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EAST AFRICAN MAMMALS

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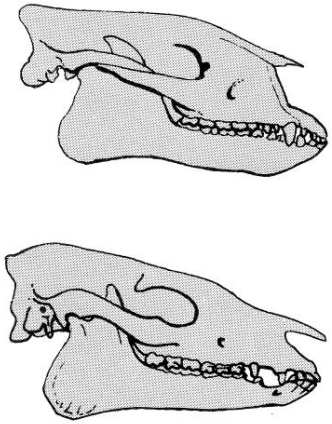
Perissodactyls

Perissodactyla
Equidae
Rhinocerotidae

Perissodactyls must have emerged from a primitive ungulate group, probably during the later Palaeocene, a period that is poorly represented in the fossil record. Their most likely ancestors are condylarths, some of which were probably omnivorous but had the general mien of carnivores or insectivores, with a full dentition, differentiated canines and a relatively long skull.

Although it is too large and too late to be considered directly ancestral, *Phenacodus* (see Volume I, p. 376) is intermediate in the structure of its heavily nailed feet and in some features of its skull and dentition between a generalized early mammal and the primitive Eocene *Hyracotherium*.

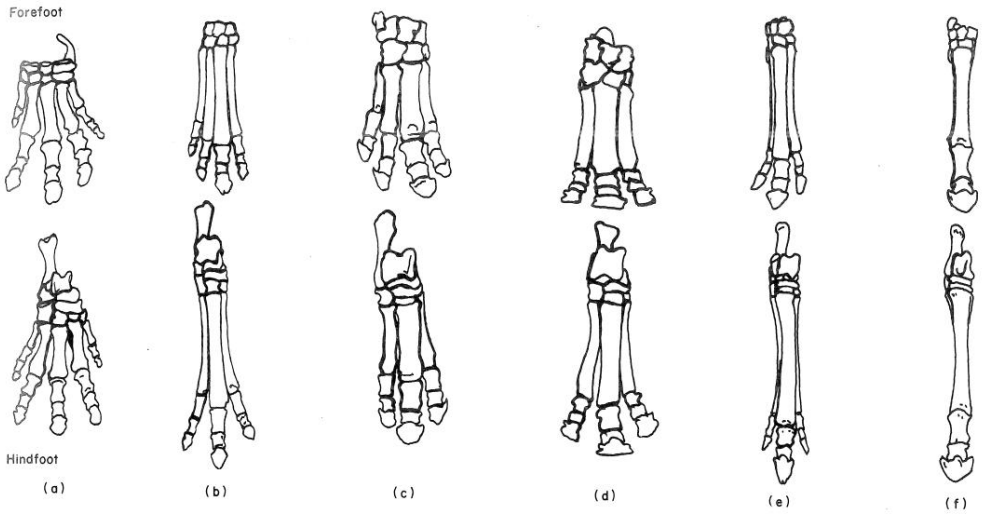


Skulls of Eocene condylarth, *Phenacodus primaevus* and *Hyracotherium* compared.

Hyracotherium is the earliest perissodactyl and may be close to the common ancestor of horses, rhinoceroses and tapirs although its slender proportions already anticipate those of the equids. Its niche may have been close to that of the living tragulids.

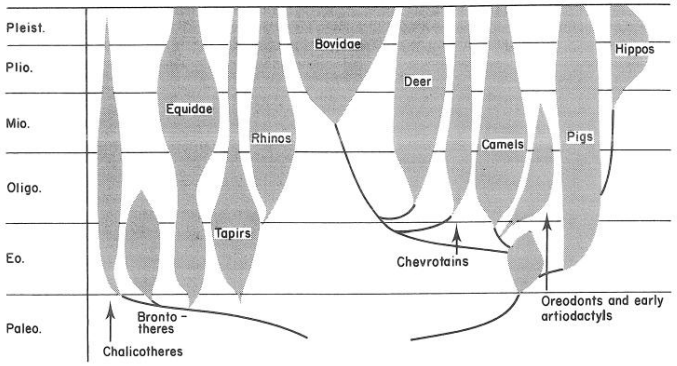
Later, perissodactyls tended to be large and to carry their weight on three toes and in modern equines on only one toe, hence the clumsy anglicization "Odd-toed hoofed mammals".

Perissodactyls diversified in the Eocene and were among the most abundant of herbivore types in America and Eurasia up to the Miocene.



Above: Perissodactyl lower limbs: forefoot above, hindfoot below.
(a) *Phenacodus* (Condylarth);
(b) *Hyracotherium* (primitive perissodactyl);
(c) *Tapirus* (Tapir);
(d) *Diceratherium* (Miocene rhinoceros);
(e) *Miohippus* (Miocene horse);
(f) *Equus*

Left: forefoot, black rhino.



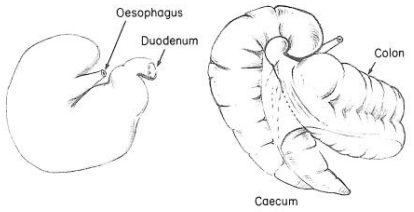
Left: *Hyracotherium* Right: *Ceratotherium*.

Superior digestive assimilation by advanced artiodactyls probably led to competition and the progressive elimination of perissodactyls from all the ordinary herbivore niches but the survivors appear to have become specialists in coarse feeding, or in the case of the grass rhino, *Ceratotherium*, an advantage may have been gained through gigantism. Browsing rhinos can feed on woody vegetation too tough for the bovids' leaf-plucking mouth and the horses have the advantage that their teeth can manage the wiriest grasses, while *Equus* may have acquired some competitively superior adaptations in their social life (see p. 128).

In Africa, perissodactyls have always occupied special niches and arrived too late ever to have been a dominant group (see Volume I, pp. 55—58).

The relatively late adaptation in Africa of *Ceratotherium* to a grass diet is interesting, suggesting that large size may confer a high level of immunity from predation and reduce the impact of competition in rich well-watered habitats.

It has been calculated that the ruminant type of digestion is advantageous up to a body weight of 1·800 kg (Van Soest in Janis, 1976). Janis (1976) regarded large size in rhinos as a strategy to avoid ruminant competition and



Stomach and caecum of *Equus*

Complex chambered stomach of an advanced ungulate

suggested that the rhinos might be regarded as representing a real adaptive response of the Tapiroidea to changing evolutionary pressures at the end of the Eocene.

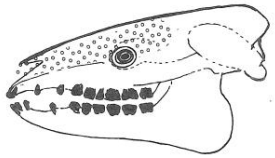
Turning to the origins of perissodactyls as herbivores, Janis (1976) thought they adopted a diet containing cellulose during the Palaeocene while they were still relatively small. She pointed out that all small-sized herbivores that eat a lot of coarse vegetable matter, lagomorphs, hyraxes and some rodents have developed caecal fermentation and she considered that the body size of ancestral perissodactyls was the critical factor in determining the type of digestion.

If quantities of herbage are always available the perissodactyl system is actually superior to rumination at digesting a high fibre content. There are no advantages in rumination for a very small animal and Van Soest (in Janis, 1976) regards 5 kg as the minimal body weight at which rumination would be viable. It is known that ruminants developed very much later than perissodactyls (see table) and it is likely that artiodactyls adopted a truly herbivorous diet when they were already relatively large.

Only two of the three living families have ever been represented in Africa and it is possible that the tapirs never entered Africa because their niche was pre-occupied by early proboscids.

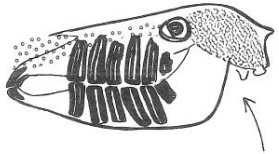
FEATURES INFLUENCING FORM IN PERISSODACTYLS

Archaic perissodactyl features



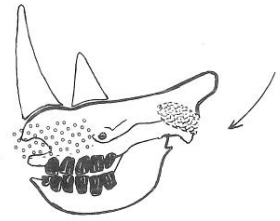
Vegetarian diet; rel. high crowned molars, deep jaws. Increasing size trend. Well developed olfaction in extended cylindrical skull.

Equid features



Medium-large size. Elongation of neck, legs and skull. Vision well developed; high head carriage. Diastema, molars with very high crowns with deep rooting. Incisors cut and pull grass. *Defence:* speed. *Weapons:* teeth and hooves.

Rhinocerotid features



Great size and weight. Heavy head, low carriage. Short plantigrade limbs. Vision poor; olfaction good. Incisors and diastema lost, lips gather food. *Defence:* size and horns. *Weapons:* nasal horns.

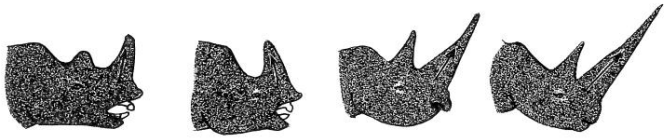
Ceratomorphs

Ceratomorpha
Rhinocerotidae

Genera

Diceros
Ceratotherium

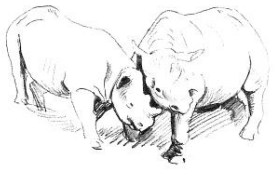
When animals have become as scarce as the rhinoceroses are today it is difficult to describe them as successful without tedious qualification. Yet there is good reason to regard the living African rhinos as advanced and successful representatives of a family that has seen a very wide range of species and types in the past.



Dicerorhinus *Rhinoceros* *Diceros* *Ceratotherium*

Their name describes that unique peculiarity, the nasal horns: a characteristic that is probably as highly developed in the living species as it has ever been in any of their ancestral forms. It is interesting to note that there is a gradient in the size of horns in different rhino species. *Ceratotherium*, living a semi-social life in the most exposed habitats, has the longest horns while the Oriental rhinos, living a more solitary existence in dense jungle, have the shortest. It is possible that long horns get more in the way in a dense habitat but their employment in intra- and extraspecific defence is probably more developed in the former species. Furthermore there are phylogenetic implications; the short-horned oriental *Dicerorhinus* is a genus known from the Oligocene, whereas *Ceratotherium* only evolved in the Pliocene and is undoubtedly much more advanced.

In the long-horned African rhinoceroses, horns tend to be used more as clubs than rapiers, particularly in the early stages of a fight. These sideways swipes, which occasionally cause horns to split, probably have a phylogenetic origin in defensive movements that deflected direct thrusts of the horns but have become ritualized into an effective and relatively harmless way of testing strength and may even be accompanied by shoulder pushing without horn stabbing (p. 115). A major conflict is of relatively rare occurrence because a dominant rhino is recognized by his scent and behaviour and elicits



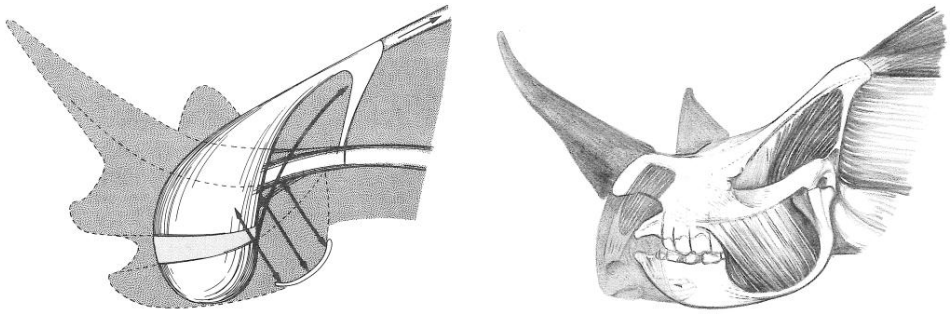
From a photograph by F. Hartmann (1970).

submission or avoidance in all other rhinos living in his territory. The richer the resources and the more open the environment the more frequent are contacts likely to be. It is therefore possible that ritualization has proceeded further in the African species than in the short-horned, forest-dwelling rhinos of Asia. It would be interesting to compare the details of horn fights or clashes in the more primitive *Dicerorhinus* and *Rhinoceros* with those of the African genera. The imminent extinction of *Dicerorhinus* makes the possibility of such comparisons sadly remote. Females are well able to defend themselves but they seldom fight. A mother protecting her offspring during a capture campaign has been seen to toss a 450 kg horse high into the air easily, which illustrates the strength of rhinos and emphasizes how dangerous all-out fighting with horns can be.

Very occasionally a rhino is born without horns. Conversely, the rudiments of a third or fourth horn may sometimes appear either behind the others or on other parts of the body. The famous engraving of an Indian rhino by Dürer shows just such a supplementary horn on its nape; however this picture was a copy from a Portuguese artist's work and the spike might have been an artistic elaboration. Areas of reinforced and rugose bone on fossils suggest that there was a general tendency towards clusters of knobs or horns on the head of various extinct rhinos.

Left: Great Indian rhinoceros, showing sites of small accessory horns above the eyes and on the forehead. Right: Black rhinoceros from a photograph by K. Sheldrick (1975).

The earliest and most primitive ancestral families, Hyrachidae and Hyracodontidae had no trace of horns and small "running rhinoceroses" were evidently fast and agile and would have resembled something between a tapir and a horse in appearance.



