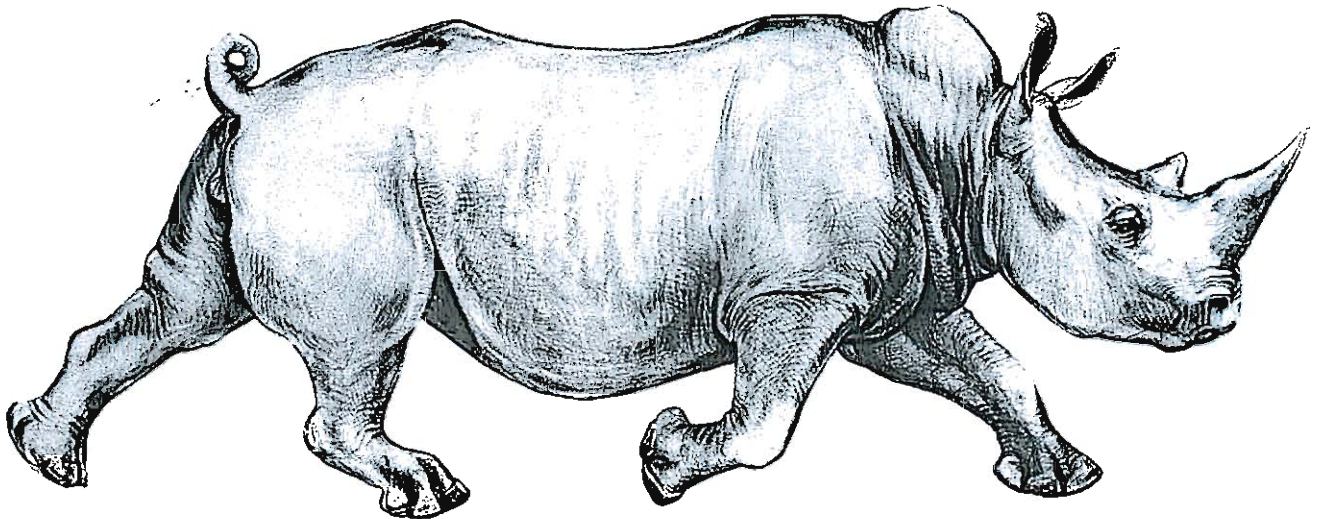


***Ceratotherium simum* WHITE RHINOCEROS (GRASS RHINOCEROS, SQUARE-LIPPED RHINOCEROS)**

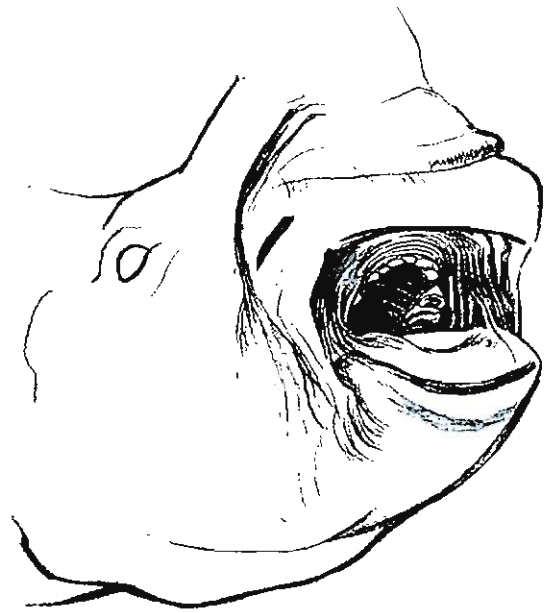
Fr. Rhinoceros blanc; Ger. Breitmaul-Nashorn

Ceratotherium simum (Burchell, 1817). Bull. Sci. Soc. Philom. Paris: 96–97, pl., figs. 1, 2. 'L'interior de L'Afrique Méridionale vers le vingt-sixième degré de latitude'; since fixed as South Africa, North-West Prov., Chue Spring (= Heuningveli), about 26° 15' S, 23° 10' E; see Grubb 1999).

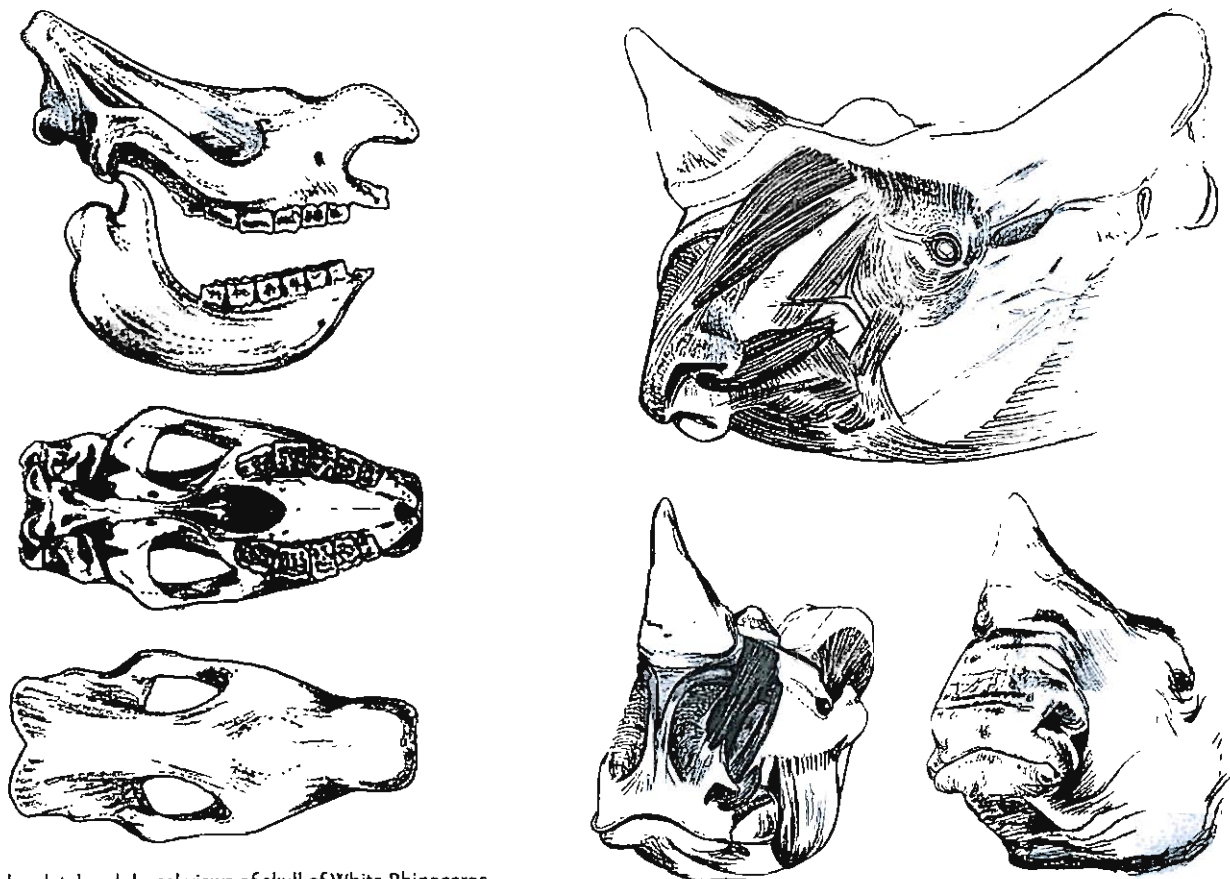
White Rhinoceros *Ceratotherium simum*.

