does not attempt to drive the former holder off the territory. He either takes little notice of the other bull, or makes a checked approach, or engages in occasional brief confrontations; thus exhibiting the behaviour patterns typically displayed by a territorial bull towards a subordinate bull (see Section V.C.2.1.). Correspondingly, the deposed bull displays the nervous watching and defensive threats typical of a subordinate bull. In the case of the bull _A_, it seems that _A_ did not accept subordinate status until after the second fight. Notably, he also continued spray-urinating until then (see below).

d. Relationship between the new territory holder and other subordinate bulls

Case 1. When the bull _I_ took over _H_'s territory in October 1969, there were two subordinate bulls present: an elderly bull _N_, who had been subordinate bull there since June 1966;

and a young adult male <u>HH</u>, who had been there at least since November 1968.

Eight encounters between <u>I</u> and <u>N</u> were seen in the month following the takeover, In seven, <u>I</u> took little or no notice of <u>N</u> (Example 59). In one, <u>I</u> advanced on <u>N</u>, but turned aside before meeting (Example 59). The subordinate bull watched <u>I</u>'s movements, snorted, snarled or shrieked when <u>I</u> approached, but did not move away from <u>I</u>.

Five meetings between <u>I</u> and <u>HH</u> were observed during the month following <u>I</u>'s takeover. In four, <u>HH</u> moved away tail curled on noticing <u>I</u> at ranges of 25-70 m, and in one of these instances <u>I</u> chased after him for 70 m (Example 60). One encounter lead to a brief horn to horn confrontation, with <u>HH</u> snarling defensively, then <u>I</u> moved away.

In the other two territory takeovers, there had been no subordinate bulls in the newly occupied territories.

The new territory holder <u>I</u> thus exhibited tolerance towards an old subordinate bull, but once chased after a young subordinate bull. This may have been related to the nervousness shown by the young bull in the presence of the new bull (the previous territory holder <u>H</u> had paid little attention to him).

e. <u>Orientation and marking behaviour of the new territory holder</u>

EXAMPLE 59. Encounters between the new territory holder I and a previously resident elderly subordinate bull N (Madlozi, 25 November'69)

0807 sADm.N defecates, makes 10 kicks afterwards; tADm.I grazes 100 m away; I looks up, walks slowly towards N, N watches him turning his head slowly from side to side, his body inclined 45° away from I, his head turned to face towards I; at 70 m I turns away and resumes grazing/ 0810 I turns to graze towards N who is now 37 m away, N immediately snarls, I grazes away without looking up /0820 I pauses in the shade of an acacia, lies down /0840 N lies down 50 m from I.
0930 shrieks are heard, I advances on N, N backs away a few metres before him with shrieks; I turns away, pauses to sniff at the dungheap where N had defecated earlier, sniffs for about 1 minute then moves away, commences grazing /1010 I grazes 30 m from N, N stands watching him /1030 I walks steadily E, then turns towards N, N stands watching him, his tail slightly raised, edges backwards; I stops 18 m from N, then continues on past him; N resumes grazing.

EXAMPLE 60. Encounter between the new territory holder I and a previously resident young subordinate bull HH (Madlozi 29 Oct'69)

1023 I walks slowly towards HH, HH turns slowly and walks slowly away, tail curled, 25 m from I; I turns away, scrapes and urinates sprays /1123 I move towards HH, HH turns and trots away when I is 70 m away, for 20 m, then stands; I defecates, then wallows /1142 I wanders on, HH hastens away 50 m ahead, I walks after him, HH walks on, I breaks into a gallop and chases HH, making gruff squeals, for about 70 m, then stops; HH continues walking away, crossing over the territory boundary.

Case 1. On 28 October (5-12 days post-takeover), the new territory holder I defecated with 8 preceeding and 9 succeeding kicks. He was seen spray-urinating once, but the sprays were weak, projecting only about 1.2 m backwards. On 29 October, I was watched exploring along the eastern border of his new territory. He scraped and urinated sprays repeatedly (20 times in 2 hours) while moving along the boundary. He then explored across the boundary, penetrating as far as 130 m into the adjoining territory in two circuits, but each time veered back into his own territory (see Example 3). He scraped and urinated sprays once while over the border, but horned and scraped twice more without urinating. He dug his horn vigorously into the border dungheap of the neighbouring bull, but did not defecate there. Instead, he dunged with kicks at the border dungheap within his own territory. On 31 October, I was with a cow, and blocked her movements at the northern border of the territory. On 3 November, I was still with the same cow, and blocked her movements both at the eastern and northern borders of the territory. While doing so, he spray-urinated a record frequency of 29 times in 122 minutes. The eastern and southern boundaries adopted by I seemed almost identical to those held by H. The northern boundary respected by I lay about 300 m further south than that of H's territory, so that I occupied a smaller territory than H had (135 ha vs. 190 ha, see Figure 28).

Case 2. On 26 May (1-4 days post-takeover), H blocked the movements of a cow at the south-eastern border of the territory. On 27 May, he flanked the cow on the west at the western border of the territory. On 4 June, he was observed patrolling and marking along the southern boundary of the territory. The boundaries adopted by H seemed similar to those respected by X, except in the south-west where H incorporated additional ground which had formed part of the small territory he himself had formerly held there.

Case 3. On 6 June, only a day or two after having moved into A's territory, X was watched turning back nervously from the northern boundary (in the same location respected by A) (Example 4). Two days later X looked up, then turned aside at the southern border, which adjoined the territory that X himself had formerly held. The eastern boundary adopted by X likewise seemed identical to that held by A, but in the west X lost a strip about 300 m wide incorporating a pan to the neighbouring bull C. While under observation over the five days 5-9 June, X spray-urinated repeatedly throughout the extent of the territory. By 9 June, the profusion of fresh scrapemarks was striking. I noticed several cases in which scrapemarks had been duplicated over adjacent bushes only a metre apart, an unusual occurrence suggesting that X had been marking over scrapemarks placed by the previous holder A. X defecated with 8 proceeding and 9 succeeding kicks on 8 June, and gave 7 preceeding and 9 succeeding kicks when defecating on 9 June.

New territory holders seem to have no difficulty in orientating with their newly acquired territories, blocking the movements of cows appropriately within a few days of settling. In general they adopted identical boundaries to those held by the previous holder (as was also observed in several other cases), but in two cases some ground was lost to a neighbouring bull. New territorial bulls clearly devoted particular attention to establishing their own urine marks on the territory, and also immediately defecate in the manner of an established territorial bull.

f. Orientation by the deposed bull

Case 1. On 28 October (5-12 days post-takeover), H was encountered within the central region of his formerly held territory. On 29 October, he walked following the new northern border of I's territory for several hundred metres, then commenced grazing across on C's side of the border. On 30 October he was seen near the north-western corner of the territory. On 31 October he was found lying near the north-eastern corner in the morning, but in the afternoon grazed through the central short grass area. Through November and

December, he was seen ranging fairly centrally through I's territory, and apparently remained on here until late January or early February. On 23 January and again on 28 January, he was found lying near the Nyonikazane Spring (which was then the only water supply in the study area), and was last seen in I's territory on 1 February. Thereafter he apparently occupied a small territory adjoining the spring.

Case 2. The defeated bull X was still within his former territory on 26, 28 and 29 May, but not in any border region. He was next seen on 5 June in A's territory.

Case 3. On 9 June, with fresh wounds evident, A spent most of the day either lying or grazing near the new western border of X's territory. On 10 June, he was watched all day as he grazed first along the eastern border of X's territory, then along the neighbouring bull L's side of the northern border. On the morning of 11 June, A was still on L's side in the region of the north-east border. He then walked southwards on the neighbour G's side of the eastern border. That afternoon he was grazing along the south-eastern border of X's territory, and this was where the second attack by X took place. The next day (12 June), A was lying at the eastern border of X's territory in the early morning. He walked northwards, then turned westwards following the northern border on L's side, then moved along the northwestern border before pausing to graze. On 13 June, he spent the morning sleeping in the vicinity of the western boundary, then grazed in the afternoon in the northern boundary zone. On 14 June, he was seen briefly at the eastern border. On 16 June, he moved along the western border, then settled to sleep there. That evening he appeared near my caravan at the eastern border. He was next seen on 22 June, again grazing in the eastern border region. When next sighted in August, and thereafter, he moved through the complete extent of X's territory.

Thus, one of the deposed bulls seemed to avoid the new territory holder by keeping to territory border regions for 10-15 days following the change. However, he also seemed to be inhibited from intruding far into any of the neighbouring territories. Another bull also seemed initially to orientate towards territory boundary regions, notably in this case observing the new location of the northern boundary established by the new owner.

g. Urination by the deposed bull

Case 1. The deposed bull H was not seen urinating until 2 November (10-17 days post-takeover), though he had been watched for a total of eight hours over the preceeding five days. He then adopted the legs straddled, tail upcurled posture and urinated in a steady stream, and urinated in similar fashion

in three subsequent observations through November and December.
<u>Case 2</u>. On 26 May (1-4 days post-takeover), <u>X</u> straddled his hindlegs apart and urinated in a stream. Later that day he gave a single urine spray while standing staring at the new territorial bull (see Example 58).

<u>Case 3</u>. <u>A</u> continued spray-urinating over the three days 5-7 June after <u>X</u> had moved into his territory, so that both <u>A</u> and <u>X</u> were spray-urinating at the same time in the same territory. On 9 June (one day post fight), <u>A</u> was not observed urinating during 7 1/2 hours observation. On 10 June, <u>A</u> spray-urinated 8 times in 17 minutes while moving along the eastern border of the territory, but did not urinate during the remaining six hours for which he was under observation. On 11 June he scraped and urinated sprays repeatedly while moving in the region of the eastern border, including a spell of 8 spray-urinations in 47 minutes while grazing in the south-eastern boundary region in the afternoon; this preceded the second fight with <u>X</u>. On 12 June <u>A</u> horned and scraped, but instead of sprays there were two squirts then a short pulsed stream of urine. Next <u>A</u> scraped and urinated three very weak sprays, followed by a fluctuating stream for 55 sec. Again <u>A</u> scraped, this time urinating one weak spray followed by six pulses of diminishing intensity, the last merely a weak stream. Later in the day, however, <u>A</u> scraped and urinated

a good spray. On 14 June, A was seen urinating in a stream with hindlegs straddled. On 15 June A followed defecation by standing with upcurled tail and hindlegs straddled, and urinated in a stream for 130 sec. Thereafter, he always stream-urinated.

Evidently, bulls cease spray-urinating immediately or within a day or two after being deposed as territory holder. In the case of the bull A, final defeat apparently occurred only after the second fight.

h. Defecation by the deposed bull

Case 1. When seen defecating on 30 October (7-14 days post-takeover), the bull H made no preceding kicks, but gave 8 subsequent kicks. On 2 November he defecated with no preceding and 10 succeeding kicks. On 17 November he again omitted preceding kicks and gave 9 following kicks but these were slow in action and only gently pushed the dung pile backwards. On 20 November he defecated and gave 5 slow kicks afterwards. On 21 December he dunged at a border dungheap and gave 5 slow kicks aftergards; only 3 of these made contact with the dung pile, but hardly disturbed it. On 10 January, H gave only a single slow kick after defecation.

Case 2. On 26 May, between 1 and 4 days after losing his territory to H, the bull X was seen defecating; he shifted his weight from one hindleg to the other without kicking, then made a few more vigorous movements which may have been kicks (a bush obscured my view) prior to defecation; afterwards he gave 3 kicks. On 28 May, X sniffed at a dungheap, shifted into a central position, then as his tail began curling he made one token kick, defecated, gave another half-powered kick, then walked off. On 29 May, X stood shuffling his weight from one hindleg to the other without kicks for several seconds, defecated, then walked on without giving succeeding kicks.

Case 3. On 10 June (2 days post-fight), A paused at a dungheap, kicked twice, defecated, then kicked 7 times. Later that day he defecated at another dungheap with 5 preceding and 7 succeeding kicks. On 11 June, he gave 4 kicks before defecation and 11 afterwards. On 12 June after the second fight, he defecated with 8 preceding and 5 succeeding kicks. On 13 June he defecated with 5 vigorous preceding kicks and 14 succeeding kicks. On 16 June he defecated twice while under observation; the first time he gave 1 preceeding and 8 succeeding kicks, all of good power; the second time he kicked 4 times before and 12 times after defecation. He was next observed defecating on 16 September, three months after loss of territorial status. This time he gave no preceeding kicks, and made only 3 slow action, delayed succession kicks afterwards.

Thus, dung-kicking waned more gradually over a period of several weeks. Initially, preceding kicks were omitted; then the vigour of succeeding kicks diminished, so that these became merely token gestures which did not scatter any dung.

i. <u>Behaviour of the deposed bull towards other bulls</u>

<u>Case 1</u>. Four encounters were seen between the deposed bull <u>H</u> and the bull <u>N</u> who had formerly been his subordinate. In three of those in which <u>H</u> was upwind, <u>H</u> watched <u>N</u> nervously, making sudden snorts or grunts when <u>N</u> moved. In one, in which <u>H</u> was downwind, <u>N</u> snarled while <u>H</u> grazed calmly ignoring <u>N</u> at 10 m range. No encounters were observed between <u>H</u> and the other subordinate bull <u>HH</u>.

On 31 October, an encounter was seen between <u>H</u> and the neighbouring territorial bull <u>C</u>, which took place in the region of the new northern territory boundary. <u>H</u> faced <u>C</u>'s approach with a series of loud snarls, backing away a few metres; <u>C</u> stopped and turned away before quite meeting <u>H</u> (see Plate 16).

<u>Case 2</u>. No encounters between <u>Y</u> and any other bull were seen.

<u>Case 3</u>. On 11 June, in the morning preceeding the second fight, <u>A</u> spent nearly three hours in the company of a pair of young adult males (<u>VV</u> and <u>VI</u>). He approached one of these young males with a few hics, and also exhibited flehmen at the urination site of this male; which was rather strange

behaviour, more appropriately directed towards a cow. On 15 June, 4 days after the second fight, A stood facing one of these young males giving loud snarls and shrieks; A was downwind.

Thus, deposed territorial bulls immediately adopted the defensive snarl posture when uncertain of the identity of any nearby bull. If downwind, and thus presumably able to recognize by scent the other bull, a deposed bull took little notice of another subordinate bull.

j. Behaviour of the deposed bull towards cows

Case 1. On 28 October (5-12 days post-takeover), H circled round and approached a cow and calf from downwind, but his approach seemed somewhat hesitant, and he seemed somewhat inhibited as he stood sniffing at the cow from 5 m away; he quickly backed away 1-2 short steps when the cow snorted while grazing in front of him. On 2 November H again approached a cow and calf slowly and hesitantly until he got downwind, stared at the cow intently, then moved away. On 3 November he approached a cow edging forwards slowly from downwind, backed away hastily when the cow made and advancing snarl, stared again intently, then turned and moved away.

Case 2. No meeting between X and a cow was seen, except in the presence of the new territorial bull H (Example 58).

Case 3. On 10 June (2 days post-fight) while moving spray-urinating along the eastern border of his formerly held territory, A suddenly noticed a cow and adolescent ahead of him. He quickly turned and walked away rapidly. Two hours later he encountered the same cow and adolescent 40 m away in front of him. He stared displaying great hesitation, alternating between stepping forwards then back again, then moved away (Example 61). Four hours later, A reencountered the same two individuals. He stared, stepped back, horned the ground, then advanced; at a snort from the cow, he relaxed and commenced grazing (see Example 61).

Thus, deposed bulls approached cows, but did so with great hesitation; possibly uncertain, until near, whether the other individual was a bull or a cow.

k. Behaviour of neighbouring territorial bulls

On 31 October 1959, 8-15 days after the takeover of the adjoining territory of H by the new bull I, C was watched moving through what had been the northern part of H's territory. C spray-urinated repeatedly as he explored through this area within which he had never been seen before. This was the area that became transferred to C's territory. C met and confronted briefly both the deposed bull H and the neighbouring subordinate bull N in the region of the new boundary established between C's territory and that of the new neighbouring bull I. On 17 November, C was observed blocking a cow at this new

EXAMPLE 61. Encounters between the newly deposed bull A and a cow and adolescent (Madlozi, 10 June 1970)

1125 A grazes WSW on the neighbour L's side of the northern border of his former territory; he pauses looking intently ahead, moves his head sideways in a sudden brief gesture, takes 2 quick paces backwards, stands looking; takes another 2 quick paces backwards, stands looking intently; a cow and adolescent companion are 40 m away ahead of him at a pan /1128 A drops his head as if to wipe his horn, then stands looking again; turns moving slowly, scrapes and urinates sprays, moves on SSW with slow movements, horns scrapes and urinates 8 m further on, pauses looking towards the cow and adolescent from 30 m; A takes a pace forwards then almost simultaneously a sudden pace backwards, stands looking; takes 3 backwards steps, pauses, backs 3 more paces, turns partly away, stands looking, wipes his horn over the ground, stands looking again, turns away, moves slowly N, scrapes and urinates, walks N then SW circling round the cow and adolescent.
1545 A looks up from grazing to find the same cow and adolescent grazing about 40 m W of him (still in the N border region); A takes one backwards step, stands; takes 3 backwards steps, turns 45° away from the cow and adolescent, stands with head angled low; takes a backwards step, turns to face towards the cow and adolescent, they graze around 35 m away from him; A takes 2 backwards steps, turns 90° away from the cow and adolescent, stands hesitantly, backs several paces, turns to face 45° towards them, horns the ground but does not scrape or urinate, advances towards the cow and adolescent; the cow snorts at 25 m range, A continues advancing, stops 18 m from the cow, the cow continues grazing; A turns and stands facing 60° away from the cow, his head low in relaxed posture.

southern territory border.

The location of the border between I's territory and that of the neighbouring territorial bull to the east, L, did not change. It may be significant that L was accompanying a cow at the time of the takeover.

In association with the takeover of A's territory by X, the neighbouring territorial bull Q incorporated a 300 m wide strip, including a pan, into his own territory (this had previously been part of A's territory). However, I was not able to confirm this change until several months later.

It seems that neighbouring bulls can sometimes detect a change in ownership of an adjacent territory and establish a claim to additional land at this time, presumably by establishing their urine marks before the new bull has had a chance to establish his. This did not occur in the case of the bull L, possibly because bulls accompanying cows avoid coming into the close proximity of territory boundaries.

Removal of territorial bull experiment

An unplanned removal experiment occurred when the bull J, who occupied a territory peripheral to the Madlozi study area, was caught by the rhino capture team and transferred to Mocambique. I kept an intermittent watch on this territory for signs of occupation by a new bull, looking particularly for fresh scrapemarks and marks of dung-scattering at the dungheaps. Nothing was noted until 11 days after _J_'s removal. Then the neighbouring territorial bull from the south, _PP_ was discovered in the territory; but _PP_ ran off nervously back into his own territory at my approach. Fresh scrapemarks were evident, and there was freshly scattered dung at one of the dungheaps. Fresh scrapemarks were noticed within the territory on several succeeding checks. Several months later I was able to confirm that _J_'s territory had been subdivided by the two neighbouring territory holders, _PP_ from the south and _D_ from the east.

Occupation of a territory by a subordinate bull

Several observations were made on the bull _N_, (who had been a subordinate bull in _H_'s, later _I_'s, territory), over the period during which he transferred himself to a small territory one kilometre further east, where he became a territorial bull. This occurred about two months after the takeover of his former home territory by the new bull _I_. _N_'s new territory had formed the western part of the territory held by the bull _M_, but following _M_'s disappearance in October 1969, so far as I was aware, no other bull had established a claim to the area. The remainder of _M_'s territory had been claimed by the neighbouring bull _K_, but the combined area of this territory plus _K_'s original territory was probably too large for _K_ to patrol adequately.