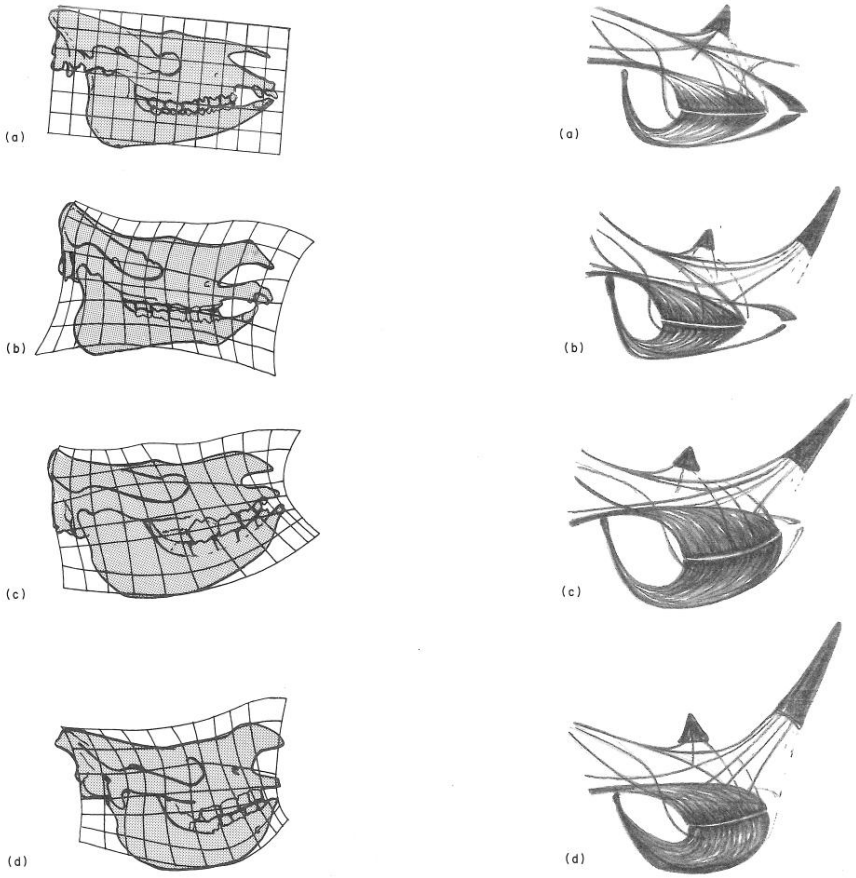
Ceratotherium: principal mass of skull in relation to mastication, horns, vertebral column and suspension.

All the perissodactyls have retained their dependence on the sense of smell for information and intraspecific communication, but the rhinos live in a world in which scents are the prime regulators of their social existence. Both their rhinencephalon and olfactory chamber are exceptionally large (Friant, 1955). The latter is accommodated beneath the cantilevered nasal bones which have had to be well buttressed to take the stress of the keratinous horn (see drawing). The massive teeth have even stronger bony bases and reinforcement of the forehead and occipital area allows an adequate support for the weight of such a heavy head as well as providing a bony shield for the brain. Enclosing large cranial, olfactory and buccal cavities, articulated by huge jaw and neck muscles, reinforced against its own weight and the extension of its horns, a rhino skull is a splendidly architectural model of form and function.

Ancestral rhinos, such as *Trigonias* and *Caenopus* had a diastema, incisors, even canine teeth and the nearly extinct *Dicerorhinus* of South-East Asia has retained short tusks in the front of its mouth. The African rhinos, instead, have lost their incisors and there are now only bony vestiges in front of the cheek teeth which have made a phylogenetic migration forward to the front of the mouth and head while the lips alone do all the cropping or plucking of food. A habit that may derive from the time when they had incisors is the snarl; Oriental rhinos actually bite but the African species employ the snarling gesture when they are on the defensive and being threatened by a superior.

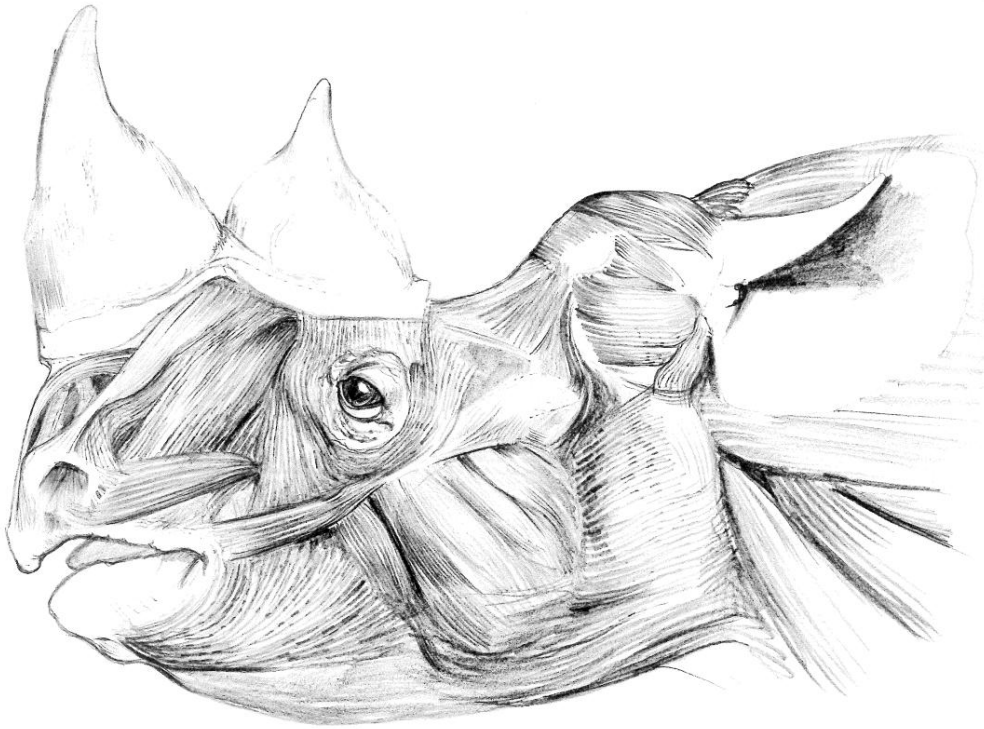
Dicerorhinus has been found in the Upper Oligocene in Asia and in Europe and Africa in the Miocene and members of this genus were once very widespread. The woolly rhinos of the ice ages, *Coelodonta*, were closely related to this genus.

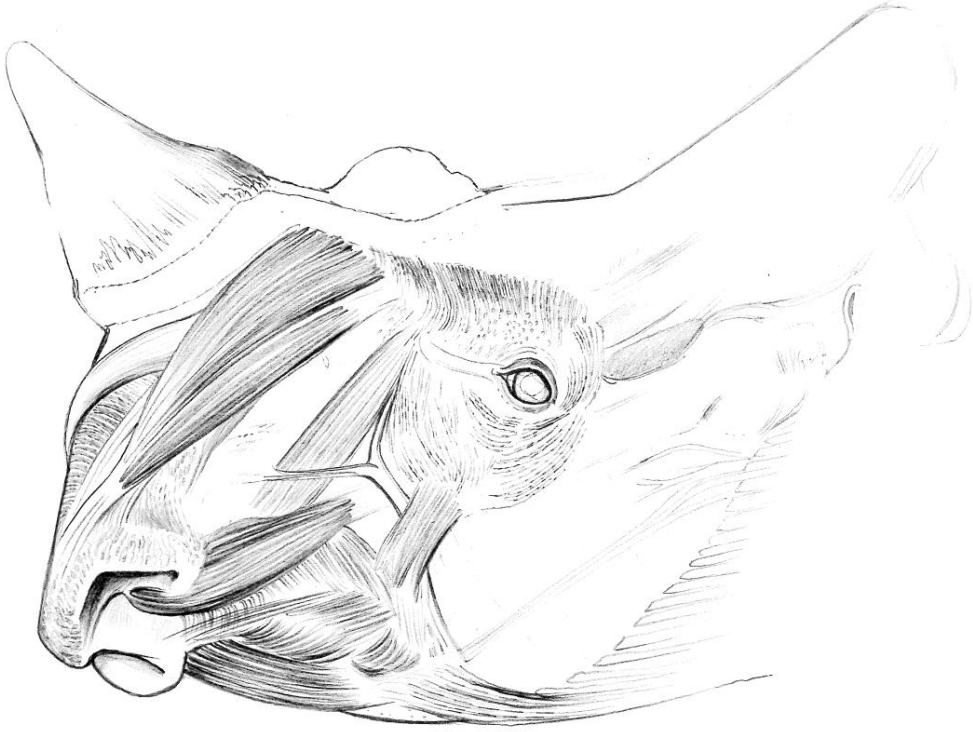
At least one rhinoceros species, *Paradiceros mukiri*, appears at Fort Ternan and this species may have been ancestral to both living species as well as to the extinct *Diceros pachygnathus* which occurred in Europe. Previous to this the hornless *Aceratherium* and *Brachypotherium* (belonging to separate and dead-end branches) appear in the East African Miocene.



Buttressing of the skull in rhinoceroses in relation to teeth and horns.
(a) *Caenopus* (Oligocene);
(b) *Dicerorhinus* (Oligocene-Present);
(c) *Paradiceros mukiri* (Pliocene);
(d) *Ceratotherium* (Pleistocene-Present).

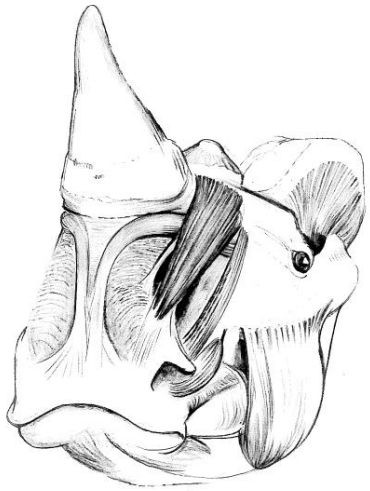
By the early Pleistocene both modern genera are present, *Diceros* in its present form while *Ceratotherium praecox* from Chemeron (4 million years old) still shows decided resemblances to *Diceros* but is probably directly ancestral to *C. simum* (Hooijer and Patterson, 1972). A Pliocene rhino from Samos, *Diceros pachygnathus*, has some characteristics of both genera and it has been suggested that they should be lumped in a single genus. Examining blood proteins, Osterhoff and Keep (1970) noted a great genetic variability in *Ceratotherium* while *Diceros* showed no variability whatever. Inferring from work on domestic animal breeding, they link this variability with an active stage of development, in which case the black rhino should be the more stabilized species. *Diceros* possesses 84 chromosomes while *Ceratotherium* has 82.

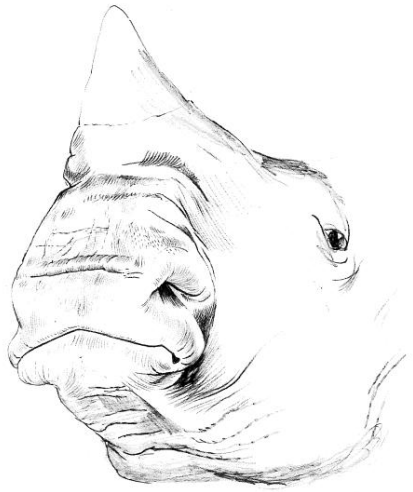


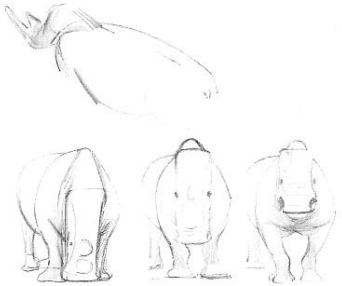


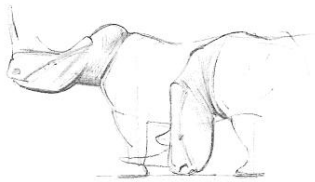
Above and below: *Diceros*;
Opposite: *Ceratotherium*.

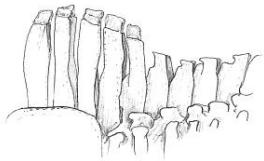
By invading the open grassland, *Ceratotherium* has departed furthest from the ancestral rhino niche of browsing coarse vegetation in thick undergrowth. The implications of this change are readily manifested in a comparison between *Ceratotherium* and *Diceros*. The most commonly described difference between the two species is in the structure of the mouth. The upper lip of *Diceros* is a pointed prehensile organ capable of wrapping round twigs, leaves, fruit and grass and thorns and drawing them into the mouth where they can be chewed or snapped off by the premolars. *Ceratotherium*, on the other hand, has flat-fronted lips, a very broad mouth which is especially adapted to crop short or medium-length grass and more hypsodont teeth. The acquisition of grazing habits has had far-reaching effects on form. Like horses, the ancient, gracile rhinos had relatively long necks so that dropping the mouth down to ground level was no problem, but as the true rhinos developed towards their present proportions they followed the common trend of increasing size, as body and head became heavier, limbs and neck got shorter. Contrary to popular belief, rhinos are not slow ponderous beasts because the greater leverage and flexibility of a light long-limbed animal has been replaced by the greater thrust and power of their well muscled bodies











Thoracic vertebrae of *Ceratotherium*.

(Smith and Savage, 1955). A more compact form allows tighter control of balance when galloping so that the neck must be short and the trunk relatively rigid. Paradoxically the browsing *Diceros* has a longer neck than the grazing *Ceratotherium* which has instead lengthened the head to reach the ground. Most particularly the occipital crest of *Ceratotherium* is exceptionally high, this may be influenced by the height of the glenoid condyle but the greater depth behind the poll improves leverage from the neck musculature while the backward sweep of the occipital crest slightly shortens its extent. Nonetheless, when the head is in the grazing position, the angle between the back of the head and the thoracic spines is wide and shallow; at least three times as wide as when the head is raised in the galloping or alert position. To overcome the shallowness of the angle, the last cervical spine is exceptionally long and mobile and acts as a fan spoke extending the arc of the hypertrophied *ligamentum nuchae*. The blade-like thoracic vertebrae are also exceptionally tall and have a unique adaptation to improve their flexibility without loss of strength; each spine has a posterior slot along its length into which the forward edge of the next spine can insert. As this arrangement only occurs in the white rhino it is evidently adapted to the extraordinary amount of contraction involved in raising a long heavy head. The demand for both strength and flexibility in the area of greatest bending moments would be particularly great during the gallop, at which time the head may be carried quite high (see drawing).