Taxonomy First described by Burchell from a specimen collected 150 km north of Kuruman in what is now the North West Province in 1812 (Burchell gave the type locality as 'Interior of South Africa near 26° S'). He applied the name *Rhinoceros simus*, the genus *Ceratotherium* being proposed by Gray in 1867. Two subspecies are recognized: *C. s. simum* in southern Africa, and *C. s. cottoni* in north-east Africa. The nucleotide sequence divergence between them is only 1.4% (George *et al.* 1993). Groves *et al.* (2010) recognized *C. s. cottoni* as a distinct species. Synonyms: *burchellii*, *camperis*, *camptoceros*, *camus*, *cottoni*, *crossii*, *kiaboaba*, *kulamane*, *kulamanae*, *oswellii*, *prostheceros*. Chromosome number: $2n = 82$, and there is no diagnostic karyotypic difference between the two subspecies (Heinichen 1967, 1969b, Houck *et al.* 1994, 1995); the X chromosome is a large submetacentric, the Y is a small submetacentric, and the autosomes are telocentric and acrocentric (Houck *et al.* 1995). Chromosomal polymorphism, resulting in three individuals with a diploid number of $2n = 81$, has been noted in the Northern White Rhinoceros (Houck *et al.* 1994). Robinson *et al.* (2005) recently confirmed a case of inter-specific hybridization in rhinoceroses, wherein a calf was born to a young White Rhino cow and a Black Rhino bull held in captivity; the hybrid showed a mixture of phenotypic traits characteristic of the two species.

Description Largest extant rhinoceros species, but closely rivalled by the Indian Rhinoceros *Rhinoceros unicornis*. Skull is lengthened and lips broadly squared, with a hump on the neck containing the ligament and associated muscles supporting the massive head. Pointed ears fringed with hair, but otherwise body hairs are sparse and detectable only on close examination. Body is barrel-shaped due to the extended rib cage, with a prominent vertebral crest in the dorsal region and, particularly in the southern subspecies, rib-like markings on the trunk

White Rhinoceros *Ceratotherium simum* detail of open mouth.

There are several theories to explain the origin of the name 'white rhino', the most popular explanation being that 'white' is derived from the Afrikaans 'wyd' or Dutch 'wijd' (meaning wide). However, there is no basis for this conjecture, since earliest reports consistently refer to the 'white rhinoceros' or 'witte renoster' (see Rookmaaker 2003a, Feely 2007). The name 'white rhino' may derive from the pale colour of the first specimens encountered where calcareous soils predominate. The more accurately descriptive names 'Square-lipped Rhinoceros' and 'Grass Rhinoceros' have been coined quite recently.



ABOVE LEFT: Lateral, palatal and dorsal views of skull of White Rhinoceros *Ceratotherium simum*.

ABOVE RIGHT: White Rhinoceros *Ceratotherium simum* lips and musculature adapted to grazing.

of the body. There are prominent folds of skin near the top of the forelimbs, and in the flank where the upper part of each hindlimb joins the body. Skin colour is battleship grey, but is modified by the colour of the soil used for wallowing. Limbs are thick-set, with three toes bearing broad, stout nails on each foot. Tail short with a sparse fringe of bristly hairs. Females bear a pair of inguinal nipples. Males lack a scrotum, and the muscular penis points backwards when enclosed in its sheath. Preputial glands are present. Apart from genitalia there is little sexual dimorphism, except that ♂♂ attain a body mass about one-third larger than ♀♀ and have noticeably more heavily set heads, chests and necks.

Two keratinous horns lacking a bony core grow in tandem on the snout, the anterior longer than the posterior. The horns are made up of a mass of tubular filaments similar in substance to hair, and are actually outgrowths of the skin not attached to the bone of the skull. Front horn has a straighter transverse edge in front when compared with that of the Black Rhino. Male horns have a greater mean anterior basal circumference than female horns, while ♀♀ generally bear more slender, and sometimes longer, anterior horns than ♂♂. Adult ♂♂ have heavier horns than ♀♀. Mean mass of horns of adult White Rhinos was 5.2 kg ($n = 163$) for anterior horn and 1.9 kg ($n = 153$) for posterior horn (Pienaar *et al.* 1991, Pienaar 1993). No difference between adult sexes in intrinsic anterior horn growth (mean rate of 50 mm per year; range 25–66); intrinsic horn growth rate is rapid in young animals, about 150 mm in the first year of life, but growth rate of anterior horns decreases with age (Pienaar *et al.* 1991, Pienaar 1993; see Horn Measurements).