The bull _I_ took over _N_'s home territory in late October 1969. Through December and January, _N_ was seen in various locations, and was evidently wandering around; though some of this movement was related to the severe drought prevailing then. _N_ was seen at or returning from the Nyonikazane Spring on five occasions, was watched exploring or resting in the neighbouring territory of _L_ to the east on four occasions, and was only twice seen in _I_'s territory. On 15 January 1970 he was seen returning from the spring in the direction of _I_'s territory displaying fresh wounds. On 19 January, he was found in his new territory, accompanying an old cow and her three adolescent companions. He scraped and urinated sprays twice while under observation, but the sprays were weak; and he gave only 2 and 3 sprays on each occasion, fewer than that typical of a territorial bull. In another instance he horned vigorously over a bush, scraped and curled his tail, but no urine spray appeared. _N_ also made a few hics while approaching the adolescent female companion of the cow. The next day _N_ scraped and urinated sprays 9 times in 37 minutes while under observation, though giving only 2-3 sprays each time. He defecated with at least 4 preceeding and 11 powerful succeeding kicks. Thereafter he was always found within his new territory.

2.2. Senescence

The deposed bull A had remained as a subordinate in his former territory for 15 months by the conclusion of the study. Judging by the massive appearance of his posterior horn and wrinkled appearance, he was an aged individual, and may have been passing beyond the stage of active competition for territories. Notably, while a territorial bull A had never shown any wounds, and evidently he had not had to fight to maintain his territorial status until X's challenge in June 1970. After having become a subordinate bull, A was seen exploring outwards through other territories on two occasions, and thus evidently had not abandoned the quest for a new territory.

The elderly bull N had been a subordinate bull for at least 2.5 years before becoming a territory holder, though the territory that he took over was a poor one. Another old bull E occupied a small poor quality territory adjoining the Nyonikazane Spring for several months before being displaced by the bull H. After H's takeover of X's territory, E became a subordinate bull in H's new territory.

At Gqoyini, two subordinate bulls that were clearly of advanced age frequented one of the territories adjoining the Hide pans. Both were profusely scarred and rather phlegmatic in nature, sometimes not even bothering to rise when I passed close by. They were never seen in the company of a cow, and were not recorded outside the limits of the single territory.

At Nqutsheni, one of three subordinate bulls coinhabiting a single territory appeared aged. This bull died during an attempt to ear-tag him; while lying partly on his side under the influence of the drug, he shook his legs a few times and quietly passed out. Post-mortem examination by NPB veterinarian Dr. M. Keep confirmed that he was of advanced age. Numerous pulmonary nodules were present, but nothing of extreme pathological nature was apparent, and arteriosclerosis was minor. Dental surfaces were worn, but teeth would still have projected well above the gumline; wear was greater on one side than on the other.

At Madlozi there was an old cow with a long anterior horn who was conspicuously wizened and shrunken in appearance. She also limped badly on her right lindleg and her carpal joint was swollen. She had no calf with her in 1966, nor through 1968-1969. However, in August 1970 she bore a calf which was still with her at the termination of the study a year later. Another cow with a very long anterior horn had a calf in 1966, but was not seen with a calf through 1968-71. However, who was recorded in oestrus and being mounted by a bull in March 1970. It seems likely that she had calved earlier but had lost the calf. In the cases of two other elderly cows, calving was delayed beyond the usual interval (see Section VII.2.5.).

The potential longevity of a white rhino could not be established during the present study. The oldest zoo specimen of knowledge is a female 25 years old and still alive at Pretoria zoo in 1971. For the black rhino, Goddard (1970) cites one individual that was 36 years old and still alive in the Chicago zoo; accordingly he assumes a potential ecological longevity for the black rhino of 40 years. For the Indian rhino, Reynolds records a maximum attained longevity of 47 years. For the hippopotamus, Laws (1968) cites a maximum longevity record of 49 1/2 years, and assumes an ecological longevity of 45 years. For the African elephant, Laws (1966) assumed an ecological longevity of 60-70 years based on recorded lifespans of over 65 years in the Indian elephant.

Accordingly, a potential lifespan of up to 45-50 years may be assumed to hold for the white rhinoceros.

Discussion

A new territory holder immediately displays all the behavioural actions appropriate to a territorial bull. He confidently moves about his new territory establishing his own scent marks, and consorts with cows and blocks their movements unhesitantly at boundaries. The continued presence on the territory of the former territory holder is tolerated;

towards him the new holder displays merely occasional approaches and brief confrontations as are typically shown by territorial bulls towards resident subordinate bulls.

A deposed territorial bull behaves like a subordinate bull in his former territory. He gives defensive snarls or other separation maintaining threats when challenged or approached by the new territory holder or other bulls. He shows hesitation in approaching cows, possibly unable to distinguish them initially from bulls. He immediately ceases spray-urination, and more gradually eliminates dung-scattering. It is as if an internal switch had been transferred to an alternate psychological state manifested by a whole new set of behavioural patterns.

The behaviour of the bull _X_ is particularly interesting in showing such a transition and also its reversal. A few days after deposement, _X_ had ceased both spray-urination and dung scattering. Several days later, having transferred himself to another territory, he once more exhibited spray-urination and dung kicking. This behaviour seemed to signify that he was claiming dominance within the new territory. Correspondingly, he also maintained dominant posture when challenged by the resident territory holder. The continuation of spray-urination by the bull _A_ for several days after the first fight seemed to indicate that he had not yet relinquished his claim to dominance in the territory. The second fight evidently settled the dispute, as shown by the extinction of spray-urination by the defeated bull thereafter.

A puzzling problem remaining unsolved concerns the manner in which the dominance transfer was accomplished in those cases in which there was no evidence of a fight. It is possible that a few telling blows by one bull may have been crucial in destroying the confidence of the other. Alternatively, a ritualized form of combat may have taken place. This could possibly take the form of a pushing contest as was observed in play bouts between adolescents. This explanation is suggested also by questions raised by V. Geist (pers. com.) concerning the functional significance of the posterior horn; it could serve to hold the heads of the two animals together during such a pushing match. However, such action was not observed during serious fights.

Territory changes also provide further evidence for the significance of scent marking for demarcating boundaries. It was observed that new territory holders generally adopted the self-same boundaries that had been held by the previous owner. Considering the infrequency of direct encounters between neighbouring bulls, this could only have been on the basis of the scent marks of the previous holder and neighbouring bulls. Also, in one (or possibly two) cases, the defeated bull orientated preferentially along territory boundary regions, though no longer scent marking himself. Since the bull kept mainly on the neighbour's side of the boundary, this could not have been based on any psychological security offered by his own boundary scent marks from several days earlier. Rather, it seemed that he was avoiding scent marks associated with the bull that had defeated him, but at the same time was inhibited from intruding far into the neighbour's territory. Such a location also offers greatest security in the event of a challenge by either bull, since retreat is possible in either direction. Such observations provide evidence that the significance of scent marks is not limited merely to that of defining the home area for the originator. Similarly, neighbouring bulls were evidently able to detect the occurrence of a change in ownership of an adjoining territory, presumably by noting the absence of fresh scent marks of the former holder.

Bulls may undergo several transitions between territorial bull and subordinate bull status during their lifetimes. However, it seems that the most capable bulls tend to remain territorial bulls during their prime, merely taking over another territory when deposed. Subordinate bulls include some up-and-coming young bulls, who have still to stake their first claim to a territory, some old bulls that have probably "retired" from active competition for territories, and some prime individuals that are biding time for an opportunity to challenge successfully for a territory. Significantly, however, no case was known in which a subordinate bull deposed a territory holder within whose territory he had been resident. Also, in most cases of change, bulls did not move very far to claim a new territory. I have no observations to show how previously subordinate bulls challenge established territory holders.

The presence of subordinate bulls does not seem to be an artificial situation created by atypically high population densities. Rather, it seems likely that subordinate bull status is a natural stage in the life cycle of males, just as in many antelopes males may alternate between holding a territory and recuperating in a bachelor herd (see Leuthold 1966; Estes 1969). As bachelor herds contain a predominance of young and old animals with fewer prime individuals (most clearly shown by Joubert (1972) for the mountain zebra, so subordinate bulls show a similar age distribution. For any prime individual unable immediately to claim a territory, a choice exists between moving away to seek out a territory in a less densely populated area, or remaining on awaiting an opportunity in a more favourable habitat. The latter may be the more successful evolutionary strategy.

F. ON THE EVOLUTION OF TERRITORIALITY

The territorial system results proximately from behaviour patterns displayed by males in encounters with other males and in response to their scent marks. The ultimate question is, how is it that males achieve selective advantages as a result of the territorial dispersion? The relative genetic contribution of males is related to access to survival influencing resources, to sexual success in mating with females, and to the viability of the offspring resulting from such matings.

(a) Survival. The grazing resources of a territory are shared among numerous cows and immature animals and with resident subordinate bulls. There is evidently some pressure on males to disperse to less crowded areas; the adult sex ratio in favourable habitat was 0.67m:1f, compared with an overall population average of 0.8m:1f (Section VII.B.3). Thus the population density of adult males in such areas is reduced by 16%, and overall white rhino biomass by about 5½%. This may result in some enhancement of the survival of resident territorial bulls. However in compensation territorial bulls are prevented from utilizing areas of hillslope grassland favoured by cows during the late dry season if these do not fall within territory limits. Notably, the behaviour of territorial bulls does not prevent other males from feeding within the territory if the latter behave submissively, and cows do not exhibit territorial exclusion, though they would benefit from any survival enhancing effects of such behaviour. No competitive displacements related to feeding areas were observed. White rhinoceroses are relatively unselective grazers in Jarman's (in press) terms, and food quality is fairly uniform over extensive areas even during periods of dry season food stress. It seems more advantageous for individuals to concentrate on rapid intake of food rather than expend energy driving away competitors, as was described by Kruuk (1972) for hyenas.

It was suggested by Wynne-Edwards (1962) that territorial exclusion might provide an upper limit to population density and thereby avoid overutilization of food resources. However, there was no indication that the territorial system of white rhino males had any influence on the population density of females nor on their fecundity, despite the conditions of habitat deterioration prevailing during the study period.

At wallows and restplaces, individuals of all social castes tolerated spacings less than those usually maintained while feeding. Adult white rhinos of both sexes are virtually invulnerable to predation.

(b) Sexual success. With only a single exception in unusual circumstances, only resident territorial bulls were observed to mate with females. Neighbouring territorial bulls did not intrude across territory boundaries even in the presence of oestrous females, and subordinate bulls did not contest rights of access to oestrous females. Special manoeuvres were performed by territorial bulls to confine potentially oestrous females to within territory limits. The long drawn out courtship and copulation thus proceed without interference from other males.

Copulations were observed too infrequently to serve as a measure of relative sexual success. By excluding one thrid of the adult males from breeding, territorial bulls in general enhance their reproductive contribution by 50%. Territorial bulls occupying territories particularly favoured by cows during the wet season when oestrus levels are highest may enhance their success further. The northern study area territories were probably among the most favourably situated in this regard. The best territory held an average population of 4.2 cows (Table 55), indicating a potential enhancement of access to oestrous females by the resident territorial bull by 3.4 X relative to the average adult male. However, in terms of the proportionate amount of time spent accompanying oestrous females, much less variability is evident among study area territorial bulls. It may be concluded that the most successful bulls probably increase their reproductive contribution by a factor of 2X to 3X% while retaining territorial bull status; but since transitions between territorial bull and subordinate bull status occur diring any individual lifespan, the overall reproductive enhancement would be lower. (c) Progeny viability. Males do not remain with females after servicing them and thus have no direct influence on progeny survival. As discussed above, the effects of the slight reduction in population density seem to have relatively minor consequences for access to food. The behaviour of the mother has far more important effects on progeny survival, and cows exclude other rhinos only from the immediate vicinity of a calf.

The selective advantage achieved by prime territorial bulls in terms of enhanced mating success clearly outweighs other consequences of the territorial system for genetic fitness. Resident territorial bulls have unchallenged sexual access to oestrous females present within their territory limits. If dominance is defined in terms of this priority of access (Gartlan 1968), each territorial bull can be seen to exert a spatially localized dominance over all other males. The behaviour patterns characteristic of resident territorial bulls are manifestations of this dominance. Other adult males need not be driven from the territory, if they demonstrate acceptance of subordinate status by appropriate behaviour. The intermittent challenges of resident subordinate bulls by territorial bulls are probably important in reinforcing this dominance-subordinance relationship. Significantly, no case was known in which a subordinate bull took over dominance from the territorial bull whose territory he had shared.

The territorial system of the white rhinoceros is thus ultimalely a consequence of intrasexual competition among males for mating opportunities. The question remaining is, why has such a system evolved rather than an alternative form of organization of male dominance relationships. This will be considered in a separate publication (Owen-Smith, in prep.).

VI. INTERSPECIFIC RELATIONSHIPS

A. MUTUALISTIC RELATIONSHIPS

Five species of bird were seen associated with white rhinos. Two of these are of benefit to the rhinos by the removal of ectoparasites.

Commonly foung with rhinos was the red-billed oxpecker (*Buphagus erythrorynchus*). These birds settled on the body of a rhino in small flocks of perhaps four to six individuals. They clambered about on the animals apparently picking off ticks particularly from around the ears, nostrils and perineal region; rhinos were quite tolerant of such attentions. After a period of a few minutes or longer, the birds flew off elsewhere. The well-known alarm relationship between oxpeckers and rhinos will be discussed later.

Pied crows (*Corvus albus*) also commonly settled on rhinos, particularly while the latter were lying down sleeping. They walked around picking off food morsels, probably ticks. Rhinos showed no response to the croaking calls of crows.

Fork-tailed drongos (*Dicruris adsimilis*) were seen on several occasions using the back of a rhino as a perch from which to hawk flying insects. Probably parasitic flies associated with rhinos would be among the insects caught.

Glossy starlings (Lamprocolius nitens) commonly walked along near the feet of grazing rhinos, seemingly looking out for insects flushed by the rhinos. Cattle egrets (Bubalis ibis) were seen doing the same, but were uncommon in Umfolozi (though common immediately outside the reserve among cattle).

Rhino dungheaps are also of signigicance to several other animal species, as well described by Player and Feely (1960). Large black and smaller green rhinoceros beetles (Scarabeidae) seemed to be dependent largely on rhinoceros dung, which they formed into balls and rolled away to lay their eggs in. Their large maggots were also commonly found in dungheaps, in addition to those of parasitic flies associated with the rhinocceroses. The invertebrate fauna associated with the dungheaps commonly attracted the attention of insectivorous birds, particularly of guinea fowl, francolins and pied crows, and occasionally also of banded mongooses. Warthogs were on a few occasions seen feeding on rhino dung.

B. RELATIONSHIPS WITH OTHER UNGULATES

Other grazing ungulates, including wildebeest, zebra, buffalo, warthog, waterbuck, impala and reedbuck, are potential food competitors of the white rhino. Greatest overlap in diet is likely with wildebeest and warthog, which similarly prefer short grass. White rhinos feed on taller grass during the late dry season, and may then also come into direct competition with zebra and buffalo.

I commonly observed white rhinos, wildebeest, zebras and warthogs grazing in the same areas, but on only a few occasions could I ascertain the food plants being taken by the latter three species. Warthogs and wildebeest were noted feeding in the wet season on the same short grasses favoured by white rhinos. However, feeding records of zebra and buffalo showed a predominance of *Themeda triandra*, while white rhinos in the same area were taking mainly species of *Panicum* and *Urochloa*.

Detailed studies on the food habits of the various species are needed to reveal the extent of overlap in diet. Recent East Africa work suggests that direct competition between grazers is avoided not so much by selection of different species of grass, but rather by differential selection of plant parts and growth stages, and differing seasonal patterns of food utilization (Bell 1971). For example, warthogs may feed on the same stoloniferous grasses as the white rhino during the wet season, but in the dry season concentrate on grass rhizomes which are unavailable to other grazers (Cummings 1971).

White rhinos commonly paid little attention to other ungulates in the vicinity. The latter in turn moved slowly out of the way if approached directly by a white rhino, but otherwise took little notice. Wildebeest males staked out their territories within the territories of white rhino males, and commonly rested under trees within a few metres of white rhinos. One wildebeest bull lowered its head with a horn tossing gesture, then turned to stare away into the distance, clownishly, when approached by a white rhino calf. The white rhino calf stared, then moved away. At a waterhole, a warthog male approached to stand 0.3 m away in front of a white rhino bull, making a head nodding gesture at the latter's horn; the white rhino bull looked at it briefly, then turned away. On another occasion, a white rhino cow with a small calf snorted at a group of zebras drinking 4 m away, then lifted her head to look towards them with a soft rumble; the zebras jumped away a few metres, then remained standing and were ignored.

On a few occasions, white rhinos reacted nervously to other ungulates. A subordinate bull drinking at a waterhole swung round with a loud snarl when two warthogs moved behind him, then relaxed. A wandering white rhino bull swung round with a snarl when a wildebeest ran up behind him; the wildebeest ran on past, and the white rhino trotted on nervously.

When a wildebeest suddenly stampeded 10 m from a white rhino territorial bull who was returning from water at night, the white rhino swung to face it with a snarl, but then relaxed. A subordinate bull on a wandering excursion turned and ran off back towards its home territory when a waterbuck male approached. In all these cases, the white rhino concerned was a bull outside his home territory, and perhaps mistook the other animal for an approaching white rhino bull.

Pienaar (1970) records a fight between a white rhino bull and an elephant which occurred at a waterhole in the Kruger Park. The white rhino was fatally gored; signs suggested that a "tremendous battle" had taken place.

Rhinos usually did not respond to the alarm calls of other ungulates. Not uncommonly a lone wildebeest bull detected my presence, and pranced around snorting repeatedly. Nearby white rhinos sometimes responded by looking around, butfrequently then resumed previous activities. However, if zebras, wildebeest, reedbuck or some other species stampeded close past white rhinos, the white rhinos commonly ran off with them. The alarm calls of other species may commonly be given in response to predators besides man, which are of little consequence to white rhinos. Thus there is little reinforcement of any need for white rhinos to react rhino. I observed 13 encounters between the two species, 3 of which occurred at Hluhluwe North. In all except one case, the white rhino responded to the presence of the black rhino. The black rhinoceros, on the other hand, paid no overt attention to the nearby presence of the white rhino in 6 cases. An approach was made by one or the other in 10 cases; 6 of these approaches were made by the white rhino, 1 by the black rhino, and 3 by both simultaneously. Five approaches led to a meeting with gentle nudging together of the horns, and 3 of these developed into slow, playful horn wrestling matches. Actions resembled those commonly displayed in meetings between white rhino adolescents, though in one case the white rhino concerned was a territorial bull. In the other 5 cases, one rhino turned away after starting an approach. Four meetings were terminated when the black rhino moved away, and one by the white rhino moving away. Examples 62-64 describe the detailed sequence of actions in three of these encounters. In one, the quick, excited movements of the black rhino contrasted strongly with the slow, phlegmatic movements of the white rhino. Two additional meetings between the two species reported by rangers (Steele and Deane 1960) followed a similar course to those I witnessed. However Hitchins (in lit.) observed evidence of a fight between a black rhino and a white rhino to them. A stampede, in contrast, is likely to be associated with the presence of human intruders.

The concept of an interspecific "biological rank", as discussed for example by Backhaus (1964), seems of little significance in interpreting relationships. Other ungulates form part of the environment perceived by the white rhino, but are of little interest to them except as occasional indicators of danger.

Relationship with the black rhino

As the black rhinoceros is almost entirely a browser (Goddard 1968), there is negligable food overlap between the two species of rhinoceros. Correspondingly, black rhinos reach greatest densities in shrubby well wooded habitats such as prevail at Hluhluwe, where white rhinos are less common, and are uncommon in the more open woodlands typical of Umfolozi. Only four black rhinos were frequented the Madlozi study area, which contained an average population of about fifty white rhinos, and these evidently ranged widely. Sightings of the single black rhino bull indicated a home range of about 25 km^2; those of a cow and calf encompassed an area of about 15 km^2 (the fourth individual was the older adolescent female offspring of the cow).

