

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

..... TERRITORY BOUNDARY

Fig. 19: Distribution of dungheaps within a territory. Figures indicate the number of times each dungheap was marked by an  $\alpha$  ♂ over a five day period

into the dungheap after sniffing; in six instances, this could be related to the known or likely presence of the dung of another  $\alpha$  ♂ there. However, in two other cases where the dung of another  $\alpha$  ♂ was known to be present, no response was given.

Urination by an  $\alpha$  ♂ was almost always carried out in a powerful backwardly directed spray in 3-5 spasmodic bursts (Fig. 20). Spray-urination was commonly preceded by first wiping the anterior horn sideways over a low bush or on the ground, then dragging the hindlegs stiffly over this site. The urine droplets fell over the scrapemarks left on the ground or coated the leaves of the bush. In 7/636 instances only, an  $\alpha$  ♂ urinated in a continuous stream with hindlegs straddled.

It was rare to find two successive instances of spray-urination at the same site, though scrapemarks were sometimes only a few metres apart over adjacent bushes. Spray-urination was performed throughout the extent of a territory, but occurred particularly frequently while an  $\alpha$  ♂ was grazing or walking along



Fig. 20: Spray-urination by an  $\alpha$  ♂

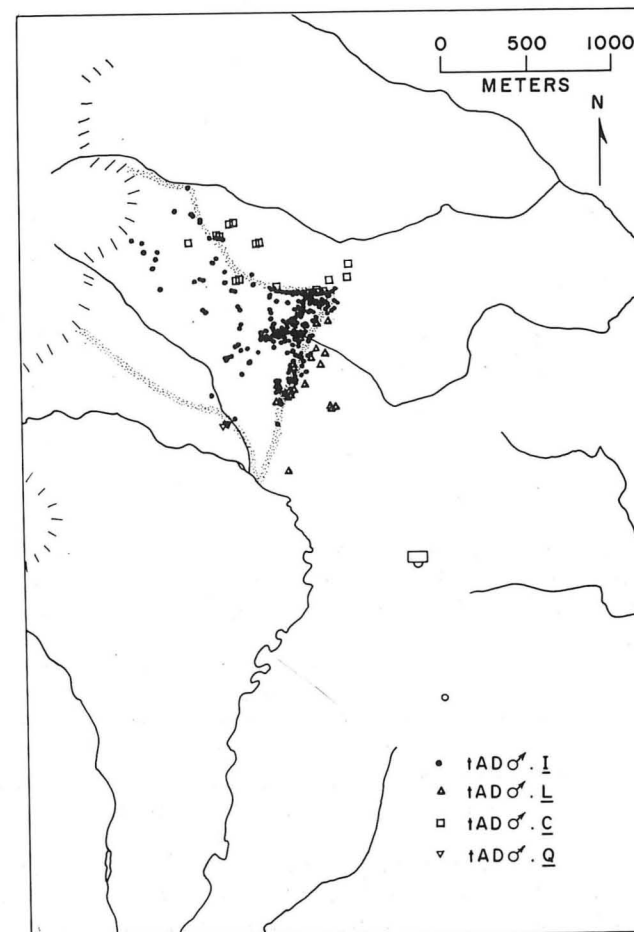


Fig. 21: Distribution of spray-urination sites by a resident  $\alpha$  ♂ and neighbouring  $\alpha$  ♂ ♂. All observed instances of spray-urination over a two year period have been plotted

a boundary region; an average of 2.0 spray-urinations per hour ( $N = 40$  hours) was recorded centrally within a territory, compared with 10.0 per hour ( $N = 12$  hours) in border regions. As a result spray-urination sites were more concentrated in boundary regions (Fig. 21). A mean density of four scrapemarks per 1000 m<sup>2</sup> was recorded within 50 m on either side of the putative boundary line in a survey conducted four days after rain had obliterated older scrapemarks. In another survey conducted twelve days after rain, an average of one scrape-mark every 25–30 m was recorded within 3 m of rhino trails following territory borders, and one scrapemark per 38 m alongside a well-used trail passing centrally through a territory. Evidently, urination sites may be concentrated beside well-used trails as well as along boundaries.

### 3. Behaviour associated with territory changes

Eleven reciprocal changes between  $\alpha\delta$  and  $\beta\delta$  status were recorded during the study period. Three strange adult  $\delta\delta$  appeared in the study area displacing one of the resident  $\alpha\delta\delta$ ; three formerly  $\beta\delta\delta$  displaced an  $\alpha\delta$  in an adjacent or nearby territory; four  $\alpha\delta\delta$  occupied part or all of a neighbouring territory after the formerly resident  $\alpha\delta$  had disappeared; and one chain displacement occurred. A newcomer  $I$  displaced a resident  $\alpha\delta H$ ;  $H$  remained in the same territory as  $\beta\delta$  for three months, then occupied a small territory 2 km away, then four months later displaced  $X$  as  $\alpha\delta$  in an adjoining territory;  $X$  stayed on only a week, then displaced  $A$  as  $\alpha\delta$  in the next territory;  $A$  still remained as  $\beta\delta$  in this same territory 15 months later. Three of the displaced  $\alpha\delta\delta$  disappeared, another stayed as  $\beta\delta$  in the same territory, while a fifth transferred to an adjoining territory and was still present there with  $\beta\delta$  status 19 months later. One unplanned removal experiment took place when an  $\alpha\delta$  from a territory adjoining the study area was captured and moved to Mozambique; the vacant territory was eventually subdivided by two neighbouring  $\alpha\delta\delta$ . One young  $\delta$  aged about nine years moved into the study area alone and took up residence within one of the territories as a  $\beta\delta$ .

No case was known in which a  $\beta\delta$  subsequently became  $\alpha\delta$  in the same territory that he had occupied as a  $\beta\delta$ .

In three cases, detailed behavioural observations were made on the  $\delta\delta$  concerned following a territory changeover. These involved the takeover of the territory of  $H$  by the newcomer  $I$ , subsequent displacement of  $X$  by  $H$ , and finally  $X$ 's displacement of  $A$ .

In no case was the crucial contest which presumably decided the transition observed. In two of the cases I simply found the new  $\delta$  behaving as  $\alpha\delta$  in the territory. In the third case I watched both  $X$  and  $A$  occupying and spray-urinating in the same territory for 4 days, but the only encounter witnessed was a brief horn to horn confrontation glimpsed from long range on the first day. Afterwards both  $\delta\delta$  moved away in different directions. On the fifth day  $A$  was discovered exhibiting numerous bloody wounds. Two days later I glimpsed the end of a fight in which  $X$  attacked  $A$  with a succession of vigorous horn blows;  $A$  then broke away and galloped off with  $X$  in pursuit. However, in the other two cases the deposed  $\delta$  was virtually unmarked, and apparently some more ritualised form of contest had taken place.

The newly instated  $\delta$  immediately displayed all the behaviour patterns typical of an  $\alpha\delta$ . He spray-urinated and scattered his dung, turned back cows at appropriate boundaries, and confronted resident  $\beta\delta\delta$ , including the former  $\alpha\delta$ , in typical fashion. Following the change, the profusion of fresh scrape-

marks in the territory was striking, and some overlapping scrapemarks beside the same bush were noted, an unusual occurrence.

The former  $\alpha\delta$  in turn behaved as a  $\beta\delta$ . He immediately or within a day or two ceased spray-urination (in the case of  $A$ , only following the second fight). He more gradually, over a period of a few days or weeks, stopped scattering his dung, first omitting preceding kicks then diminishing the intensity of succeeding kicks until these became merely "token" gestures. He approached cows more hesitantly. When approached by the new  $\alpha\delta$ , he stood giving snarls. However, deposed  $\delta\delta$  did not vacate the territory.

In the case of  $A$ , it was particularly clear how the deposed  $\delta$  orientated along the borders of the territory for 1–2 weeks following the takeover, tending to locate himself just across on the neighbouring  $\alpha\delta$ 's side of the boundary. Notably, at one border he observed the *new* boundary established between  $X$  and the neighbouring  $\alpha\delta$ . In two cases, sudden boundary shifts took place following a changeover. In one case I observed the neighbouring  $\alpha\delta$  spray-urinating around in the transferred section (where he had not been seen previously) about 8–15 days after the transition. Subsequent sightings of the  $\alpha\delta\delta$  concerned confirmed the new boundary locations, which thereafter remained stable.

Two months after the occupation of  $H$ 's territory by  $I$ , the old  $\beta\delta N$ , who had been resident there for at least 3.3 years, left and occupied an area 1 km away. This locality had formed part of the territory of an  $\alpha\delta$  who had disappeared three months earlier.  $N$  settled there and thereafter behaved as an  $\alpha\delta$ .

Some  $\beta\delta\delta$  exhibited profuse scarring, which may have been the marks of the fight in which they had lost  $\alpha\delta$  status.