Skull elongated, occipital crest rising high at the rear of the skull, with a broad rugose area on top of the skull providing a broad area for attachment of the neck muscles. Zygomatic arches heavily built and provide firm attachment for masseter muscles that operate the lower jaw. Lower jaw massive, condyles very broad and fitting into deep sockets. Adult dental formula is $I^{0/0}, C^{0/0}, P^{3/3}, M^{3/3} = 24$. Four premolars in deciduous dentition; no incisors or canines in deciduous dentition, which are sometimes present in Black Rhinos. Upper and lower second molars are the largest of the cheekteeth (Skinner & Chimimba 2005). Patterns of tooth eruption are discussed by Hillman Smith *et al.* (1986).

Geographic Variation

C. s. simum: Southern White Rhinoceros; southern Africa only, though introduced to Kenya, Uganda (where the species, but not subspecies, formerly occurred) and Zambia.

C. s. cottoni: Northern White Rhinoceros; formerly in Central African Republic, Chad, Sudan, Uganda and NE DR Congo; now probably extinct in the wild. Dorsal outline of the skull less concave than in the southern subspecies, a shorter toothrow length, slightly longer legs relative to body length (Heller 1913), slightly smaller size overall (see Measurements), and generally higher head carriage.

Similar Species

Diceros bicornis. Sympatric, over various parts of the range of the southern subspecies. Considerably smaller, with hooked upper lips; skull shorter and broader, with occipital part not produced backwards behind condyles; head generally held high; more rounded ears with ear tips pointing upwards; and concavely saddled outline to the back.

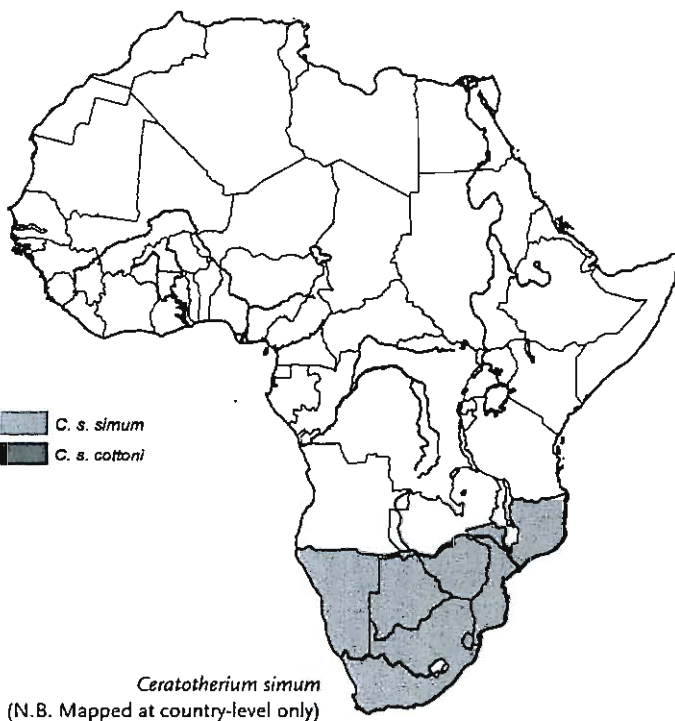
Distribution

Historical Distribution The southern subspecies formerly occurred from the Zambezi R. southwards into South Africa, in the east as far as NE KwaZulu–Natal, and in the west through the Northern Cape north of the Orange R. into NE Namibia. That they ever occurred naturally in Zambia is not definitely known; Ansell (1978) notes they may have occurred between the Zambezi and Mashi Rivers in the south-west of the Western Province, but considers the Zambezi R. as the northern boundary of the southern subspecies. White Rhinos were particularly abundant in the North West Province of South Africa, E Botswana and SW Zimbabwe. The species was absent from the highveld region of interior South Africa. Through hunting the species was almost exterminated, except for a remnant of a few score animals that persisted near the Umfolozi R. in the extreme south-east of the range. This core population has recovered such that White Rhinos have been re-introduced into many parts of their former distribution in southern Africa, and even to parks in East Africa outside the historic distribution range (see also Conservation).

The northern subspecies was found historically to the west of the upper Nile R., from NW Uganda and NE DR Congo northwards into S Sudan and into adjoining parts of the Central African Republic and southern edge of Chad. A feature of the historic distribution of the species as a whole is the limitation by major rivers, presumably because of a limited swimming capability.

White Rhinos formerly occurred through much of East Africa, as is attested by abundant fossil remains in early to mid-Pleistocene deposits in places like Olduvai Gorge. Teeth found on the soil surface in Kenya, and rock paintings in Tanzania, suggest that the species persisted in East Africa until a few thousand years ago (Hooijer & Patterson 1972). Rock engravings in Algeria indicate that the distribution range extended into North Africa in the early Holocene.

Current Distribution South Africa remains the stronghold for this subspecies, with sizeable populations in Kruger N. P. and Hluhluwe–



Umfolozi, but also occurring in numerous protected areas and private reserves throughout the country. There are also smaller re-introduced populations within the historical range of the species in Namibia, Botswana, Zimbabwe, Swaziland and Mozambique (Emslie *et al.* 2007). Populations have also been introduced outside of the former range of the subspecies to Kenya, Uganda and to Zambia. A population introduced to Côte d'Ivoire is considered semi-captive (Emslie & Brooks 1999, 2002a).

The northern subspecies is now extinct in Uganda, Chad, Central African Republic and at least up until 2006 survived in the wild only as a tiny remnant in Garamba N. P. in DR Congo (Emslie & Brooks 1999, Hillman Smith 2001, Emslie *et al.* 2007). The subspecies is now probably extinct in the wild (Milliken *et al.* 2009, Emslie 2011). Reports of rhinos surviving in S Sudan are unconfirmed; none were reported during the survey by Fay *et al.* (2007).

Habitat In southern Africa White Rhinos are typically associated with drier forms of savanna woodland, with mean annual rainfall under 750 mm. In Hluhluwe–Umfolozi Park they favour thornveld dominated by *Acacia* spp., but in Kruger N. P. they have settled abundantly in broadleaf savanna on granitic soils where *Combretum* spp. predominate (Pienaar *et al.* 1993a). Selous (1899) reports that they were partial to broad grassy valleys within savanna woodland regions of Zimbabwe. They were not recorded historically in treeless grasslands of the Highveld and interior KwaZulu–Natal. Being water-dependent, White Rhinos are seldom found further than about 5 km from surface water.