While on the brink of extinction today, rhinoceroses were evidently very widespread in the past. Numerous fossil rhinos have been found scattered across Africa and Eurasia. The woolly rhinoceros was carved and painted by stone-age artists right across the Palaeartic zone and preserved remains have been excavated from the permafrost of Siberia and the bogs of Europe. Schaurte (1960) reviewed the cave paintings and other early representations of rhinos. Likewise images of African rhinos are found wherever there are wall-paintings by cave-dwelling hunters and grass rhinos appear in rock paintings in North-central Tanzania, in the rock engravings from numerous localities in the Sahara and in the Kalahari, all areas where they long ago ceased to exist.

Grass rhinos depicted in Kisese rock shelter near Kondoa, Tanzania.

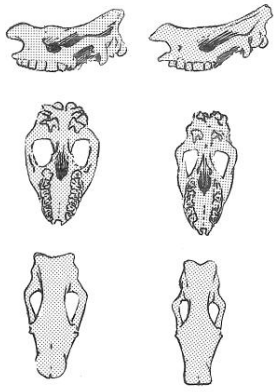
The ecological speciality of the rhinos was probably their capacity for

feeding on coarser plant material than most of the artiodactyls, yet with greater selectivity and less damage to the vegetation than elephants. Originally rhinos may have lived wherever there was a perennial supply of such food and water.

African rhinos depend on water for temperature control and they are capable of sweating to the point where their bodies are streaming with moisture. These scent-oriented animals have also a secondary use for water in their dependence on frequent sprays of urine for communication. Although it is only the sexually active minority that employ this device, the system would be less effective for a physiology designed to be economical of water.

Wallows are another necessity for rhinos and the wallowing habit probably assists temperature control, although it may have other incidental benefits.

Drought has been known to kill large numbers of rhino of both species. There was a massive mortality of *Diceros* in Tsavo in the drought of 1961. As conditions worsened in this area, rhinos from a wide catchment area concentrated around the only permanent water. Some months before the drought reached its peak there were reports of widespread and severe fighting among the rhinos. This phenomenon was possibly the product of the ecological disturbance shattering the established land-tenure network and is discussed later.



Diceros *Ceratotherium*

Thousands of elephants concentrated along the river and inflicted colossal damage on the surrounding bush. The forage for rhinos was thus reduced still further or actually destroyed. At the height of the drought rhinos were mainly dying of starvation but disease and stress were also playing a part. Elephants therefore appear to compete for browse with *Diceros* during periods of stress for both species. Whether grazing ungulates compete directly with *Ceratotherium* under similar conditions is not known, for relevant observations of the 1932 drought in Zululand are not available but Foster (1961) reported a decline in numbers at this time. However, there is a strong implication that both rhino species are susceptible to severe droughts and to the competition for reduced resources that attend them.

Large requirements of food and drink militate against rhinos during periods of extreme stress and their slow breeding inhibits a rapid recovery afterwards, so non-competitiveness with other herbivorous animals is most apparent over such periods and one can guess at similar factors leading to the decline of extinct rhino species.

The two modern genera are probably more adaptable and competitive than their collaterals and ancestors. Furthermore their recent decline is mainly due to man, but they also provide contemporary models for our understanding of the process of extinction.

Unaffected by rinderpest, they also appear to have a high level of resistance to anthrax, which is said to be endemic in African rhinos (Heppes, 1958). A low level of natural mortality has been noted in most rhino populations and this trait may be linked with their slow breeding rate.

Contemporary predators very rarely tackle an adult rhino and their imperviousness to predation is probably of long-standing. (Sabre-tooths might have been a major hazard in the Pleistocene but numbers of other pachydermatous mammals would also have been proportionally greater.)

Both species adapt their activity to the seasons, in that they rest for much longer in the middle of the day during the dry season. Otherwise their activity tends to alternate between feeding and resting throughout the day and night. Well-marked paths going to water or connecting feeding areas and wallows show that their habits are regular. These paths often pass through thick vegetation when it would be just as easy to skirt round it and the rhinos seem actively to seek the scratching sensation of twigs and thorns; they also like to rub on stumps and stones. In addition to the rewards of scratching an itch these habits may serve rhinos to help advertise their presence for the flakes of mud deposited or dropped off in this way possibly carry enough scent to be detectable to another rhino. If this is so, it is only one of several ways in which rhinos communicate with one another by scent. Apart from oestrous females only territorial male rhinos squirt urine and Owen-Smith (1974) showed that the frequency of squirting was highest in boundary areas between two *Ceratotherium* territories. He also considered this to be the main sign of territorial behaviour as a vanquished bull ceases squirting the moment he loses a contest. Urine probably identifies a rhino and his/her condition for other rhinos. Dung middens also serve as scent posts throughout the animals' home range, but Owen-Smith saw territorial bull *Ceratotherium* visiting particularly large middens on the borders of their territories where deep hollowing testified to the vigour with which the feet were scraped through them. He also saw non-territorial males use the same middens but with less ritual, as they may fail to wipe their feet in the dung or do it with less vigour and so probably make less smelly trails.

Scent trails provide the means by which both rhino species can meet or avoid conspecifics and encounters have been seen to be actively sought out by rhinos sniffing along trails. Non-territorial rhinos or territory holders off their own ground probably avoid other males, but there is evidence that resident males hasten to challenge invaders and that the distinctive urine ceremony is connected with territorial assertion. A male usually sprays urine over a landmark, a tussock, bush, stone or occasionally over a dung midden site, after which he lowers the head and thrashes his horn from side to side as if in the preliminaries to a challenge. This may be accompanied by backward shuffling or foot-scuffing and quick forward steps as if to challenge a non-existent rival. At times, the weaving of the head and horn turns into a savage onslaught on the bush or tussock. This horning behaviour has impressed many observers and has been widely interpreted as redirected aggression against an enemy. Owen-Smith's study established that *Ceratotherium* males have a well defined territorial system and although *Diceros* has been less intensively studied, there seems little doubt that the broad outlines of their social system are very similar. Only mature males are solitary and tend to restrict their movements even more than other classes. Both the density of rhinos and the food resources of the region are likely to influence the size of male territories.

Both these factors vary enormously. As many as 23 *Diceros*, of all sexes and ages, have been known to live in the 3 sq km of Lerai, Ngorongoro, 17 of them permanently. Even in the midst of inhospitable and extensive lava flows, *Diceros* can exist at surprisingly high densities and Root (personal communication) has seen 18 animals living in an area of about 15 sq km. Both species of rhino tend to crowd a suitable habitat rather than disperse out rapidly in

search of new ground. Five *Ceratotherium* per sq km of the Umfulozi Park has led to deterioration of the habitat and it is unlikely that densities of this order could be matched elsewhere; in the Kyle National Park, Condy (1973) found two *Ceratotherium* per 3 sq km and territories of 5—11 sq km. In Kidepo National Park, the overall density of black rhinos in 1970 was estimated at one per 10 sq km. The existence of male territories is obscured from casual observation by the tolerance of territory owners to other male rhinos (including former owners), so long as they show subordination in the dominant male's presence. Because the subordinate animal often displays noisy behaviour that gives every sign of being threatening, this has also tended to hide the true nature of confrontations between males, as has the behaviour of a territory owner the moment he steps outside the strict limits of his land. At such times, as on a trip to water, his movements become more tentative and should he meet any other rhinos, whether bull, cow or adolescent, while off his territory, he tends to avoid them. Owen-Smith (1974) has described some of the varied responses of other classes to a territorial male *Ceratotherium* on his own ground.

> "A subsidiary bull responds to an approach by a territorial bull by standing his ground, uttering loud rasping bellows with forward thrust head and flattened ears. He may even take a few quick paces towards the territorial bull. Despite their seemingly intimidatory nature, these gestures are to be interpreted as defensive threats. This snarl-threat is employed by cows and adolescents against an approach by a bull, and, among subadults, usually by the smaller animal. The territorial bull may approach simply to stare horn to horn, or may clash horns briefly. Such a horn clash is fended off by the subsidiary bull to the accompaniment of trumpeting shrieks. Engagements between a territorial bull and a subsidiary bull which is resident within his territory are usually very brief, and the territorial bull soon walks off, leaving the other bull standing. More often, however, the territorial bull simply wanders on past as if oblivious of the other bull's presence, despite nervous snorts and grunts from the latter. The two bulls may not infrequently be observed grazing or resting together peacefully only 20—30 m apart."

When there is a true contest for a territory the vanquished animal is seldom pursued far, nor is he normally attacked any further once he has fallen. There are scattered reports of extensive fighting among rhinos, which have usually been interpreted as competition by bulls in rut, but closer observation suggests that these outbreaks, which occur in both species, are mainly contests for territories by wandering males and are most likely to occur when the equilibrium of land tenure has been upset by ecological or other disturbances.

Unless they are in oestrus, females do not have their movements impeded by other rhinos and the extent of their range is determined by the resources of the area. These resources are shared by other females, subadults and non-territorial males. Females or subadults of both species wander over an average range of 10—12 sq km, with a wide range of variation. These classes, which are completely non-territorial and tolerant of other rhinos, are most frequently in twos. Most females accompany their latest young one and this association is the closest and most consistent bond in rhino society and is only broken just before the birth of a new calf. The rejected three- or four-year-old then forms a new bond, preferably with another youngster of the same

sex, or it may link up with an unattached female. Very occasionally the mother may tolerate its return some time after the birth of the new calf and, if the new baby is lost, the old association may be resumed. It has been suggested by Owen-Smith (1975) that the main social difference between *Diceros* and *Ceratotherium* is that the subadults of the latter are more gregarious.

When drinking sites become scarcer during the dry season, rhinos may walk greater distances away from their normal home range and especially attractive food or wallow sites may also draw numbers together into temporary congregations. The behaviour of such commuting rhinos is seldom indicative of their social status, as all classes tend to be equally diffident off their own ground.

Sexual behaviour would seem to be initiated entirely by the scent clues produced by the oestrous females. Courtship is cumbersome and exceptionally lengthy. The male on whose territory a female stands blocks her departure and, by attending her constantly appears to forge a temporary bond for the period of her oestrus, and very occasionally for a longer period. As she is invariably accompanied by her last young one or by some older female, the bull's advances involve a triangle. In the early stages of courtship, the cow and her satellite both repel his approaches and the bull may actually attack the cow's companion; she in turn may defend the victim and quite serious fighting can break out. The risk of conflict is evidently offset by the male being extraordinarily cautious but also persistent in his courtship. His capability for damaging the young or the female is probably countered to some extent by the fact that females are just as well armed and sometimes nearly as heavy as the males. The fact that subadult companionships may be between members of the opposite sexes as well as between bachelors, shows that the only period in which rhinos assume obvious sexual roles are when a female comes into oestrus. Both the oestrous female and the dominant male advertise their sex and their condition by means of economic but frequent sprays of urine, and any other form of sexual differentiation is superfluous. I have observed a female with a small calf at heel make frequent sprays while threatening another female at a waterhole so the squirting may have a more general link with assertive behaviour.

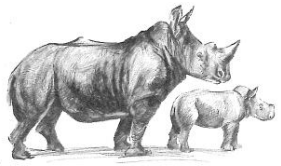
Owen-Smith (1975) pointed out that the rhinos' peculiar form of territoriality provides a most efficient and economic way of regulating competition for reproductive rights. He noted that at population levels that are close to the carrying capacity of the habitat, territoriality is favoured by a limited potential for surplus food, by relatively sedentary and solitary habits, by the physical risks of fighting, by year-round breeding and by the vulnerability of very prolonged courtship to interference.

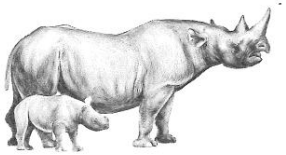
Copulation is only effected after the male has thoroughly accustomed the female to his approach and broken down her defensive reactions. Unusual calls, circling and posturing, as well as prodding on her belly and chin resting on her rump, appear to appease her and enlist her co-operation. There are several observed instances of young female *Diceros* behaving towards the male in a manner resembling a playful calf, with active curiosity alternating rapidly with flight impulses.

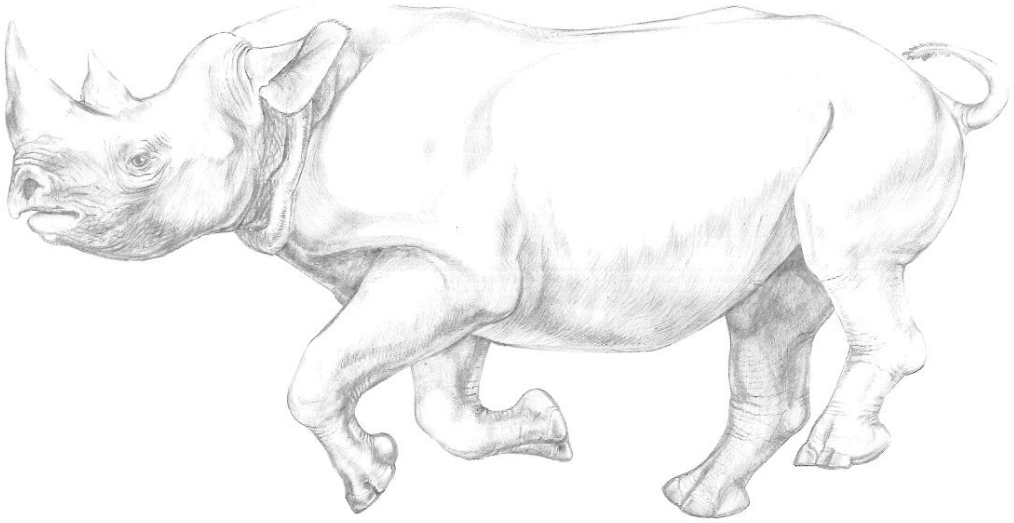
Although breeding is continuous, there is evidence that mating peaks occur in both species and these have some correlation with the end of the dry season and early rains, so that a connexion between fresh green growth and the stimulation of oestrogens in the female is possible.