### 4. Intra-group interactions

Group companions while grazing commonly chose orientations which maintained them in close proximity. Frequently they grazed side by side for several minutes. If the individuals happened to drift apart, close spacing was restored by one individual turning and moving closer to the other before resuming grazing. Calves and subadults were more active in moving nearer to a companion cow than vice versa (Table 16). The differing spacing typical of different group types (Table 2) was the result of older animals tolerating greater

Table 16: Intra-group interaction frequencies

Group type	hours intens. observ.	moving nearer (times recorded)		initiation of moves (times recorded)		tactile contact (times recorded)		threats (/hour)	
		cow	other indiv.	cow	other indiv.	cow	other indiv.	cow	other indiv.
Cow + juvenile	37	4	13	7	1	2	6	0	0
Cow + subadult	32	2	6	12	1	2	3	0.3	0.07
Cow + cow	19	4	3	5	4	3	1	0.08	0
Subadult + subadult	7	0	0	2	2	3	1	0.4	0
Cow + several subadults	3	0	2	1	1	-	-	0	0.6
Temporary subadult with cow-subadult ♀ dyad	30	0	20	15	0	0	3	0.3	0.9* 0.06*
Cow + alpha ♂	47	0	n	n	0	0	0	2.3	0

\* By subadult companion of cow against temporary subadult.

+ By temporary subadult against cow or her subadult companion.

n = numerous.

separations before moving nearer. In the case of two companion cows, both individuals seemed equally active in moving nearer.

Sometimes after moving nearer, or simply when passing by, one individual made tactile contact by rubbing its side against that of the other in passing, or occasionally by rubbing its head against the other's body. Cows initiated such tactile contacts with a calf or subadult companion as well as vice versa. Acceptance of such action probably has a proximity maintaining function.

A change in location was initiated by one individual walking steadily in a certain direction. Frequently the companion followed almost simultaneously. If not, the initiator paused waiting after 10—15 m. Sometimes the initiator then returned to walk close past the companion, in some instances rubbing against it in passing, or making a panting sound as it moved thereby drawing its attention (this sound functioned in several contexts as a contact or proximity maintaining signal). In cow-calf and cow-subadult groups, most moves were initiated by the cow, though occasionally a cow followed a directed movement initiated by the younger individual. In a cow-multi-subadult group, the cow appeared the focus of the group. Though one of the subadults sometimes initiated a move by walking ahead, if the cow did not follow the move was abortive. Nearest neighbour analysis revealed no preferential associations between any of the subadults. In a three-subadult group, control was exerted by the older ♀. Moves initiated by the other two were less likely to be followed. In even-aged homosexual subadult dyads, both individuals seemed equally able to initiate moves. In the case of the two companion cows, both were equally active in this regard. Subadults that were only temporarily attached to a particular group maintained greater spacings and seemed to orientate to the group in general rather than to any specific individual. They were less attentive to the movements of the others, and sometimes got left behind when the group shifted on. In cow-*a*♂ associations it was always the *a*♂ that followed the movements of the cow.

While moving, companions walked within a few metres of one another either in single file or side by side. The initiator of the move seldom led the move; calves and subadults tended more often to walk ahead of a cow than behind her. After settling to rest, close companions lay down almost touching. No supplanting interactions were observed between close companions in this context or any other. However, cows commonly advanced on accompanying *a*♂♂ with a snort or snarl if the latter blocked their path of movement, and once a cow displaced an *a*♂ from a shade rest-place in this manner. Alpha ♂♂ readily yielded to such threats.

Upon a disturbance (usually caused by detection of a human intruder), group companions rushed together making panting sounds. They then either stood with their rear ends together facing outwards in different directions, or stampeded off making pants. Juvenile calves always ran off ahead of their mothers, responding to any changes in direction by her. White rhinos rarely charged towards the source of a disturbance in the manner of black rhinos; cows with very small calves stayed close beside the infant. ♂♂ hastened towards or after cows with pants, never vice versa.

Threats between close companions were rare, being limited to an occasional soft snort when the companion moved close behind or beside. Two 11—12 year old sa♂♂ made 3 brief snarls during a 3.2 hour observation session, an unusually high rate; but the significance of this is questionable, as other companion dyads occasionally had "off-days" when several threats were exchanged, while on other days none were recorded. In a three subadult group, the two sa♀♀ never exchanged snorts while under observation, while the older sa♀ directed several snorts or horn prodding movements at the sa♂, and the latter snorted at

the younger sa♀ on several occasions. Four months later the sa♂ broke away from the group leaving the two sa♀♀ together (and accordingly he has been regarded as a peripheral group member in compiling Table 16). Where several subadults were associated with the same cow, several exchanges of snorts or horn prodding gestures among them were noted. When additional subadults were temporarily associated with a cow-subadult dyad, the subadult companion of the cow was the more active in directing snorts and horn prods towards them. In cow-*a*♂ associations, the cow snorted or snarled if the bull approached closer than about 10 m.

## 5. Reproductive behaviour

Though reproduction was not seasonally restricted, seasonal variations were evident in the incidence of both oestrus and parturition. Peak oestrus levels, estimated by the proportion of cows being accompanied by a ♂, tended to occur in November and February, while few cows were accompanied by ♂♂ during the dry season months of July—September. Calving peaks were evident in March and July, in accordance with the estimated gestation period of sixteen months (allowing for some non-fertile oestruses). However, there were year to year variations which could be related to the prevailing rainfall regimes. Oestrus seemed to be stimulated by conditions of freshly sprouting green grass following rain.

The approach of oestrus was first indicated by a persistent association between a cow and an *a*♂. All such associations lasting more than a day or two could be related to probable oestrus. Cows known to have been pregnant (from subsequent parturition) were recorded as having an *a*♂ associated with them in only 2.5% of sightings (N = 728) (compared with 13.0%, N = 2499, for all cows combined), and none of these associations was seen to last longer than a day or two. The pre-oestrus consort period usually lasted 1—2 weeks (range 4—20 days). The *a*♂ followed the cow everywhere in her movements, but there were no other signs of oestrus evident to me. The cow snorted or snarled if the *a*♂ came nearer than about 10—15 m, and the *a*♂ accordingly kept his distance from the cow, except in one set of circumstances.

If the cow's movements took her into the proximity of a territory boundary region, the *a*♂ hastened ahead squealing to stand in front of her blocking her progress (Fig. 22). The *a*♂ made loud squeals, horn wiped, scraped and urinated sprays repeatedly (once 29 spray-urinations were recorded within 122 min), and persistently moved to stay between the cow and the boundary. Sometimes there was a short confrontation, with snarls from the cow and squeals from the *a*♂, but almost always the *a*♂ succeeded in turning the cow back. Occasionally I disturbed the animals and the cow ran off past the *a*♂; in such cases the *a*♂ set off in haste after the cow attempting to cut her off, but if she got past him he did not pursue more than 100—200 m beyond his territory limits. There were four cases in which the *a*♂ encountered a neighbouring *a*♂ at the boundary while blocking a cow, and a short confrontation developed, during which the cow slipped over the boundary. The cow was then joined by the new *a*♂, and the previous *a*♂ did not follow. However, though the noise associated with such territory boundary blocking interactions was audible for several 100 m, neighbouring *a*♂♂ never crossed territory boundaries to interfere, even when they were close by. Usually an *a*♂ commenced territory boundary blocking manoeuvres about 100 m within his own territory limits, and positions of such interactions confirmed territory boundary locations (see Fig. 8).



Fig. 22: An  $\alpha$  ♂ (on the right) blocks the advance of a cow and calf at a territory border. The ears back posture of the  $\alpha$  ♂ is unusual, perhaps due to his being particularly hard pressed by this cow

The onset of oestrus was indicated by the commencement of repeated courtship advances by the  $\alpha$  ♂. The  $\alpha$  ♂ approached behind the cow making a wheezy hiccup sound. Initial advances were checked by separation maintaining vocalizations from the cow. After several hours of persistent approaching, the  $\alpha$  ♂ was tolerated when he placed his chin briefly on the rump of the cow. Several approaches led to this position before the initial mounting attempts, and usually the first few attempts were abortive. During later stages the cow emitted little squirts of urine each time the  $\alpha$  ♂ approached, though still resisting with snorts and snarls. Sometimes an  $\alpha$  ♂ mounted a few times without achieving erection, then full erection and intromission finally occurred. Copulations lasted 15–28 min ( $N = 7$ ), with ejaculations every 2–3 min revealed by rapid quivering movements. Copulation took place about 24 hours after the first hiccup approaches had been recorded, and only a single copulation took place, except in one instance when copulation was repeated after an interval of three hours. The consort relationship persisted for a further 1–5 days. Some cows were not seen with an  $\alpha$  ♂ again until after the birth of the calf 16 months later. However, other cows were rejoined by an  $\alpha$  ♂ a few days later, and it appeared that oestrus recurred at intervals of about 30 days if conception did not result.

With one exception,  $\beta$  ♂ ♂ did not form such persistent attachments to cows, though they sometimes followed after cows for a few hours. Of the seven copulations observed, six were by  $\alpha$  ♂ ♂, and one by a  $\beta$  ♂. However, the latter was associated with unusual conditions. It took place in a section of the former home territory of the  $\beta$  ♂ concerned which had shortly before been transferred to the neighbouring territory in association with a territory takeover. There was no preceding or succeeding consort period by the  $\beta$  ♂, nor was any  $\alpha$  ♂ seen with the

cow. The mating was evidently not fertile, since the cow was being persistently accompanied by an  $\alpha$  ♂ a month later.