Heller (1913) described the habitat of the northern subspecies in Sudan as an open savanna containing scattered *Combretum* trees, and tall grass over 2 m in height during the wet season. The recent range in Garamba N. P. is likewise mostly tall *Loudetia/Hyparrhenia* grassland on lateritic and granite-derived sandy soils with widely scattered trees of *Vitex doniana* and *Terminalia mollis*. Falling within the Sudano-Guinean Savanna belt, the natural state of this area is tree/bush savanna or *Combretum/Terminalia* woodland, but the southern part of Garamba, where the rhinos are protected, is maintained as more open grassland by frequent intense fires and high elephant density. The area is regularly dissected by flowing rivers with patches of gallery forest. Rainfall from 1980 to 1988 averaged 1265 mm per year, though from 1957 to 1963 the average had been 1627 mm (Hillman Smith 1989). A crucial feature of this habitat is the presence of regularly spaced termitaria clearings. They cover 10–12% of the surface area of the grassland, but an average of 42% of all rhino observations over a ten-year period were in termitaria clearings. The *Loudetia* grass is unavailable to the rhinos as a food source above 0.5 m in height, but in the long grass seasons the termitaria clearings are the site of smaller, more palatable species. The long grass areas are used by the rhinos for cover, both for resting during the day and when disturbed, but it is the termitaria within the long grass that provide the combination of protection and airflow (K. Hillman Smith pers. comm.).

Abundance The Southern White Rhino is the most numerous of all rhino taxa, and its recovery from just a few score individuals has been recognized as among the world's greatest conservation success stories. As of 31 December 2010, there were an estimated 20,160 animals surviving in the wild, the majority of which (18,796) were in South Africa. Namibia (469), Kenya (365) and Zimbabwe (290) are the only other countries with over 250 wild Southern White Rhino, and together they conserve 82% of the subspecies outside of

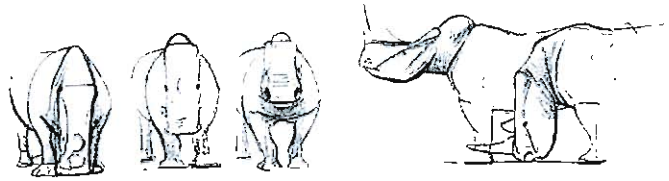
South Africa. Smaller populations exist in Botswana (135), Swaziland (88), Uganda (9), Zambia (7) and Mozambique (6) (Emslie 2011).

In iMfolozi, Southern White Rhinos had attained local densities exceeding 5/km², and a regional density of 3/km², at the time of Owen-Smith's study in 1970 (Owen-Smith 1973). The species constituted about half of the total biomass of large mammalian herbivores. Numbers have subsequently been held below this level through regular live removals. The former high abundance of the species in favourable habitat is attested by reports from early explorers of up to 80 animals being seen during a day's journey with wagons through the Magaliesberg region of South Africa's North West Province (Harris 1838). In Kruger N. P., the growing White Rhino population has attained local densities of 0.5–1.4 animals/km² (Pienaar *et al.* 1993b).

The northern subspecies was locally, rather than generally, abundant (Roosevelt 1910), but several thousand must have occurred in five countries at the start of the twentieth century. In 1960, the population was estimated to have stood at about 2230 individuals (Emslie & Brooks 1999). Four animals were last seen in Garamba N. P. in the Democratic Republic of Congo in 2006 and only spoor found in 2007. Since then there have been no signs of rhino despite intensive ground-based searches, except for a 2–3-year-old poached carcass found in 2008, and it is now believed this population is extinct (Milliken *et al.* 2009, Emslie 2011).

Adaptations The most notable adaptations are those facilitating a grass diet, in particular the lengthened head, widened lips, absence of incisor and canine teeth in both jaws, and high-crowned premolars and molars, possessing convoluted enamel layers on their biting surfaces adapted to grinding up coarse food. The skin is extraordinarily dense, tough and inelastic, varying in thickness from 18 to 24 mm, although the epidermal layer is only 1 mm deep. Large apocrine sweat glands, with myoepithelial cells arranged round the ducts, are distributed over the body. Following extreme exertion, White Rhinos may suddenly become covered in sweat over the whole head and trunk region. Wallowing in pools of water or in mud aids in thermoregulation, although wallowing is not restricted to the mid-day period. The ears may play an additional role in heat loss, being moved around restlessly even when animals are apparently sleeping. The body temperature is fairly low (34–37°C), and may vary over a 3–5°C range during the course of the day (Allbrook *et al.* 1958, Wallach 1969). During mid-day, they congregate in shady rest-places usually situated on ridge-crests. Here they may slumber for up to 8 h during mid-summer, but the rest period is reduced during the cooler winter period. During cold, windy weather animals seek shelter in dense woodland patches. A subcutaneous layer of fat up to 50 mm in thickness may build up on the abdomen, providing a buffer against malnutrition during the dry season.

The nasal sinuses take up almost as much space in the skull as the brain, indicating strong dependency on olfaction. White Rhinos may respond to human scent at ranges as great as 800 m, and can follow the tracks of other rhinos over an hour later. Animals of the southern subspecies walk with head held low and nostrils close to the ground, such that in sandy soil the mouth may make a sinuous track, but the northern subspecies holds the head higher, probably because of the longer grass habitat. Hearing is sharp, but vision poor. Animals react to a person walking past in clear view at ranges of 80 m, but with some uncertainty. However, they appear unable to identify a motionless human observer at ranges greater than 15–20 m.



White Rhinoceros *Ceratothorium simum* grazing and head lift diagram.

The White Rhino is a hindgut fermenter with a capacious large intestine where digestion of plant fibre occurs. The mean retention time of dye-marked food particles in the digestive tract was around 60 h (Foose 1982). As a result of the prolonged retention about 50% of cell wall components of a standard grass hay may be degraded, a digestive efficiency lower than that of grazing ruminants but better than equids. Grass is cropped by grasping material between the upper lip and a pad on the lower lip, then breaking it off by inward movement of the lips or slight jerk of the head. The width of the bite is around 20 cm, the biting rate as much as 80/min, and height of cropping down to as low as 10 mm above ground level (Owen-Smith 1973, Shrader 2003). This enables these large animals to obtain an adequate rate of intake even from short grass swards. Defecation takes place 4–6 times per 24 h, and the boluses contain much coarse grass material.