In encounters between the two species, the black rhino appears somewhat dwarfed by the much larger bulk of the white

EXAMPLE 62. Encounter between black rhino and white rhino; curiosity by white rhino, little notice by black rhino (Nadlozi, 1 Nov '70)

1000 A white rhino subadult male approaches a group of four black rhinos; he stands 4 m away beside the black rhino bull, looking towards a black rhino cow and calf which are lying down a few metres away; the black rhino cow rises with a short snort; the white rhino quickly turns away, walks off close past the black rhino bull again, the latter turns slowly towards him but pays little attention to the white rhino and appears quite relaxed.

EXAMPLE 63. Meeting between black rhino bull and white rhino territorial bull, with horn wrestling (Dengozi, 5 Nov. '69)

0715 a white rhino bull walks a few paces towards a black rhino bull which lies 80 m away, apparently scenting it; the black rhino rises and comes forwards a few paces towards the white rhino, they stand; the white rhino advances a few paces, stands; the black rhino advances a few paces, stands; both appear relaxed; both advance simultaneously, the white rhino then continues the advance and makes contact; they rub horns gently together, stand thus /0722 the white rhino presses its head against that of the black rhino pushing the latter back a pace, then the black rhino pushes the white rhino back two paces; they continue wrestling horns slowly, mostly rubbing the two horns together gently, either singly or simultaneously /0730 the black rhino makes two head down feints, they stand heads raised, horns touching, then lower heads again; the black rhino feints twice more, then rubs its horn gently on that of the white rhino /0733 the white rhino slowly backs away two paces, stands; the black rhino turns away, walks a few paces, stands; the white rhino walks away, stands rubbing on a tree; the black rhino slowly moves off.

EXAMPLE 64. Meeting between black rhino and white rhino, which contrasts the temperment of the two species (Madlozi, 6 Feb.'71)

1635 a white rhino subordinate bull and black rhino subadult female stand facing; the black rhino backs and shakes its forequarters up and down, the white rhino stands looking passively; the black rhino turns and runs off with puffs, the white rhino walks after it, the black rhino advances, rubs its head on the white rhino's horn, the white rhino stands, looks confused, retreats slightly, stands, then advances; the black rhino makes a horn feint gesture with a puff, the white rhino looks on /1640 the black rhino turns and gallops away 25 m, stops and turns; the white rhino follows at a slow walk, before they meet the black rhino feints with its horn and jumps forwards with puffs, the white rhino stands head low quietly in front of it; the white rhino advance head up to touch horns, the black rhino rubs its horn on the white rhino's horn, they stand; the white rhino advances, the black rhino feints horns; the white rhino turns and wanders off.

which resulted in both individuals falling into a pool and drowning. A case was also reported in which a white rhino bull suddenly attacked a black rhino near a wallow (Bailey, pers.com.).

In all the encounters that I observed, the black rhino seemed relaxed and at ease in the presence of the white rhino. One may therefore conclude that attacks by white rhinos are unusual.

Notably, the white rhino generally displayed the greater curiosity towards the other individual. Visually, a black rhino could resemble an adolescent white rhino. In three instances, the white rhino turned away after smelling either the black rhino or its tracks. Because of the much greater size of the white rhino, visual confusion the other way round is less likely. However, that there is recognition of the basic similarity of the other species is suggested by the occurrence of horn wrestling matches. In an enclosure at Natal Parks Board headquarters, Pietermaritzburg, I saw a young black rhino and a young white rhino moving around as a close pair, though I do not know how long this relationship persisted.

There are no recorded matings between the two species. It would seem that they are too different in size for this to occur, at least under natural conditions.

C. PATHOLOGY AND PARASITES

1. Pathogens

The Zululand white rhino population seems little affected by disease. Heppes (1958) reported a similar conclusion for the Uganda population. Anthrax was endemic in the Uganda population, but responsible for few deaths. The species is apparently not susceptible to rinderpest (Shortridge 1934; Heppes 1958). Tsetse flies, vectors of trypanosomes, formerly occurred in the Umfolozi region, but were eliminated during the 1940's. White rhinos introduced to Meru Game Reserve in Kenya where tsetse flies occur seem unaffected by Trypanosomiasis.

It is possible that, in Zululand, some pathogens were lost from the population during the period when population size was very low. It is therefore difficult to evaluate how significant mortality from disease may have been in the past.

2. Parasites

In the two dissections of dead white rhinos that I was able to observe, a profusion of nematode worms was found in the stomach and small intestine, and large numbers of gyrostigmid fly larvae, up to 4 cm long, were attached to the stomach walls. Judging from the observations of Hitchins (pers.com.) on black rhinos, such parasitic infections are common in healthy appearing animals. The eggs of gyrostigmid flies are commonly evident on the heads of white rhinos, particularly around the horn bases; how they reach the digestive tract is unknown.

Rhinos usually have associated with them a swarm of large blood-sucking flies, Rhinomusca dutoiti, which are host-specific to the two rhino species. These flies normally rest in a compact clump on the sides of the rhino, all individuals facing head down, and are present year-round. A stampeding rhino frequently dislodges a swarm of these buzzing flies, which fly off after the direction taken by the animal. When a rhino defecates, some of these flies leave to settle on the fresh dung. Their eggs are laid in the dung, and their larvae develop in the warm moist environment provided by dungheaps. I also observed large numbers of small flies settling on rhino dung, which are presumably of the genus Lyperosia. These are also blood sucking, and are listed as occurring on white rhinos by Hitchins and Keep (1970). They are reportedly common on black rhinos in Tsavo Park, Kenya (Parsons and Sheldrick 1964).

Numerous ticks have been recorded on white rhinos (Baker and Keep 1970), and two rather colorful species show a host preference for the two rhino species (Zumpt

1964).

Skin lesions behind the shoulders such as are characteristically present on black rhinos in Zululand do not occur on white rhinos. A microfilarial parasite is apparently responsible for these sores (Hitchins and Keep 1970).

Small piroplasms (Babesia sp and possibly also Theilaria) have been found in blood specimens from the white rhino (Keep 1970).

There is no evidence that these parasites have any serious debilitating effect on white rhinos.

D. PREDATORS

1. Non-human predators

Lions. The last lion was eliminated from Umfolozi Game Reserve in 1915 (Vincent 1970). In 1958, a single adult male settled at Umfolozi, and in 1965 two lionesses joined him (Steele 1971). Since then the lion population has increased rapidly; in 1972, 63 lions were counted during the helicopter survey (Hitchins 1972). The original nucleus spread out from a base near the White Umfolozi River, and the first signs of lions I encountered in the Madlozi area were fresh tracks seen in April 1970. After this time, lions or their tracks were seen regularly at the Mphafa Pool, and a few times in the central Madlozi study area. They also entered the Nqutsheni area during the course of 1970.

At Gqoyini and Dengezi, lions had been irregular visitors since 1968 or earlier.

I observed three encounters between white rhinos and lions.

In one encounter at Madlozi, a white rhino subordinate bull took little notice as a group of seven lions walked past 15-20 m away, then lay down to sleep while the lions settled down about 30 m away. A black rhino cow and calf present about 30 m away seemed uneasy; the cow stared at the lions, then made a short charge of a few paces which caused the lions to scatter.

In another encounter at Madlozi, a group of four adolescent lions was filmed as they lay watching a white rhino cow and her year old calf from about 15-20 m range. The calf stood head up for several minutes, appearing uncertain how to react to the lions, then resumed grazing ignoring them. The cow grazed, moving as far as 15 m from the calf, paying no attention to the nearby lions. The lions appeared unexcited, and made off after about ten minutes when a tourist car disturbed them.

A group of seven lions was watched at night for two and a half hours at the Gqoyini Hide Pans while numerous white rhinos moved past to drink. A cow with an adolescent companion advanced towards two lions as she approached the pool, and the lions bounded out of her way at 12 m range. The rhinos continued past giving no response. Later, a cow with a two year old calf approached and stood looking at two lions which lay about 5 m in front of them. The calf backed nervously away from the lions a few paces, then jumped away with a gasp-snort when the lions rose and moved away. The cow stood facing away from the lions, and appeared unconcerned. The lions made a few fruitless attempts to stalk zebras and a duiker near the pool.

A white rhino bull was killed by lions in the south west of Umfolozi Game Reserve; no details are available (Hitchins in lit.). This is the only recorded instance of predation in the Complex. In Kruger Park, one white rhino calf is know to have been killed by lions, and a white rhino bull was attacked by lions and mauled so badlythat it had to be destroyed (Pienaar 1970). In East Africa, attacks by lions on black rhinos are rarely observed (Goddard 1967). Goddard observed one instance in which a black rhino cow swung round and fatally gored a lion that had attacked her from behind. Another attack by lions on a black rhino is described by Tatham Warter (1971).

Leopard. Leopards seem always to have been fairly numerous in Umfolozi Game Reserve, though infrequently seen. I observed only one encounter between a white rhino and a leopard, this taking place at the Gqoyini Pans at night. The leopard moved away hastily at 5 m range when a 2 1/2 year old approached; the white rhino continued on its way without responding.

Cheetah. Cheetahs were reintroduced into Hluhluwe Game Reserve in 1966 and later into Umfolozi; their present population numbers perhaps 40. I observed two encounters between a white rhino and a cheetah. In one, the cheetah rose and slunk away about 5 m in front of a white rhino bull; the white rhino showed no response. In the other case, four cheetahs wandered by 25 m from a white rhino bull; neither paid any attention to the other.

Hyena. Hyenas are abundant in Hluhluwe Game Reserve, and in Umfolozi have increased in numbers following the general buildup in game numbers; from 1968 through 1971, they were commonly heard at night at Madlozi and elsewhere. On two occasions I observed hyenas walk by about 30-40 m from white rhinos, but no interactions occurred.

In Hluhluwe Game Reserve black rhino calves are frequently seen with lacerated ears (Hitchins, pers.com.); Kruuk (1972) observed hyenas grabbing black rhino calves preferentially by the ears and tail at Serengeti. Hitchins feels that hyenas may be a significant cause of mortality among black rhino calves at Hluhluwe. In contrast, no white rhino calves with torn ears were noted either by me or by Hitchins, and white rhino calf mortality was very low (Section VII.B.4).

2. Man

Most of the time during observations, the rhinos remained clearly unaware of my presence. If I remained immobile, they were apparently unable to distinguish me visually at distances over 20-30 m (Section III.D). If I moved while in clear view, they reacted usually by swinging round and running off at a rapid trot. Sometimes they appeared uncertain, shuffling about agitatedly, perhaps turning to make off but then swinging round to face back again. In several instances when I was squatting or sitting on the ground, usually partly obscured by bushes or next to a tree, rhinos approached hesitantly but curiously to within 2-5 m. The sudden click of my Leica shutter at such ranges caused them to jump in fright and run off. On occasions when I had suddenly to move out of a rhino's way at very close ranges of 10 m or less, they seemed less startled than when I suddenly appeared nearby at greater distances.

To the repetitive thud of human footsteps, or to a sudden cracking sound as of a twig snapping close by, rhinos also reacted usually with flight. To more subtle sounds, they usually reacted by shuffling looking around uncertainly. Sometimes, in such circumstances, the rhino advanced a few quick paces towards the source of the sound; such action was usually effective in causing me to move, and the rhino then turned and ran off.

To human scent, rhinos usually reacted with instant flight, invariably running downwind. If the breeze was eddying with no clear direction, they shuffled about facing in different directions displaying great agitation, until able to detect the location of the person by sight or sound, then they ran away.

Rhinos also reacted immediately to the alarm calls of red-billed oxpeckers. These birds commonly made "chip" calls or soft "churrs" as they clambered about on the rhinos without disturbing the animals. The alarm call given on detecting the nearby presence of a human intruder was a repeated harsh strident "churr", and rhinos responded to this by looking around apprehensively. Sometimes the birds remained on the rhinos while calling, on other occasions the flock took off with loud "churrs". The latter action commonly caused rhinos to stampede. Flocks of oxpeckers sometimes gave the harsh "churr" call while flying overhead if there was a person below, and rhinos in the vicinity responded by looking about nervously. Usually I remained immobile and the rhinos were unable to detect the source of the birds' alarm; they turned to face in different directions displaying great agitation, which persisted for some time after the birds had left. I heard oxpeckers give the alarm only to a human intruder, except on one occasion when the birds called as a lanner falcon flew close overhead; the rhinos they were sitting on reacted nervously.

The white rhinoceros has no specific alarm call. The pant is commonly given in situations of alarm, but is also made in several other contexts (Section V.C.1.). When one rhino in a group detected my presence, it usually hastened towards its companion(s) and stopped abruptly beside them in head up alert posture, sometimes emphasising its presence with pants as it did so. Such action usually caused the companion to look around nervously. As discussed earlier, the pant seemed to function merely to draw attention to the performer, and alarm was communicated by his excited movements. The pant was not given while stationary in contexts of alarm. Sometimes a single rhino that had detected by presence seemed unable to communicate his alarm to the group when they had detected nothing (Example 65).

When approached on foot from a vehicle near one of the tourist roads rhinos were less likely to run off than when encountered away from the roads; particularly if the approach was made openly rather than furtively. The white rhinos that frequented the vicinity of the roads in the southern part of Hluhuwe

EXAMPLE 65. Unsuccessful communication of alarm by one individual on detecting a human intruder

1145 I sit on the ground in the open, near an association of six white rhinos: a territorial bull together with a cow and calf; two six year old adolescent males; and a subordinate bull; one of the adolescent males, M, sees me moving at 35 m range; he springs round with a few pants, but the other rhinos do not react /1148 M walks a short way towards the cow and calf with pants, but they stand quietly ignoring him /1150 M walks slowly towards me; at 25 m range he turns away and trots off past the other rhinos a short way; now the other rhinos look around, then stand; M approaches me, then trots away again; the bull resumes grazing, the other rhinos stand /1200 M walks towards me, then turns and trots away and stands, giving two pants /1203 the other adolescent male N lies down, the remaining rhinos stand quietly /1206 the bull turns towards M with a low rumble, M quickly turns away /1215 M walks curiously towards me to within 7.5 m range before I make a slight move; M springs away with a startled pant, shuffles around then stands; the other rhinos do not react /1219 M takes a few steps towards the cow and calf 35 m away with a few pants; but the territorial bull advances towards him with several quick paces with a gruff squeal and M moves away a few metres.

Game Reserve commonly take no notice of humans approaching on foot to within a few metres. However, the same individuals were likely to run away if approached away from the roads (Deane, pers.com.). Rhinos in the Wilderness area, which are also used to frequent approaches by parties of wilderness trailers, also seemed more inclined to stand rather than run off.

Rhinos approached directly near the roads commonly stood staring, swinging their heads in a low arc as if to sniff the ground or turn away but staying put; their tails were curled repeatedly. A group of adolescents or adolescents with a cow commonly responded to such situations of mild alarm by standing together with their rumps almost touching or in contact, facing outwards in different directions (Plate 21). This posture I will term the rump-to-rump formation. A bull sometimes backed towards a female companion when alarmed, but cows gave snorts or snarls preventing close contact.

In some instances, rhinos ran towards me instead of away when disturbed. However, if I emphasised my presence with a shout or clap or hissing sounds ("ksssk"), they almost always turned aside. Seemingly they had been confused as to my location, or advanced when they turned curiously to face towards me continuing trotting. On a few occasions, mostly involving a cow that was following a calf, rhinos held to their initially chosen direction despite my noises, and ran close past the bush behind which I had taken shelter.

On only two occasions, during the 3 1/2 year study period, did I observe actions which could be termed directed charges.

On the first occasion, I stood somewhat carelessly behind a small bush expecting a lone rhino bull that was about 15 m in front to move out of the way. The rhino noticed me and approached to stand staring about 5 m away. I exposed myself to one side of the bush expecting the rhino to run off, but the bull instead immediately rushed towards me. The grass was wet after rain, and I slipped and fell, and struggled to regain my feet with the rhino about 2 m away. I braced for an impact, but found myself lying on the ground untouched; apparently the rhino swerved at the last instant when I stood up in front of it. I turned round to see my assistant flying through the air having been tossed aside as he tried to run away from the rhino. The rhino continued on its way.

On the second occasion, a week later, I stood about 13 m away from a bull which had been blocking the movements of a cow at a territory boundary. The bull shuffled about nervously, apparently getting a whiff of my scent but unable to ascertain my location. When I clicked my camera, he immediately rushed towards me. I ducked behind a nearby bush clump, but when I turned round the rhino was still coming straight towards me; I shouted and it turned aside a few metres away.

Rhinos which were still groggy from drugging responded to the sudden appearance of an object ahead by dropping their heads so that the horn pointed forwards; an action which would be preparatory to an upwards thrusting movement of the head.

An African woman was reportedly attacked and killed by a white rhino just outside the game reserve in 1965. White rhinos which have wandered out into Bantu reserve areas, where they are sometimes harassed, are said to be far more dangerous to approach than those inside the game reserve.

Discussion

White rhinoceroses in Umfolozi show little fear of non-human predators, and predatory losses even of young animals are rare. In Umfolozi white rhinos have been in contact with lions for only a few years, and lions have abundant alternative prey. However, observations on white rhinos in Kruger Park and on black rhinos in East Africa indicate that attacks by lions on rhinoceroses are unusual. Notably in the single recorded Kruger Park attack on an adult the lions were unsuccessful in overcoming their victim, and would presumably learn to avoid such prey. The white rhinoceros is clearly highly successful in its anti-predator adaptations. In considering the evolutionary origins of observed strategies, one must bear in mind not only extant predators, but also the extinct sabre-tooth cats and giant hyenas which occurred in Africa during the early Pleistocene (Cooke 1968).

Because of their large body size and tough hide, it is difficult for even a lion to kill an adult white rhino. Sabre-tooth cats may have been more successful; their enormous canine tusks are believed to have been adaptations enabling them to reach the vulnerable organs of very large mammals. Adolescent white rhinos are potentially more vulnerable, and the rump-to-rump formation is a defensive stand probably effective against an attack by group-hunting carnivores such as hyenas or lions. The vulnerable rear is protected and the attacker is confronted by several horns backed by powerful neck muscles. This formation resembles the "hedgehog" formation adopted by muskoxen towards wolves. Clearly, it is advantageous for young white rhinos to be associated in groups. Young calves may be protected against predator attack by the physical involnerability of the mother, provided they remain close beside her. Their habit of always running ahead of the mother facilitates this. The differences in horn shape that occur between the two sexes may be related to the fact that in cows the horn is more important for predator defense than for intraspecific fighting. The long slender horns or extremely forwards projecting horns exhibited by some cows would be more effective in warding off a predator, giving the cow a longer reach.

It may be advantageous for a female with a small calf to run off to escape the attentions of a pack of hyenas; the latter may give up pursuit when confronted only by the body of the cow. Standing ground would generally seem the best response for a white rhino to adopt against a non-human predator; but such behaviour would make them vulnerable to organized bands of primitive human hunters armed with spears or arrows (consider the hunting success of pygmies against forest elephants). Hence, flight can be viewed as a response adapted specifically against humans.

Rhinos, apart from those habituated to tourists, react with instant flight either to human scent or to the warning calls of oxpeckers when the source of the latter's alarm can be located. To a human detected visually, they display considerable ambivalence, wavering between the alternative responses of standing their ground or fleeing. The impression conveyed has been aptly described by one observer: "They seem so confused and helpless, one feels like comforting the huge pachyderms". This may be related to the poor visual acuity of the animals; a human intruder can be identified unequivocally only by scent or through the aid of the superior vision of oxpeckers. This hesitancy makes them easily approachable from downwind; the difficulties of a hunter are mainly those of dispatching the thick-skinned animal with primitive weapons.

The alarm call given by oxpeckers specifically to a human intruder is interesting, since the birds have nothing to fear themselves from man. It seems that this has probably evolved from a rallying call given by the flock before taking off, since the approach of humans is generally followed by stampede by hosts (which include several other ungulates besides rhinos).