In two instances,  $\beta$  ♂ ♂ remained only 20–50 m away during courtship and mating, but displayed little excitement. In several other instances,  $\beta$  ♂ ♂ moved past consort pairs showing little interest. Once an  $\alpha$  ♂ clashed horns briefly with a nearby  $\beta$  ♂, but thereafter ignored his presence. Once a  $\beta$  ♂ made courtship advances towards a cow the day after she had been courted by the  $\alpha$  ♂. The  $\alpha$  ♂ clashed horns briefly with the  $\beta$  ♂ three times, but the latter stayed close by for several more hours before wandering off.

There was one case in which a  $\beta$  ♂ formed a consort attachment to a cow at a time when the  $\alpha$  ♂ was accompanying another cow. However, two days later the  $\alpha$  ♂ was seen courting and mating with the first cow, while the  $\beta$  ♂ moved around agitatedly nearby. After mating, the  $\alpha$  ♂ confronted the  $\beta$  ♂ and clashed horns three times, but then wandered off. The  $\beta$  ♂ remained with the cow and attempted courtship advances, but the cow warded off all further approaches. This  $\beta$  ♂ had been the  $\alpha$  ♂ in the neighbouring territory a year previously.

Calves commenced nibbling at grass at two months and were grazing concentratedly by four months. Nursing usually continued until the calf was about a year old, but in one case was prolonged as long as 18 months. Cows came into oestrus again when the calf was 6–12 months old, and intercalving intervals averaged 2.5 years (range 22 months to about three years,  $N = 29$ ). The older calf was driven away by the mother at the time of the birth of the new calf; only two instances were recorded in which an older offspring later rejoined its mother and the new calf (out of 45 births observed). Juvenile mortality was low, only two calves under a year old disappearing and being presumed dead.

#### IV. Discussion

##### 1. Characteristics of the social system

Features of the social structure of the white rhinoceros include (i) the limited extent of group formation; (ii) the spatial dispersion of adult ♂ ♂ in discrete areas, each occupied by one reproductively active ♂ and perhaps one or more subsidiary ♂ ♂.

Previous authors have reported the white rhinoceros to live in family groups or herds numbering up to 14 individuals (e.g. RIPLEY 1958, HEPPEL 1958), contrasting this pattern with that of the more solitary black rhinoceros. However the group structure observed in this study differs only slightly from that reported for the black rhinoceros (KLINGEL and KLINGEL 1966, GODDARD 1967, SCHENKEL and SCHENKEL-HULLIGER 1969). In Zululand, HITCHINS (pers. com.) found that 1.7% of black rhino groupings included more than three individuals, while for the white rhino in the same region the corresponding figure is 3.4% (this study). The largest black rhino grouping seen by HITCHINS included seven individuals, but this was probably a temporary aggregation. KLINGEL and KLINGEL (1966) reported an association of five black rhinos (two cows, a calf, a subadult ♀ and a bull) in Ngorongoro Crater which remained together for four days. The main difference between the two species is that whereas in the black rhino subadults are usually found solitarily, in the white rhino subadult associations including several individuals are relatively common. This difference may be partly a consequence of the much higher population densities maintained by the white rhinoceros (3/km<sup>2</sup> in Umfolozi Game Reserve overall) compared with those typical of the black rhinoceros (about 0.8/km<sup>2</sup> in Hluhluwe Game Reserve and 0.3/km<sup>2</sup> at Ngorongoro). What previous authors have prob-

ably misinterpreted are temporary grazing or resting aggregations formed by white rhinos. Different groups may bunch together when disturbed, conveying the impression of a larger cohesive group.

In the white rhinoceros, stable associations seem limited to dyadic attachments. These may be based either on a mother-offspring bond, a "surrogate" mother-offspring bond between a cow lacking a calf and a subadult driven away by its mother, or a close "friendship" between two subadults. Larger groups arise mostly when several subadults attach themselves to the same cow. The occasional associations between two adult ♀♀ and between young ♂♂ nearing maturity are interesting as they presage the formation of multi-♀ herds and bachelor ♂ groups by the more highly sociable ungulates. Evidence suggests that such associations need not be based on a genetic relationship between the individuals concerned.

The system of mutually exclusive areas occupied by  $\alpha\delta\delta$  seems essentially similar to the territorial systems described for many African bovids (well documented examples include kob *Kobus kob*, LEUTHOLD 1966, wildebeest *Connochaetes taurinus*, ESTES 1969, Thomson's gazelle *Gazella thomsoni*, WALTHER 1964 and 1972 a, waterbuck *Kobus defassa*, SPINAGE 1969, and bontebok *Damaliscus dorcas*, DAVID 1973), and also for Grevy's zebra *Equus grevyi* (KLINGEL 1972), pronghorn *Antilocapra americana* (BROMLEY 1969), vicuna *Lama vicugna* (KOFORD 1957), and black rhinoceroses in Zululand (HITCHINS 1972). As in Thomson's gazelle, the territories of white rhino ♂♂ have sharply defined boundaries that are patrolled and scent marked. In this they differ from the centripetally focussed territories of wildebeest and bontebok ♂♂, for which boundaries seem diffuse. Territory sizes observed for Umfolozi white rhinoceroses are not large in relation to the body size of the animals, being exceeded in extent by those of Grevy's zebra (2.7–10.5 km<sup>2</sup>, KLINGEL 1972), black rhinoceros (4 km<sup>2</sup>, HITCHINS 1972), sable antelope *Hippotragus niger* (2.5+ km<sup>2</sup>, ESTES 1974) and tsessebe *Damaliscus lunatus* (2–4 km<sup>2</sup>, JOUBERT 1972). However for an introduced population of white rhinos in Kyle National Park, Rhodesia, where the population density was 0.7/km<sup>2</sup>, CONDY (1973) found territories to be 5–11 km<sup>2</sup> in extent.

Spatial location in relation to the territorial structuring strongly influences the nature of behavioural interactions among ♂♂. Unlike wildebeest, neighbouring white rhino territorial ♂♂ do not actively seek meetings; encounters seemingly occur only accidentally when two ♂♂ happen to patrol the same boundary at the same time. In border confrontations, conflicting tendencies to advance and withdraw are strikingly displayed, and actions appear highly ritualised. Aggressive tendencies are redirected in the form of vigorous horn wiping, or limited to momentary horn clashes. A charge can be interpreted as an action which serves to confirm the status of the other rhino. Alpha ♂♂ meet charges silently, other rhinos make snarls. Horn wiping appears in several contexts, but since it is performed only by  $\alpha\delta\delta$  it can serve as a manifestation of presence which also identifies status.  $\alpha\delta\delta$  on their home territories confidently approach all other rhinos. Such action differs from the hesitant approaches made by all other rhinos and without requiring further emphasis functions as an intimidatory challenge. It seems that, in order to maintain relative status, an  $\alpha\delta$  must always respond to such a challenge by a neighbour with corresponding displays, even when trespassing on the neighbour's territory. However, in the latter circumstances the intruding  $\alpha\delta$  yields ground steadily until he regains his own territory. Apart from infrequent contests for territory ownership, fights may also develop when an intruder meets a neighbour some distance from his own territory limits. Unfortunately, support for this is based on a single obser-

vation only. Further observations would also be desirable to support another suggested pattern: that an  $\alpha\delta$ , on crossing the boundary from the neighbouring territory to the territory once removed, apparently suddenly switches to the behaviour patterns of a  $\beta\delta$ . This suggests that  $\alpha\delta\delta$  recognize not only their own territory limits, but also those of neighbouring territories.

The loud roars of  $\beta\delta\delta$  in the snarl display contrast strongly with the silent confrontations of  $\alpha\delta\delta$ . To a human observer the snarl display appears strongly intimidatory, especially when coupled with advancing steps or horn waving gestures (and was accordingly misinterpreted by PLAYER and FEELY 1960). However, gestures suggestive of fear are evident on close observation: the overall tenseness of the posture, which contrasts with the relaxed bearing of the confronting  $\alpha\delta$ ; a tendency to step backwards, or make intention movements to do so; the rise in pitch of the roar to a shrill shriek at any move by the  $\alpha\delta$  suggestive of attack; and a curling of the tail. The snarl display when adopted by  $\beta\delta\delta$  appears to function as a defensive threat. It signals clearly that the displayer is not challenging, while maintaining a position in which he is able to defend himself if necessary. The use of such a display, rather than withdrawal, can be understood on the basis of the physical characteristics of the white rhinoceros. Subtle visual gestures of submission are likely to pass unnoticed by a rival endowed with such poor vision. Running is energetically highly expensive in so large an animal, and furthermore exposes the fleeing animal to attack from the rear unless it is capable of outdistancing the pursuer (notably only subadults or young adult ♂♂ respond by fleeing). There is no safe refuge to which a  $\beta\delta$  can retreat; on adjoining territories he is liable to be challenged by other  $\alpha\delta\delta$ , and there is no unclaimed ground. A  $\beta\delta$ 's best strategy is accordingly to stand his ground ready to deflect attacking moves by the challenger, repeatedly assert non-challenge, and wait until the challenger tires and goes away. On the part of the challenging  $\alpha\delta$ , an attack if pushed through would draw forth defensive responses, exposing the  $\alpha\delta$  to the risk of receiving injuries himself. Having confirmed that the other ♂ is not a challenger, he wastes no further time and energy and moves away.