White Rhinos drink daily during the wet season when water is abundant. During the late dry season when animals must travel perhaps several kilometres to water, they may drink only every 3–4 days. Drinking generally takes place during the late afternoon or early evening through to midnight, so that travelling to and from water occurs during the cooler hours. After wallowing in mud, animals rub various parts of the body against convenient trees, rocks or termite mounds, which become quite highly polished. This action may serve to remove ticks along with the mud. The mud coat may also serve some protection against biting flies.

Despite their large size, White Rhinos move quite gracefully with marked flexure of the carpal joints. The walking speed is 3.0–3.8 km/h. Animals generally trot with a high-stepping action while hastening from a human intruder, and can maintain this gait for several kilometres at a speed of 29 km/h. Galloping takes place only over short distances except by small calves, and the top speed is reported to be 40 km/h. In a study of locomotion and bone strength in the White Rhino, Alexander & Pond (1992) found that the stresses developed in the long bones in running are rather low, in comparison with other large mammals, suggesting that rhinoceros skeletons may be built to unusually high factors of safety.

Foraging and Food Strictly a grazer, with forbs normally constituting no more than about 1% of the diet. Occasional instances reported of White Rhinos chewing on woody stems, otherwise no browsing observed. In Hluhluwe–iMfolozi Park, they favour short grass areas where species of *Panicum*, *Urochloa*, *Digitaria*, *Sporobolus* and *Cynodon* predominate. Such species can constitute over 50% of the diet during the wet season. Since some of these grass species grow in a tufted form elsewhere, a prostrate growth form appears to be cultivated by the grazing pressure of White Rhinos. Much foraging occurs around termite mounds, sites of former human habitation and other areas where nutritious short grasses prevail. During the dry season White Rhino transfer their grazing more towards taller tuft-forming grass species, especially *Panicum maximum* growing

under tree canopies and *Themeda triandra* in more open areas. The latter species can constitute up to half of the diet at this time of the year. Under extreme conditions they may extend their foraging up hillsides where tall grass reserves remain. Apart from lawn-forming species like *Cynodon dactylon* and *Dactyloctenium australe* growing under shade canopies, fibrous grasses growing in sandy soil areas are eaten little. Aromatic grasses like *Cymbopogon* spp. are rejected, although *Bothriochloa* is eaten when short. The grazing impact of White Rhinos promotes the formation of a mosaic interspersed of short and tall grasslands (Owen-Smith 1988, Waldram *et al.* 2007).

White Rhinos of the northern subspecies have been observed feeding on medium-tall grasses of the genera *Hyparrhenia*, *Panicum*, *Chloris*, *Heteropogon* and *Brachiaria* (Foster 1967, Van Gysegem 1984). In Garamba N. P., *Loudetia arundinacea* was only grazed by White Rhinos when the grass was below 0.5 m in height. Recent park management promoted mosaics of short grass for feeding and long grass for cover, but the remaining rhinos were not at sufficiently high density to maintain lawns themselves. In the later wet season, their feeding was largely restricted to medium-tall grasses of the genera *Brachiaria*, *Pennisetum*, *Sporobolus*, *Cynodon*, bordering termitaria or occurring sparsely elsewhere, certain forbs growing on termitaria, and *Eleusine* along rivers.

White Rhinos are typically active for about 50% of the 24-h cycle, distributed equally between day and night, with most of this time spent foraging. Peak grazing activity occurs during the early morning and late afternoon, extending into the night. However, when food is plentiful daytime foraging activity is reduced. Foraging time tends to decline during the dry season, perhaps to conserve energy when only poor-quality grass is available. Greatest daytime activity occurs during the period of new grass growth at the start of the early wet season, and frequent wallowing indicates that animals are under much thermal stress at this time of the year when their feeding time extends towards the hot mid-day period.

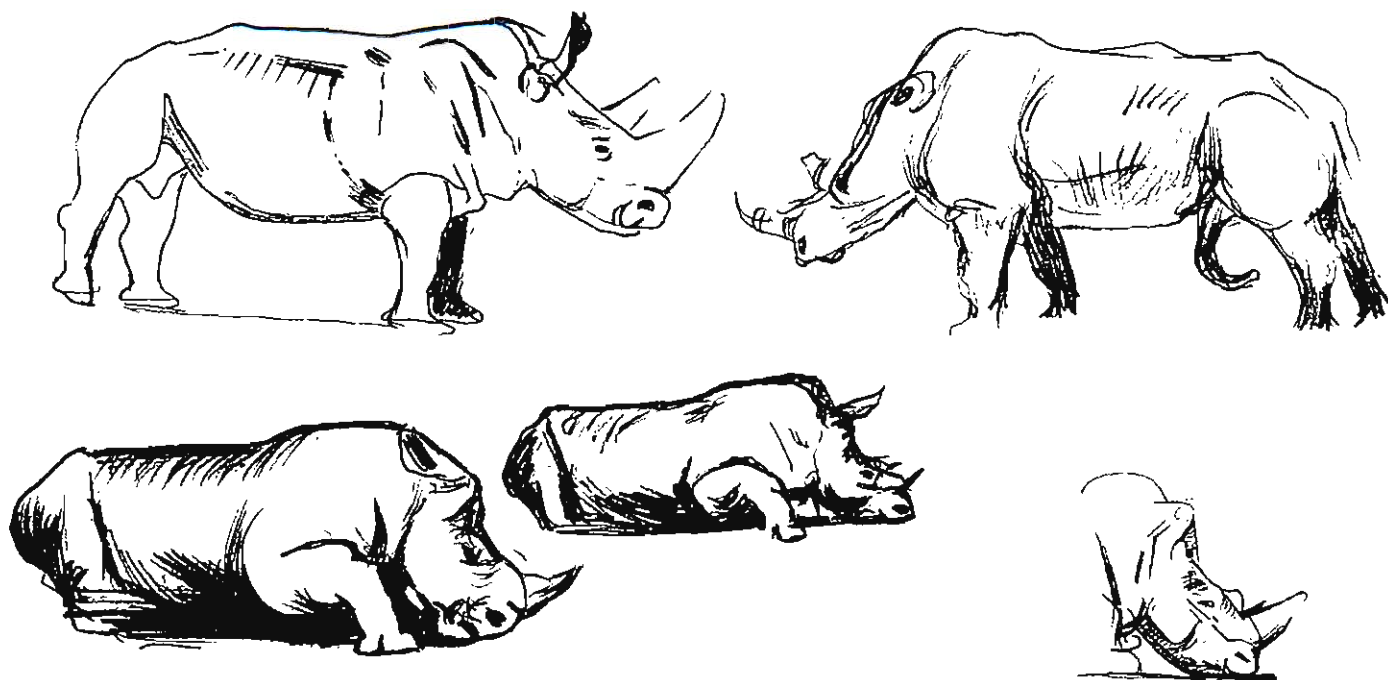
Social and Reproductive Behaviour Social organization is structured around the territorial system of adult ♂♂. Territories are occupied year-round by a dominant adult ♂, and perhaps shared with one or more subordinate adult ♂♂. They encompass 0.8–2.6 km² in high-density regions of Hluhluwe–iMfolozi Park (Owen-Smith 1975) and 2.6–9.0 km² elsewhere in this park (White *et al.* 2007), and are also larger in less favourable habitat: 2.5–13.9 km² in Ndumo G. R. in KwaZulu–Natal (Conway & Goodman 1989), 1.7–3.7 km² in Kruger N. P. (Pienaar *et al.* 1993b), 1.4–5.0 km² at Matobos in SW Zimbabwe (Rachlow *et al.* 1999), and 5–11 km² in SE Zimbabwe (Condy 1973). However, territories as large as 50–100 km² to more than 100 km² have been documented for low-density populations elsewhere (Roche 2000, P. Kretschmar pers. comm.).