Gestation lasts 15 to 16 months and the young are on their feet in less than half an hour. After a period of some weeks' seclusion within a small sheltered locality, the mother wanders more widely with her young one, who keeps extremely close to her. Females of *Ceratotherium* tend to follow their young, whereas *Diceros* generally lead theirs. The dependence of the young on the mother is total and orphans usually starve unless they are weaned or can form an attachment to another female.

Favourite zoo animals, rhinos are generally not difficult to keep and breed and have a life expectancy of 35 to 50 years.







Black rhinoceros, Browse rhinoceros (Diceros bicornis)

Family Rhinocerotidae
Order Perissodactyla
Local names
Faru (Kiswahili), Kifau (Kisambara), Infwoko (Kingiha), Mbusya, Mbila (Kikamba), Bia (Siha, Chagga), Huria, Munyi (Kikuyu), Mburia (Kipare), Mpuria (Kimeru), Mpenbee (Kinyaturu), Mpembele (Kinyiramba), Mpela (Kitaita, Kizima), Pera (Kirabai), Isabhi (Kijita), Mela (Kihehe), Omuga, Amuka (Lwo), Enkula (Luganda), Muni (Kisamburu), Emunyi (Masai), Enkura (Lunyoro), Ejiji (Madi), Amosing (Ateso), Kipsirikto (Kalenjin), Kurrbatit (Sebei), Kipsirichet (Kipsigis), Kibawit (Elkoni), Warses (Kiliangulu), Weyil (Somali).

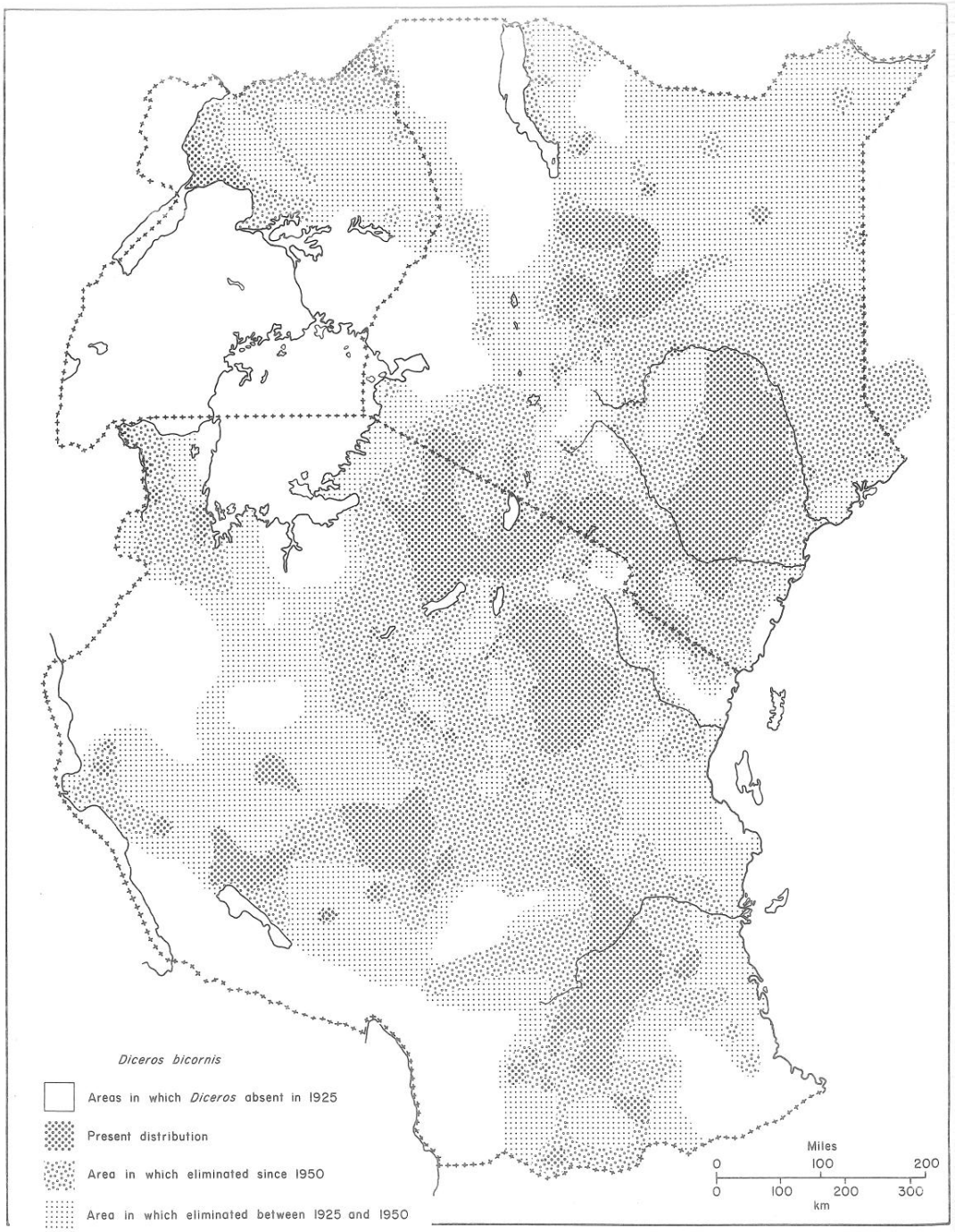
Measurements
head and body
3·4 (3—3·75) m
height
1·66 (1·4—1·8) m
tail
70 cm
weight
996—1,362 kg

Black rhinoceros, Browse rhinoceros (Diceros bicornis)

This rhinoceros is subject to considerable variation, some of which may represent local genetic traits; animals from the more arid habitats tend to be smaller and the highly variable skull proportions may also tend to show some degree of regional consistency. However, it is doubtful if any racial subdivision is justified.

This species probably ranged over a large part of sub-Saharan Africa at one time and it was found in practically all but the very driest areas of East Africa until relatively recently, commonly at altitudes up to 2,700 metres. It seems to be absent from the hot, humid lowland forest belt from Nigeria to Uganda but small population pockets were reputed to exist in the forests of the Middle Congo and Cameroon (Blancou, 1954). Because it needs to drink regularly it is only found within range of permanent water. Although it disperses into a wider area in the rains, its maximum dry season range is about 25 km from water. On open grassland and in closed canopy areas of the *Brachystegia* woodlands rhinos have always been very scarce or absent, and their favoured habitats are along the edges of thickets and wherever there are extensive areas of short woody growth, the thin regenerating twigs of which provide, together with legumes, their main food, however these may be heavily augmented by grass in some marginal habitats. Where there is a permanent source of water and plenty of shrubs and herbs growing within easy reach, the rhinoceros is capable of becoming a major animal in the ecological community because its diet includes resources which are used by few other animals except elephants. The black rhino was therefore very common and widespread until recently and it is still capable of reaching astonishing densities when protected in suitable habitats. In the Ngorongoro crater twenty-three rhinos live in the 2·6 sq km of Lerai Forest, a grove of *Acacia xanthophloea* trees with thin canopy and continuously regenerating undergrowth which provides the animals with ideal conditions. Of these twenty-three rhinos, Goddard (1967a) never saw seventeen outside this area in three years of intensive study. Pointing out its unique dietary niche and ecological role, Frazer Darling (1960a) considered that this animal might be a key species in the management of indigenous African vegetation.

Some 200 species of food plants from 50 families have been recorded by Goddard (1970b) and some of the commonest foods are dominants in the thicket, hard-pan Acacia and riverine communities that are favourite rhinoceros haunts. Thus *Acacia*, *Commiphora*, *Grewia*, *Cordia*, *Lannea*, *Euphorbia*, *Adenia*, *Sanseviera* and *Aloe* are commonly observed rhino foods. Shenkel (1969) also lists *Aerva persica*, *Bauhinia*, *Blepharis*, *Ehretia titensis*, *Sericomopsis* spp. and *Crotalaria*. In spite of being uncommon, *Caesalpinia trothae* is a favourite food; also green clover, *Trifolium*, is greatly favoured while certain dominant plants such as *Boscia* and *Thylachium* are never eaten at all. Salt may be a factor in the rhino's liking for *Suaeda monoica*, a shrub growing in saline soils. Rhinos are soon regular visitors to the artificial salt licks that have been set up beside many tourist lodges.



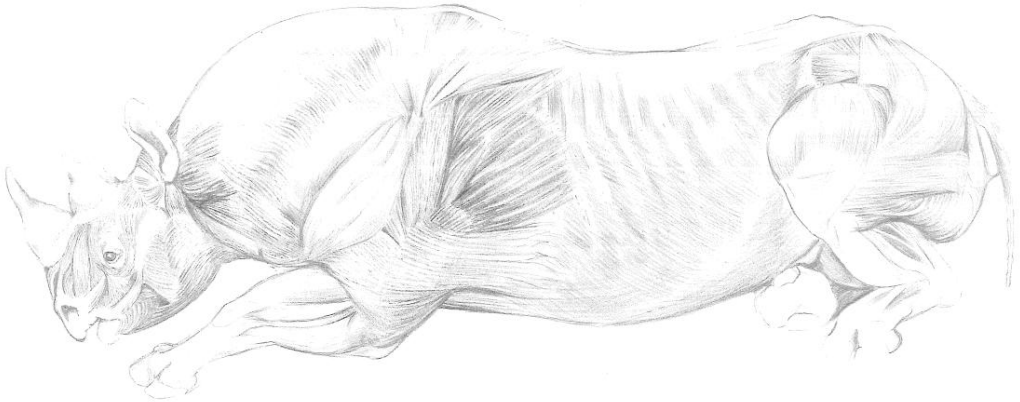
The importance of the prehensile upper lip in gathering twigs into the mouth has been mentioned and it is interesting that rhinos on the floor of the Ngorongoro crater, where grass is normally an important food, took to picking up gnu dung for some days when the grass was only 7—8 cm long following a fire. Klingel and Klingel (1966c) suggest that this may have been to correct a mineral deficiency but, more simply, it may have been due to the difficulty the rhinos faced in cropping short grass. As several hundred gnu were in the area, their dung would have answered the rhinos' need for bulk food more effectively than attempting a task for which their mouths are ill-adapted.

Various fallen fruits are readily picked up and the large sausage-like fruit of *Kigelia* are favoured, as are those of various *Acacia* and *Grewia* species. Roots, particularly those of succulents, are occasionally eaten. The horns have been seen to dig them out as well as to break branches above the reach of the mouth. Rhinos have even been seen to balance on the backlegs to reach twigs nearly 3 m off the ground.

Digging for water is not uncommon in rhinos and in the sand of river beds they use their forelegs quite effectively to this end. Water is needed in some quantity as sweating is the principal cooling mechanism of the rhinoceros. Notwithstanding the habit of hanging around waterholes, they generally drink rapidly and finish in less than five minutes. I have followed rhinos over 10 km back to their regular haunts, which they reached in less than three hours with very little feeding on the way. Well-worn tracks, usually shared by a variety of other animals, lead to and from water to wallows. In areas where many rhinos are concentrated there is a maze of subsidiary tracks running parallel to the main ones. In thickets rhinos can become important path-makers for other animals if they use a track often enough but many of the plants such as *Lannea* and *Commiphora* are sufficiently pliant to spring back after the rhino's passage. Following a rhinoceros in such country can sometimes mean crawling on hands and knees for long periods.

Resting and sleeping in mud wallows is common, but the heat of the day is normally spent sleeping under shade, while the most intense feeding periods are in the earlier part of the morning and evening. In areas where they are persecuted they become largely nocturnal. Wallowing in mud or water is a conspicuous habit. During the 1960—61 drought when hundreds of rhinos died of nutritional anaemia (Tremlett, 1961), a high proportion ended up in the shallow waters of the Athi River, where they presumably found some relief from the heat and biting flies. Schenkel and Schenkel (1969) have suggested that wallowing protects the skin from flies as well as conditioning it. As wallows are most commonly used during or after the hottest part of the day, cooling is likely to be the most direct incentive for the individual's behaviour. Incidental effects might include protection from sun and insects, also the blazing of pathways with flakes of scented mud, which are probably valuable identity tokens for the scent-orientated rhinoceros.

Rhinos so frequently pass under or through bushes when they could just as easily have skirted them, that one suspects that scraping and scratching must be a rewarding sensation for the animal; shedding flies and mud flakes could be incidental benefits of this behaviour. As well as using mud wallows, rhinos will roll in fine dust or the ash of burnt trees or branches. They are



often attracted by bush-fires and have even been known to scatter burning logs with their horns. I once found the impression of a rhinoceros that had rolled in ash so perfectly recorded that the animal could be recognized by its scars and creases. Such impressions also show that the depression immediately behind the shoulder may miss being coated in ash or soil. As this spot is the commonest area for "rhino sores" the protective function of mud and ash seems evident.

Exposed areas of skin are very thick and inflexible—the effect is of armour plates. Between these plate units movement demands more flexible and thinner skin and lions attacking rhinos have been seen to seize the throat and chest, after which they can easily unbalance the top-heavy animal and bite the softer underparts.