Beta ♂♂ are equivalent in status to the non-territorial ♂♂ which typically group into "bachelor herds" in the more sociable ungulates. In some species, for example wildebeest (ESTES 1969), such bachelor ♂♂ are excluded from the territory mosaic and occupy peripheral marginal habitat. They are tolerated within territories, to varying degrees, in Grevy's zebra (KLINGEL 1972), Grant's gazelle *Gazella granti* (WALTHER 1972a), bontebok (DAVID 1973) and impala *Aepyceros melampus* (JARMAN and JARMAN 1974), but range through several territories. In the white rhino, there is the unusual situation in which such "bachelor ♂♂" restrict their movements mostly to the territory of a single territorial ♂. Since all available habitat is divided up into territories, it seems most advantageous for a white rhino  $\beta\delta$  to settle in a particular territory, gradually habituate the resident  $\alpha\delta$  to his presence so that challenges become less frequent, and conserve time and energy until an opportunity to challenge for  $\alpha\delta$  status occurs. As in the social bovids, the status of bachelor or  $\beta\delta$  is only a temporary phase in the life of an adult ♂; though the time scale is considerably more drawn out in the white rhino. The occasional wandering movements made by  $\beta\delta\delta$  can be interpreted as exploratory sallies to investigate the situation in surrounding territories.

Elsewhere (OWEN-SMITH 1971) it was suggested that the presence of subsidiary ♂♂ could be a consequence of high population density. However, it seems more likely that the class of  $\beta\delta$  is a typical feature of white rhino social organization. There will probably always be present some young and aged indi-

viduals incapable of maintaining the status of  $\alpha\delta$ , plus a few prime  $\delta\delta$  awaiting opportunities in favourable areas rather than dispersing out into less propitious conditions.

On the part of  $\alpha\delta\delta$ , it is difficult for animals unable to detect intruders at ranges exceeding 50–70 m to maintain surveillance over an area of 2 km<sup>2</sup>, and actively exclude all intruding  $\delta\delta$ . Instead,  $\alpha\delta\delta$  simply challenge other  $\delta\delta$  when encountered, forcing them to demonstrate whether they have tendencies to reciprocate the challenge. If they show submission, they are left on the territory. The recurring brief confrontations of resident  $\beta\delta\delta$  serve to reinforce periodically the relative status of the two individuals. Notably, no  $\beta\delta$  was ever observed to depose the  $\alpha\delta$  in the same territory.

Direct interactions between neighbouring  $\alpha\delta\delta$  occur too infrequently to account for the observed stability in territory boundary locations. The scent marking system seems of prime significance here. The concentration of spray-urination sites along boundaries seems adequate to delineate their location and provide evidence of the continued presence of the neighbouring  $\alpha\delta$ , without a need for direct interactions. Dungheaps on the other hand are more widely dispersed. Kicking movements could transfer dung scent to the feet and thereby distribute it more widely, as was suggested by GODDARD (1967) for the black rhino. However, though  $\alpha\delta\delta$  frequently made use of border dungheaps while patrolling boundaries, there was no evidence that they did so particularly before beginning a patrol. Dungheaps provide focal points for investigation, and potentially reveal the presence in the vicinity of other individuals of all classes (RIPLEY'S [1958] suggestion that they function as "family bulletin boards" therefore has some merit, if the word "family" is deleted). The conspicuous presence of the scent of the  $\alpha\delta$  on the dungheap emphasises his occupation of the locality in which the dungheap is situated. The large border dungheaps, which probably consist mainly of the dung of the  $\alpha\delta$ , could demonstrate to neighbours his continued residence. However, such information seems redundant, being supplied also by spray-urination sites.

Such scent marks could function either by reassuring the originator that he is on home ground, or by repelling rivals. In practice it is difficult to separate these alternatives. On one side of a territory boundary an  $\alpha\delta$  is surrounded primarily by his own scent marks, on the other mainly by the scent marks of the neighbour; it is the difference between these two situations which is likely to affect his relative confidence.

There is, however, evidence that in the white rhino scent marks have significance not only for the originator.  $\beta\delta\delta$  observed the same boundaries as  $\alpha\delta\delta$ , though they did not exhibit special scent marking patterns. Newly resident  $\alpha\delta\delta$  exhibited no difficulties in orientating to the limits of the territory they had just occupied. Two such  $\delta\delta$  were watched veering back after exploring across a boundary. Such  $\delta\delta$  could only have identified boundary locations on the basis of the scent marks of the previous resident and the neighbours. In cases where neighbouring  $\alpha\delta\delta$  claimed extra ground at the time of a territory changeover, apparently they detected the absence of fresh scent marks of the former  $\alpha\delta\delta$ , and established their own scent marks on the area before the new  $\alpha\delta$  had established his (otherwise trespassing was rare). Notably, a deposed  $\delta$  orientated himself along the neighbours' sides of boundary lines, as if avoiding the area scent marked by the ascendant rival but at the same time fearful of intruding further into the areas scent marked by neighbours. Finally, I had the impression that wandering  $\delta\delta$  seemed frequently to move along territory boundary regions while passing through a strange area.

## 2. Relationship to concepts of territoriality and dominance

Territoriality is conventionally identified on the basis of a "defended area", following NOBLE (1939). However, the criterion of defence is difficult to substantiate in the case of the white rhino. The distracting teleological connotations can be avoided by accepting as examples of "defence" any actions which demonstrably cause another animal to move away from, or desist from approaching, some geographically fixed spatial area.

Clearly, white rhino territories are not defended against resident or intruding  $\beta\delta\delta$ , since they are not necessarily driven away (an intruding  $\beta\delta$  may choose to stay and settle). Also, border confrontations between neighbouring  $\alpha\delta\delta$  do not demonstrate defence; the neighbouring  $\delta$  would not have intruded even if there had been no confrontation. Only cases in which a trespassing  $\delta$  retreated before a resident's advance can be accepted as exemplifying defence. However, these were rare, only four being observed in three and a half years of concentrated observation; perhaps too rare to serve as a practical criterion. It may be argued that border confrontations probably inhibit later intrusions, and thereby function as a form of "indirect defence", while scent marking constitutes a further form of "indirect defence". However, this can only be substantiated by demonstrating that other  $\alpha\delta\delta$  in fact rarely trespass on the marked and patrolled territorial space; which is equivalent to following PITELKA'S (1959) definition of territory as an "exclusive area". The existence of such exclusive areas can be demonstrated clearly and unequivocally, but, except where active interception and driving out occurs, the mechanisms by which such exclusion is maintained may remain hypothetical. This is especially likely to be the case for the more olfactorally orientated mammals in which indirect manifestations of presence by scent marking, coupled with avoidance of areas scent marked by rivals, are probably the main mechanisms by which such exclusion is maintained. Other authors have also found difficulties in applying the criterion of defence to mammals, for example SCHENKEL (1966) (who proposed substituting "intolerance"), LEUTHOLD (1970) (who used indirect evidence) and WALTHER (1972b) (who emphasized the importance of sharply delineated boundaries). However, white rhino territorial  $\delta\delta$  tolerate  $\beta\delta\delta$  and  $\alpha\delta\delta$  passing through to water, while wildebeest and blesbok territories have diffuse boundaries.

A territory is perhaps better characterised behaviourally in terms of EMLEN'S (1957) definition, as the area within which a resident shows supreme dominance with respect to certain categories of intruder. The displays typical of  $\alpha\delta\delta$  can be seen as manifestations of this claim to dominance. Another  $\delta$  can respond to such displays either by submissive displays, by retreat, or by reciprocation. Alternatively the area occupied by a dominance claiming rival may be avoided. If dominant displays are reciprocated without retreat, a fight is the likely result. A territory transfer involves a change in dominance status within its area, and associated with this, a change in a whole set of coupled behaviour patterns by the  $\delta\delta$  concerned. The rapidity of the switch suggests that the underlying physiological coupling is neurological rather than hormonal; though testosterone levels may subsequently respond to the change in dominance status, as was demonstrated for rhesus macaques by ROSE *et al.* (1971) and suggested for impala (BRAMLEY and NEAVES 1972). It is the spatial localization of dominance that distinguishes territoriality from other forms of dominance relationship.

Where two  $\beta\delta\delta$  share the same territory, there is no evident difference in their relative status; both are subordinate to the resident  $\alpha\delta$ . Among  $\text{♀♀}$  and

subadults, the concept of dominance has little significance. No supplanting interactions were observed, competitive situations with regard to food do not arise, and threats seem related merely to the maintenance of a small "personal space" (MARLER and HAMILTON 1966). A cow appears dominant when she displaces an accompanying  $\alpha\delta$  from a shade rest-place, but at a boundary it is the  $\delta$  that forces the cow to yield. The strategy of the accompanying  $\delta$  is simply that likely to be most effective in keeping the cow within his territory until she is receptive to mating.