Female home-ranges extend over 10–20 km² in Hluhluwe–iMfolozi Park, including a favoured core encompassing 5–10 km² where each ♀ spent most of her time while food and water remained abundant, but some individuals may move over much larger ranges (Owen-Smith 1975, White *et al.* 2007). Home-ranges of 40–50 km² are reported from elsewhere in southern Africa (Pienaar *et al.* 1993b, Rachlow *et al.* 1999). White Rhinos of the northern subspecies introduced into the E Nile region of N Uganda moved over annual ranges approaching 100 km² (Van Gysegem 1984). In Garamba N. P., where the population is at very low density, adult ♂♂ ranged over areas of 125–

230 km², while ♀ home-ranges covered 200–500 km² (K. Hillman Smith pers. comm.). Both total home-ranges as well as the core areas of ♀♀ generally overlap extensively. Female home-ranges also encompass several female territories (Owen-Smith 1975, Pienaar *et al.* 1993b, White *et al.* 2007). Adult ♀♀ may temporarily abandon their home-ranges during adverse conditions, but return to them thereafter, although some individuals may shift home-ranges over their life-span (Owen-Smith 1973). In Garamba N. P., shifts in the home-range of a ♀ were sometimes associated with the birth of a new calf. Animals peripheral to a ♀ and her current calf tend mainly to be the older offspring of that individual (K. Hillman Smith pers. comm.).

Adult ♂♂ older than 10–12 years are basically solitary, but territory holders were temporarily associated with a ♀ and her companions on about 40% of occasions seen (more in the wet season, less in the dry season). Subordinate adult ♂♂ are likewise usually found alone, and associate only briefly with ♀♀. Adult ♀♀ are most commonly found in dyads consisting of a mother and her offspring, or a ♀ accompanied by a subadult that is generally not her progeny (Owen-Smith 1975). However, in Garamba N. P., 50% of female calves remained with or re-joined the mother and her next offspring (K. Hillman Smith pers. comm.). Occasionally, two adult ♀♀, both lacking an offspring, may join together for a period, and sometimes a young subadult attaches itself to a cow–calf pair to form a triad. Larger social groups may be formed where several subadults join up with a ♀ lacking a small calf, the largest such unit including eight individuals. Subadults most commonly form same- or mixed-sex pairs, triads or larger groups. Temporary associations numbering up to 16 individuals can be observed, usually with an adult ♀ as the core, especially where animals congregate around resting areas or waterpoints. Bonds between individual subadults can endure for several years. Subadult ♂♂ persistently form attachments until about ten years of age. Young ♀♀ separate from subadult companions following the birth of their first calf around seven years of age (Owen-Smith 1988).

Territory holders confine their movements year-round to within their own territories, except for excursions to seek water for drinking during the dry season. Territories are marked through spray-urination concentrated along boundaries, and dung scattering performed at large hollowed-out dung heaps at borders. Territory holders also add their contributions to the middens formed where other rhinos have defecated. Subordinate ♂♂ restrict their movements mostly to a single territory, but do not scatter their dung or spray-urinate. Two dominant ♂♂ meeting at a mutual territory border engage in silent, repetitive horn-against-horn contacts interrupted by wiping the anterior horn on the ground. After periods varying from a few minutes to an hour or longer, the ♂♂ disengage back into their own territories. Fights may develop where a territory holder crossing a neighbouring territory on his return from water is accosted by a rival ♂, and unable to back away to his own territory. Otherwise territorial ♂♂ behave subordinately while off their home territory. Subordinate ♂♂ stand their ground with loud roars and shrieks when confronted by a territory holder, and hold their ground until the territory holder wanders off, having reinforced the dominance relationship. A ♂ displaced as territory holder may remain on as a subordinate, or seek to claim dominance in another territory. Fights can be quite severe, with ♂♂ battering one another around the head, belly and groin with their horns, and not uncommonly result in the death of the loser (Owen-Smith 1975).



White Rhinoceros *Ceratotherium simum*.