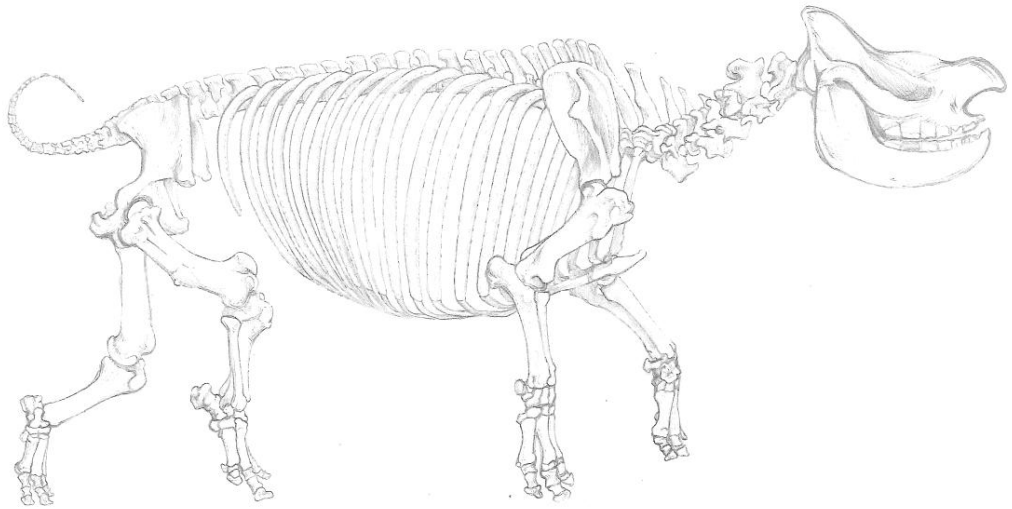
Rhinoceroses cannot roll across their sharp spines from side to side but lie down with hindquarters resting on one leg and then roll sideways until the spine throws them back. They will generally half rise or even get up and turn round before rolling on the other side. Abrupt rising and a few brisk movements, even interrupting a period of complete immobility or preceding a long sleep, are characteristic of rhinos. A rhino may sleep lying on its brisket, chin or cheek on the ground or it may doze standing with its head hanging. The ears continue to move even when it is asleep.

Rhinos are not slow and can make sharp turns even in the middle of a charge at some 50 km per hour. An alerted rhino tries to focus its ears on a source of alarm and may swing from side to side with the head up and nostrils flaring as it sniffs.

Although eyesight plays an inferior role to hearing and smell, the common claim that rhinos are half blind is misleading. Long-distance vision is of little importance to them but they give every sign of responding to visual stimuli at

close quarters. In some encounters, swinging movements seem to have the character of ritualized head-flagging. Bulls, particularly, raise their forequarters in a stiff-legged walk with erect head, in which they turn with some deliberation and posture in profile. It has been suggested that this is in order to see better out of one eye than ineffectively out of two, but head-on vision is functional in spite of a broad muzzle and horns (see drawing). However, myopic the rhinoceros seems to be, it is certainly capable of perceiving the silhouette of a massive neck, head and horns. Bulls tend to meet at wallows and waterholes and encounters are characterized by mutual displays which may or may not develop into sparring matches.

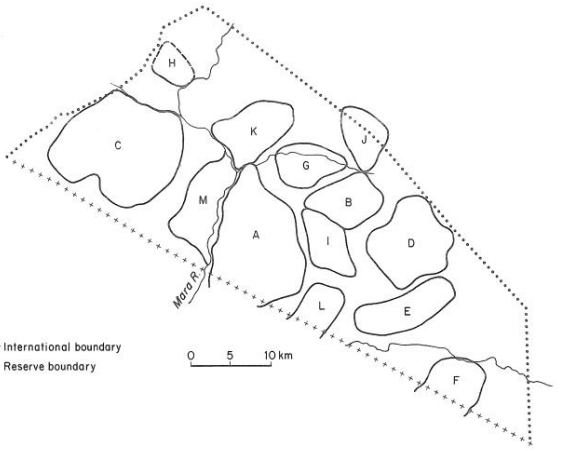
Alarms and threats are accompanied by short snorts but it is evident that snorts probably have shades of meaning for the rhino. A male approaching a female punctuates his slow progress with a series of three or four snorts, pausing momentarily after the first before giving two more in quick succession; the effect is somewhat like morse. When excited they also make a deep wheeze, which has been likened to a man gasping for breath. I have heard a similar call in a captive when approached by his keeper; it may imply pleasurable excitement or it could be an adult modification of the high-pitched noises of very young rhinos at play. These are different to the squealing distress call of the young. During his immobilization and tagging programme, Goddard (1970a) witnessed a calf attract an adult male from over a kilometre away in response to its squealing. Another very high-pitched call is uttered by mothers calling their young. When threatening or fighting one another, rhinos grunt loudly or else scream.



Like many other mammals, male rhinos scent the boundaries of their home range with urine. Bushes, tufts of grass, stumps or stones are sprayed with a scattering of urine drops which dry out into white flecks. These landmarks are generally temporary but Ritchie (1963) and others have reported that a hard deposit similar to the "dassiepiss" of hyraxes may form on rocks that are used for many years, possibly by generations of rhinos. This habit is mainly an adult male's prerogative and the penis is well adapted to direct a horizontal squirt between the hindlegs. Females make a finer spray while they are in oestrus or during encounters with other rhinos in the presence of their young, but it appears to be at random (Schenkel and Schenkel, 1969). These authors report that in the early mornings some bulls may make a more or less circular tour sniffing and urine squirting. Rhinos also use well established dung deposits, some individuals wiping their hindlegs through the dung immediately afterwards. Single deposits are common on roads and paths but these may represent no more than the reaction of animals encountering a strange element in their surrounding. The cumulative dung middens, however, tend to be added to by rhinos of either sex that come across them. Mukinya (1973) found a relationship between the degree to which a pile was shared (and hence its size) and the frequency with which a path or area was used by other rhinos. The social nature of dunging behaviour is betrayed by young rhinos that soon follow the mother's example. Sheldrick, who reared a young rhinoceros, could make it defaecate by scraping the earth with his boots.

As with many scent-oriented animals, an important function of these deposits may be connected with reassurance within the home range, by extension of the "self"and may favour the regulation of social and sexual contacts by allowing animals in the same area some choice in contacting or avoiding one another. Both these functions are well illustrated by Goddard's experiments in Ngorongoro while he was trying to learn more about the significance of scent trails. He dragged bags of rhinoceros dung behind a vehicle, laying out complicated trails for distances up to two miles. Most rhinos were able to follow every twist and turn of the bag, 60% of them followed their own dung trail and most of them chose to defaecate on it and an even larger proportion, 70%, followed the dung of animals with which they shared the home range. However, only 20% of them defaecated over it. The least response (30%) was for the dung of distant rhinos.

Goddard (1967a) was unable to find any consistent pattern in the deposits of dung, which are apparently random in distribution. Urine on the other hand, may be the main way of marking out the area used by an individual. Rhinos, particularly adult males and particularly in dense habitat, are essentially solitary but Goddard (1967a), noting their tolerance of well known neighbours, described the rhinos resident within a restricted locality as a community. Joubert and Eloff (1971) have used the word "clan" and they regarded a watering point as the focus for all social activity. In such circumstances rhinos are often tolerant of one another. In a study of the ecology and behaviour of 108 black rhinos in the 750 sq km of the Masai-Mara game reserve, Mukinya (1973) was able to delineate thirteen areas of variable size, within which resident rhinos associated with each other but were never seen

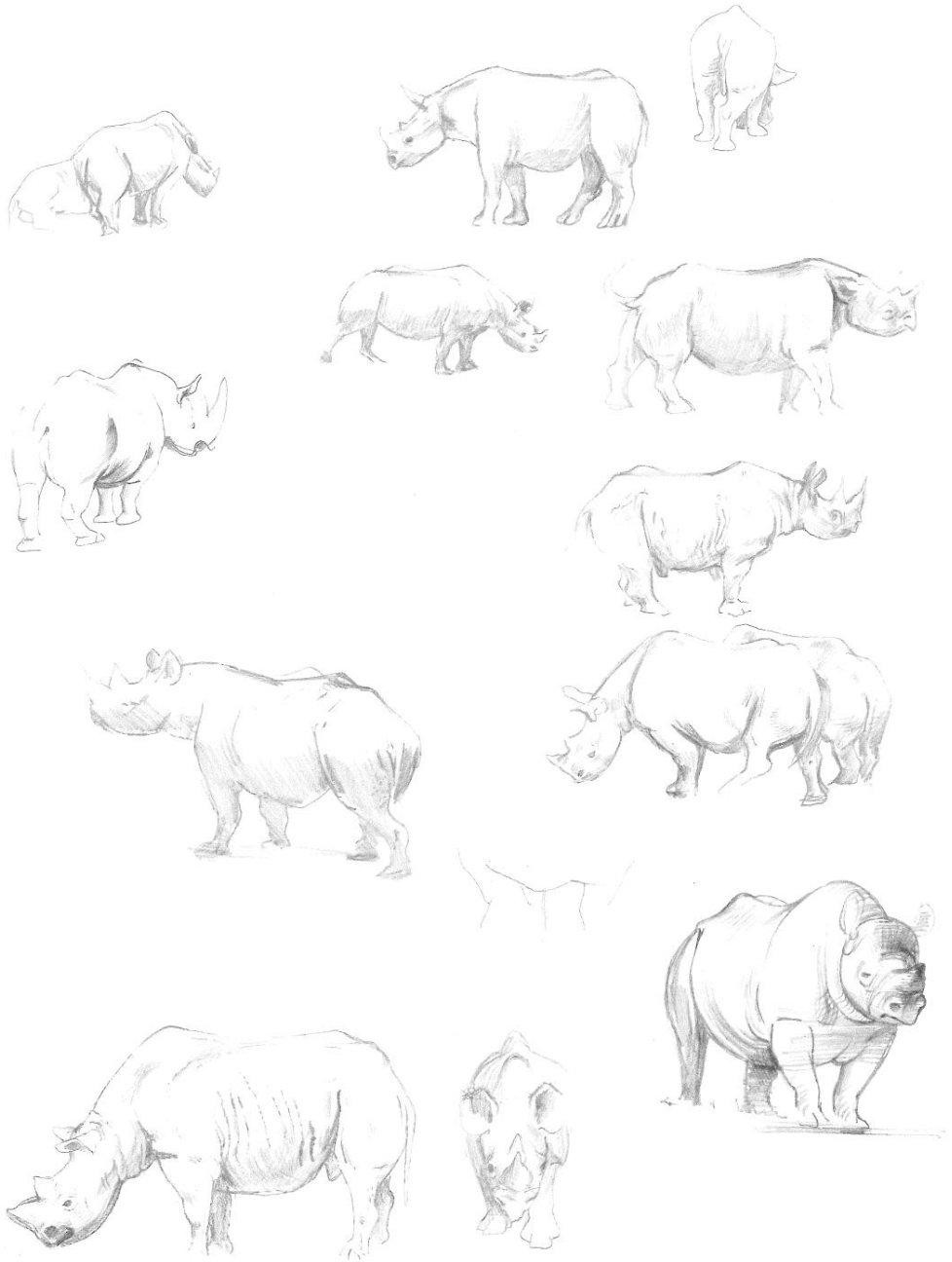


Rhinoceros distribution or "clan" areas in Masai Mara Game Reserve, from Mukinya (1973).

with individuals from another area. As many as thirteen have been seen together in a wallow in Ngorongoro but such aggregations are very temporary and soon disperse into singles and groups of two or three. Female rhinos are hardly ever alone. Most of their life is spent with their current offspring, sometimes in company of an earlier daughter. If without any young, females form attachments with neighbouring females. When the long-sustained bond between a mother and her offspring is broken by the birth of a new calf, the subadult rhinoceros is quick to seek out a new attachment irrespective of its sex. At this stage subadult rhinos range over a larger area. Occasionally a rhinoceros disturbed by a vehicle gives the impression of actively seeking contact with a large moving object. This was noticeable when a solitary subadult animal that had recently lost its mother tried to follow my Land-Rover.

Only when they are fully adult do males become solitary and even then they may associate with other neighbours for variable lengths of time.

In Ngorongoro, Goddard (1967a) thought adults of both sexes had similar-sized ranges and estimated an average of about 15·5 (2·6—44) sq km in open grassland, a third of which was regularly shared with other rhinoceros. In the more barren Olduvai gorge, the average was about 25 (3·6—90) sq km and males appeared to have slightly smaller home ranges. Comparing a well-thicketed area with more open savanna in South Africa, Hitchins (1969) found similar orders of magnitude with many more animals living within



smaller ranges in thickets. After marking all the resident rhinoceroses, Goddard was able to affirm that conflicts between males in the crater usually concerned strangers wandering into an established range and that strange females were not treated as violently as males. Nursing females were found to have larger ranges than single females or single males by Mukinya (1973). He recorded an incident in which one animal snarled and screamed at another which simply stared, after which both animals ran off in opposite directions. It was perhaps in cases where the invader was dominant that Goddard saw resident animals scream and snarl at a silent stranger. In one instance the intruding bull from another area displaced a resident male, which in turn moved into a neighbour's range, illustrating what might happen when the status quo is upset by ecological or other disturbances. A chain of displacements might have been a factor in the situation reported by the warden of East Tsavo shortly before the 1960—61 drought, when all the rhinos seen in that area were covered in fresh wounds and a number died as a result of fighting.

Fighting over females has been reported but it is also known for several bulls to court a female without conflict and Schenkel and Schenkel (1969) considered that there is not very much direct competition for oestrous females. Males do not associate closely with females except while they are in oestrus.

Watching the Tsavo rhinos during a period of drought, Schenkel and Schenkel (1969) thought that the females were generally intolerant of one another. However, in certain circumstances they seem capable of giving one another some degree of mutual protection. Ellis (1958) saw four rhinos come out of a forest together and cross a plain. "Three of these fully-grown rhinos were moving in a strange manner, pressed shoulder to shoulder, with the fourth one following behind. On closer inspection it was seen that the three front ones were cows, and that the centre one, very heavy in calf, was being helped along by her companions. One of the attendant cows actually rubbed the pregnant animal's flank with the side of her head and horn. Rangers reported the birth of a calf three days later." Perhaps pregnancy elicited maternal or protective responses in the other females but, unusual though it is, this observation serves to show that apparently altruistic social behaviour is not unknown in black rhinos.