The inoffensive nature of the white rhino contrasts strongly with the excitable, unpredictable temperament of the black rhino. Many so-called charges made by black rhinos are merely curious advances, or short rushes effective in forcing a person to reveal his location, such as I observed occasionally also from white rhinos (Hitchins, pers.com.). Other black rhino charges appear to be disorientated rushes which carry the animal past the person should he get out of the way. A person running away in front of an animal is likely to be chased; white rhinos also show tendencies to do this. Nevertheless, a person working where both rhino species occur develops a high degree of reliance that a white rhino will run the other way, whereas such confidence is not felt towards a black rhino. Besides being more likely to rush towards an intruder, the movements of black rhinos are more sudden, and they couple their rushes with steam-engine like puffs; all of which help to create a frightening impression. The temperamental difference between the two species is reflected by physiological differences in their response to the narcotic drug Etoprphine Hydrochloride (M.99). Though only half the weight, black rhinos require the same dosage (1.5-2 mg) for immobilization. After injection of the drug antagonist, a black rhino regains consciousness within a minute or two, and is immediately highly aggressive and likely to charge a nearby vehicle. A white rhino in contrast remains sleepy and shows diminished responsiveness toward the surroundings for several hours (Keep 1971).

The frightening charges of black rhinos are clearly adaptations for inhibiting predator attacks, probably effective against human hunters as well as carnivores. These may not always be successful, nevertheless any rhino displaying such aggression is less likely to be killed than an individual behaving more docilely.

African elephants also commonly respond aggressively towards human intruders. The inoffensive nature of the white rhino therefore is anachromous and needs explaining, since it seems a less effective way of responsing to a potential enemy.

Both species of rhinoceros attained their present form before the emergence of Hominids as efficient predators. On account of its greater physical invulnerability the white rhino has less need to react aggressively to non-human predators. A high threshold for aggressive excitability has advantages for social reasons and also for energy conservation. Having strongly suppressed aggression for social and energetic reasons, the white rhinoceros may now lack the evolutionary potential to reverse this adaptation.

The significance of man as a predator of white rhinos is shown by the fear that the Umfolozi white rhinos continue to show towards man, despite the fact that they have not been hunted for some fifty years, beyond the lifespan of any individual. There may be an innate basis to this fear response particularly towards human scent; but clearly this is not deterministic, since individuals can become quite habituated to tourists, and most of those captured for zoos become tame within a short period. Probably inherent tendencies to respond nervously to human scent or simply to strange objects are reinforced by the peculiar behaviour generally displayed by humans towards rhinos where contacts are infrequent. African game guards usually continue walking straight towards any white rhinos in their way and scare them off with noises. Tourists orientate towards rhinos, approach furtively or remain standing nearby, and sometimes make strange noises to encourage the rhinos to move for photographs.

The confused reactions shown by white rhinos towards humans illustrate the potential vulnerability of such giant mammals to organized hunting by man, and support the arguments of Martin (1973) regarding the significance of early man as an agent in the late Pleistocene extinction of the North American megafauna. Having evolved large body size as an effective defense against non-human predators, there is less strong selective pressure favouring increased sensory capacities, fleetness of foot, and "intelligence".

VII. D E M O G R A P H Y

A. NUMBERS AND DISTRIBUTION

1. Population size

Regular aerial censuses of the white rhino population have been conducted by the Natal Parks Board since 1953; since 1970, these have been carried out by helicopter. Vincent (1969) has described the techniques used in the counts by fixed-wing aircraft. Parallel strips about 1100 m apart were flown, using two observers and a recorder in addition to the pilot. Helicopter censuses have been conducted by intensive low altitude coverage of successive blocks. The results of these counts are presented in Table 61.

Counts by fixed-wing aircraft are clearly far less complete than those by helicopter. A fixed-wing aircraft count conducted a week later than the helicopter census in 1970 accounted for only 54% of the number of white rhinos seen from the helicopter. However, the number of animals recorded in the 1970 fixed-wing aircraft count was lower than that of previous years. By comparing results it seems that on the average, the relative counting efficiency by fixed-wing aircraft is about 60%.

The fraction of the total white rhino population recorded

TABLE 61. Results of counts of the white rhinoceros population in the Umfolozi-Corridor-Hluhluwo Complex

Data from Kluge (1950), Player and Feely (1960), Vincent (1969 and 1970), Hitchins (1971 and 1972)

Area Method*	1932 g	1936 g	Dec 1948 g	Sept 1953 f	Aug 1959 f	Aug 1960 f	Aug 1962 f	Aug 1965 f	June 1967 f	July 1968 f	Oct 1969 f	Aug 1970 f	Aug 1970 h	Aug 1971 h	Aug 1972 h
Umfolozi G.R.:															
between rivers,															
W. of Mpila				292	324	387			515	446	655	504	910	1054	884
E. of Mpila				33	63	82			62	48	121	82	193	155	158
subtotal				325	387	469	476	560	577	530	776	586	1103	1209	1042
S. of W. UMF,															
inside G.R.							93	100	148	187	153	120	258	320	294
outside G.R.							115	82	61	24					
subtotal				69	130	141	208	182	209	211	153	120	258	320	294
TOTAL, UMF.G.R.	220	226	554	394	517	610	684	742	786	741	929	706	1361	1529	1336
Corridor,															
S. of Hlabisa rd.				28	50	55			119		153	156	237	256	269
N. of Hlabisa rd.					(20)	(20)			(20)		84		76	90	106
W. of Mona str.				15			39	13	10	15	(20)				
TOTAL, CORRIDOR				43	70	75	133	117	149	175	257		313	346	375
Hluhluwo G.R.:															
South											35		52	70	67
North											7		38	57	46
TOTAL, HLU.G.R.				(20)	(20)	(20)	31	(40)	55	89	42		90	127	113
GRAND TOTAL FOR COMPLEX				457	607	705	856	912	1000	1020	1228		1764	2002	1824

* g = ground count, f = fixed wing aircraft count, h = helicopter count, ( ) = estimate

in helicopter counts is probably close to 100%. Independently, the average population density of white rhinos in the three western study areas was calculated, by "Territory Occupancy Index", to be 5.7/km^2 (Table 63); this estimate should be unbiased. The helicopter counts of 1970 and 1971 indicate an average white rhino population density for the whole of the 250 km^2 extent of the western section of Umfolozi Game Reserve of 3.6-4.0 /km^2. The study areas represent local pockets of high white rhino density, and it is not unreasonable to assume that population densities in such areas are 50% higher than the average population density over a much more extensive area including sections of hill-slope and dense woodland relatively little frequented by withe rhinos.

The total white rhino population in the Umfolozi-Corridor-Hluhluwe Complex in 1970-71 was thus evidently, on the basis of the helicopter counts, about 2000 animals. Of these, about three quarters were located within Umfolozi Game Reserve, with most between the two Umfolozi rivers. About 350 animals occurred in the Corridor, and only about 130 in Hluhluwe Game Reserve.

2. Population distribution

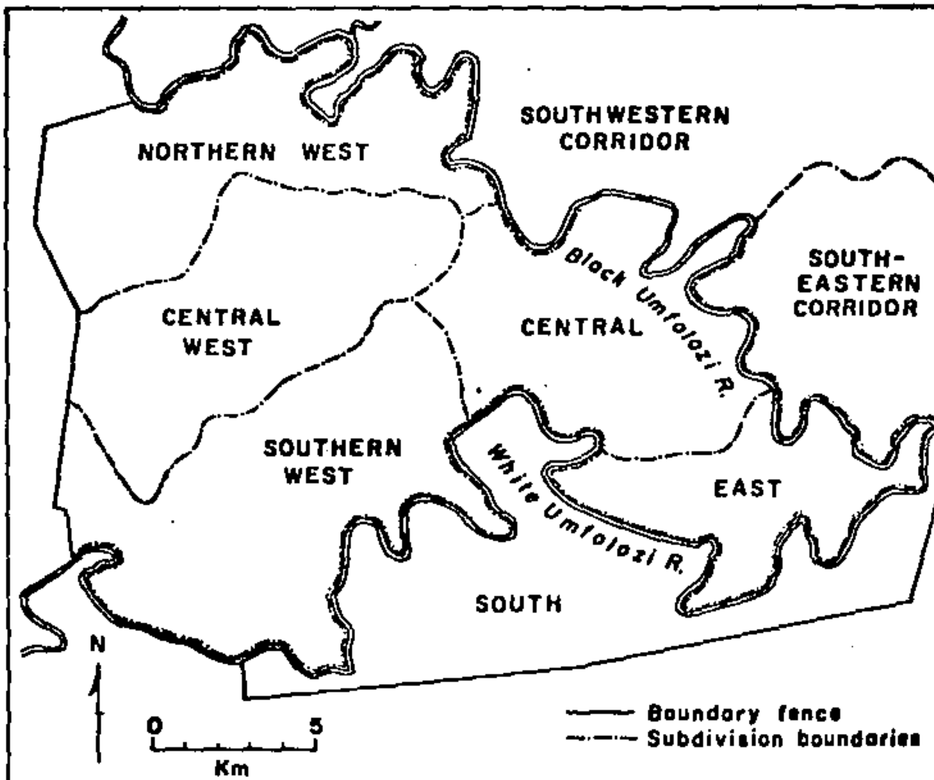
All official counts have been carried out during the late dry season, when visibility is best following loss of leaves from the deciduous trees. To obtain comparative information on wet season distribution, and additionally more detailed information on distribution patterns, I undertook two special counts by fixed-wing aircraft. These were carried out in August 1970 and February 1971 with the aid of Natal Parks Board officers.

The same basic technique was used as had been employed in previous counts by fixed-wing aircraft. Two observers seated one on each side of the aircraft reported all rhinos seen, and an additional recorder noted the positions of these as accurately as was feasible on 1:50 000 sectional maps. In addition to recording general distribution, information was also desired on variations in population composition between different sections. All rhinos seen were therefore categorized as follows on the basis of known patterns of social grouping (Section V.B): (i) all single animals were recorded as adult males; additional adult males that were associated with cows and calves could be distinguished by their size; (ii) all small individuals judged to be under about three years of age that were associated with an adult were regarded as calves; (iii) all adults accompanied by calves were recorded as cows; (iv) groups consisting of similar sized individuals were tallied as subadults. Single animals other than adult males are rare, and adult males almost never join together (See Table 15); hence the proportion of adult males estimated in this way was expected to be a fairly accurate reflection of the true proportion. Some animals recorded as calves may have been approximately three year old adolescents that had joined cows whose calves had been caught and removed, but other very small calves may have been overlooked; hence the proportion of calves recorded was similarly expected to be close to the true proportion. However, some cows that had subadult companions could not be distinguished and would be included among the subadults. Only the area south of the Hlabisa road through the Corridor was counted in this way.

In analyzing results, natural boundaries such as rivers, waterholes and ranges of hills were used to subdivide the population into local units (see Figure ~~46~~ 45). The total number of rhinos recorded south of the Hlabisa Road in the August 1970 count by fixed-wing aircraft was 54% of that recorded in the helicopter count carried out the preceeding week; population density estimates were corrected in this basis, assuming the helicopter figure to be an accurate estimate of the true population. An additional correction was applied to the February 1971 data for the 82 rhinos that were caught and removed between August 1970 and February 1971.

Highest white rhino population densities were present

FIGURE 45. **UMFOLOZI GAME RESERVE, showing subdivisions used in analysing population distributions**



in the western part of Umfolozi Game Reserve, averaging 3.5-3.8 per km^2 over the total extent of 250 km^2 (Table 62). Densities were only 1.0-1.4 per km^2 in the Corridor, and 0.4 per km^2 in Hluhluwe Game Reserve.

Estimates of local population densities in each of the study areas are also available, (locations are shown in Figure 2). Wet season population densities for the three western study areas varied between 5.1 and 7.0 per km^2 (Table 63). However, the high white rhino density recorded at Nqutsheni was probably the result of an influx related to the unusually dry conditions that prevailed during January and February of 1969. A partial movement of rhinos out of the central Madlozi study area during the dry season is suggested. This is probably related to watering movements to and from the vicinity of the Mphafa Pools and later the White Umfolozi River.

Comparison of the results of the two counts suggests general dry season movements away from the Black Umfolozi River in the western part of UGR, and towards the vicinity of the White Umfolozi River; and also into the eastern triangle and the southern Corridor. Such movement would be largely by the more mobile cows and calves, and appropriate changes in the proportions of adult males and of calves were observed. However, during the helicopter count a week

TABLE 62. Population distribution, Umfolozi-Corridor-Hluhluwe Complex

Regional distribution based on two counts by fixed-wing aircraft. Overall population size corrected on basis on total count for same area recorded in helicopter census of 10-13 August, 1970. February count data additionally corrected for removals made between counts, but assumes no reproductive increase.

	area (km^2)	18-19 August, 1970 count	cor. pop. est.	pop. dens. (/km^2)	ADm %	calf %	18-19 February, 1971 count	cor. pop. est.	pop. dens. (/km^2)	ADm %	calf %
1. Umfolozi Game Reserve											
a. northern west	76	122	226	3.0	29.5	13.1	116	305	4.0	21.6	21.6
b. central west	73	135	250	3.4	19.3	26.7	115	284	3.9	15.7	22.6
c. southern west	99	210	389	3.9	19.1	21.9	149	356	3.6	20.2	19.5
SUBtotal, UGR west	248	467	865	3.5	21.8	21.0	380	945	3.8	19.2	21.1
d. central	71	55	102	1.4	20.0	18.2	37	84	1.2	24.4	24.4
e. east	42	62	115	2.7	14.5	17.8	39	89	2.1	12.8	15.4
f. south	94	120	222	2.4	29.2	20.8	114	259	2.8	28.0	19.3
TOTAL, UGR	456	704	1304	2.8	22.4	20.4	570	1377	3.0	20.9	20.5
2. Corridor											
a. south-east	68	71	132	1.9	22.5	19.7	40	91	1.3	35.0	20.0
b. south-west	148	86	159	1.1	24.4	24.4	55	125	0.8	25.4	20.0
subtotal, southern Corridor	216	157	291	1.4	23.1	22.4	95	216	1.0	29.5	20.0
TOTAL, UGR + S. CORRIDOR	672	861	1595	2.4	22.5	20.7	666	1593	2.4	20.9	20.5
c. Northern Corridor	57	-	87	1.5							
3. Hluhluwe Game Reserve											
a. south	156	-	42	0.3							
b. north	57	-	37	0.7							
TOTAL, HGR	213	-	79	0.4							
GRAND TOTAL	942		1761	1.9							

TABLE 63. Population density and structure, study areas

Average population density for four UGR study areas calculated by territory occupancy index; for Hluhluwe North, based on number of different individuals recorded.

Study area	period	extent (km^2)	aver. popul.	pop. dens. ($/km^2$)	ADm %	ADf %	subad. %	calf %
Madlozi	Nov'68-Jan'69; Oct-Dec'69	8.88	48.9	5.5	16.5	31.7	26.2	25.6
	July-Sept'69		42.8	4.8	17.8	30.6	30.6	20.8
Nqutsheni	Jan-Feb'69	5.08	35.4	7.0	23.3	27.5	21.9	27.2
Gqoyini	Mar-Apr'69	7.52	38.7	5.1	20.9	22.8	34.4	22.0
THREE WESTERN SA's COMBINED		21.48	123.0	5.7	19.8	27.6	27.5	25.0
Dengezi	May'69	6.10	22.6*	3.7*	15.1	27.6	31.0	26.4
Hluhluwe North	April'69	66	30	0.5	16.7	6.7	70.0	6.7

* probably 50% too high

earlier in August, more rhinos were seen in the vicinity of the Black Umfolozi valley, and fewer in the region of the White Umfolozi River. Thus, such distributional changes seem to be merely the result of temporary day to day variations related to dry season movements to and from water. The Mphafa Pools still held water at the time of the August counts. From study area observations, an influx of rhinos into the White Umfolozi valley may occur following the drying up of these pools, as a result of individual journeys to water every three to four days by a proportion of the rhinos grazing the central region of UGR west.

The dry season distribution recorded in the August 1970 count shows little influence due to distance from water. However, only a small section of UGR, running through the northern part of the Madlozi study area, was then more than 3 km from the nearest water supply. The main influence on distribution pattern seemed to be food. Concentrations of rhinos were noted along the slopes of ranges of hills with a good cover of long grass, particularly the Nqolothi and Mbulunga ranges. This is in accord with study area observation indicating a tendency to graze increasingly on hillslope Themeda grassland as the dry season progresses (Section IV.A.3).

In summary, seasonal shifts in the population seem to be small and due mainly to local movements related to changes in the distribution of water supplies and food.

In general, highest white rhino densities are associated with gently undulating terrain on which vegetation forms a catenary sequence from open *Acacia tortilis* woodland on the interfluves to *A. nilotica* woodland on the lower valley slopes, with a prevailing ground cover of short grass. Low white rhino densities occur in areas with more steeply undulating hillsides and ridges based mainly on sandstone as are found along the southern boundary of UGR, in the central region around Mpila, and over much of the Corridor. The higher rainfall grasslands and more steeply undulating terrain typical of much of Hluhluwe Game Reserve have only recently been colonized by white rhinos and apparently form less favourable habitat.

Variations in the relative proportions of particular age/sex classes in different sections of the complex were fairly consistent between the two counts (Table 62). Cows with calves were most concentrated in the central part of the western region of UGR, and subadults in the eastern triangle. The portion of UGR south of the White Umfolozi River and the southern Corridor contained a relatively high proportion of adult males.

B. POPULATION DYNAMICS

1. Population trend

Information on population trend is available from the aerial counts which have been carried out regularly since 1953, and from three earlier ground counts (Table 61). To determine the natural rate at which the white rhino population has been increasing, these count data need to be corrected for the varying efficiencies of different census techniques, and for the cumulative effects of the rhino removal program.

A comparison of results of counts by fixed-wing aircraft and by helicopter suggests that the former method accounts for an average of only about 60% of the number of rhinos seen from the helicopter. (See Section A.1). Helicopter censuses will be assumed to be complete; as discussed earlier, it seems unlikely that they miss more than 5-10% of the population. The efficiency of ground counts is unknown; it will tentatively be assumed to be 100%.

Records of the numbers of white rhinos removed were available from Natal Parks Board files. For calculation of the effects of these removals on population trends, allowance has also to be made for potential recruitment by these animals had they remained in the population. This will be assumed to be 10% per annum, similar to the net rate of increase calculated for the whole population (see later). This is an approximation, since a large proportion of the animals removed were subadults; such females would not have reproduced for 1-4 years, but their reproductive rate thereafter would have been higher than that of the overall population.