If a territory holder detects that a ♀ is about to enter oestrus, he attempts to hold her within his territory until receptivity develops. This entails blocking any movements by the ♀ and her companions to cross over a territory border region, accompanied by loud squeals by the ♂ and threatening roars in response by the ♀. This pro-oestrous consort period lasts a few days to two weeks or longer. Periodically the ♂ sniffs urine deposits, exhibiting the lip-curl (flehmen) posture, as well as dung from the ♀. Courtship begins with approaches by the ♂ accompanied by a hic-throbbing sound. Initially, the ♀ wards off such advances with aggressive roars. After several hours of repeated advances her aggression becomes muted, and the ♂ is able to rest his head on her rump. Eventually mounting, and ultimately intromission, takes place. Copulations last 15–30 min, with repeated ejaculations. A single mating is the rule, with the ♂ continuing to accompany the ♀ for a few more days thereafter without further advances. Subordinate ♂♂ may sometimes attempt courtship when a ♀ is not accompanied by a territory holder, but opportunities are rare and ♀♀ ward off advances from subordinate ♂♂ quite vigorously (Owen-Smith 1975).

The ♀ seeks the seclusion of dense bush, long grass or other remote areas prior to giving birth. Calves follow after the mother when just a few days old. They are very inquisitive, and young animals display great curiosity upon meeting other groups. Calves and subadults, and sometimes even adults of both sexes, may approach each other to engage in playful horn wrestling, and sometimes counter-chasing, for a period. Calves continue to accompany their mothers until around the time of birth of the next offspring (i.e. until about 2–3 years of age). The older calf may be driven off shortly before the birth of the new infant, but in low-density populations ♀♀ may rejoin the mother.

Subadults tend to settle in home-ranges similar in extent to those of adult ♀♀, but these are usually somewhat transient. Subadults form temporary associations with adult ♀♀ or other subadults, and these companionships enable them to explore a wider area than that covered by their own home-ranges, through what has been termed a 'buddy system' (Shrader & Owen-Smith

2002). By reducing the risk of being attacked by territory holders, and uncertainty of finding food in the novel area, such shifting companionships facilitate later dispersal by subadults beyond the region where they were born. Females establish fixed home-ranges around the time of birth of their first calf, ♂♂ when they settle within a territory either as a subordinate or eventually as a territory holder. During their adult period, ♂♂ alternate between territory holder and subordinate status. Testosterone levels are higher in territorial than in non-territorial ♂♂ (Rachlow *et al.* 1998). The average duration of territory tenure within a particular territory exceeds five years. Ageing ♂♂ may eventually settle in retirement within a territory as a subordinate and forego further aspirations to reproduction.

White Rhinos make a variety of sounds, the most frequently heard being the snorts and roars associated with maintaining spacing among individuals. The squeals made by ♂♂ blocking ♀♀ at territory boundaries resemble squeals made by calves seeking to nurse from their mothers. Soft pants serve as a contact sound between companions, and are also made by a mother calling a lost calf. Calves may also make high-pitched mewling sounds when moving. White Rhinos have no alarm call, animals communicate alarm to companions solely by their agitated movements, and in Garamba N. P. have been recorded stamping on the ground and kicking their bellies to make a drum-like sound.

White Rhinos are often found in association with Fork-tailed Drongos *Dicrurus adsimilis*, which hawk insects by flying along the sides of resting rhinoceros, and with Red-billed Oxpeckers *Buphagus erythrorhynchus*, which feed on ticks and skin secretions. The birds also give a harsh alarm call to which the rhinos react immediately by looking around agitatedly to detect the source of the birds' reaction. Any sound or movement causes the animals to run off. Rhinos may remain alert and sensitive to the slightest sound for half-an-hour or longer. Why the birds should give this alarm is not obvious, but the call may serve as a rallying signal in anticipation of their host running off due to some impending danger.

Reproduction and Population Structure In the wild ♀♀ undergo their first oestrous cycles around 4–5 years of age (youngest 3.8 years), and produce their first offspring around 6.5–7 years of age (Owen-Smith 1988, Hillman Smith 2006). In captivity, ♀♀ as young as 4.3 years have given birth (Rieches 1998), but perhaps only because they had reached near adult size by this age due to a high plane of nutrition. In the wild, ♂♂ show reproductive interest around eight years of age, but are not able to contest for territorial dominance until they reach full size around 10–12 years of age (Owen-Smith 1975). In captivity, ♂♂ as young as 4–5 years of age have sired offspring (Rieches 1998).

Births in the wild occur throughout the year, but there is a peak during the early dry season months (Mar–Jul in southern Africa and Dec–Mar in the northern subspecies) (Owen-Smith 1988, K. Hillman Smith pers. comm.). This seems to be an outcome of the stimulating influence of fresh grass growth induced by rainfall on oestrous cycling 16 months earlier, indicated by a marked rise in the number of ♀♀ being accompanied by ♂♂ from Oct–Nov when the wet season commences. During the dry season few ♀♀ show signs of oestrus, and dry spells during the wet season also suppress behavioural indications of oestrus. Hormone profiles obtained from faecal samples indicate that cycling continues, although at a lower amplitude, during these periods of 'quiet oestrus' (R. Swaisgood pers. comm.). Under captive conditions some ♀♀ show irregular oestrous cycles, while others go for long periods without overt reproductive activity, and some even switch off completely.

Reproductive activity almost never develops when White Rhinos are housed as male–female pairs in zoos, but the species is not difficult to breed when kept in groups in large enclosures. The presence of more than one ♂, or introduction of a new ♂, seems to be a requirement for ♀♀ to solicit matings (Lindemann 1982, Patton *et al.* 1999). This phenomenon, which enables ♀♀ to exert some control over their choice of a mate, probably operates in the wild as well.

Gestation lasts 16 months with a single offspring born. Calves weigh about 65 kg at birth (range 45–75 kg), or around 3.5% of maternal weight. At birth, the skin is pale grey with a pink tinge. The outer horny layer of the skin is moulted at about 1.5–4.0 months, revealing a new paler skin, and a further moult takes place at about 10 months (Bigalke *et al.* 1950). The calf is born hornless, but in one study animal the anterior horn pierced the skin at five weeks, grew to 39 mm at three months and 100 mm at seven months. Infants less than two months old nurse hourly, while among older calves nursing takes place about every 2.5 h. Calves start nibbling grass at around two months of age, while weaning off mother's milk takes place from 12–18 months, although occasionally extends to 24 months. The milk is low in fat and protein and high in carbohydrates.