Births are about two to four years apart and Klingel and Klingel (1966) estimated that about 28% of the Ngorongoro females bred each year. Births have been recorded at all times of the year but mating peaks have been suggested for September—November and also for March—April in Kenya. The gestation period is about fifteen months, 446—478 days.

Courtship has sometimes been described as being phlegmatic and without display but it is not unusual for the female to attack the male and he is often very slow and circumspect in his initial approach and movements. More than one male has been seen to try and court a cow, pairs form and break up very easily and Cowie watched a male copulate with two females in succession. Goddard, however, saw one pair associate for four months after mating. Males make a distinctive display towards females, which Schenkel and Schenkel (1969) have interpreted as symbolic aggression against a rival; it consists of sideways swipes with lowered horns directed at the ground or at a

bush, short forward and backward rushes on stiff legs accompanied by the shuffling and scraping of the hindlegs that normally accompanies foot-scenting together with urine-squirting. Schenkel and Schenkel have also described a young female becoming very excited as she repeatedly approached and fled from a big male only to return again and repeat her approaches. Another observer in a car also interrupted a courtship in which the female appeared to take an active role. The precipitate flight of the male had passed unnoticed by the female, which continued for about fifteen minutes to display towards the motionless car. After a retreat brought no response, she stopped and pranced; then she took a tuft of grass in her mouth and tossed it into the air. After approaching closer with a stilted walk she suddenly caught the scent of the car and charged into the vehicle's bumper.

Circling the female, the bull may prod her belly with his horn, curl back his lip in a spectacular *flehmen* gesture and lay his head on her back before attempting to mount her, standing in an upright posture and keeping up with her steps. Copulation may last over half an hour and may be repeated intermittently over a few days.

The birth of a wild rhinoceros was witnessed by Park Scouts Edy and Malinda in Manyara National Park. They had been descending one of the game trails along the rift wall when they found a female rhinoceros lying down in their path:

> "thinking the animal was probably dead, they first threw some stones in her direction, with no result. They approached closer and found the surrounding ground was covered with liquid. Within a few minutes the rhino got up and with little effort the calf was seen to appear. Within approximately ten minutes, the calf was dropped. The mother then turned round and started removing the birth sac with her mouth and ten minutes later the baby was on its feet, twitching its ears." (T.P.R., 1961).

Mothers are extremely intolerant of any disturbance for some days after a birth and it is probably at this stage or just before the birth that the former calf is driven off. The new calf is about 40 kg at birth and sucks within three hours. Twin calves are unknown but it is possible that adoptions take place. Thereafter the calf sucks briefly but frequently. Schenkel and Schenkel noticed that mothers with recently born young avoided wallowing even though the wallows are preferred areas for suckling. The young bleat for their mothers and continue sucking when they are so enormous it is necessary for them to lie down to get their heads under the mothers' bellies. They keep very close indeed to the mother and respond to every detail of her behaviour. Normally the calf follows but in an alarm the mother attempts to interpose herself between the baby and the cause of alarm and she tends to swing broadside on to the source of the disturbance, which hides the calf more effectively. Both animals tend to get their backsides together and as the calf gets older this behaviour turns into a very characteristic radial formation with which any group of subadult or adult rhinoceroses first responds to an alarm.

Very young calves can be quite frolicsome and will rush around tossing vegetation. Frame (1971) watched three calves taking turns at picking up and mouthing a stick without biting or chewing it.

Although it becomes independent at about two-and-a-half years a rhinoceros is not fully grown until about seven. However, it is sexually mature between five and six. Ages of about forty years have been reached by zoo animals and the animals are probably fertile to the end.

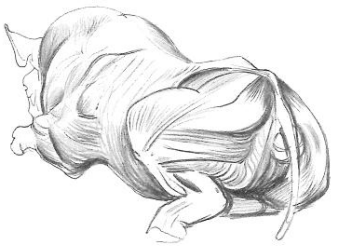
Goddard (1970a) estimated an annual mortality of about 16% in the first two years of life, dropping to 9·8% between the ages of five and twenty-five. Recruitment in Ngorongoro is about 7% but it would be difficult to find a truly undisturbed rhinoceros population today and all the results of population dynamics must be calculated in the light of very local conditions.

In their preferred thickets rhinoceros are impossible to count accurately over large areas but Goddard (1969a) used density strata samples to estimate 6,000—9,000 animals in the Tsavo National Park. This is the largest single concentration of the species in existence today (Glover and Sheldrick, 1964). At the time of this estimate the area also supported about 36,000 elephants. While the elephants had increased over a period of some twenty years, Sheldrick considered that the rhinoceros population had fallen by half over the same period. It would be extremely interesting to learn more about the interaction of these two species and see how elephants might influence the numbers of rhinos and this should be one of the priorities for wildlife research in the region.

Where rhinos are numerous, their young and very occasionally adults may fall prey to lions, and hyaenas have also been known to kill young rhinos. Elephants, hippopotamuses and crocodiles have all been recorded killing rhinos but these are almost as isolated as the instances of rhinos attacking other animals. When resistance has been lowered by lack of food or water, disease may hasten death, but there is no evidence of rhinos suffering from widespread epidemics.

A large number of tick species and other parasites have been recorded from rhinos (see Zumpt, 1964) and the "rhino sores" found behind the shoulder are associated with a worm, *Stephanofilaria dinniki* (Schultz and Kluge, 1960), which is carried by flies and ticks. Two species of flies, *Rhinomusca* and *Lyperosica*, develop in rhinoceros's dung and, after hatching, fly on to the first rhino visiting the dung midden.

Because the rhinoceros's favourite habitats are generally well-watered and reasonably fertile, settlement of rhino habitats is continuous. When food or cotton crops are damaged, or herdsmen are chased there are demands for control or extermination. Very large numbers of rhinoceros have been killed on the assumption that any form of human enterprise and the presence of rhinos are incompatible. One hunter, a former Scottish gamekeeper, claimed to have killed 1,600 rhinos in Kenya, most of them shot officially in order to make way for government settlement schemes. It is impossible to know how many rhinos have been killed illegally for their very highly priced horns, but a fairly detailed reconstruction of the species' overall decline in East Africa has been possible (see maps).

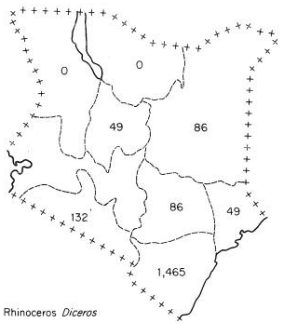


The varied disposition of rhinos is in the opinion of Ritchie (1963) related to genetic selection over many generations of exposure to hunters or to the greater tolerance of pastoralists. Given the long period of learning, it is more likely that the killing off of rhinos that expose themselves to attack has favoured those that have acquired a learnt tradition of caution and/or

truculence. The traditional attitude of Masai pastoralists towards rhinos resembled that of European country folk towards dangerous domestic bulls, avoiding provocation and giving due respect to their size and armament, and it is no coincidence that the largest populations of rhinoceros still left outside national parks are in Masailand (see map).

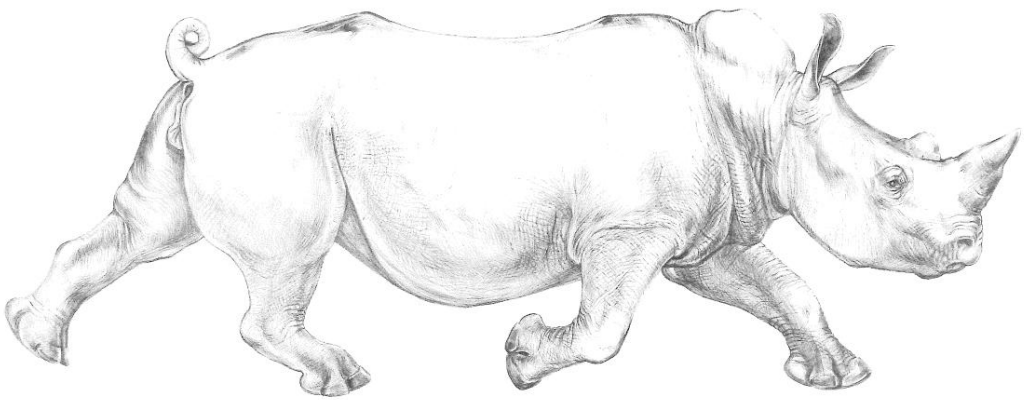
Although they are effective converters of very coarse, prickly vegetation into animal protein, they are not very suitable for regular exploitation as meat, among other reasons they grow and breed so slowly.

It is important that the species be conserved wherever possible and the details of its ecological niche be investigated further; for fossils have shown that black rhinos have been an important part of the African scene for several million years.



Rhinoceros *Diceros*

Preliminary estimate of *Diceros* numbers in Kenya rangelands in 1977. From Ministry of Tourism and Wildlife, Kenya Rangeland Ecological Monitering Unit. Aerial survey report No. 3.



White rhinocerus, Grass rhinocerus (Ceratotherium simum)

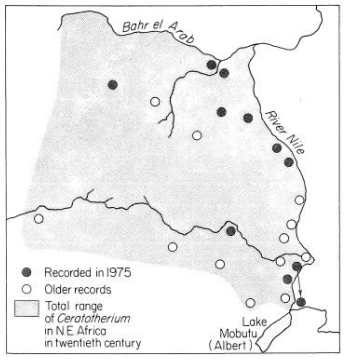
Family Rhinocerotidae
Order Perissodactyla
Local names
Kifaru ya majani (Kiswahili), Ijiji (Madi), Ubirya (Lugbara).

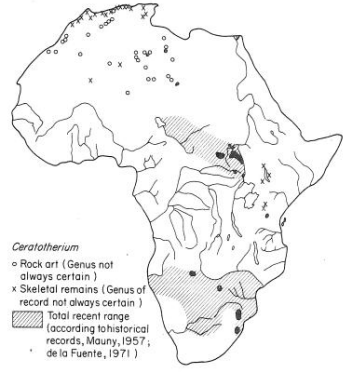
Measurements
head and body
3·6—4·2 m
height
1·5—1·85 m
tail
48 cm
weight
2,300—3,600 kg
horn
95—101 cm (Northern population)
95—200 cm (Southern population)

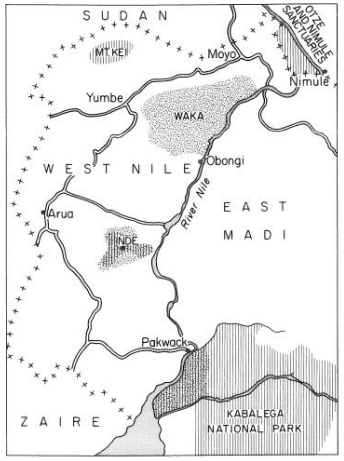
White rhinocerus, Grass rhinocerus (Ceratotherium simum)

The survival of this huge grass-eating animal, second only to the elephant in size, in two widely separated pockets, one by the Nile and the other in Zululand, has been the subject of much discussion. The two populations have been regarded as racially distinct mainly on the basis of the relative concavity of the skull forepart. Cave paintings from as far afield as the Sahara, the Kalahari and Tanzania show that this species had a very much wider range within very recent times, although it was already greatly reduced before Europeans started exploring the continent.

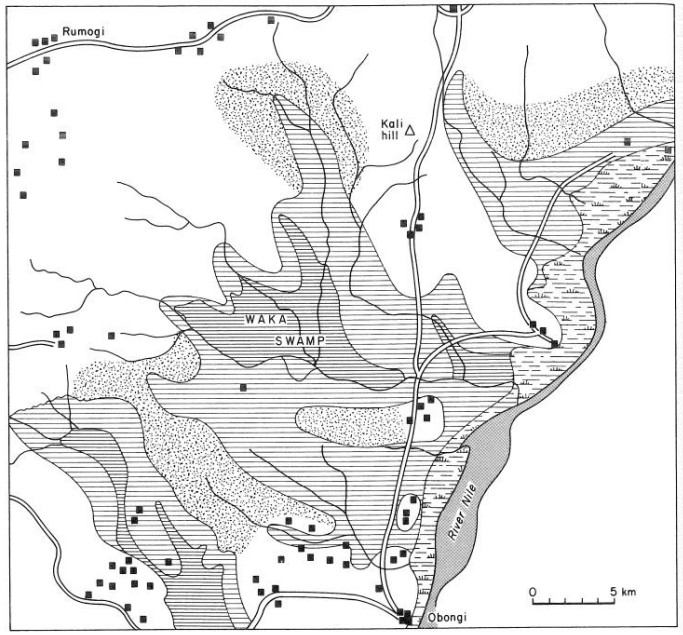
The common black rhino was known to Linnaeus in 1758, whereas the white rhino was not described until 1817 from South Africa and 1907 from Uganda. What made this animal so scarce and why has it survived in these two areas? Like all rhinoceroses it needs water (for example, many died in Zululand during a drought in 1932). Also, the grass rhino eats a lot of food; the sheer quantity needed by each rhino might be difficult to obtain during droughts, both because the vegetation has died or been burnt off and because smaller ungulates with bigger ranges, faster or more efficient cropping methods and greater numbers might converge on water supplies and compete for reduced resources. Thus areas subject to erratic rainfall have perhaps always been avoided by this species. As grazers forest, dense woodland and thickets would also have been closed to them. Recolonization of lost ground is delayed by the slow breeding and static habits of these rhinoceroses but, even allowing for this and considerable fluctuations of climate, large areas of Africa, between the two extremes of forest and semi-arid country, should have been available to grass rhinos for they do not demand very special grass species or extraordinary ecological conditions. They are almost immune to wild predators and it is perhaps this invulnerability that has encouraged a



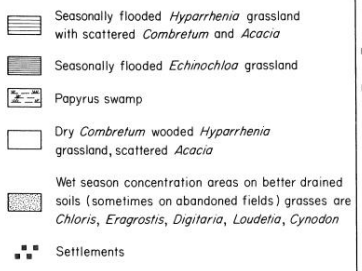


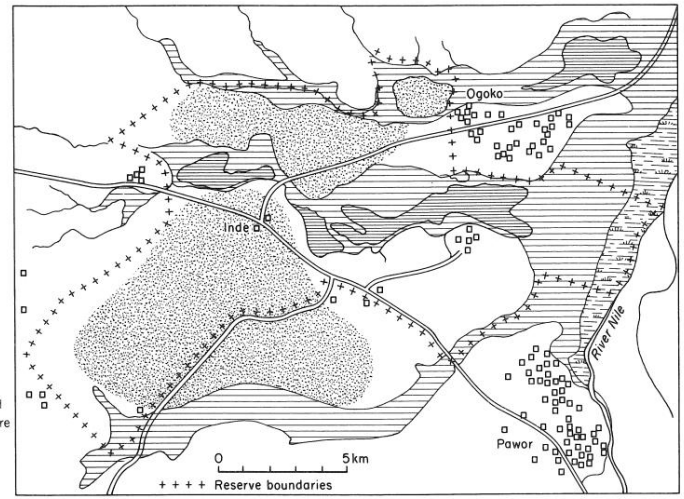


Above: Gazetted white rhino-sanctuaries and National Parks in Northwest Uganda and present range of *Ceratotherium*. Introduced into Kabalega National Park. Eliminated in Mt Kei and Otze sanctuaries. (Also exterminated in Nimule National Park, Sudan.)