With these corrections applied, it is calculated that the total population in August 1971 would have numbered 3368 white rhinos if no removals had been made (assuming also that no density dependent changes in net recruitment had come into effect) (Table 64). A logarithmic plot of the projected natural increase by the white rhino population (Figure ~~47~~ 46) yields a straight line after 1960, indicating that the rate of increase has held constant since about that time. Thus, seemingly no density dependent restraint on population increase is yet occurring. It seems unlikely that any such effects have been masked by steadily increasing counting efficiencies; identical techniques were used for the four fixed-wing aircraft counts from 1965 to 1969, and also for the subsequent three helicopter censuses. The rate of increase was evidently lower before 1960. Consequently, the age structure of the population may still be adjusting to the higher rate of increase, and this effect could obscure small changes in age-specific fecundity and mortality. But

TABLE 64. Estimated potential increase of white rhino population in the absence of removals

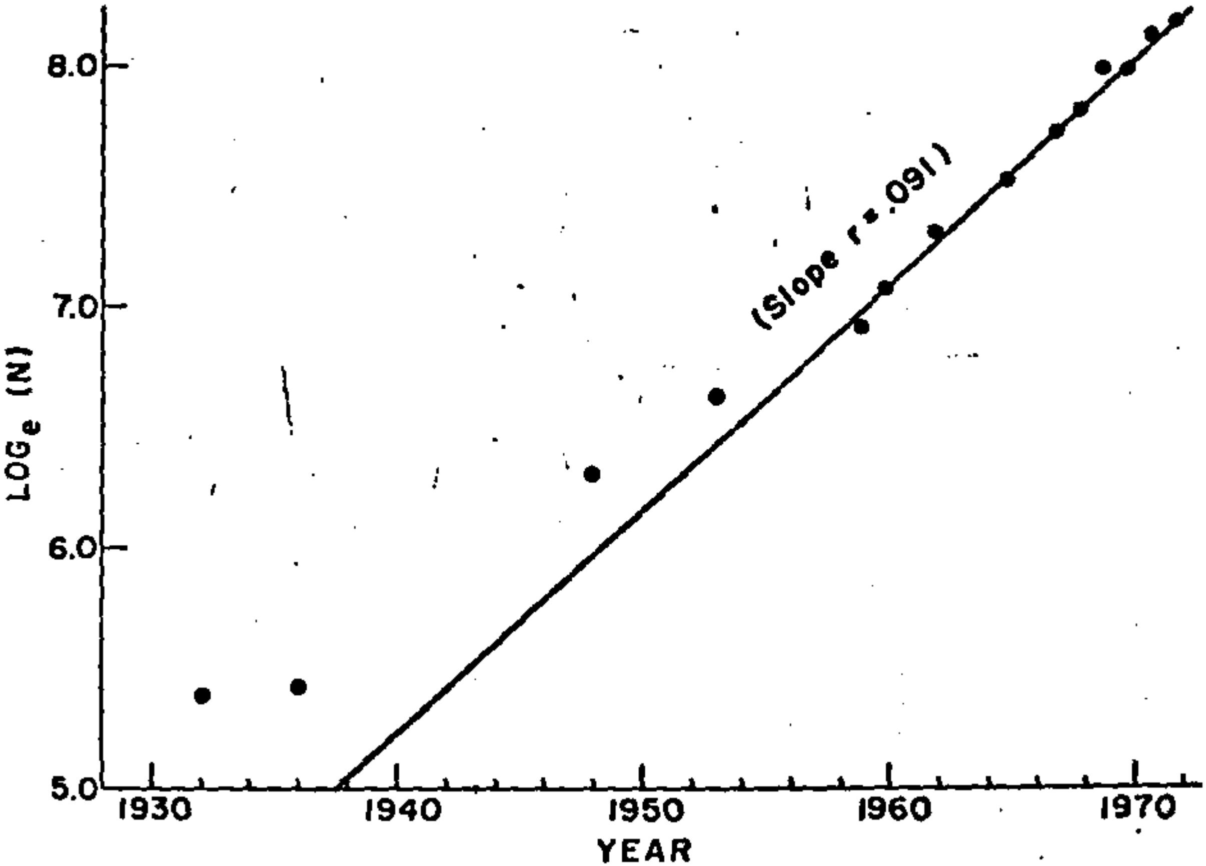
Allowance made for the animals removed from the population in the capture program
Assumptions: (a) counting efficiency by fixed-wing aircraft = 60%
(b) anticipated recruitment by removed animals = 10% p.a.

year	1932[1]	1936[1]	Dec 1948[1]	Sep 1953[2]	Aug 1959[2]	Aug 1960[2]	Aug 1962[2]	Aug 1965[2]	June 1967[2]	July 1968[2]	Oct 1969[2]	Aug 1970[3]	Aug 1971[3]	Aug 1972[3]
count	220	226	554	457	607	705	856	912	1000	1020	1228	1764	2002	1824
corrected popul. estim.	220	226	554	762	1011	1175	1429	1520	1667	1700	2024	1764	2002	1824
cumulative no. removed							60	288	493	603	714	851	990	1248
potential recruitment by removed segment							5	45	111	160	220	291	376	475
PROJECTED TOTAL POPULATION	220	226	554	762	1011	1175	1494	1853	2271	2463	2958	2906	3368	3547
$\log_e N$	5.394	5.421	6.317	6.636	6.919	7.080	7.309	7.525	7.728	7.809	7.992	7.975	8.122	8.174

[1] ground count [2] fixed-wing aircraft count [3] helicopter count

References: Player and Feely, 1960; Vincent, 1969; Hitchins, 1972; Natal Parks Board files.

FIGURE 46. Logarithmic plot of projected increase in white rhinoceros population in the absence of removals



any such influence is probably slight bearing in mind the preferential removal of young animals in the capture program.

From Figure 47, the current exponential rate of increase (*r*) of the white rhino population is calculated to be 0.091. This is equivalent to a finite net rate of recruitment of 9.5% per year.

2. Age composition

Eight size classes of white rhino were originally defined but these were found not to correspond to unitary year classes (Table 6). Since differentiation between these size classes was initially somewhat subjective, they will generally not be used in the following analysis. Subsequent evidence of seasonal variations in reproduction allowed immature animals to be assigned to particular year classes, but it was not possible to apply this knowledge to an adequate population sample during the present study.

The white rhino population will therefore be subdivided simply into three age categories: (i) adults - animals not reliably distinguishable from fully mature individuals; (ii) subadults - immature individuals not attached to a cow, or judged to be over three years of age if with a cow; (iii) calves - immature animals with a cow that are not over three years of age. Precise application of the three years of age subdivision was seldom needed, since most calves separate from the mother before three years of age. However, since intercalving intervals vary between 2 and 3 years, some individuals in the age range (2-3) years will be classed as calves and others as subadults. The subadult age category corresponds closely with the social class of adolescent as defined in Section V.A; it includes males up to 9 or 10 years of age, and nulliparous females up to about 7 years of age.

Estimates of population structure are available (i) from repeated sampling of study area populations (Table 63); (ii) from several extensive foot tours outside the study areas (Table 65); and (iii) from the two aerial counts of August 1970 and February 1971 (Table 62). The aerial count data supply the needed extensive coverage of the population range, but are most prone to observational errors, since animals had to be classified on the basis of brief glimpses from above. To reduce such effects categories were chosen such as to be readily distinguishable at a glance (see above). Lone cows or single large subadults would be recorded as adult males but since these comprised only about 1% of the population (see Tables 15 and 16), errors are likely to be small. Additionally, a few small calves may have been overlooked through being hidden by the bodies of their mothers. Cows that were accompanied by large subadults or another cow would be recorded as subadults. It was intended to use

TABLE 65. Population structure, other samples

(a) Samples obtained from extensive foot tours outside study areas

Area	Period	sample size	ADm %	ADf %	subad. %	calf %
Madlozi environs	Aug-Sept'69	138	16.0	22.5	43.5	18.1
Nqolothi-Mfulumkhulu	Oct.'69	24				
Mqutshomi environs	Jan.'69	45	13.3	31.1	26.7	28.9
Gqoyini environs	Mar.'69	18				
COMBINED, UGR WEST		225	16.0	25.8	37.3	20.9
South of W. Umfolozi R.	Feb.'71	61	27.8	28.5	21.3	21.3

(b) Aerial count data, corrected for removals which took place between March, 1969, and date of count

Area	Date of count	sample size	ADm %	ADf %	subad. %	Calf %
UGR West	Aug.'70	545	19.8	-	-	21.0
UGR West	Feb.'71	477	18.4	23.8	35.3	22.5

extensive ground sampling of population composition as a control for the accuracy of the aerial count data, but several factors precluded this except for a few areas. The study area and other ground samples from the western part of UGR, and a ground sample from the area south of the White Umfolozi River (Tables 63 and 65) can be used for this purpose.

However, before a direct comparison of results can be made the aerial count data have to be corrected for the effects of the removals made between 1969 and the dates of the two counts. In all, 159 rhinos were removed between March 1969 and August 1970, and a further 82 before February 1971. With the exception of 4 individuals, all were taken from the western part of UGR. The approximate age classes and sexes of these animals are recorded in Natal Parks Board files; they consisted mostly of subadults, with some adults and a few calves. If the animals removed are added to the observed aerial count samples for the western part of UGR, making allowance for counting inefficiencies, they change the age class proportions to those presented in Table 65b. These represent the age composition expected if an aerial count had been conducted in the western part of UGR in February 1969. Population structures in other sections may have been affected indirectly by the removals, but any such effects will be ignored. No rhinos were removed from within the game reserve between February 1967 and March 1969 (animals were taken from south of the boundary fence during this period). The population structure in early 1969 was thus relatively little affected by the removal program, and this period will hence be used as a time base-line.

There is close agreement between the proportions of adult males for UGR west calculated from the aerial count data (19.8% and 18.4%) and from the three western study areas combined (19.8%); other ground samples from UGR west give a lower proportion (16.0%). The proportion of adult males recorded in the ground sample in the area south of the White Umfolozi River is identical to that obtained in the aerial count carried out during the same month. It will thus be assumed that the aerial count data overestimate the true proportion of adult males by 1%. The various estimates of the proportion of calves agree within a few percent: for the western part of UGR, 21.0% and 22.5% from the two aerial counts, 25.0% for the three study areas combined, and 20.9% from the ground samples; for the area south of the White Umfolozi River, 20.8% and 19.3% from the aerial counts, and 21.3% from the ground sample. The average proportion of calves recorded in the two aerial counts will be assumed to underestimate the true proportion of calves by 1%. The proportion of adult (parous) females cannot be obtained directly from the aerial count data, but may be estimated from the cow:calf ratio. On the basis of study area populations and other ground samples, this is calculated to be 116 cows : 100 calves (Table 66), and this ratio will be assumed to hold for the entire population.

Based on these assumptions, the overall composition of the white rhino population in the whole Complex in early 1969 is calculated to have been: adult males - 20.5%; adult females - 25.6%; subadults - 32.1%; calves - 21.9% (Table 67).

It must be emphasised that the above figures refer to the total population. Within any local section population composition will differ. For example, population structure in the western part of UGR where an estimated 57% of the population was concentrated was estimated to be: adult males - 18%; adult females - 27%; subadults - 32%; calves - 23%. In contrast, in the southern section of UGR adult males outnumber adult females, while in the Corridor approximately equal proportions of both sexes occur. This is a consequence of the sprinkling of adult males occupying hilly areas not favoured by the bulk of the population, (presumably as a result of territorial pressures). These outlying males have to be taken into account in estimating overall population structure.

TABLE 66. Estimation of cow: calf ratio

Population sample	no. of cows	no. of calves
Study areas:		
Madlozi, Jan.'69	32	28
Madlozi, Aug.'71	39	31
Nqutsheni, Feb.'69	43	38
Gqoyini, Mar.'69	28	25
Dengezi, May'69	30	29
Other ground samples:		
UGR west, 1969	58	49
UGR south, Feb.'71	18	13
ALL SAMPLES COMBINED	248	213
RATIO	116	100

TABLE 67. Estimated overall population composition as of early 1969

Population distribution based on aerial count data of February 1971, with the addition of the animals removed between February 1969 and the date of the count; age composition for each region estimated from aerial count samples of Aug.'70 and Feb.'71 as follows: (i) percent ADms = aver. % recorded from both counts, minus 1%; (ii) percent calves = aver. % recorded from both counts, plus 1%; (iii) percent cows = 1.16 x % calves; (iv) percent subadults obtained by difference; population structure in HGR south is assumed to be the same as that recorded for the Corridor; population structure in HGR north is based on the study area population.

Region	population size	ADm	ADf	sub-ad.	calf
UGR - west		(18)	(27)	(32)	(23)
	1100	198	297	352	253
- central		(21)	(26)	(30.5)	(22.5)
	84	18	22	26	19
- east		(12.5)	(20.5)	(49.5)	(17.5)
	93	12	19	46	16
- south		(27.5)	(24)	(27.5)	(21)
	259	71	63	71	54
Corridor		(25.5)	(25.5)	(27)	(22)
	303	77	77	82	67
HGR - south		(25.5)	(25.5)	(27)	(22)
	42	11	11	12	9
		(16)	(7)	(70)	(7)
	37	6	3	26	3
GRAND TOTAL	1918	393	492	615	421
PERCENT		20.5	25.6	32.1	21.9

Upper figure (in Brackets) is estimated percentage
Lower figure is calculated total number

3. Sex ratio

The adult sex ratio can be calculated from the estimated proportions of adult males and adult females in the total population (Table 67). For the overall population, this ratio is 80 males: 100 females. Estimation is based on the populations samples observed in the two aerial counts (Table 62) which represented 46% and 35% respectively of the estimated total adult population. With this consideration, the ratio calculated for the total population is significantly different from 1:1 at the 99.9% confidence level; but is based on the assumptions concerning possible biases.made above. For UGR west alone where all the excess adult females appear to be located, the adult sex ratio was estimated to be 67 males: 100 females. Over the remainder of the Complex, approximately equal proportions of adult males and adult females in the adult cohort can be ascribed to the differing rates of attainment of maturity in the two sexes (see below).

The sex ratios of immature age classes can be estimated from population samples observed in the study areas and on foot tours through other regions. For calves and for younger subadults, equal numbers of both sexes were observed (Table 68). Among older subadults, males predominated; this is to be expected, since males remained distinguishably subadult until 9 or 10 years of age while females were regarded as

TABLE 68. Sex ratio of immature age classes

Based on number of different individuals recorded in various sample populations

Area	calves			subadults class I*			subadults class II*		
	N	m	f	N	m	f	N	m	f
Madlozi (Jan'69)	31	15	16	32	16	16	18	11	7
Nqutsheni	30	11	19	21	9	12	23	20	3
Gqoyini	18	10	8	28	14	14	5	4	1
Dengezi	15	10	5	14	7	7	6	2	4
Other areas	22	11	11	21	11	10	13	10	3
COMBINED	116	57	59	116	57	59	65	47	18
ratio m:f	97:100			97:100			261:100		

*Class I approx. 3-6 years of age

adult after the birth of their first calves at an age of about 7 years.

Assuming (i) that 32% of the population is subadult (from Table 67); (ii) that 33% of the subadults are over about 6 years of age (from the relative proportions of subadults observed, Table 68); (iii) that of subadults over 6 years of age, 72% are males (the observed ratio in the population sample, Table 68), the sex ratio for all animals over about 6 years of age is calculated to be 98.5 males: 100 females, which is not significantly different from parity.

Estimation of the secondary (natal) sex ratio is based on the sexes of calves born into the Madlozi population and of calves seen elsewhere that were under one year of age. Since infant mortality is under 10% between birth and one year of age (see next section), the sex ratio observed in this sample should not differ greatly from that at birth. The observed sex ratio was 178 males: 100 females (Table 69), which is significantly different from 1:1 ($N = 128$, $t = 3.3$, $p = 0.001$). All samples showed an excess of males except that from Gqoyini. A similar preponderance of males among sub-yearling calves was observed by Hitchins (in lit.) during a helicopter survey carried out in 1972; 26 male calves were observed and only 14 females. Hitchins also observed an

TABLE 69. Secondary sex ratio

Based on calves born into the Madlozi study area population, plus calves less than one year old encountered in other areas.

Area	N	m.	f.	ratio m:f
Madlozi:				
1968	13	8	5	
1969	15	11	4	
1970	13	9	4	
1971	12	7	5	
Madlozi, combined	53	35	18	195:100
Nqutsheni	22	15	7	
Gqoyini	22	10	12	
Dengezi	14	9	5	
Other areas	17	13	4	
All other areas, combined	75	47	28	168:100
ALL AREAS COMBINED	128	82	46	178:100

excess of males among immature animals aged 1-4 years (95 males and 61 females), only part of which can be accounted for by the preferential capture of females.

These observations lead to the conclusion that there is a considerable excess of males among calves born, but that by adulthood the age-specific sex ratio has become even; suggesting a higher mortality among males than among females.

4. Mortality

Approximate estimates of mortality can be made from the histories of known individuals at Madlozi. Five deaths were recorded during the study period, including 2 bulls, 1 cow and 2 calves (the latter aged 12 months and about 18 months respectively). Calculated mortality rates per year were thus: adult males - 3.5% (Table 70). Only some subadults were individually recognizable, and none of these was known to have died. However, 3 unrecognizable subadults were found dead at Madlozi during the 3.3 year observation period, during which the average subadult population in the study area was estimated to be about 15 individuals; suggesting a subadult mortality rate of about 6% per year.

Since infants were usually not observed until they were about 2 months of age, the above estimate of calf mortality does not include immediately post-natal losses. One infant was known to have disappeared between 2 and 7 days of age,

TABLE 70. Mortality estimates based on histories of individually known animals in Madlozi study area

age class	no. of dif. indiv.	animal-years observed	no. dying	Mortality % p.a.
ADm	25	54.8	2	3.5
ADf	42	98.5	1	1.0
calves	40	57.8	2	3.5

TABLE 71. Mortality records from Natal Parks Board files

From Vincent, 1969, and Natal Parks Board files

Period	years	adults + subadults m.	f.	total	juveniles m.	f.	total	total
Aug'62-Aug'65	3	19	8	31	5	3	13	44
Aug'65-June'67	2	23	13	49	0	1	5	54
June'67-July'68	1	6	6	14	1	0	1	15
July'68-Sept'69	1	11	4	18	1	0	4	22
Oct'69-Sept'70	1	3	2	12	0	1	2	14
Sept'70-Mar'17	1/2							11
TOTAL	8.5	62	33	124	7	5	25	160
%		54	29				17	

TABLE 72. Age/sex structure of animals dying furing the study period, supplemented by nine additional skulls obtained

	adults m.	f.	total	subadults m.	f.	total	juveniles m.	f.	total	total
Number	14	5	22	2	1	9	2	1	7	38
%			58			24			18	

but this was detected only because its mother was equipped with a radio transmitter. However, known inter-calving intervals varied between 1.8 and 3.5 years (see next section). Thus, if a cow had not calved over a four year observation period, it could be assumed that she was either barren, or had aborted, or had lost the infant shortly after birth. There were only 3 cows that did not produce calf as expected, while 45 calves were known to have been born, of which 44 survived beyond one week of age. The observed reduction in recruitment was thus 4/48 or 8.3%, only part of which may have been due to post-natal mortality.

Records of white rhino deaths have been maintained by the Natal Parks Board since 1962. Recorded mortality in the Complex has averaged about 20 individuals per year, of which 17% were classed as juveniles, while 65% of the remainder were males (Table 71). I noted the ages of those animals dying during the study period, supplemented by the ageing of nine additional skulls found; of these 38 animals, 58% were adult, 24% were subadult, and 18% were juveniles (Table 72).

Coverage is certainly incomplete, since I knew of five rhinos that died in the vicinity of my study areas that were not recorded in official records. On the other hand, the carcases of adult and subadult rhinos are conspicuous attracting large concentrations of vultures for several days, and it is the duty of NPB officers to collect the horns from all dead rhinos; so that it is unlikely that a large proportion is missed except probably in the case of calves. Carcases and bones of animals under about a year of age disappear almost completely within a day or two, from the work of hyenas, and are most likely to be missed. Recorded mortality over the entire complex has averaged about 20 individuals per year, of which 17% were classed as "juveniles". Arbitrarily, it will be assumed that about two-thirds of all adult and subadult deaths are recorded, and accordingly it is estimated that about 25 adults plus subadults die each year on the average.

Making the above assumptions, the following mortality estimates were derived from Natal Parks Board records (assuming age structure as in Table 67): adult males - 12, or 3.0%; adult females - 6, or 1.2%; subadults - 7, or 1.1%. The estimated adult mortalities are similar to those calculated from study area observations, while a lower estimate for subadult mortality resulted.

It is possible that a higher proportion of subadults than of adults might be missed in the NPB records. Hence the following annual mortality rates will tentatively be assumed to apply: adult males - 3%; adult females - 1.2% (or overall adult mortality = 2.0%); subadults - 3%; calves (excluding post-natal mortality) - 3.5%. Pre- and post-natal losses will be assumed to amount to 8%. Overall pppulation mortality, apart from early post-natal losses (which normally to unobserved) was calculated for the early 1969 population to be 51 individuals or 2.7%.