The ultimate significance of dominance is in enhancing access to some significant resource for the more dominant individual. White rhino  $\alpha\delta$  not only accept other rhinos within their territories, but even allow them to graze close by unhindered. Food is of a relatively uniform quality over wide areas, and under such conditions it appears more advantageous for a  $\delta$  to concentrate on rapid intake of food rather than expend energy driving away competitors (as argued by KRUUK (1972) in explaining hyena feeding strategies). The significance of dominance appears only in the sphere of reproductive rights. Resident  $\beta\delta$  do not contest matings, and neighbouring  $\alpha\delta$  do not intrude across territory boundaries even in the presence of oestrous  $\text{♀♀}$ . The long drawn out courtship and copulation hence proceed without interference. Territoriality can thus be seen as a system partitioning access to oestrous  $\text{♀♀}$  among competing  $\delta$ , whereby each  $\alpha\delta$  has unrestricted access to oestrous  $\text{♀♀}$  within his own territory limits.

### 3. Selective consequences of territorial dominance

Selection may operate through enhanced access to survival influencing resources, increased reproductive opportunities, or improved progeny viability (CROOK 1972, GOSS-CUSTARD *et al.* 1972). The selective consequences of the spatial dominance exerted by white rhino  $\alpha\delta$  for each of these processes needs to be appraised more critically.

(a) Survival. The food resources of a territory are shared by the  $\alpha\delta$  with one or more  $\beta\delta$  and numerous cows and subadults. There is evidently some pressure on  $\delta$  to disperse to less crowded areas; the adult sex ratio in the western section of Umfolozi where habitat conditions were particularly favourable, was 0.67  $\delta$ :1 $\text{♀}$ , compared with an overall population average of 0.80  $\delta$ :1 $\text{♀}$  (OWEN-SMITH 1973). This is equivalent to a reduction in adult  $\delta$  density by 16%, but in total white rhino biomass by only 5½%. This effect seems relatively insignificant. In compensation  $\alpha\delta$  are prevented from gaining access to particular stretches of grassland which might offer temporarily favourable grazing conditions where these lie outside their territory limits.

It was suggested by WYNNE-EDWARDS (1962) that territorial exclusion could provide an upper limit to population density thereby preventing over-utilization of food resources; such benefits to the population having arisen through interdemic selection. However, there was no evidence that the territorial system of  $\delta$  had any influence on either the density of  $\text{♀♀}$  or on their fecundity, though habitat deterioration was causing serious concern. Thus it can have no population regulatory function.

At wallows and rest-places, individuals of all social categories tolerated spacings even less than those usually maintained while feeding. Predator evasion benefits can be discounted in a species in which adults are virtually invulnerable to non-human predation.

Notably  $\text{♀♀}$  do not exhibit territorial exclusion, though they would benefit from any significant survival enhancing consequences; while their food supply is of critical significance also to the survival of their offspring.

(b) Reproduction. The reproductive contribution of certain  $\delta$  may be enhanced by (i) delaying the reproductive maturity of subadults, (ii) causing the death or emigration of a proportion of adults, (iii) producing an unequal apportionment of mating opportunities among remaining  $\delta$ .

(i) The sex ratio for all individuals over about six years of age was estimated to be 0.98  $\delta$ :1 $\text{♀}$ ; while for socially mature adults it was 0.8  $\delta$ :1 $\text{♀}$  (OWEN-SMITH 1973). This resulted because  $\text{♀♀}$  attained socio-sexual maturity at 6—7 years (upon the birth of their first calf) and  $\delta$  at 11—12 years (upon taking up solitary residence in a territory). The consequent reproductive enhancement accruing to mature  $\delta$  is 1.2 times.

(ii) The adult sex ratio in prime habitats was 0.67  $\delta$ :1 $\text{♀}$  compared with 0.8  $\delta$ :1 $\text{♀}$  overall.  $\delta$  resident in such favourable habitats consequently enhanced their reproductive access to  $\text{♀♀}$  by a further 1.2 times.

(iii) Within prime habitats about one third of the adult  $\delta$  had  $\beta\delta$  status and were excluded from mating (with only rare exceptions). This enhanced reproduction by  $\alpha\delta$  by a further 1.5 times.

Thus by maintaining territorial dominance in a favourable region an individual  $\delta$  can increase his reproductive contribution by about 2.7 times on the average. Certain individuals would fare even better. The most favourable study area territory held an average population of 4.2 cows during the mating period (see Table 10). However less variability is evident in the proportion of time spent consorting with  $\text{♀♀}$  by individual  $\alpha\delta$  (Table 17). It is concluded that the most

Table 17: Relative reproductive potentials of individual  $\alpha\delta$  occupying territories in the central study area

Alpha $\delta$	C	L	X	I	A
total no. days seen	135	170	97	204	65
propn. days accompanying AD $\text{♀}$	.40	.41	.41	.30	.32
mean AD $\text{♀}$ popul. in territ.	4.2	3.8	2.7	2.8	1.5

successful  $\alpha\delta$  probably enhance their mating opportunities by between 3 and 4 times while holding  $\alpha\delta$  status. However, since transitions in status take place, the overall reproductive enhancement integrated over an individual lifespan would be lower.

(c) Progeny viability.  $\delta$  do not remain with  $\text{♀♀}$  after mating and thus exert no direct influence on the survival of their offspring. As discussed above, the effects of the slight reduction in population density achieved on food access by kin seem likely to be slight.

The selective advantage achieved by prime  $\delta$  in terms of enhanced reproductive opportunities clearly outweighs other consequences of the territorial system for genetic fitness. It may be concluded accordingly that territoriality has arisen through a process of intrasexual selection among  $\delta$  competing for limited mating opportunities. However, there are alternative systems of ordering reproductive competition which can result in even higher mating success accruing to prime  $\delta$  (OWEN-SMITH, in prep.). Thus it remains to be considered why territoriality has been favoured evolutionarily, rather than some alternative form of regulation of mating competition among  $\delta$ .

#### 4. Evolutionary origins of territoriality

This leads to a consideration of the explanatory arguments put forward by ESTES (1974), JARMAN (1974) and GEIST (1974a and b).

ESTES contended that territoriality was a primitive bovid trait which had been lost only by the most highly advanced species. Being regarded as a primitive ungulate group, the rhinoceroses might therefore be expected to retain territoriality. However, though territoriality has been reported for all three rhinoceros species which have been studied adequately, the form it takes in the Indian rhinoceros (*Rhinoceros unicornis*) is quite different from that in the two African species. Individuals of both sexes drive away other rhinos from small grazing areas (covering about 10 000 m<sup>2</sup>) on the meadows surrounding ponds, and also reportedly defend separate sleeping territories (ULLRICH 1964). During the mating season there are wild chases in which individual ♂♂ drive oestrous ♀♀ well away from their usual haunts (RIPLEY 1952) (perhaps thereby achieving spatial separation from competing ♂♂). Thus reproductive territories are not general in the rhinoceroses. Work on primates suggests that social systems are responsive to prevailing ecological circumstances (CROOK 1970), and the primitive-advanced dichotomy furthermore does not explain why territoriality has been lost in supposedly more advanced species.

JARMAN, considering only antelopes, proposed that feeding styles under the influence of predation determine grouping patterns, and also influence body size, habitat choice and degree of localization. Accordingly, highly selective feeders on particular plant parts are generally solitary or pair forming, relying on concealment to escape predators; while relatively gross feeders eating grass or browse at varying growth stages aggregate in large cohesive herds which may confront predators in mass. In species with small to medium sized ♀ herds, territoriality is superimposed by ♂ competition for mating rights. In species forming very large ♀-herds (such as the African buffalo *Syncerus caffer* and perhaps the eland *Taurotragus oryx*), a number of ♂♂ are simultaneously associated and a rank hierarchy prevails.

While the white rhinoceros is a relatively unselective feeder, like the African buffalo, it contrastingly does not form large herds. This can be accounted for on the basis of its relative invulnerability to predation as a factor promoting group formation, since a solitary adult is likely to be successful in warding off a lion or any other predator except man. Notably, groups are based largely on associations by subadults, which are more vulnerable to predation. Consequently upon the small ♀ groupings and their relatively localized movements, territoriality by adult ♂♂ is predicted.

However, JARMAN's arguments do not account for the absence of territoriality in some ungulate groups, notably most north temperate cervids and caprines.

GEIST noted the vast seasonal superabundance of food in relation to population levels during summer in temperate regions. This enables ♂♂ to store energy in the form of fat, and expend it later in vigorous dominance and courtship interactions during a brief rut. In tropical regions, population levels remain closer to carrying capacity year round so that energy available for storage is more limited, while breeding seasons are commonly extended. The high plant diversity and productivity typical of tropical regions further increases the predictability of food and hence also ♀ locations, favouring territorial localization. Thus territoriality is prevalent in tropical species, but with rare exceptions (pronghorn, roe deer) is absent in north temperate ungulates. A need to reduce the incidence of combat can also be related to morphology, particularly

that of weapons. Small injuries may become fatal where predator density is high, as is typical of tropical areas. Highly developed horns or antlers allow vigorous contests with relatively low risk of serious injuries, while species with dangerous weapons (e.g. sharply pointed horns) should fight less frequently.

GEIST's arguments can be extended further (OWEN-SMITH in prep.). The wide roaming habits and vigorous contesting possible for north temperate ungulates permits higher reproductive gains by the most successful ♂♂ than those attained in a territorial system. Under conditions of more limited energy surpluses, ♂♂ are forced to play for more limited gains, otherwise lifespans would be attenuated and hence overall reproductive fitness lower. Territoriality seems the most efficient way of organizing reproductive competition with the lowest expenditure of energy and injury risks.