Right: Ungazetted refuge for *Ceratotherium* in area of Waka seasonal swamp.





Ajai's White Rhino Reserve, Inde, Uganda

fatal tameness. In 1927 Pitman visited West Madi and described walking within 3 m of them. In no single instance did an animal show any aggression towards him, although the rhinos were aware of his presence and were watching him with interest. In such circumstances an animal is exceptionally easy to kill, even with the most primitive of weapons and there is no doubt whatever that hunting has been entirely responsible for their decline and continues to endanger present-day populations. Furthermore, if we turn the coin, it is possible that their survival both in Zululand and West Nile was assisted by the traditional attitudes of the local people. In the former area, the flesh is regarded as dangerously inedible and in Uganda a formerly sparse human population tended to avoid the malarial rhino habitats. In 1924 Game Warden Salmon was told that the rhinos were scarcely ever molested in West Nile prior to the demand for their horns.

Because their habitats are so restricted today it is difficult to be certain that these are representative or even include optimum ecological conditions for the species. Their present refuge on the seasonally waterlogged margins of the Nile is possibly less favourable than their former haunts on the higher ground around Moyo, Kei and Inde Hill. Brooks (1959) noted limited seasonal movements in West Madi, the rhinoceroses moving further inland and on to the hills during the dry months of January and February. At this time the dominant tall grass species of this area, *Hyparrhenia*, *Themeda* and *Setaria* are short tufted after the fires and are, therefore, suited to close grazing and are also at their most palatable stage. Once the rains have started, the rhinoceroses avoid the tall grasses and Brooks found them concentrated in July (the wet season) on short grass meadows. *Digitaria*, *Cynodon dactylon*, *Heteropogon contortus* and *Chloris gayana* are grazed at this time. Other species recorded are *Brachiaria brizantha*, *Urochloa* spp., *Eriochloa*, *Panicum* and young *Phragmites*. The cropping of short grass is not entirely unselective and Foster (1967) noted that they were not eating the widespread *Sporobolus festivus* during December and June.

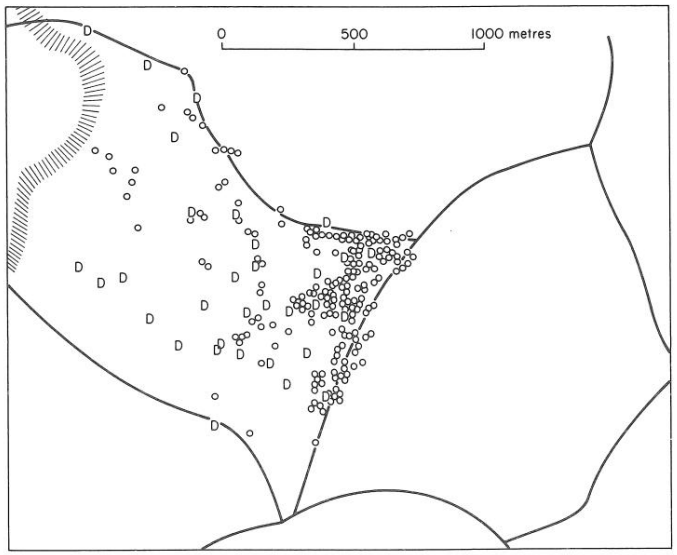
Although they prefer grass shorter than 10 cm they will crop grass up to one metre high in the absence of anything shorter. In addition to grass they may occasionally eat small shrubs and, in Zululand, Foster (1961) noted them commonly feeding on dwarf *Euphorbia*, *Stapelia* and a creeper, *Sarcostemma viminale*.

Grazing is generally sustained for a few hours and alternates with resting spells. This may continue throughout the day and night in cool weather, but the midday rest becomes progressively longer as the dry season advances. Several observers have noted a tendency for these rhinos to congregate on exposed ridges during the middle of the day, even neglecting to use available shade and it is possible that biting flies may influence this behaviour as harassment is worse along watercourses and near thicker vegetation. Foster (1961) suggested that wallowing habits were influenced by the prevalence of flies, but temperature regulation is clearly the most important factor and Owen-Smith (1975) noted that wallowing became more frequent in hot weather. Wallows are most readily formed on hardpan soils and rhinoceroses join warthogs and buffalo in maintaining short grass patches on these pans for much of the year; walking from one meadow to the other along well established paths.

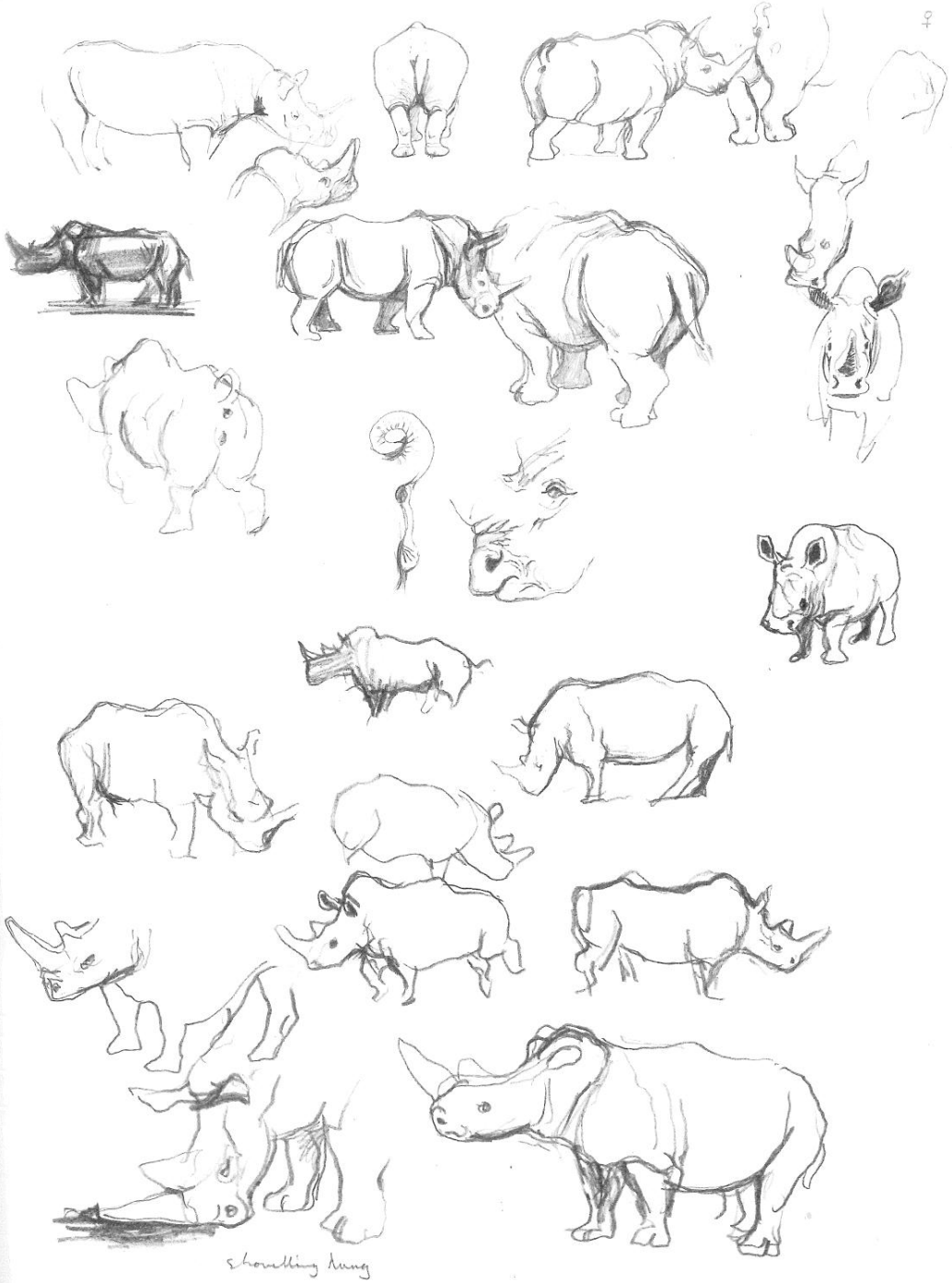
Water is needed every two to four days and very regular drinking habits are attested by well worn paths leading to their drinking stations. In the dry season water may lie 10 km or so from the home range.

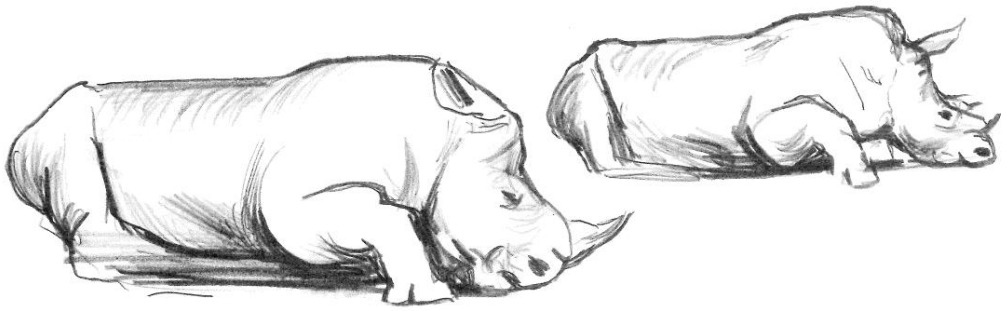
While the rhino is grazing, the head hangs vertically and only during excitement is the head raised very high, causing a tight constriction at the back of the short neck, which gives this species a highly characteristic neck hump. Even when it is running, the head is not carried very high. Galloping is moderately fast, about 40 km per hour, but cannot be sustained for very long and Foster (1961) described Zulu dogs soon winding them in a chase. While attempting to immobilize rhinos in Zululand, Player (1967) had a horse tossed into the air by a rhinoceros and a captive showed considerable agility in climbing over a gate 2 m high.

Scent, as with all rhinos, is very important and dung middens are conspicuous throughout country occupied by white rhino. Rhinos tend to add dung to an established deposit but dominant males only use a limited number of deposits which according to Owen-Smith (1975) average about thirty to a territory. Here the bull kicks and scatters the dung pile every time he uses it, whereas other classes do not disturb it. While the dung deposits are scattered throughout the territory, urine sprays are instead essentially boundary markers and Owen-Smith recorded an average of ten sprays per hour. The dominant male also makes scuffling scrape marks along his boundary trails as well as on any other favourite paths but Owen-Smith found the boundary scrapes were more frequent (one every 28 m instead of one every 38 m).



Distribution of urine sprays (O) and dung piles (D) in a grass rhino territory. (After Owen-Smith, 1975.)





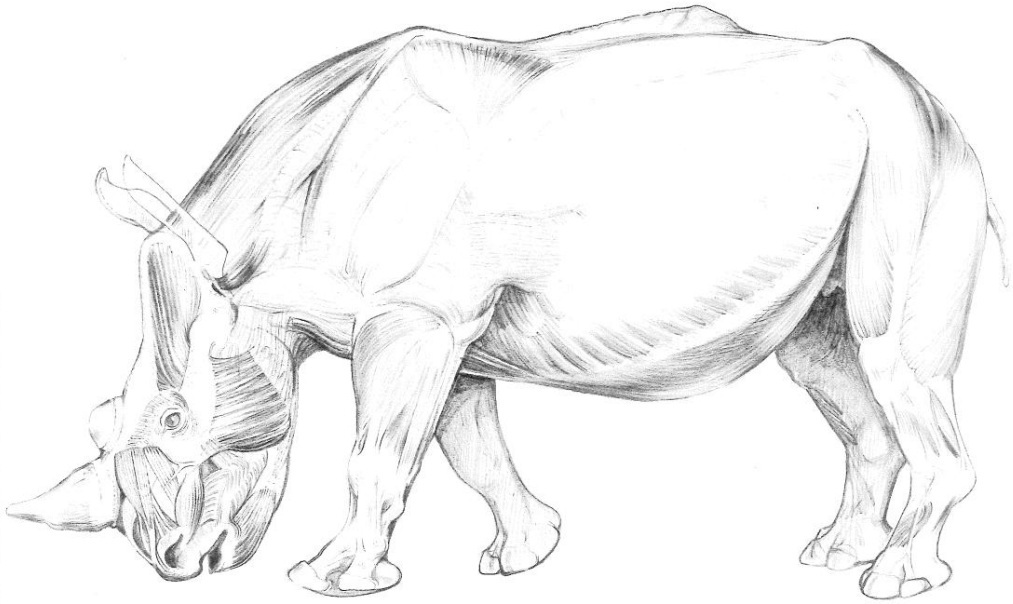
Rubbing posts are also used regularly and I have the stump of an ebony tree, picked up in West Madi, that has been rounded and polished through the regular abrasion of rhino buttocks. They also wallow regularly and occasionally roll in dust.