Photographs taken of the newborn infant that died show that it was clearly less robust than other infants observed, and this may be the origin of most post-natal losses. Other known causes of death included the following: (i) accidents: a post-mortem examination on the study area cow that died revealed acute peritonitis, following the bursting of an abscess surrounding a piece of sprung steel wire that had been swallowed some time previously; one adult male fell down a 10 m high cliff while conditions were slippery after rain, and had to be destroyed; another adult male found dead had evidently fallen down a 3 m high embankement, but this may have occurred during a fight; a subadult female found dead had become trapped under a leaning tree in a wallow; an old female died after having become stuck in mud; subadult was seen floating down the Black Umfolozi River during a flood; (ii) fighting: one adult malewas reported killed by injuries received in a fight, and another which died also showed numerous wounds; there were signs of a fight in the vicinity of the skeleton of a male presumed to have been the former territorial bull of the area; two adolescent males reportedly died from horn wounds; (iii) a year old calf was listless and clearly sick the day before its death; one subordinate bull was noted to be in very poor condition before its disappearance (bones were later found); (iv) senescence: only three individuals dying were clearly aged.

Overall, it is clear that mortality rates are very low and most deaths seem to be accidental or from fights among males. There were few deaths from old age. This is not surprising, since individuals dying of old age would presumably have been born between 1920 and 1930 when the total population comprised probably only 200-300 individuals. Assuming a recruitment of 10% and survival to old age of 33% of the individuals born, only about 8 individuals would be expected to die of old age during 1969.

5. Natality

The natality rate estimated from the history of a cohort of about 45 individually known cows at Madlozi was 34.2% per female per year (Table 73). Similar cohorts of individually known cows were established in other study areas, but the removal of some calves from these during rhino capture operations precluded the calculation of natality rates.

Specific inter-calving intervals were also obtained in

TABLE 73. Natality of study area cohort of cows

Based on history of individually known cows at Madlozi

Year	no. of cows observed	no. of calves born	specific natality (% per ADf per year)
1968	42	13	31.0
1969	45	15	33.3
1970	43	13	29.5
1971	40	17	42.5
TOTAL	(170)	58	34.2

35 cases (Table 74). These were based on estimating the ages of calves when first seen; precision is estimated to be better than ± 1 month for calves up to 6 months of age, and ± 2 months for calves 6-12 months of age. Considerable individual variability is evident. The shortest known inter-calving interval was an accurately determined record of 22 months, while the longest recorded was about 42 months. Four successive records for particular cows show individual consistency. For example, the 1967 calf of the cow LL was estimated to be under two years of age at the time of the birth of her next calf, and her next calving interval was recorded more precisely to be 22 months. For the cow DD, one inter-calving interval of 27 months was noted, and her anticipated date of next calving gave an interval of 25 months. For the cow TT, both records indicated an interval of about 27 months, while for the cow K, two intervals of 30 months and 29 months were suggested.

The average inter-calving interval based on 29 cows is calculated to be 30 months.

Three records relate to the interval between the first and the second calf born to a particular cow. These are for the cows DD, NN and ZZ in Table 74, and the intervals are 27 months, 28 months and 33 months respectively. Certain other cows were judged to be relatively old individuals, on the

TABLE 74. Specific inter-calving intervals

Interval between successive calves	identity of cow	Number of cows
1 year 10 months	LL	
1 year 11 months	LL, P	- 4
2 years 0 months	W+	
2 years 1 month	(DD)*, KK, PP	
2 years 2 months		- 7
2 years 3 months	DD*, TT, (TT), (S*)	
2 years 4 months	NN*, R	
2 years 5 months	HH, I+, (K)	-6
2 years 6 months	K	
2 years 7 months		
2 years 8 months	H, SS, U	- 4
2 years 9 months	(ZZ*)	
2 years 10 months	T, UU	
2 years 11 months	VV	- 4
3 years 0 months	AA	
3 years 1 month	Y	
3 years 3 months	FF	
3 years 4 months	MM	- 7
3 years 5 months	(N+)	
over 3.5 years	D+, J+, YY	
no calf born during 4 year observ. period	B+, GG+, II+	- 3

( ) = based on anticipated calving date, from time of last known oestrus
* = young cows, accompanied by either first or second calf
\+ = elderly cows

basis of the length and degree of wear shown by their horns. About 33% of the cows showing inter-calving intervals of over 30 months were judged to be elderly, and only 10% of those with shorter intervals. One particular cow D seemed of advanced age, being wizened with an extremely long anterior horn and a bad limp. She had no calf with her in 1966, nor in 1968, but gave birth to a calf in August 1970. All three of the cows that failed to produce calves appeared elderly. One of these, B, was known to have calved in 1965 and was noted in oestrus in March 1970. This evidence suggests that she very likely calved again in 1968 or 1969 but lost the calf. It thus appears that reproduction continues throughout the lifespan of a cow, but that with advancing age inter-calving intervals lengthen and cows become more susceptible to infant mortality.

Alternatively natality rate can be estimated from the estimated 9.5% net rate of increase of the population and 2.7% overall mortality rate. Gross recruitment was thus calculated to be 12.5% per year (Table 75).

Calculation of specific natality rates depends upon estimation of the proportion of subadult females which are fertile. Since first oestrus occurs at about 5 years of age, the fertile cohort includes all females over 5 years of age. The age structure of subadults was not known, but could be

TABLE 75. Natality estimates derived from observed rate of increase of population and estimated mortality

Population structure assumed to be as in Table 67. Immediately post-natal mortality is incorporated as reduced recruitment.

(a) Gross recruitment rate

Net recruitment = 9.5% p.a. 109.5%
Mortality rate (overall) = 2.7% 3.0%
112.5%

∴ Gross recruitment = 12.5%
= 240 individuals for population size of 1920

Percentage of sub-yearling calves (allowing infant mortality of 3.5%) =236/2100
=11.2%

(b) Specific natality of female cohort

Fertile cohort - 492 adult females plus estimated 116 subadult females aged 5-7 years = total of 608

∴ Specific natality of fertile cohort = 240/608
= 39.4%

Estimated production of calves by 56 subadult females in age class (6-7) years, all of which calve at age 7 (allowing *% post-natal mortality) = 52

∴ Specific natality of parous cohort = 240/548
=43.7%

Specific natality of multi-parous cohort = 188/492
= 38.2%

Average calving interval of fertile cohort = 608/240
= 2.54 years
or, assuming 8% post-natal loss undetected
= 608/260
= 2.34 years

Average calving interval of parous cohort = 548/240
= 2.29 years
or, assuming 8% post-natal mortality undetected
= 2.11 years

estimated from the known attributes of the popu
specific natality for the fertile cohort of fem
calculated to be 39.4% per year (Table 74b). H
estimation of the proportion of fertile subadul
several assumptions, and the directly observabl
that of the parous cohort, including all female
already born calves plus primiparous females pr
first calves; this is calculated to be 43.7%. F
parous female segment alone, natality is calcula
38.2%.

These variations in specific natality rates
result of age class effects; thus, no calves ar
be born to females between 5 and 6 1/2 years of
females are expected to calve between 6 1/2 and
none of these females are then likely to calve f
16 months. Such effects are exaggerated in the
white rhino population on account of the high pr
subadults present.

The best estimate of average intercalving in
taken to be the mean between those calculated for
and parous cohorts. This is estimated to be 2.4
infant mortality is overlooked, but 2.2 years if
infant mortality of 8% is allowed (see Table 75b).

The natality calculated for the study area c

principle equivalent to that of the parous coho...
practice, however, it included only two primipa...
this is probably the result of the removal of f...
would have fallen into this category during thi...
prior to February 1967. It should therefore be ...
with that calculated above for the post-parous ...
is fairly good agreement between these two esti...
ering the many assumptions made (34.2% and 38.2...
discrepancy could be ascribed either to slight u...
tion of the proportion of adult females in the p...
or to slight overestimation of mortality rates. ...
it may be that specific natality rates for the l...
at Madlozi are lower than the average for the wh...
this is not unreasonable, considering that the Ma...
has been a centre of high population for a long t...
thus be expected to contain a higher proportion o...
females than other areas.

It will be assumed that the best estimate of ...
rate for adult (= parous) cows is the mean of the ...
estimates, 36.1%, and that the average intercalvi...
is 2.5 years.

6. Dispersal

Dispersal movements westwards, southwards and ...
out of Umfolozi Game Reserve are prevented by the ...

fence in the south than the total population there at any one time (J. Daniel, pers.com.) - evidence that dispersal movements southwards took place in the past. Most of the animals caught were taken from the region of the south-western corner of UGR, where there is no physiographic barrier to movement and where natural vegetation similar to that inside the game reserve remains. Two records of extensive movements by adolescent females from my study areas also indicated a tendency to move southwards (Section V.E.1.3).

Unusually severe floods which occurred in July 1963 markedly altered the nature of the Black Umfolozi River. Extensive deposition of silt resulted in the river becoming shallower and slower flowing at low water than it had been in the past (Vincent 1970), and this has probably facilitated white rhino movements northwards into the Corridor. A range of tall hills along much of the western boundary of the Corridor inhibits movements in that direction, while elsewhere dispersing animals are likely to encounter the strange and inhospitable environment of agricultural fields. In 1971, fencing of the western and eastern boundaries of the Corridor was completed. The only remaining direction of movement is northwards into Hluhluwe Game Reserve. The south-western section of Hluhluwe Game Reserve has always held a small resident population of white rhinos, but the hilly northern part was colonized by white rhinos only after 1961.

Information on the process colonization of the Hluhluwe north area was kindly made available by P. M. Hitchins (in lit.). The first white rhinos were seen in Hluhluwe north in 1958, but these did not remain. In 1961, two young males moved into the area and after a period of exploration settled down there. Between 1965 and 1968 an influx of white rhinos occurred, and the 1971 white rhino population in Hluhluwe north was estimated to number about 50 individuals (Hitchins and Vincent 1972). Colonization was by adolescents of both sexes plus a few adult males. In 1969, only two cows with calves were present, and both were young animals that had given birth to their first calves after arrival in the area (Hitchins pers.com.). Among the 30 different individuals that I identified there in 1969, there were 5 adult males, and two young subadults (a male and a female) aged about three years. The remaining 19 individuals were older subadults between five and ten years of age, of which two-thirds were males. Between 1968 and 1972 the first colonization by white rhinos of the hilly north-eastern section of Hluhluwe Game Reserve was observed. (Hitchins, in lit.), the first individuals consisting of a few lone adult males. In 1971 Hitchins observed a group comprising an adult male and two subadults, a male and a female aged 4-7 years, moving into a new area.

They were apparently attracted by the fresh grass sprouting after a spring burn. When the grass grew too long they moved to a nearby area and were still there a year later. By then the adult male had split off and was exhibiting territorial behaviour (Spray-urination plus dung scattering). No cows had been seen in this area as of March 1972.

There is thus evidence that dispersal movements out of the game reserve would occur were it not for the boundary fence. Most of this movement would evidently be by older subadults of both sexes, with males predominating, supplemented by some adult males.

Discussion: Population regulation in the white rhinoceros

Since a shortest inter-calving interval of 22 months was recorded, white rhino females may potentially calve every second year. However, it seems unlikely that an average interval as short as this would prevail in a population. For the African elephant Laws (1969) reported one intercalving interval as short as 2 3/4 years, though the average intercalving interval prevailing under favourable conditions seems to be about 4 years (see also Hanks 1969). Thus, for the white rhinoceros it seems that the existing average calving interval of about 2.5 years is the minimum to be expected for the species.

The mortality rates operative in the white rhino population in Umfolozi during the study period are very low; lower than has been recorded for any other population of large ungulates (Table 76). Though mortality estimates were based on several assumptions, it seems unlikely that these estimates are too low in view of their consistency with other population parameters.

With high natality, low mortality and restricted dispersal, the white rhino population is probably expanding at close to the maximum intrinsic rate of increase possible for the species. There is as yet no evidence that population regulation, in the sense of a reduction in rate of increase with increasing population size (Gilbert 1970) is as yet occurring. In Table 77, the detailed structure of a hypothetical population increasing at a constant rate of 9.5% per year, with similar characteristics to the existing Zululand white rhino population has been calculated. Its age composition agrees closely with that estimated for the real population. Minor discrepancies can be accounted for on the grounds that the real population has probably not attained a stable age distribution, and thus contains a slightly higher proportion of adults.

As yet, the animals apparently show no adverse effects from overpopulation. Fertility is high, mortality is low, and the general physical condition of the animals seems to

TABLE 76. Population dynamics statistics for various African large hervivores

Species	Mortality (% p.a.) post-natal	juv.	adult	Natality sub. yearl. calves %	specific per ADF p.a. %	sexual maturity (yrs) male physical	male social	female oestrus	female parturition	longevity yrs	reference
African elephant	-	8	4	6.5	25	15	26	12		60	Laws, 1966; Laws etal, '70; Laws, '73
White rhinoceros	5	3.5	1.5	11	40		12	5	7	50	This study
Black rhinoceros	16	16	10	11	40				5.5	40	Goddard, 1970
Hippopotamus	45	15	4	9.5	33-50	7		3-9	4	40	Laws, '68; Pienaar etal, '66; Laws and Clough, 66
African buffalo		25	12	6-12	58	3	8	3			Pienaar, 1969
Plains zebra		5			50	3	5	1.5	3.5		Klingel, '69 a and b
Waterbuck		.50	12		120		5		3	13	Spinage, 1970
Wildebeest		80	8	38	95		3	1.5	2	18	Talbot & Talbot, 1963

TABLE 77. Composition of hypothetical population increasing at a constant rate of 9.5% per annum, after attainment of stable age distribution

Assumptions: (i) size of total population about 1918 individuals; (ii) age-specific sex ratio constant = 100:100; (iii) mortality rates as follows: juveniles (0-3 years), 3.5% p.a.; subadults (3-7 yrs), 2% p.a.; adults, 1.5% p.a.; plus terminal mortality of all individuals reaching 45 years of age.

Age range	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-13	13-14	14-15	15-16	16-17	17-18	18-19	19-20	20-21	21-22
No. of indiv.	200	177	157	140	126	113	101	91	82	74	67	60	54	49	44	39	35	32	29	26	23	21

age range	22-23	23-24	24-25	25-26	26-27	27-28	28-29	29-30	30-31	31-32	32-33	33-34	34-35	35-36	36-37	37-38	38-39	39-40	40-41	41-42	42-43	43-44	44-45
No. of indiv.	19	17	15	14	13	11	10	9	8	7	7	6	5	5	4	4	4	3	3	3	2	2	2

	No.	%
Adult males (over 9 yrs)	363	19.0
Adult females (over 7 yrs)	449	23.5
Subadults (ms 2.5-9 yrs; fs 2.5-7 yrs)	644	33.7
calves (0-2.5 yrs)	455	23.8
TOTAL	1911	

Mortality of cohort (adults + subadults over 3 yrs) = 26 or 1.8%

Specific natality: fertile cohort = $\frac{202}{556}$ = 363%; parous cohort = $\frac{202}{449}$ = 450%

post-parous cohort = $\frac{110}{357}$ = 30.8%

Proportion of individuals in age range (0-1 yrs) = 10.4%

remain good with only a few individuals showing any notable decline in condition during the dry season over the study years (see Keep 1971 for estimation of physical condition).

Though the white rhinos thus seem still able to secure their nutritional requirements from the vegetation with little difficulty, the extent of degradation of the grass cover within Umfolozi Game Reserve has become the cause of serious concern. Observers seem agreed that the following trends are occurring: (i) areas of tall themda grassland are being extensively replaced by short grass cover; (ii) areas of denuded eroding soil are becoming increasingly prominent; (iii) many springs no longer flow. Habitat deterioration is most advanced in the eastern triangle, over much of the White Umfolozi valley particularly around the Mfulumkhulu and Madlozi drainages, and in parts of the Black Umfolozi valley. On the other hand, extensive reserves of tall grass still remain on the slopes of most of the hill systems, and in a few places at lower elevations.

I noticed such changes proceeding in the Madlozi area during the study period. Sections which in 1966 had been recorded as having a long grass cover remained in closely cropped condition year-round after my return in late 1968. Over much of the eastern slopes of the upper Madlozi valley the soil had become bare and sheet erosion was prominent.

The alluvial soils bordering the Madlozi stream, a favourite grazing area in 1966, had become virtually denuded of grass. Within both these areas experimental plots had been fenced off in 1967 to exclude all ungulates; these retained a good grass cover. The upper Madlozi Spring, which had been an important water source in 1966, produced only a small seep in 1969, and dried up altogether in 1970. In contrast, immediately to the north of the Madlozi valley the illuvial flats below the Zintunzini range mostly retained a good cover of tall and short grassland mosaic. There was an excellent cover of luxuriant themeda grassland on the slopes of the Zintunzini range and on Khandaladuba hill further north. The Zintunzini slopes were heavily grazed by white rhinos and other ungulates in late 1968 after burning, but grazing pressure was insufficient to prevent tall grass growing back again.

However, the explanation of observed habitat trends is not simple. The year 1966 was one of good summer rains, while drought conditions prevailed to varying degrees through 1967 to 1971. Some of the reduction in tall grass cover could be only temporary, to be reversed after the return of wet conditions. The influx of wildebeest and zebra into the Madlozi area which took place between 1966 and 1968 was an additional influence trend. Nevertheless, on the basis of relative biomass (Table 3) over 50% of the grazing pressure on the habitat is exerted by the white rhino. Therefore, it seems that at existing levels the white rhinoceros population is overgrazing its habitat.

The characteristics of the white rhinoceros population are essentially those of one undergoing an irruptive phase of expansion. Such irruptions have been recorded for other ungulate populations terminated by drastic population crashes. The most spectacular cases have occurred in introduced island populations. On St. Paul island in the Pribiloffs, 25 reindeer introduced in 1911 had increased to 2000 in 1938. A rapid decline then ensued, and only 8 individuals remained in 1950 (Scheffer 1951). On St. Matthew Island in the Bering Sea, 29 reindeer introduced in 1944 had increased to 6000 animals in 1963; the severe winter which followed elimated all except 42 (Klein 1968). In both cases the crash was ascribed to the heavy decimation of the lichens essential as winter food. On Isle Royale, Lake Superior, moose which colonized the island in 1905 had increased to between 1000 and 3000 by 1930. A die-off then enued, and only 400-500 remained in 1936. There was a second expansion to 800 in 1948, followed by a decline to 300 in 1957. The die-offs were correlated with a reduction of the browse essential as winter food. Since 1957, the moose population has apparently stabilized at about 600 under the influence of wolf predation (Moch 1966). Other population irruptions followed by crashes have been observed in mainland populations of deer. The best known is that of the Kaibab mule deer herd (Rasmussen 1941), though the data are speculative (see Caughley 1970). Other examples for mule deer and white-tailed deer in North America have been documented by Leopold et al (1947) and by Martin and Krefting (1953), and for elk by Banfield (1949). In Africa, a population of reedbuck in Kyle National Park, Rhodesia, recently crashed in similar fashion (Ferrar and Kerr 1971). The most spectacular African example however is that of the Tsavo elephant population. Details still remain to be documented, but it is evident that several thousand elephants died of apparent starvation around water sources during the severe drought of 1971.

These population irruptions can be understood on the basis of a model developed by Riney (1963) on the basis of observations on introduced ungulates in New Zealand, which is also applicable to natural populations where there is a large discrepancy between population levels and potential habitat carrying capacity. Such populations apparently proceed through four stages: (i) an initial stage of rapid expansion into the superabundant habitat with low mortality; (ii) a period of temporary stabilization as population levels reach then exceed carrying capacity; (iii) a stage of rapid decline in numbers as populations adjust to a lowered carrying capacity; such mass mortality is likely to be associated with critical habitat conditions such as a drought year; (iv) a period of final stabilization at a much lower population level in a degraded habitat. The irruptive cycle is held to arise from an interaction between the expanding population and the vegetation. The intensifying effects of feeding by the expanding population reduce the productivity of the food plants upon which it depends. Though age specific natality and mortality rates may later adjust to those operative in stable populations, the population continues to increase for several more years as results of the continuing recruitment into the adult cohort of the high proportion of young animals resulting from the expansive phase. Thus, a considerable excess in population size over carrying capacity is built up, resulting in severe habitat destruction.