Validation of these arguments requires more critical information than is currently available on energy intakes and outputs, and on the frequency and nature of interactions in a variety of species.

In conclusion, it may be stated that territoriality in the white rhinoceros has probably been favoured evolutionarily by the following conditions: (i) relatively unselective feeding habits and low predation risk related to large size, leading to ♂♂ being dispersed singly and relatively localized in their movements; (ii) relatively small seasonal variations in forage productivity in relation to population levels, which limit energy surpluses; (iii) morphology including directly functional horns which increase the injury risk in combats; (iv) extended reproductive season, requiring year-round reproductive readiness by ♂♂; (v) prolonged courtship and mating sequence which would be especially vulnerable to interference by other ♂♂.

#### Acknowledgements

This paper is dedicated to JOHN T. EMLÉN on the occasion of his retirement, for his friendly guidance and encouragement during the long years in the field and at the writing desk.

The idea of a study on the white rhino was suggested by G. A. PETRIDES, then Visiting Professor of Wildlife Management at the University of Pretoria.

The study was made possible through the generous facilities and support provided by the Natal Parks Board. In particular I am grateful to R. C. BIGALKE for initiating the study, valuable assistance also rendered by R. S. CRASS, D. R. M. STEWART, J. VINCENT, P. M. HITCHINS, M. KEEP, B. DOWNING, P. G. STEWART, O. BOURQUIN, R. PORTER, I. C. PLAYER, N. A. STEELE, G. BAILEY, J. DANIEL, K. ROCHAT, M. ASTRUP, J. TINLEY, B. THRING, G. ROOT, D. DENYER, M. NKOSI and B. NKOSI.

From the University of Wisconsin, D. CHANDLER, J. LUND and W. HOLTHAUS helped with photographic and recording equipment, and T. NEALON helped in many ways. C. HUGHES aided by J. DALLMANN patiently prepared the numerous diagrams.

Radio transmitters used were designed by F. ANDERSON and supplied by the South African Council for Scientific and Industrial Research. P. M. HITCHINS developed techniques for their use on rhinos and helped with their instalment.

During the course of this work I was supported by fellowships from the Natal Parks Board and the Wisconsin Alumni Research Foundation. Accommodation, equipment and running expenses were funded by the Natal Parks Board, and by U.S. National Science Foundation grant No. GB-15304 to J. T. EMLÉN.

Earlier drafts of this manuscript were criticized by J. T. EMLÉN, P. MARLER, V. GEIST, J. KAUFMANN, W. LEUTHOLD, G. STEPHENSON, M. DEMMENT and A. BLEED, and subsequent improvements were aided by their comments.

#### Summary

The social system of the white rhinoceros is analysed in fundamental terms to allow consideration of the evolutionary importance of phylogeny, morphology, ecology and energetic factors. Data were collected during a 3½ year field



study carried out in the Umfolozi-Corridor-Hluhluwe game reserve complex in South Africa. All animals, except for some immatures, were recognized individually, and radio telemetry was used to follow the movements of 10 individuals. Two social categories of adult ♂ were distinguished and termed  $\alpha\delta\delta$  and  $\beta\delta\delta$ . ♀♀ up to 7 years and ♂♂ up to 10–12 years were regarded as subadults.

Cows were accompanied either by a single offspring or by one or more subadults (the largest group numbering seven); infrequently two adult ♀♀ were associated together. Cow home ranges covered about 10–15 km<sup>2</sup>, with a core area of 6–8 km<sup>2</sup> favoured during optimum conditions. The home range was extended by corridors leading to permanent water supplies during the late dry season. Cow home ranges overlapped extensively and no discrete home range groups could be distinguished. In encounters, cows usually ignored one another or approached for reciprocal nasonasal contact, which sometimes developed into playful horn wrestling. Sometimes mild threats (snorts) were used to maintain a small personal space.

Subadults not with cows were associated in subadult groups including up to 5 individuals of both sexes, but groups larger than two were unstable. Some subadults occupied settled home ranges while others shifted about seminomadically. Subadults frequently engaged in nasonasal contacts and horn wrestling with other subadults and with cows.

Group companions maintained close spacings, usually less than 5 m. A cow was always the control animal if present, or alternatively a subadult ♀. Where two cows or two even-aged subadults of the same sex were associated together, both individuals were equally active in influencing moves. Dominance interactions were absent.

All adult ♂♂ were basically solitary, except for temporary periods of attachment to oestrous cows by  $\alpha\delta\delta$ . Alpha ♂♂ occupied mutually exclusive territories year-round, and each territory was shared by 0–3  $\beta\delta\delta$ . Boundaries were sharp and patrolled by neighbouring  $\alpha\delta\delta$ . Alpha ♂♂ scent-marked by spray urination and by scattering their dung at dungheaps. Other rhinos used the same dungheaps, but did not scatter their dung and urinated in a stream. Within their home territories  $\alpha\delta\delta$  confidently approached other rhinos. At borders, there were ritualised confrontations between neighbouring  $\alpha\delta\delta$ . Intrusions were rare, except in the late dry season when ♂♂ had to cross other territories to water. Intruding ♂♂ were challenged by a horn to horn confrontation, then the resident  $\alpha\delta\delta$  moved away. An intruding neighbouring  $\alpha\delta\delta$  retreated steadily if confronted;  $\alpha\delta\delta$  on distant territories and  $\beta\delta\delta$  stood defensively with loud snarls. This snarl display was used also by cows and subadults. Beta ♂♂ sharing the same home territory were challenged less frequently and more briefly by resident  $\alpha\delta\delta$ , and showed no avoidance. Territory changes involved the assumption of  $\alpha\delta\delta$  status by a new ♂; while the former  $\alpha\delta\delta$  assumed  $\beta\delta\delta$  behaviour patterns, but did not vacate the territory. Some  $\beta\delta\delta$  later became  $\alpha\delta\delta$ , but always in a different territory.

Reproduction was year-round with seasonal fluctuations. There was a pre-oestrus consort period during which the accompanying  $\alpha\delta\delta$  confined the cow within his territory by blocking her at boundaries. Courtship advances consisting of hiccup approaches spanned 24 hours, and copulation lasted 16–28 minutes. With one exception  $\beta\delta\delta$  did not form consort relationships, and the single observed copulation by a  $\beta\delta\delta$  took place in unusual circumstances. Beta ♂♂ did not interfere with matings and neighbouring  $\alpha\delta\delta$  did not intrude across boundaries.

The limited extent of group formation is related to the relative invulnerability of adults to predation on account of their large size. Groups seem based

on mother-offspring bonds, or a surrogate mother-offspring relationship between a cow and an unrelated subadult, or on friendships between two subadults.

Relationships among ♂♂ are characterized as a spatially localized dominance exerted by each  $\alpha\delta\delta$  within his home territory. Other ♂♂ respond either by avoidance or by submissive displays. Scent marks seem important in maintaining spatial exclusion, but direct interactions are infrequent, and there are difficulties in invoking concepts of "defence". This territorial dominance has little influence on food access or population regulation, and its exclusive functional significance is to confer unhindered access to oestrus ♀♀. It has apparently evolved through intrasexual selection as a system regulating reproductive competition among ♂♂. By maintaining territorial dominance in favourable areas, individual ♂♂ may enhance their reproductive success by a factor of 3–4 times. However, this gain is lower than that possible in other mating systems. It is suggested that the evolution of territoriality has been favoured by (i) relatively limited food surpluses for energy storage, making more active forms of contest less successful, (ii) small relatively localized ♀♀ groupings, (iii) potentially high injury risks associated with combat, (iv) the extended reproductive season and drawn out courtship.

#### Zusammenfassung

Die Grundzüge des Sozialsystems des Weißen Nashorns wurden analysiert, um die Bedeutung phylogenetischer, morphologischer, ökologischer und energetischer Faktoren für die Evolution abzuschätzen. Die Daten wurden in 3<sup>1/2</sup>-jähriger Freilandarbeit im Umfolozi-Korridor-Hluhluwe Wildreservat-Komplex in Südafrika gesammelt. Alle Tiere (außer einigen Jungtieren) waren individuell bekannt. Mit Radio-Telemetrie wurden die Wege von 10 Tieren verfolgt. Zwei soziale Kategorien von adulten ♂♂,  $\alpha\delta\delta$  und  $\beta\delta\delta$ , werden unterschieden. ♀♀ bis zu 7 Jahren und ♂♂ bis zu 10–12 Jahren gelten als Subadulte.

Kühe werden entweder von einem einzelnen Jungtier oder von einem oder mehreren Subadulten begleitet (die größte Gruppe umfaßte 7 Individuen); manchmal schlossen sich auch zwei ♀♀ zusammen. Der Aktionsbereich von Kühen betrug etwa 10–15 km<sup>2</sup> mit einem Kernstück von 6–8 km<sup>2</sup>, das unter optimalen Bedingungen bevorzugt wurde. In fortgeschrittener Trockenzeit wurde das Streifgebiet über Korridore zu Dauer-Wasserstellen erweitert. Die Streifgebiete der Kühe überlappten beträchtlich. Bei Begegnungen ignorierten Kühe einander gewöhnlich oder näherten sich zu gegenseitigem Nasonasal-Kontakt, der manchmal in spielerisches Horn-Ringen überging. Manchmal schufen schwache Drohungen (Schnauben) einen kleinen Individual-Abstand.