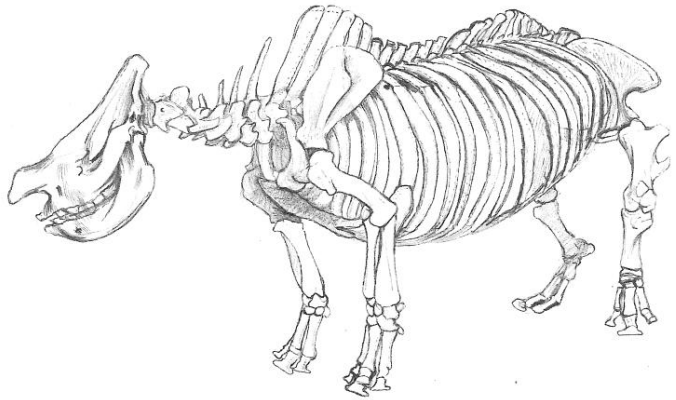
Their vocabulary includes a panting contact call which is common in groups, a squeal of distress and a whining want call in juveniles. Threat is implied by a deep bellow or rumbling growl and inferior animals on the run from others utter peculiar chirping cries, which probably signify submission. A loud wail is made by a courting male trying to restrict the movements of a female and Owen-Smith (1975) described the courting call of an approaching male as "hic-throbbing".

Owen-Smith (1975) summarized the interactions of the various classes of rhinos as follows. An alpha male usually approaches any other rhino within his territory but avoids contacts of any sort outside it. Females are sniffed at, subsidiary males are commonly confronted with a brief apposition of horns while intruding males face a more prolonged confrontation if they do not retreat. However fights are rare and it is almost invariably the resident alpha male that moves off first. Females and subadults are remarkably indifferent to one another but playful horn wrestling is common in these classes as well as in calves. All rhinoceroses, except the very young, tend to respond to the approach of an alpha male with snarling threats, which Owen-Smith saw as "separation maintaining displays". In this display the lips are retracted from the open mouth, the head is raised and the ears held back. A loud snarling roar rises to a shriek if the alpha male makes any threatening movement.

Owen-Smith explains the function of snarl displays as follows:

> "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 males respond by fleeing). There is no safe refuge to which a beta male can retreat, on adjoining territories he is likely to be challenged by other alpha males and there is no unclaimed ground. A beta male'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."





In the Zululand Park, where the very numerous rhinos have virtually no space for their expanding population, Owen-Smith (1975) found land divided up into a mosaic of single male territories averaging 1·65 sq km (0·75—2·60) with very narrow overlapping margins. Territorial males patrol their boundaries and reinforce them by challenging any male that contests them. At the time of Owen-Smith's study as many as a third of the adult males were each living under the subordination of one or more territorial bulls, tolerated within the territories for as long as they gave way to the owner. Except for the period of oestrus females and their young wander freely over the male territories. For example, one territory in Zululand was visited by a total of twenty-six different females (Owen-Smith, 1975). However, females also tend to live

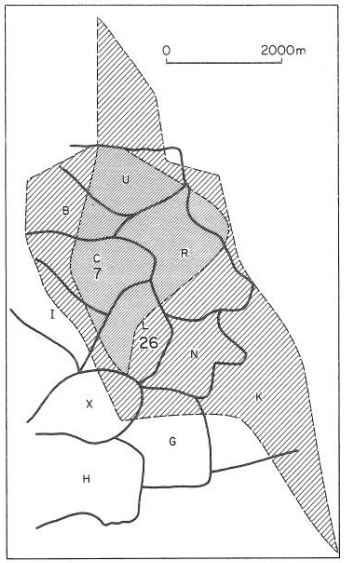
Aggregations of more than two or three animals are commoner in this widely, but others tended to range over an area of only 4—10 sq km. within a limited area of about 10—12 sq km but do not defend land and they share good grazing with other animals. Their normal home range overlaps that of several other cows with their attendant young.

The subadult young are driven off by their mothers at the birth of a new baby, whereupon they tend to pair up with an age-fellow in a similar condition and preferably of the same sex. Alternatively, they may join an unattached female, which occasionally acquires more than one satellite in this way. Many of the adolescent rhinos studied by Owen-Smith wandered species than in the black rhino and they usually centre on wallows, water or a choice area of grazing. Owen-Smith noted that subadult rhinos oriented towards groups rather than to individuals so that cows with immature young are a natural but temporary social focus and may be accompanied by up to six subadults. Of more stable associations lasting a month or more over 40% were with other subadults and 21·5% with a single cow. Only 2·7% of all subadults sighted were solitary; 0·4 cows were solitary, whereas 61·6% of alpha males and 91·8% of other males were on their own. Bonds between mothers and female offspring last longer than with males and Owen-Smith (1975) calculated an average of 10·3 months for the former (with a maximum of 26 months) and 8·1 months for the latter.

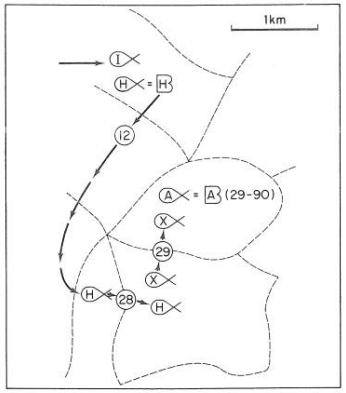
The large grazing ungulates share a general tendency towards greater sociability. Aggregations probably help maintain grass in a condition suited to regular cropping. Rhinos may be favoured by the presence of other grazers as long as grass and water are still adequate for all.

Owen-Smith only recorded conflict among territorial males as a result of trespass. Richards (1972) saw two males fight while female and calf stood nearby. He also recorded a male trying to herd two females and in incidents where a female is present, it is likely that a clash between males will take place on a boundary.

As in the black rhinoceros, preliminary sparring may take the form of sideways swipes with the horn and in this way it is possible for horns to be split. However, Foster (1961) witnessed a remarkable incident that illustrated the ritualized nature of rhinoceroses' contests. "The fight had evidently been going on for some time, as there was an area of roughly 50 feet in diameter where the ground was trampled and the shrubs and trees broken. The two rhinos were battering at each other with their shoulders, like two enormous battering rams and not once while being watched did they use their horns.



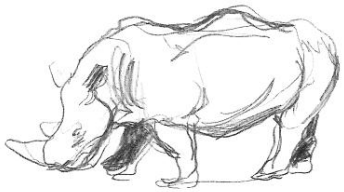
Overall home range and core area of a female grass rhino superimposed upon a mosaic of male territories. The numbers of females recorded visiting two neighbouring territories are indicated; territory L was considered to offer optimum habitat. (After Owen-Smith, 1975.)

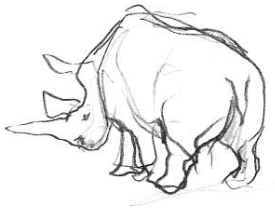


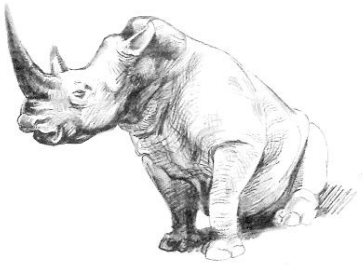
Chain displacement of territory holders. Male I displaces H. H becomes subsidiary (beta) male. After 12 weeks H moves to small territory. Sixteen weeks later H displaces X in neighbouring territory whereupon X displaces A as dominant (alpha) male. A remains as beta male for over one year. (After Owen-Smith, 1975.)

Their shoulders were bruised and appeared quite wet." Only in the most serious fighting are direct upwards stabs with the point of the horn employed. This suggests that the originally defensive components of fighting have been isolated from the aggressive one of direct thrusting and ritualized into a less dangerous fencing contest. Defeated bulls are not driven away but they adopt subordinate gestures to the victor; they stop spraying urine and gradually scatter their dung less as they progressively reduce the intensity of their foot wiping. They are also precluded from accompanying females and Owen-Smith (1975) recorded only 8% of all sightings whereas 39% of the alpha or dominant bull sightings were in the company of females. Owen-Smith also noted a chain displacement of territorial males resulting from the ingress of a single bull. The new owner was never observed to rise from the rank of subsidiary male within the same territory but such males can move into a neighbouring territory and displace an alpha male there. They immediately assume all the behaviour of a dominant animal, tending females, confronting other males, spraying boundaries and scattering dung. Boundaries are sometimes altered but are commonly inherited intact by the new tenant. Even more significant is the observance of territorial limits by the subsidiary males which have played no part in the establishment of these boundaries. Presumably the risk of unnecessary challenges are avoided in this way. The displaced bull ceases to spray urine and gradually stops scattering dung. Territories can be taken over after fights in which one or both contestants are wounded or there may be no evidence of a fight at all.

It is possible that outbreaks of fighting that have been observed in West Nile were the product of a similar upset in the territorial system. But the social life of grass rhinos has not yet been studied in East Africa. Although there are occasional fatalities from fighting, the slow breeding and maturation of this species is obviously related to a very low rate of natural mortality. Shortage of water has never been a problem on the banks of the Nile, yet the density of population has never even begun to approach the numbers reached in contemporary Zululand.







Young are born at intervals of two or three years and females in Zululand do not give birth until they are six-and-a-half to seven years old (Owen-Smith, 1975).

A female only elicits interest from the male when she is in oestrus, a condition she advertises by repeated sprayings of urine samples. A female may come into oestrus between six and eight months after giving birth, but Owen-Smith has suggested that a flush of green grass after a dry period may trigger oestrus and encourage the observable mating peaks seen in this species (October—December in South Africa and February—June in West Nile). A birth peak between July and November has been noted in Uganda.

Courtship is prolonged and Owen-Smith saw couples consorting together for 5—20 days. The male is usually cautious but persistent in his approaches to the female, which tends to threaten him at first, as does her calf. A territorial male tries to keep an oestrous female within his territory by heading her off and blocking her way, meanwhile uttering peculiar panting or hic-throbbing calls or actively chasing her back from a boundary with loud wails or squeals. He scrapes, urine-sprays and wipes his horn repeatedly (Owen-Smith, 1975). After 15—20 hours of persistent attendance the male's closer approach is tolerated and he lays his head along her back. Once the female stands still and curls her tail, the male may mount and copulation can last up to half an hour. That the whole affair places considerable demands upon the male was shown at Whipsnade Park Zoo when a copulating male had a heart attack and fell so heavily upon the female that she broke her back.

After a gestation of sixteen months the female chases off her previous offspring and gives birth well away from other rhinoceroses. Although the newborn rhino can stand within an hour, the mother remains in a secluded spot for a few days with the rather shaky youngster keeping very close. After

a few weeks they may join up with other rhinos and the young one starts grazing at two months. However, suckling is maintained for over a year, with the young one whining for its drink and taking its fill in two or three minutes.

A curious difference between *Ceratotherium* and *Diceros* is the tendency for calves of the former to take the lead. Even in flight the female appears to follow the direction taken by the young one.

Calves are often alert and curious but never leave their mothers out of reach. While it lasts this relationship is close and enduring but the necessity for a close companion is not lost when the juvenile is rejected. The subsequent rapid link-up of adolescents or unattached females suggests a continuing need by the immature for companionship.

Until recently this species has been rare in zoos but they have proved to be almost ideal zoo animals, easy to feed and maintain in good health. They breed well in captivity and are generally tame and tractable; they can also be controlled by means of tranquillizing drugs.

A female has been recorded still bearing calves at 36 years old (Player and Feely, 1960) and total life expectancy is probably in the region of 40—50 years.

The vicissitudes of the Uganda population have been patchily chronicled in the annual reports of the Uganda Game Department. In 1924 an article was published in the Bulletin of the Zoological Society of New York which focused conservationists' attention on the status of the white rhinoceros. Largely as a result of this article, protective legislation and a summary census were attempted. Quantities of horns were on sale at this time and there are official records of some 182 horns from animals killed between 1923 and 1928. In the latter year a marked diminution in numbers and a total estimate of 133 Uganda rhinos was suggested (UGR, 1928). Over the next 20 years casualties were rare and the rhinos were almost unmolested; by about 1950 a healthy population of approximately 500 rhinos were scattered throughout the uncultivated areas of West Nile. At about this time the price of rhino horn rose, so over the next ten years poaching was very heavy and the rhinos were killed out in all their gazetted sanctuaries. By 1963 the sum total of Uganda rhinos was believed to number 71 (Hayes, 1964). Between 1961 and 1964, fifteen rhinos were darted and moved to Murchison Falls National Park and their last stronghold at Inde (Ajai's reserve) was gazetted as a rhino sanctuary. Since then poaching has continued on a reduced scale but a virtually domesticated rhino (nick-named Obongi and pictured in this profile) was killed within the national park.

Throughout this century and probably for several hundred years grass rhinos have lived in proximity with people. In the wake of local shifts or fluctuations in human settlement the rhinos have benefited, like the kob, from the clearings that surround old villages and the swards that form on abandoned fields. No conservation measures for the grass rhino can be successful without the support of the local people of West Nile. Unscrupulous and predominantly foreign middlemen offering to buy horns have been the opponents of the Uganda Game Department (and, in recent years, of a dedicated rhino warden, Dr Ted Williams of Kuluva Hospital). It is not only penalties that have encouraged the people to maintain their traditional

tolerance of these animals. In 1972 there were 120 rhinos in Ajai's Reserve; by early 1978 they had been reduced to 80. About 25 animals are now living in the Kabalega National Park.