Caughley (1970) examined the validity of Riney's predictions for the introduced New Zealand population of Himalayan thar (Hemitragus jemlahicus). Four sample populations were observed at increasing distances from the initial point of release of the animal sixty years previously, it being populated that these would represent each of the four stages of population adjustment. Variability in natality and mortality rates and in body condition as expressed by kidney fat reserves were shown to accord with Riney's predictions. Regulatory changes were most striking in terms of first year mortality. Differences in fecundity were less notable except for the proportion of two year old females becoming pregnant. These changes were related to a depletion of the snow tussock grass which was a key plant for winter forage.

In Riney's terms, the Umfolozi white rhinoceroses represent a "Stage 1" population still in the expansive phase. However considering the evidence of habitat destruction, a rapid transition through to "Stage 4" may be anticipated to commence soon, unless management is instituted to avert this.

A contrasting situation prevails in the Hluhluwe black rhinoceros population, which appears to be either stable or even declining slowly in numbers (Hitchins, pers.com.). Black rhino density in HGR is considerably lower than that of the Umfolozi white rhinos, averaging only $0.76/km^2$ over the 215 km^2 area (compared with about $4/km^2$ for white rhinos over the 250 km^2 area of UGR west). Fecundity appears low, with many females remaining unaccompanied by calves despite showing signs of oestrus and being seen to be mated, suggesting that infant mortality is high. Hyenas seem to be the agents of some of this mortality, judging by the ear mutilations seen on several surviving calves. However the ultimate cause may be that calves are born of subnormal weight on account of nutritional deficiencies (see Sadleir 1969). The black rhinoceros population thus presents all the characteristics of a "Stage 4" population without having undergone an interuptive cycle.

The subject of population regulation in ungulates remains, in general, poorly understood. Because of the intense pressure such large herbivores can exert on the habitat, they would seem to be particularly in need of population regulatory mechanisms which would avoid direct starvation. This is especially so for the white rhinoceros, for which predation seems unlikely to be significant as a controlling factor. For the white rhinoceros population to achieve stability, changes must come about in existing rates of natality, of mortality, or of dispersal, or all three. To understnad the present situation, it is necessary to consider how the operation of these processes may have been diffenent in the past, and what changes might be anticipated under present conditions.

<u>Influences on mortality</u>

Current mortality rates are very low. For comparison, Goddard (1970) for the Tsavo black rhino population estimated average annual mortality rates of 10% for adults and 16% for juveniles (versus 2% for adults and 3.5% for juveniles in the white rhino, this study). Even for the African elephant, Laws (1966) estimated an average mortality rate for adults of 4% per annum for adults, under the favourable environmental conditions prevailing in Queen Elizabeth National Park, Uganda (though some of this mortality may have been due to shooting).

Under present condition, mortality in the Umfolozi white rhino population from predation and disease seems to be close to zero (Sections VI.D and C). Higher mortality rates through these agencies may have operated in the distant past.

The Umfolozi lion population is relatively new in the area and has an abundance of alternative prey. With more limited prey availability, lions might kill a few immature white rhinos. But judging from Kruger Park observations and observations of black rhinos in East Africa (see p. 663 it seems unlikely that lion predation would form a significant mortality factor.

Currently few if any white rhino calves are taken by hyenas in the complex. However, if white rhino calves were born less robust through nutritional deficiencies, and thus less well able to keep up with the mother, losses through hyena predation might be higher.

Currently, there are almost no poaching losses, since penalties are high and it is difficult to hide a white rhino carcass. The significance of human predation in the past is difficult to evaluate. Rhinoceroses sometimes appear in the rock paintings of Bushmen people, but they do not seem to have been a favoured prey species. Probably they were difficult to kill with the primitive weapons and small hunting bands typical of the Bushmen. Of the Bantu tribes who later settled in South Africa, the Tswanas used pits to capture rhinoceroses (see p.28), while the Zulus did not regard rhinoceroses as edible. Thus, while human predation may have been locally significant, it seems unlikely that it was a consistent mortality factor.

Parasites and diseases seem currently to have little effect in the white rhino population, but it may be that some disease pathogens were eliminated while the population was at a very low level before protection became effective. Without any other long-established population for comparison, little more can be said.

Nutritional deficiencies, could lead directly to starvation during critical periods, or at least make the animals more susceptible to the effects of disease and parasitism. During the study period, animals showed some loss in condition during the dry season, but this seemed of a relatively minor nature. However, large-scale mortality probably related to starvation occurred during the very severe drought of 1933, when at least 100 white rhinos reportedly died (Player and Feely 1960). During another prolonged drought in 1965, increased mortality was also noted and the proportion of animals in poor condition was higher than in previous years (Steele, unpublished report in NPB files), but, as reflected in the mortality records (Table 71) this was evidently on a much smaller scale. Since population densities at the time of the 1933 drought were probably only about 20% of those currently existing, such mortality is apparently density independent in its action. This can be understood from knowledge of the food ecology of the species (Section IV.A). During short drought periods such as prevail every winter, food quantity is not limited, but the animals are forced to subsist for a period on forage which is submaintanance in its protein levels. If such conditions are prolonged, mortality of a portion of the population due to starvation may ensue, such mortality being related to the lenght of the drought period rather than to pre-existing population levels. Density dependent effects may be superimposed, since with higher population densities better quality forage is grazed down earlier during the wet season, thus reducing later food intake per unit time making the animals less capable of building up adequate fat reserves.

The animals are thus forced to turn their attention to poorer quality forage earlier in the dry season and as a result lose condition more rapidly. This effect seemed to be occurring during the study period considering the fairly extensive utilization of the less nutritious hillslope grasslands taking place. However, though rainfall was low and erratic during study years, late rains fell so that the length of the dry season was shorter than usual. It may be predicted that if a prolonged drought should ensue under present conditions, extensive mortality would result. Catastrophic mortality of this nature associated with an unusually severe drought was probably irregular in its action in the past, perhaps knocking back population levels at intervals without restricting population growth during intervening more normal years.

Nutritional deficiencies are likely to be reflected more sensitively through infant mortality. Vermes (1962, quoted by Klein 1970) demonstrated experimentally the strong influence on infant survival of dietary deficiencies in pregnant and post-partum white-tailed deer females. Poor quality diets increased post-natal mortality from 7% to as much as 90%, resulting from the following factors: (i) poor condition of the fawn; (ii) fawn too small to reach the teats of the doe; (iii) doe not permitting the fawn to suckle; (iv) delayed lactation or no lactation by the doe. For the high density hippopotamus population in Queen Elizabeth Park, Uganda, Laws (1968) reported a first year mortality rate of 45%. In the excessively high elephant population in Murchison Falls National Park South, Uganda, juvenile mortality over the period 0-4 years increased from 29% to 43% between 1946 and 1966.(Laws 1973). In contrast, post-natal losses are estimated to be under 10%, and total juvenile mortality between 0 and 3 years under 20% for the Umfolozi white rhino population (Section 4). Mortality related to starvation was probably the main factor limiting population size in the African buffalo population in Serengeti National Park, Tanzania (Sinclair in press). Hirst (1969) found that non-migratory populations of impala, kudu and giraffe in the Timbavati Nature Reserve in the Eastern Transvall were limited mainly by recurrent starvation losses during the dry season. To understand how such mortality may also have operated in the white rhino population in the past, it is necessary to consider the interrelationships between various grazing ungulates and the vegetation in a much broader perspective.

Present conditions in Umfolozi Game Reserve are probably much changed from those that existed in "pristine" times 150 or more years ago. There has evidently been an increase in woody vegetation at the expense of grassland judging by changes in animals populations. Zebras and buffalo, both long grass grazers, were formerly abundant in the region (Vincent 1970). Currently large numbers of woodland inhabiting nyala and impala occur, neither of which was recorded historically in the area. A vegetation shift towards denser woodland may have been initiated by the elimination of elephants from the area in 1890 (Vincent 1970), considering the impact this species can have on vegetation in other areas (see Bourliere 1965).

In the past, the area in the vicinity of the two Umfolozi Rivers probably formed a dry season concentration area for such mobile grazers as zebra, buffalo and wildebeest. During the wet season, populations of these species were probably widely dispersed. More sedentary species such as warthog and white rhinoceros would probably have had ample supplies of forage, on account of the absence for much of the year of such migratory grazers. As the dry season advanced, an influx of these migrant species would have occurred, attracted not only by the reliable water supplies, but also bythe Themeda grasslands of Umfolozi which remain relatively more nutritious during the dry season then surrounding higher rainfall grasslands. During the later dry season, populations of white rhino, buffalo, zebra and wildebeest would all have been dependent on the remaining reserves of _Themeda triandra_, and the quantity of food available to the white rhino population must thus have been reduced by the competitive grazing effects of the other three species. Warthog would be able to avoid food competition by seeking out rhizomes and tubers unavailable to other grazers.

In the absence of migration, populations of buffalo, zebra and wildebeest are now probably much lower than those which occurred in Umfolozi in the past during the dry season and present numbers have been built up relatively recently. Warthogs have been numerous for some time, but their biomass in insignificant compared with that of white rhinos. Thus, in the virtual absence of grazing competitors, the white rhino population has enjoyed a superabundance of winter forage. This has probably allowed it to reach higher population densities than those which occurred in the past without significant winter mortality.

Current high white rhino population densities coupled now with year-round grazing by large numbers of wildebeest inhibiting recovery of grasslands during the wet season. Constant foliage removal from tall-growing species such as Themeda triandra prevents seeding, and limits build-up in root storage nutriments for the dry season. Plants thus die and are replaced by closegrowing stoloniferous species. Though these may be more nutritious on account of their lower fibre content, than taller species, the resulting heavy removal of plant material leaves the soil unprotected from the eroding effects of wind and rain during the dry season. Under certain soil conditions this may lead to a progressive denudation in grass cover. In the absence of fires, such areas are likely with time to be colonized by woody vegetation. The habitat can thus be considered to be in the process of a natural adjustment to the changed grazing regime, which will result in a reduced carrying capacity for grazers. If this interpretation is valid, it implies paradoxically that ultimately a higher white rhino population could be sustained in the area in the presence of high seasonal concentrations of grazing competitors.

From this analysis in terms of community dynamics, it seems that some chronic dry season mortality in the white rhino population has been eliminated.

Influences on fecundity

In association with the elephant overpopulation in Murchison Falls National Park South, Uganda, intercalving intervals have lengthened from four years to about seven years, and female age at puberty has been retarded from twelve to eighteen years (Laws et al 1970). These changes were related to poor nutrition which was apparently also responsible for a retardation in the seasonal occurrence of peak calving by several months. Nutritional effects on fecundity have been demonstrated in North American deer and in domestic sheep (Sadleir 1969; Klein 1970). In different cases, these can influence ovulation rates, fertility during oestrus, the incidence of twinning, or growth and survival of the foetus during pregnancy. In many ungulate populations, the proportion of yearling females which are fertile is particularly sensitive to nutritional plane. However, Hanks (1972) has suggested that fecundity changes alone are insufficient to stabilize African elephant population in the absence of increases in infant mortality.

Trivers and Willard (1973) have proposed that, for evolutionary reasons, a population in poor nutritional condition should produce a high proportion of female calves, and one in good nutritional status a high proportion of males. Poor survival of male calves has been noted in many populations under stress (see for example Klein 1970). The high proportion of male calves being born to the white rhino population (Section B.3) suggests that nutritional effects are having little influence on the white rhino population as yet. Some cows were observed to undergo several oestrous cycles before conception, and this phenomenon could be exaggerated by increasing nutritional stress, thus increasing intercalving intervals. However, the effect of this on fecundity would probably be small, perhaps reducing it by no more than 20%.

The effects of nutrition on progeny viability are likely to be more significant, and also its influence on the rate of maturation of females.

<u>Dispersal</u>.

Dispersal movements out of the game reserve are now prevented by the boundary fence. Evidence presented earlier (Section 6) indicated that emigration of a portion of the population would occur were it not for the presence of this barrier; and that such dispersal movements by subadults would be primarily a response to decreasing food and water availability during the dry season (Section V.E.1.3.). Additional dispersal movements by adult males may be related to social factors (see next section). Dispersal movements primarily by adult males and subadults has been noted for many other species (see for example Hitchins and Vincent 1972); causative factors have rarely been identified, though it has generally been assumed that social pressures are significant.

Formerly the white rhino was distributed in localized pockets of abundance (Section I.C); the area of Umfolozi Game Reserve seems to have represented one such pocket. Surrounding these pockets was sparsely populated habitat which was presumably less favourable in terms of water availability and grassland composition. Emigration of a portion of the population surplus into such areas was probably an ongoing process in the past, and if mortality rates were higher there, as seems likely, this would help to regulate overall population size.

Different species may differ in their tendencies towards dispersal. Those inhabiting seral communities are likely to produce the highest surplus for dispersal, while inhabitants of stable climax vegetation covering extensive areas gain little by dispersing (Geist 1973). Goddard (1967) emphasised that extremely low dispersal rates are typical of black rhinoceros populations. However, grazers need to adapt to widely fluctuating local carrying capacities related to broad cycles of wet and dry periods, which reach greatest extremes in arid and semi-arid regions (De Vos 1969). The white rhinoceros is a grazer which, from its former distribution pattern, is adapted to the dryer forms of grassland. As Laws (1968) emphasised for the African elephant, dispersal must have been an important mechanism limiting the degree of overutilization of local food resources.

Social influences on mortality, fecundity and dispersal

Territoriality is held by some, notably Wynne-Edwards (1962), to be an adaptation for limiting population size within the food carrying capacity of the environment, thus avoiding overutilization of food resources. However, this interpretation is controversial, and convincing evidence for seemed generally tolerated by adult males and adult females alike, and dispersal movements of females cannot be accounted for on the basis of social factors.

Thus the major population regulatory mechanisms which probably operated in the past, but which are precluded under present conditions, seem to be these: (i) mortality and reduced recruitment resulting from dry season nutritional stress at lower population densities than those currently existing as a result of more intense grazing competition; (ii) emigration of a portion of the subadult population. Additional losses through occasional predation on young animals, though small, may have reduced still further the excess of recruitment over mortality. Animals in the present population have grown up under conditions of environmental superabundance, and are likely to be particularly robust physically, and better able to maintain high natality and low mortality rates under currently existing conditions than might otherwise be the case.

Table 78 presents the structure of two hypothetical stable populations. Population A has similar natality and mortality rates to those operating in the real population; stability has been achieved by the emigration or death of all surplus individuals promptly at six years of age, immediately preceeding the recruitment of subadult females into the adult

TABLE 78. <u>Composition of two hypothetical stable populations</u>

Assumptions: Population A: as in Table 77, with specific natality per post-parous f of .33 p.a. stability achieved by emigration or death of surplus subadults promptly at age 6.; Population B: specific natality = 0.25 per post-parous female p.a.; first parturition at age 8; post-natal mortality (0-6 mo) = 40%; immature mortality to age 6 = 10% p.a.; Size of adult cohort in both populations adjusted to 900.

Age range		0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-13	13-14	14-15	15-16	16-17	17-18	18-19	19-20	20-21	21-22
No.indiv.	A	155	150	145	141	137	133	32	32	31	31	30	30	29	29	29	28	28	27	27	27	26	26
	B	75	67	60	54	49	44	40	38	37	36	35	34	33	32	31	30	30	29	28	27	26	26

Age range		22-23	23-24	24-25	25-26	26-27	27-28	28-29	29-30	30-31	31-32	32-33	33-34	34-35	35-36	36-37	37-38	38-39	39-40	40-41	41-42	42-43	43-44	44-45
No. indiv.	A	26	25	25	24	24	24	23	23	23	22	22	22	21	21	21	21	20	20	20	19	19	19	19
	B	25	24	23	23	22	21	21	20	20	19	18	18	17	17	16	16	15	15	15	14	14	13	13

	A		B	
	No	%	No	%
Adult males (over 9 yrs)	435	23.6	431	32.0
Adult females (over 7 years)	466	25.3	469	34.9
Subadults (ms 3-9 yrs, fs 3-7 yrs)	495	26.8	243	18.1
Calves (under 3 yrs)	450	24.4	202	15.0
TOTAL	1846		1345	
Mortality of cohort (Adults + immature over 3 yrs)	43	2.3	63	5.5
Proportion of individuals in age range (0-1 yrs)	155	8.4	75	5.6

cohort. With a total population size of 1845 individuals, the emigration of 100 six year olds per year would be necessary to achieve balance. In population B there is no emigration, and balance has been achieved by alterations in natality and mortality rates, suggesting the extent of such changes required: (i) increase in average calving interval from 2.5 to 4 years; (ii) age of first calving in females retarded from 6.5 years to 8 years; (iii) post-natal mortality (0-6 months) increased from 10% to 40%; (iv) immature mortality to age 6 increased from 3% to 10% per annum; (v) adult mortality increased from 2% to 3% per annum.

However, evidence is accumulating that ungulate populations do not in general exist in a stable state; rather there is an ebb and flo in population size in response to fluctuating environmental carrying capacities related to climatic cycles. For example, populations of wildebeest and other ungulates were drastically reduced in East Africa during the severe 1961 drought; on the Athi-Kapiti plains of Kenya, the overall ungulate biomass was reduced from 1945 kg/km^2 to 1089 kg/km^2 (Stewart and Zaphiro 1963; see also Talbot and Talbot 1963), but since then populations have been expanding steadily in numbers (Estes 1969). Elephant populations seem to exhibit long term local fluctuations in numbers, perhaps in response to the changes they themselves bring about in the vegetation

(Watson et al 1972). Other cases of mass mortality during drought periods have been recorded in Botswana, where an estimated 15,000 or more wildebeest died in 1964, and in 1970 (Child 1972). Stevenson-Hamilton (1947), first Warden of the Kruger National Park, presents an excellent exposition of such fluctuations in game numbers and associated responses by predators.

The process seems to be that during a series of favourable years recruitment exceeds mortality, and populations expand in size and colonize new areas. When severe drought conditions arise, large-scale mortality results in an overall reduction in populations size which is more extreme in less favourable habitats. This seems to be related basically to the elimination of food around the few remaining water sources. With the return of favourable conditions, populations are considerably below carrying capacities and expand outwards from optimal habitats to recolonize surrounding habitats. Limitation of population size is thus achieved largely by periodic mass mortality in marginal habitats in critical years. Population fluctuations, in more prolific species, are dampened by the effects of predation, though predators do not seem to limit overall populations sizes in favourable habitats (see Schaller 1972). In optimal habitats, reproductive rates provide, on the average, a small surplus such an effect has been presented only for the Red Grouse (Watson and Jenkins 1968; see also Tanner 1966). Though territoriality has frequently been claimed to regulate populations of songbirds by limiting breeding densities, Brown (1968) has disputed this.

In the case of the white rhino and most other territorial ungulates, territoriality is limited to adult males. It may provide pressure for some males to settle elsewhere, and may also be responsible for increased mortalities among males (but such mortality may be lower than that which would result were an alternative form of male-male competition to be adopted). It may thus restrict male population densities and hence have some influence on the grazing pressure exerted on the habitat. However, such effects seem slight, since males unable to claim their own territories can remain as subordinate bulls. More significantly, male territoriality does not seem to have any influence on population densities of females, nor does the fecundity of females seem limited in any way by availability of males for mating. Thus, territoriality exerts no apparent controlling effect on natality rates in the population.

Territorial bulls were occasionally observed chasing subadult males. This may provide an additional stimulus for such young males to emigrate. However, subadult females in natality over mortality which is available for colonization of surrounding areas. Population densities in favourable habitats are regulated by the dispersal outwards of this surplus. This mechanism ensures the continued survival of the species in the face of long term fluctuations in locally prevailing environmental favourability. As Laws (1968) has emphasised, in long-lived species such as the African elephant, dispersal is essential if population limitation within the carrying capacity of the habitat is to occur, since fecundity changes are too slow acting and adult mortality shows little response until conditions have already become critical. Similar arguements can be applied to the white rhino. This conceptual model carries considerable implications for the management of ungulate populations within National Parks, which are usually sited in optimal environments for a variety of species; these will be examined in the next section.