Subadulte ohne Kühe war in Subadulten-Gruppen bis zu 5 Individuen beiderlei Geschlechts vereinigt, doch waren Gruppen von mehr als 2 unbeständig. Manche Subadulte besetzten dauerhafte Streifgebiete, andere zogen halbnomadisch umher. Subadulte waren öfter in naso-nasale Kontakte und Hornkämpfe mit anderen Kühen oder Subadulten verwickelt.

Gruppenmitglieder blieben nahe beisammen — im allgemeinen unter 5 m. Wenn anwesend, war eine Kuh oder ein subadultes ♀ das maßgebende Tier. Waren zwei Kühe oder zwei gleichaltrige Subadulte gleichen Geschlechts beisammen, so beeinflussten beide Tiere gleichermaßen die Ortsveränderungen. Dominanzanzeichen gab es nicht.

Alle adulten ♂♂ waren im Grunde solitär, mit Ausnahme der zeitweiligen Vergesellschaftung mit brünstigen Kühen.  $\alpha\delta\delta$  besetzten während des

ganzen Jahres Reviere und teilten diese mit 0—3  $\beta$ - $\delta$   $\delta$ . Die Grenzen waren scharf und wurden von benachbarten  $\alpha$ - $\delta$   $\delta$  kontrolliert.  $\alpha$ - $\delta$   $\delta$  setzen Duftmarken, indem sie Urin verspritzen und Dung an Dunghaufen verteilen. Andere Nashörner benutzen dieselben Dunghaufen, verteilen aber den Dung nicht und urinieren in einem Strahl. Innerhalb ihrer Reviere näherten sich  $\alpha$ - $\delta$   $\delta$  anderen Nashörnern selbstsicher. An Grenzen kam es zu ritualisierten Konfrontationen zwischen benachbarten  $\alpha$ - $\delta$   $\delta$ . Eindringlinge gab es fast nur in fortgeschrittener Trockenzeit, wenn die  $\delta$   $\delta$  fremde Reviere kreuzen mußten, um Wasser zu erreichen. Eindringende  $\delta$   $\delta$  wurden mit einer Horn-zu-Horn-Begegnung herausgefordert, dann entfernte sich das ansässige  $\alpha$ - $\delta$ . Ein eindringendes benachbartes  $\alpha$ - $\delta$  zog sich bei einer Herausforderung langsam zurück;  $\alpha$ - $\delta$   $\delta$  entfernter Reviere und  $\beta$ - $\delta$   $\delta$  verhielten sich defensiv und brummen laut. Diese Laute waren auch von Kühen und Subadulten zu hören.  $\beta$ - $\delta$   $\delta$  desselben Reviers wurden durch ansässige  $\alpha$ - $\delta$   $\delta$  weniger oft und kürzer herausgefordert und wichen ihnen nicht aus. Veränderungen in einem Revier traten ein, wenn ein neues  $\delta$   $\alpha$ -Status annahm; das frühere  $\alpha$ - $\delta$  ging zu  $\beta$ - $\delta$ -Verhalten über, verließ aber das Revier nicht. Einige  $\beta$ - $\delta$   $\delta$  wurden  $\alpha$ - $\delta$   $\delta$ , aber immer in anderen Revieren.

Die Fortpflanzung erstreckt sich über das ganze Jahr, mit jahreszeitlichen Schwankungen. Im Prae-Ostrus schließt sich ein  $\alpha$ - $\delta$  der Kuh an und hindert sie am Verlassen seines Reviers, indem er sie an den Grenzen stoppt. Das Werben dauert 24 Std. und besteht aus Annäherung mit "Hick"-Lauten. Eine Kopulation dauert 16—28 min. Mit einer einzigen Ausnahme bildeten  $\beta$ - $\delta$   $\delta$  keine Paare; die einzige beobachtete Kopulation eines  $\beta$ - $\delta$  erfolgte unter ungewöhnlichen Bedingungen.  $\beta$ - $\delta$   $\delta$  griffen nicht in die Paarung ein, und benachbarte  $\alpha$ - $\delta$   $\delta$  überschritten die Reviergrenzen nicht.

Die geringe Gruppenbildung hängt mit der relativen Unverwundbarkeit der Adultiere zusammen. Gruppen scheinen auf Mutter-Kind-Bindungen zu basieren (auch auf einer Pflegemutter-Kind-Bindung) oder auf einer Freundschaft zwischen zwei Subadulten.

Die Beziehungen zwischen  $\delta$   $\delta$  sind durch die räumlich begrenzte Dominanz der  $\alpha$ - $\delta$   $\delta$  innerhalb ihres Reviers charakterisiert. Andere  $\delta$   $\delta$  reagieren mit Ausweichen oder Unterwerfung. Duftmarken scheinen für die Aufrechterhaltung der Grenzen wichtig, direkte Zusammenstöße sind selten.

Diese territoriale Dominanz hat wenig Einfluß auf die Erhaltung des Nahrungsangebotes oder die Regulierung der Populationsdichte; wichtig ist sie zur ungehinderten Paarung. Sie entstand offenbar durch intrasexuelle Selektion, um die Konkurrenz zwischen den  $\delta$   $\delta$  während der Fortpflanzung zu regulieren. Einzelne  $\delta$   $\delta$ , die in günstigen Gebieten ansässig sind, haben 3—4 mal so großen Fortpflanzungserfolg wie andere. Trotzdem bieten andere Paarungs-Systeme größere Vorteile. Man kann daher annehmen, daß die Evolution des Revierverhaltens gefördert wurde durch (1) relativ geringen Nahrungsüberschuß, der eine aktivere Form eines Wettkampfes weniger erfolgreich machte, (2) kleine, relativ ortsgebundene  $\delta$ -Gruppen, (3) hohe Wahrscheinlichkeit von Verletzungen im Kampf und (4) die ausgedehnte Fortpflanzungszeit und lange Werbung.

#### Literature cited

- BELL, R. H. V. (1971): A grazing ecosystem in the Serengeti. *Sci. Amer.* **225**, 86—93 • BRAMLEY, P. S., and W. B. NEAVES (1972): The relationship between social status and reproductive activity in male impala *Aepyceros melampus*. *J. Reprod. Fert.* **31**, 77—81 • BROMLEY, P. T. (1969): Territoriality in pronghorn bucks on the National Bison Range, Moiese, Montana. *J. Mammal.* **50**, 81—89 • CAVE, A. J. E. (1962): The pedal scent gland in *Rhinoceros*. *Proc. Zool. Soc. Lond.* **139**, 685—690 • CAVE, A. J. E. (1966): The preputial

- glands of *Ceratotherium*. *Mammalia* **30**, 153—159 • CLARK, P. J., and F. C. EVANS (1954): Distance to nearest neighbour as a measure of spatial relationships in populations. *Ecology* **34**, 445—453 • COLBERT, E. H. (1969): Evolution of the Vertebrates. 2nd edn. John Wiley Inc., New York • COLE, L. C. (1949): The measurement of interspecific association. *Ecology* **30**, 411—424 • CONDY, P. (1973): The population status, social behaviour and daily activity pattern of the white rhinoceros in Kyle National Park, Rhodesia. M. Sc. thesis, Univ. Rhodesia • CROOK, J. H. (1970): The Socio-ecology of primates. In: *Social Behaviour in Birds and Mammals* (J. H. CROOK, ed.). Academic Press, London, New York. pp. 103—166 • CROOK, J. H. (1972): Sexual selection, dimorphism and social organization in the primates. In: *Sexual selection and the descent of man* (B. CAMPBELL, ed.). Aldine Publ. Co., Chicago. pp. 231—281 • DAVID, J. H. M. (1973): The behaviour of the bontebok, *Damaliscus dorcas dorcas* (Pallas 1766) with special reference to territorial behaviour. *Z. Tierpsychologie* **33**, 38—107 • EISENBERG, J. F., and D. KLEIMAN (1972): Olfactory communication in mammals. *Ann. Rev. Ecol. Syst.* **3**, 1—32 • EMLEN, J. T. (1957): Defended area? A critique of the territory concept and of conventional thinking. *Ibis* **99**, 352 • ESTES, R. D. (1969): Territorial behaviour of the wildebeest (*Connochaetes taurinus* Burchell 1823). *Z. Tierpsychol.* **26**, 284—370 • ESTES, R. D. (1974): Social organization of the African Bovids. In: *The Behaviour of Ungulates and its Relation to Management* (V. GEIST and F. WALTHER, eds.). IUCN Public. New series No. 24 • GEIST, V. (1974a): On the relationship of ecology and behaviour in the evolution of ungulates: theoretical considerations. In: *The Behav. of Ungul. and its Relationship to Management* (V. GEIST and F. WALTHER, ed.). IUCN public., new series no. 24 • GEIST, V. (1974b): On the relationship of social evolution and ecology in ungulates. *Amer. Zool.* **14**, 205—220 • GEIST, V., and F. WALTHER (Eds.) (1974): *The Behaviour of Ungulates and its Relationship to Management*. IUCN public., new series no. 24 • GODDARD, J. (1967): Home range, behaviour and recruitment rates of two black rhinoceros populations. *E. Afr. Wildl. J.* **5**, 133—150 • GOSS-CUSTARD, J. D., R. M. DUNBAR and F. P. G. ALDRICH-BLAKE (1972): Survival, mating and rearing strategies in the evolution of primate social structure. *Folia Primat.* **17**, 1—19 • HEPPES, J. B. (1958): The white rhinoceros in Uganda. *African Wild Life* **12**, 273—280 • HITCHINS, P. M. (1972): Preliminary findings in a radiotelemetric study on the black rhinoceros in Hluhluwe Game Reserve, Zululand. Symposium on Biotelemetry, Pretoria, 1971. CSIR, Pretoria • HOOIJER, D. A. (1969): Pleistocene East African rhinoceroses. In: *Fossil Vertebrates of Africa*, Vol. I (L. B. LEAKEY, ed.). Academic Press, London and New York • HUNTER, R. F. (1964): Home range behaviour in hill sheep. In: *Grazing in terrestrial and marine environments* (D. J. CRISP, ed.). Symp. Brit. Ecol. Soc. **4**, 155—171 • JARMAN, P. J. (1974): The social organization of antelope in relation to their ecology. *Behaviour* **48**, 215—267 • JARMAN, P. J., and M. V. JARMAN (1974): A review of impala behaviour, and its relevance to management. In: *The Behaviour of Ungulates and its Relation to Management* (V. GEIST and F. WALTHER, eds.). IUCN public., new series no. 24 • JEWELL, P. A. (1966): The concept of home range in mammals. *Symp. Zool. Soc. London* No. **18**, 85—109 • JOUBERT, S. C. J. (1972): Territorial behaviour of the tsessebe (*Damaliscus lunatus* Burchell) in the Kruger National Park. *Zoologica africana* **7**, 141—156 • KLINGEL, H. (1967): Soziale Organisation und Verhalten freilebender Steppenzebras. *Z. Tierpsychol.* **24**, 580—624 • KLINGEL, H. (1972): Social behaviour of African Equidae. *Zoologica africana* **7**, 175—186 • KLINGEL, H., and U. KLINGEL (1966): The rhinoceroses of Ngorongoro Crater. *Oryx* **8**, 302—306 • KOFORD, C. B. (1957): The Vicuña and the Puna. *Ecol. Mono.* **27**, 153—219 • KRUIK, H. (1972): The Spotted Hyena. A study of predation and social behaviour. Univ. Chicago Press, Chicago • KURT, F. (1968): Das Sozialverhalten des Rehes. Eine Feldstudie. Verlag Paul Parey, Hamburg und Berlin. 102 pp. • LEUTHOLD, W. (1966): Variations in territorial behaviour of Uganda kob *Adenota kob thomasi* (Neumann 1896). *Behaviour* **27**, 215—258 • LEUTHOLD, W. (1970): Observations on the social organisation of impala (*Aepyceros melampus*). *Z. Tierpsychol.* **27**, 693—721 • MARLER, P., and W. J. HAMILTON (1966): *Mechanisms of Animal Behavior*. John Wiley & Sons. Inc. New York • NOBLE, G. K. (1939): The role of dominance in the social life of birds. *Auk* **56**, 263—273 • OWEN-SMITH, R. N. (1971): Territoriality in the white rhinoceros *Ceratotherium simum* Burchell. *Nature* **231**, 294—296 • OWEN-SMITH, R. N. (1972): The contribution of radiotelemetry to a study of the white rhinoceros. Symposium on Biotelemetry, Pretoria, 1971. CSIR, Pretoria • OWEN-SMITH, R. N. (1973): The Behavioural ecology of the white rhinoceros. Ph. D. Diss., Univ. Wisconsin • PIENAAR, U. DE V. (1970): The recolonisation history of the square-lipped (white) rhinoceros (*Ceratotherium simum simum* Burchell) in the Kruger National Park. *Koedoe* **13**, 157—169 • PITELKA, F. A. (1959): Number, breeding schedule, and territoriality in pectoral sandpipers in Northern Alaska. *Condor* **61**, 233—264 • PLAYER, I. C., and J. M. FEELY (1960): A preliminary report on the square-lipped rhinoceros *Ceratotherium simum simum*. *Lammergeyer (Natal)* **1**, 3—23 • RIPLEY, S. D. (1952): Territorial and sexual behaviour in the Great Indian Rhinoceros, a speculation. *Ecology* **33**, 570—573 • RIPLEY, S. D. (1958): Comments on the black and square-lipped rhinoceros species in Africa. *Ecology* **39**, 172—174 • ROSE, R. M.,

J. W. HOLADAY and I. S. BERNSTEIN (1971): Plasma testosterone, dominance rank and aggressive behaviour in male rhesus monkeys. *Nature* **231**, 366—371 • SCHENKEL, R. (1966): Zum Problem der Territorialität und des Markierens bei Säugern — am Beispiel des Schwarzen Nashorns und des Löwens. *Z. Tierpsychol.* **23**, 593—626 • SCHENKEL, R., and L. SCHENKEL-HULLIGER (1969): Ecology and Behaviour of the Black Rhinoceros (*Diceros bicornis* L.). A Field Study. In: *Mammalia Depicta*, Verlag Paul Parey, Berlin und Hamburg • SIDNEY, J. (1966): The past and present distribution of some African ungulates. *Trans. Zool. Soc. London* **30**, 5—397 • SPINAGE, C. A. (1969): Territoriality and social organization of the Uganda defassa waterbuck *Kobus defassa ugandae* Neumann. *J. Zool., London* **159**, 329—361 • THENIUS, E., and H. HOFER (1960): *Stammesgeschichte der Säugetiere*. Springer Verlag, Berlin • THORNTON, D. D. (1968): Intensive domestic use of rangeland. *E. Afr. Agric. For. J.* **33**, 148—158 • ULLRICH, W. (1964): Zur Biologie der Panzernashörner (*Rhinoceros unicornis*) in Assam. *D. Zool. Garten (N. F.)* **28**, 225—250 • WALTHER, F. R. (1964): Einige Verhaltensbeobachtungen an Thomsongazellen (*Gazella thomsoni* Gunther) im Ngorongoro-Krater. *Z. Tierpsychol.* **21**, 871—890 • WALTHER, F. R. (1972a): Social grouping in Grant's gazelle (*Gazella granti* Brooke 1872) in the Serengeti National Park. *Z. Tierpsychol.* **31**, 348—403 • WALTHER, F. R. (1972b): Territorial behaviour in certain horned ungulates, with special reference to the examples of Thomson's and Grant's gazelles. *Zoologica africana* **7**, 303—308 • WALTHER, F. R. (1974): Some reflections on expressive behaviour in combat and courtship of certain horned ungulates. In: *The Behaviour of Ungulates and its Relationship to Management* (V. GEIST and F. WALTHER, eds.). IUCN public., new series no. 24 • WYNNE-EDWARDS, V. C. (1962): *Animal Dispersion in Relation to Social Behaviour*. Oliver and Boyd, Edinburgh.

Author's address: R. N. OWEN-SMITH, University of Rhodesia, P. O. Box M.P. 167, Mount Pleasant, Salisbury, Rhodesia.

*Div. of Ethology, Dept. of Zoology, Stockholm University, Sweden*

## Sexual Imprinting in the Context of Species Recognition in Female Mallards<sup>1)</sup>

By THORSTEN KLINT

Received: 6. 8. 1974

### Introduction

The aim of this paper is to give some information about the role of sexual imprinting in the process of species recognition by female mallards. A contradiction in the literature was the incentive to this investigation. SCHUTZ (1964, 1965) proposed that ♀♀ of dimorphic ducks (Anatini) are not sexually imprintable but recognize the species-specific ♂♂ by means of some kind of innate ability. In agreement with this hypothesis he more specifically states that female mallards are almost non-imprintable. This point has been disputed by FABRICIUS and FÄLT (1969). These authors showed that female mallards in a two-choice experiment preferred white male mallards which they were reared with, and also that ♀♀ brought up in close contact with a human caretaker directed sexual behaviour towards people. However, there are important differences in the experiments of SCHUTZ (1965) and FABRICIUS and FÄLT (1969), which will be considered in the discussion.

### Subjects

All mallards (*Anas platyrhynchos*) used in the experiments have originally been obtained from the stocks of the Game Management School at Öster Malma and from the wild population in the surroundings of the Öster Malma laboratory about 90 km south of Stockholm, Sweden.

On a few occasions white ducklings have been hatched in otherwise completely normal broods. These birds have been selected and bred separately. All the white birds used in the experiments are offspring in the second to fourth generation from the first white parents. These white mallards perform all behaviour patterns exactly like normal ones as far as can be ascertained. Only the frequency of some sexual behaviour is suspected to differ significantly (KLINT 1973). Concerning the normal ♂♂, the nuptial plumage developed from about 14 to 18 weeks of age. Colour markings were applied both on the bill as nasal disks and around the legs as rings to secure that all the subjects could be easily identified.

### Birds reared in groups

#### Experiment 1

Experiment 1 was designed to investigate whether imprinting occurs before the time of fledging (probably about 9 weeks of age) and/or from the time when the male siblings begin to develop their nuptial plumage (about 14 weeks of age). The birds were reared in groups to imitate the natural situation.

<sup>1)</sup> Dedicated to Professor Dr. Eric FABRICIUS on his 60th birthday.