If such processes have always been successful in the past in avoiding overpopulation, the white rhinoceros need have evolved no other mechanisms to regulate population densities.

VIII. M A N A G E M E N T

A. BROAD OBJECTIVES

Management of the Zululand white rhino population cannot be viewed in isolation, but must be considered holistically in relation to the overall objectives for which the region is set aside. Both Umfolozi and Hluhluwe were established as game reserves for the purpose of protecting wild animal populations, but have since become of importance also for public viewing of wildlife. They are included in the United Nations list of National Parks and equivalent reserves (Harroy, 1971. The intervening Corridor remains as unallocated State Land, but forms an essential part of the same unit so far as animal populations are concerned. It currently has de facto status as a game reserve, and it is to be hoped that this will finally be confirmed by legislation. Were this not to come about, it would greatly compound existing problems, both for animal populations and for tourism. The Umfolozi-Corridor-Hluhluwe Complex in effect forms a single unit for management purposes, and will be considered as such.

As yet, no detailed statement of management objectives has been formulated for the area by the Natal Parks Board. However, from my familiarity with the region, I suggest that the following more specific aims need to be incorporated:

1) retention of plant and animal communities representative of those which formerly occurred in the Zululand region as a cultural resource for viewing and study by the people of South Africa and the rest of the world;

2) maintainance in particular of an adequate population of the white rhinoceros to ensure its long term survival in the area, for scientific and aesthetic reasons as a rare and unusual species;

3) designation and maintainance of part of the area as a wilderness, as an aesthetic and recreational resource; no other big game wilderness is included in the South African Parks system, and no other area is so favourably endowed for this purpose;

4) design of facilities to enable the park to function as an economic resource based on tourism, supplying income to the Kwa-Zulu homeland, which adjoins the area.

Particular problems are associated with trying to accomodate all four aims within the limited area of 950 km^2 available. Zonation will obviously be needed to avoid conflicts between objectives. Both tourism and wilderness appeal are, however, dependent on the maintainance of the wildlife resource, and the wildlife resource is in turn dependent on its habitat. Thus a simplified statement of goals in practical terms is possible, so far as wildlife populations are concerned. Management may be directed primarily towards maintaining as large and diverse a large mammal fauna, on a sustained basis as is concomitant with other aims.

Lamprey (1973) provides an excellent discussion of some of the problems associated with the management of fauna and flora in National Parks, particularly from the aspect of the dynamic nature of natural ecosystems. In Africa it is difficult, and of questionable desirability, to try to maintain historic conditions, as was proposed for U.S. National Parks (Leopold et al, 1963). Ecosystems undergo broad fluctuations in character in response to climatic variations and other influences. Such changes should not be resisted, so long as they do not lead to irreversible alterations in the fauna or flora or aesthetic qualities of the area. The management ideal may be defined as one of maintaining the ecological potential of the area in terms of highest sustained productivity and species diversity.

However, the Umfolozi-Corridor-Hluhluwe Complex is too small to retain the self-regulating properties of a natural eco-system. I therefore suggest that goals be redefined in these more pragmatic terms: that management procedures be designed to achieve an environment which, as perceived by the visiting public, represents the closest approximation to natural conditions that can practically be accomodated.

Active intervention may thus be needed to combat some trends which conspicuously change the pristine appearance of the area. However, measures adopted should not intrude so as to create an impression of artificiality. The area should resemble, as nearly as is practical, a wilderness and not a game farm.

B. WHITE RHINOCEROS MANAGEMENT - PROBLEMS

Maintainance of the white rhino population can be approached through the concepts of resource management. The white rhino population is a renewable resource dependent upon energy flow from primary production in the grasslands. Attention thus needs to be focused on the productivity of the grassland layer, the nature and degree of its utilization by the white rhinoceros and other consumers, and the effects of these on continued grassland productivity. From this aspect, the grasslands of the reserve can be divided into the following categories: (i) short grass areas in which there is near complete utilization of foliage production, mainly during the wet season; forage quality is high in terms of nutritive state, but after the growing season such areas offer little food; (ii) tall grasslands in which there is partial offtake of foliage mainly during the course of the dry season; (iii) tall grass areas which are hardly utilized, either through inaccessibility or relative unpalatibility;

they may be important as an emergency food source when critical conditions arise; (iv) over-utilized areas showing decreased productivity, either through reduced grass cover or increased proportion of unpalatible species.

Thus, grassland areas can be characterized as representing summer food sources, winter food sources, emergency food reserves and suboptimally producing areas. Trends in the areal extent of each can easily be monitored by observation from the air or high points. During the late summer, summer grazing areas will present a green carpet areas representing winter and emergency food sources will appear golden from the flowering of Themeda triandra and other grasses, and degraded areas will show bare soil. The extent of utilization of tall grass areas during the dry season can be obtained from similar observations immediately following the first good spring rains. Unutilized tall grass will remain brown, while sections that have been grazed down will flush green along with the short grass covered areas.

The optimal ratio of these four forage categories for long term maintainance of the white rhino population is not known. A satisfactory answer can be provided only by a long term program of research on grassland productivity and its utilization by consumers (a start on this was made in 1972 by Rober Porter). What gives cause for concern is the apparently increasing concentration by grazing rhinos on areas of hillslope grassland during the later dry season. Such grasslands are probably suboptimal in nutrient content (see Downing 1972). The risk of a large-scale die-off of white rhinos through nutritional stress should drought conditions be prolonged is thereby heightened.

Coupled with this decreasing availability of better quality dry season grazing is an apparent increase in the extent of areas of bare, eroding soil which are less productive of forage for summer grazing. The white rhino population is hence forced to graze increasingly into remaining stands of tall grass during the wet season. The causes of such trends are probably complex. Some of the denuded sections coincide with areas that were covered with woodland prior to the anti-nagana bush-clearing. The process may thus be one merely of reversion to the former vegetation type. There is evidence, from the observations of Downing (1973) that overgrazing may be inevitable on some of the more fertile alluvial soils, resulting in a closed woodland cover. Some soils with low permeability seem susceptible to erosion under existing grazing pressures, particularly if aided by increased slope (as on the eastern slopes of the Madlozi valley). Other soils with improved texture, particularly those derived from dolerite, seem able to support a good grass cover even though subjected to higher grazing pressures (as on the Zintunzini flats).

To halt further habitat degradation, a reduction in the white rhino population seems an urgent necessity. Evidence indicates that the white rhino population is in the process of an irruptive fluctuation. From knowledge of other cases of such cycles, it can be predicted that without intervention this trend will lead to eventually come about a stage of gross overpopulation and extensive habitat destruction, followed by mass mortality and a population crash, with stabilization of the population at much lower levels in a degraded habitat. The Umfolozi-Corridor-Hluhluwe complex in effect represents an ecological island in which dispersal is impossible, and an irruptive cycle can therefore be expected to follow the pattern typical of island populations.

The problem becomes one of deciding what are the populations of the white rhinoceros and other large mammals which can be sustained on a long term basis, and how the process of artificial regulation can best be carried out.

A crude approximation to carrying capacity may be obtained by comparing standing crop biomass of large herbivores with those existing in other African habitats. (Table 79). Highest recorded biomasses are those of Queen Elizabeth National Park, Uganda, and the adjacent Albert National Park

TABLE 79. Comparative year-round large herbivore biomasses in different African habitats

Location	extent km²	biomass kg/ha	reference
Queen Elizabeth Pk, Uganda			
(i) short grass, overgrazed	58	295	Field&Laws, 1970
(ii) shrt grass	54	168-190	
(iii) long grass	26	51	
Albert N.P., Zaire			
(i) S of Lake Edward	600	242	Bourliere, 1965
(ii) N of Lake Edward	226	89	
Umfolozi G.R., Zululand	456	79	from NPB count, 1970
Hluhluwe G.R., Zululand	215	62	
Nairobi N.P., Kenya	115	63	Foster&Coe, 1968
Ngorongoro Crater, Tanzania	311	61	Lamprey, 1964
Serengeti N.P., Tanzania	15,000	50	Hendrichs, 1970
Serengeti Ecosystem	25,500	40	Watson et al, 1969
Tarangire G.R., Tanzania	1683	11	Lamprey, 1964
" " , transect area	30	127	
Kruger N.P., South Africa			
(i) Sabi River area	1050	56	Pienaar et al, 1966
(ii) overall	18500	19	
Kafue N.P., Zambia	20000	13	Dowsett, 1966

of Zaire. Most of the biomass in these two parks is made up by three large-bodied species which have correspondingly low rates of energy turnover per unit of body weight: the hippo, buffalo and elephant. At the highest biomass of 295 kg/ha in Wueen Elizabeth Park, the habitat was regarded as overgrazed. In other habitats with lower biomasses of 168-190 kg/ha, the vegetation was showing good recovery from a previously overgrazed condition (Field and Laws, 1970). Rainfall regime is not significantly higher than that in Umfolozi Game Reserve (average rainfall for Queen Elizabeth Park is 670 mm p.a. Spinage, 1970); that for UGR is 635 mm p.a. (Downing, 1973). For most other African habitats, biomasses typically vary between 50 and 63 kg/km^2.

Of the UGR biomass of 72 kg/km^2, nearly 60% is made up by the white rhino. From the known relationship between metabolic rates and body weight (metabolism = $k \times W^{0.73}$, Hemmingson 1960), the energy demands of the white rhinoceros population should be only about 60% of those of an equivalent weight of wildebeest. Thus, existing biomass in UGR is comparable to that sustained by similar habitats elsewhere and does not in itself indicate overpopulation. However, the growing season in Zululand is shorter than that in East African habitats, because of the more extended dry season, and the replacement of the grassland by denuded areas and woodland implies a further reduction in overall grass production in the area, and hence in carrying capacity for grazing herbivores. With these considerations the existing biomass seems excessive.

C. IMPLEMENTATION

White rhino population densities need to be reduced to a sufficiently low level to halt further habitat degradation, but excessive reduction would be morally repugnant. Arbitrarily, it seems that a minimum reduction in white rhino biomass by about one third would be required. This implies a reduction by this fraction in the size of the adult cohort which makes up the bulk of the biomass. A sufficient number of immature animals would also need to be removed to overcome the considerable momentum built into the current population towards increase through the imbalance in proportion of immature animals.

Consideration of the relative proportions of different age and sex categories to be removed is facilitated by reference to Tables 77 and 78. If culling took place in accordance with existing ratios, then at the current rate of increase it would be necessary to remove 8.7% of the total population (= original population plus 9.5% increase) per year in order to halt population increase. For a total population size of about 2000, this means the annual removal

TABLE 80. Suggested removal program to reduce biomass by one third and stabilize population
Population structure in early 1969 derived from Tables 67 and 77; removals up to Aug.'72 are those actually accomplished, except that immature sex ratio has been assumed even; natality of post-parous female cohort = 36%, plus parturition by all females on reaching age 7; mortality rates ADm- 3%, ADf - 1.2%, subadults (2.5-7 yrs) - 3%, juveniles (0-2.5 yrs)- 3.5%; immatures (2-6 yrs) assumed removed proportionately to existing ratios.

		removals					age structure of population										
		adult m	adult f	imm.	juv.	tot.	0-1	1-2	2-3	3-4	4-5	5-6	6-7	ad.+subad.7+ m	ad.+subad.7+ f	tot.	TOTAL
e.1969	POPUL.						185	164	145	135	121	109	98	477	492	957	1926
	removed	13	36	109		157			32	29	26	22		13	36		
	remain						185	164	113	106	95	87	98	464	456		
Aug.'70	popul.						207	179	159	110	103	92	84	498	500	998	1940
	removed	4	13	141		158			48	34	31	28		4	13		
	remain						207	179	111	76	72	64	84	494	487		
Aug'71	popul.						211	200	174	107	74	70	62	520	523	1043	1961
	removed	26	49	183		258			74	46	32	30		26	49		
	remain						211	200	100	61	42	40	62	494	474		
Aug'72	popul.						196	204	193	97	59	41	39	509	499	1008	1837
	removed	80	80	160	80	400	40	40	79	40	24	17		80	80		
	remain						156	164	114	57	35	24	39	429	419		
Aug'73	popul.						166	151	159	111	55	34	23	435	434	869	1568
	remove	80	80	160	80	400	41	39	71	49	24	16		80	80		
	remain						125	112	88	62	31	18	23	355	354		
Aug'74	popul.						133	121	119	85	60	30	17	353	359	712	1277
	remove	40	40	80	40	200	21	19	32	23	16	8		40	40		
	remain						112	102	87	62	44	22	17	313	319		
Aug'75	popul.						110	108	99	84	60	43	21	322	324	646	1171
	remove		5	80		85			28	24	17	12			5		
	remain						110	108	71	60	43	31	21	322	319		
Aug'76	popul.						119	106	104	69	58	42	30	322	325	647	1175

white rhinos over the four year period 1971-1975. If fewer animals were removed during this period more animals would have to be removed in the long run because of continuing reproduction by animals remaining in the population. For example, if only 250 animals per year were removed, population reduction would not be accomplished until mid-1977, and a total of 1550 white rhinos would have to be taken out over the six year period.

The final size of the white rhino population to be aimed at is 1200 animals, about that which was present in the Complex in 1960 (ref. Table 64). Such a population could be held constant by the removal of 85 animals annually, if these were made up by immature animals '- the age range (2-6. years. A slight excess of females would d to be removed, because of the lower mortality rate prevailing among cows. Fewer animals per year could be removed if removals were concentrated on subadults of about age 6, and fewer still if natural population regulatory changes latered existing natality and mortality rates.

One final consideration concerns the best manner of maintaining population stability. Rather than the arbitrary removal of a fixed number of animals each year, it would be preferable to imitate natural population regulatory processes so far as is possible. A key process missing under present conditions is opportunity for subadult dispersal. To permit this, it will be necessary to create "vacuum zones" into which surplus animals can move. This could be done by the complete removal of all white rhinos from selected segments of the game reserve. The improved grazing conditions in such areas would presumably draw in individuals from surrounding areas. Culling could then be carried out by removing all white rhinos recolonizing the vacuum zones each year. These animals would represent the surplus individuals as determined by social relationships within the population in relation to local food resources. The bulk of the white rhino population would thus remain relatively undisturbed by artificial manipulation. It might be necessary to cull a few additional animals from the main population, if an insufficient number to control population increase immigrates into the vacuum areas. The vacuum areas could also be located for the most efficient removal of surplus animals, leaving wilderness qualities in the remainder of the game reserve untarnished by vehicle tracks and other disturbances.

The management program must be supported by an ongoing program of research to monitor its effects both on the white rhino population and on the vegetation. Information on vegetation trends in relation to animal populations and their dietary requirements is essential in order to ascertain the permissible carrying capacities for white rhinos and other ungulates. The size and structure of the white rhino population must be censused annually by a standard technique to reveal changes brought about by removals. In addition, a control population of white rhinos must be set aside that will remain affected as little as possible by the removal program. This will serve as a future research area to determine what population regulatory changes have come about naturally in the white rhino population, and will retain an undisturbed population for future scientific studies. This control study area must be large enough to encompass the annual movements of a representative population of white rhinos. Since individual cows may range over an area of 20 km^2 or more, it would need to encompass an area of at least 50 km^2, and should be bounded as far as possible by natural features such as hills, rivers or waterholes.

D. RECOMMENDATIONS

1. That the 1971 white rhino biomass be reduced by one third, implying a reduction in total numbers to about 1200 animals.
2. That in order to minimize further habitat degradation, such reduction be accomplished as rapidly as possible, preferably by no later than mid 1975.
3. That simultaneously the large excess of immature animals in the present population be reduced to proportions typical

of a stable population.

4. That thereafter population stability be maintained by the selective removal of all white rhinos settling within selected "vacuum zones".

5. That these vaccuum zones be located as follows: (i) in the region of the south-western corner of UGR, south of the White Umfolozi River; (ii) in the lower Madlozi valley, south of the Nyonikazane Spring; (iii) in the region of Nqutsheni camp in the north-western corner of UGR; (iv) in the eastern triangle between the two Umfolozi rivers; (v) in the northern part of HGR.

6. That removals be prohibited in a special white rhino study area, in order to retain a relatively undisturbed population for future scientific studies, and as a comparison area to ascertain the effects of the removal program.

7. That the white rhino study area be based on my Madlozi study area, and defined as a square of about 50 km^2 extent with the following limits: (i) in the north, the Sokhwezela beacon; (ii) in the south, the junction of the Madlozi and Nyonikazane Streams; (iii) in the east, the lower Mphafa Pool; (iv) in the west, the western boundary fence; furthermore, that no removals be carried out during the late dry season between this study area and the White Umfolozi River between Nqolothi and the junction of the Mphafa Stream when movements

by some animals out of the study area in this direction is likely; and that no marked individuals retaining eartags or recognizable slits in their ears, or radio transmitters in their horns, be removed, wherever they might be.

8. That high priority be given to an intensive program of research to determine environmental productivities and the food-energy demands of populations of the white rhino and other ungulates, to permit the assessment of the long-term carrying capacities for each species.

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APPENDIX I

Scientific names of mammals referred to in the text

ass, African wild	Equinus asinus
bison, American	Bison bison
bontebok	Damaliscus dorcas dorcas
buffalo, African	Syncerus caffer
bushbuck	Tragelaphus scriptus
bushpig	Potamochoerus porcus
caribou	Rangifer tarandus groenlandicus
chamois	Rupicapra rupicapra
cheetah	Acinonyx jubatus
deer, mule	Odocoileus hemionus
deer, red	Cervus elaphas
deer, roe	Capreolus capreolus
deer, white-tailed	Odocoileus virginianus
dikdik	Madoqua kirkii
duiker, grey	Sylvicapra grimmia
duiker, red	Cephalophus natalensis
eland	Taurotragus oryx
elephant, African	Loxodonta africana
elephant, Asian	Elephas maximus
elk, American	Cervus canadensis
gazelle, Grant's	Gazella granti
gazelle, Thomson's	Gazella thomsoni
gerenuk	Litocranius walleri
giraffe	Giraffa camelopardalis
hartebeest, Coke's	Alcelaphus buselaphus cokei
hartebeest, Lichtenstein's	Alcelaphus lichtensteini
hippopotamus	Hippopotamus amphibius
hyena	Crocuta crocuta
impala	Aepyceros melampus
klipspringer	Oreotragus oreotragus
kob	Kobus kob
kudu	Tragelaphus strepsiceros
kudu, lesser	Tragelaphus buxtoni

(Appendix I)

leopard	*Panthera pardus*
lion	*Panthera leo*
moose	*Alces alces*
muskox	*Ovibos moschatus*
nyala	*Tragelaphus angasi*
pronghorn	*Antilocapra americana*
reedbuck	*Redunca arundinum*
reedbuck, mountain	*Redunca fulvorufula*
rhinoceros, black	*Diceros bicornis*
rhinoceros, Indian	*Rhinoceros unicornis*
rhinoceros, Javan	*Rhinoceros sondaicus*
rhinoceros, Sumatran	*Dicerorhinus sumatrensis*
rhinoceros, white	*Ceratotherium simum*
roan antelope	*Hippotragus equinus*
sable antelope	*Hippotragus niger*
steenbok	*Raphicerus campestris*
tiger	*Panthera tigris*
topi	*Damaliscus lunatus korrigum*
tsessebe	*Damaliscus lunatus lunatus*
vicuna	*Lama vicuna*
wapiti	*Cervus canadensis*
warthog	*Phacochoerus aethiopicus*
waterbuck	*Kobus ellipsiprimnus*
wildebeest	*Connochaetes taurinus*
wildebeest, black	*Connochaetes gnou*
zebra, Grevy's	*Equus grevyi*
zebra, mountain	*Equus zebra*
zebra, plains	*Equus burchelli*

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