Cows come on heat again when the calf is about 6–12 months old, so that the modal inter-birth interval is 2–2.5 years (minimum 22 months in the wild when the previous calf survived) (Owen-Smith 1988); results from Garamba N. P. were similar, where inter-calf intervals averaged 30 months over a 20-year period, with a range of 21–57 months (Hillman Smith 2006). However, some ♀♀ appear less fertile and may undergo several oestrous cycles of about 30 days duration (range 27–34 days; R. Swaisgood pers. comm.) before conceiving. Hence, at a population level, the mean inter-calving interval is about 2.5 years (and see Rachlow & Berger 1998), or even longer under unfavourable conditions. However, under zoo conditions one ♀ produced six calves

in nine years at an average interval of 18.5 months (Lindemann 1982).

Cementum line counts from tooth sections indicate a maximum longevity of 40 years (Hillman Smith *et al.* 1986), which approximates maximum longevity of 45 years recorded in captivity (Weigl 2005). Elderly ♀♀ exhibit lengthened calving intervals, but one obviously very old ♀ gave birth after a long period with no offspring.

The overall sex ratio of the Hluhluwe–iMfolozi population was close to parity (98 ♂♂ to 100 ♀♀) based on the 1969 census, i.e. prior to distortion by removals. However, the sex ratio of calves born around this time showed a strong male bias (167 ♂♂ to 100 ♀♀, $n = 232$), which had moved up into older age classes by 1974. Early zoo records also show a bias towards male offspring (147 ♂♂ to 100 ♀♀, $n = 121$; Lindemann 1982), but this has not persisted (e.g. 43 ♂♂ to 42 ♀♀ born in San Diego Wild Animal Park; Rieches 1998). In Garamba N. P. there was a strong male bias in calves born during the disturbances of the war period, but overall the birth sex ratio was close to parity (K. Hillman Smith pers. comm.). At Hluhluwe–iMfolozi, primiparous ♀♀ produced mainly sons, and old ♀♀ mostly daughters. Hence the male-biased sex ratio of offspring may have been a temporary phenomenon related to the high proportion of young ♀♀ in the expanding population (Owen-Smith 1988).

Because ♂♂ reach maturity around 10–12 years of age and ♀♀ around 7–8 years, the functional sex ratio in Hluhluwe–iMfolozi in 1969 showed a female bias overall (80 adult ♂♂ to 100 adult ♀♀, $n = 684$). The predominance of ♀♀ and calves was greater in regions where high rhino densities occurred in favourable habitat, while in outlying areas of less suitable habitat there was an even sex ratio among adults. Subadults constituted 32%, and calves <3 years 22% (10% <1 year). Because the population was expanding at this time, it exhibited a higher proportion of young animals than would a stable population (Owen-Smith 1988). The structure of the expanding population in Garamba N. P. was similarly about 40 : 30 : 30% adults to subadults to calves (K. Hillman Smith pers. comm.).

Annual mortality in Hluhluwe–iMfolozi was 1% for adult ♀♀, 3.5% for adult ♂♂ and 3.5% for calves. Mortality appeared somewhat higher among subadults. However, these rates are for a growing population, at a time when few animals would be dying of old age. Much mortality among adult ♂♂ is as a result of fighting injuries, and some subadults are also attacked fatally by territory holders. Neonatal mortality was under 8%. Based on these mortality rates, and an effective natality rate of around 0.4 per adult ♀ per year, the maximum sustained rate of population growth is about 9% per year. The actual rate of increase of the Hluhluwe–iMfolozi population over 1960–72, adjusted for removals, was 9.5% per year, perhaps because the growing population had not yet attained a stable age distribution (Owen-Smith 1981, 1988). The Kruger N. P. population has also been growing at around 9% annually (SANParks pers. comm.). Similarly, between 1983 and 2005, 50 births were recorded in Garamba N. P., and mean annual rate of population growth was about 9% (Hillman Smith 2006). From comparison with other megaherbivores, population regulation is expected to occur largely through lengthened birth intervals coupled with retarded age at first reproduction. However, dispersal movements by subadults of both sexes make an important contribution to dampening local population increases. In Hluhluwe–iMfolozi population growth was slower in the high-density population core than in outlying areas. This indicated a dispersal rate outwards from the core of about 3% per year overall, and about 7.5% per year specifically for subadults (Owen-Smith 1988).

Predators, Parasites and Diseases Adult White Rhinos are effectively invulnerable to predation by carnivores. However, young animals are susceptible to being killed by Lions *Panthera leo* and perhaps Spotted Hyenas *Crocuta crocuta*. They gain security by associating in groups, and when disturbed adopt a rump-against-rump formation facing outwards in different directions. When threatened by the close approach of a human, ♀♀ with young calves stand guard over the calf and do not charge. The long anterior horn could aid in warding off a predator attack. When fleeing, young calves gallop ahead of their mothers, enabling the mother to maintain close contact with the whereabouts of her offspring.

A new threat has developed following the introduction of orphaned young elephants into wildlife parks where White Rhinos occur. Young male elephants nearing adulthood have directed their sexual and aggressive behaviour towards White Rhinos of both sexes, with substantial numbers of rhinos being killed (e.g. Slotow & Van Dyk 2001, Slotow *et al.* 2001). Such incidents are seldom recorded in places like Kruger N. P. where a well-established population of elephants exists.

White Rhinos in southern Africa generally have large swarms of a large blood-sucking fly *Rhinomusca dutoiti* resting on their sides. These flies lay their eggs in rhino dung middens where their larvae develop. Much smaller flies of the genus *Lyperosia* are also commonly associated with rhinos and their middens. Large numbers of gyrostigid fly larvae, up to 40 mm long, may be found attached to the stomach walls of rhinos. Small piroplasms (*Babesia* and possibly also *Theilaria*) have been found in blood samples (Keep 1970). Circumstantial evidence indicates that the deaths of three rhinos translocated into Matusadona N. P. in N Zimbabwe were due to trypanosomiasis infection (Taylor 1986), and mortality among animals translocated to East Africa could have been due to the same cause.

Theiler (1962) provided a detailed checklist of ixodid ticks recorded from White Rhinos, and Baker & Keep (1970) a checklist from KwaZulu-Natal. More recently, Knapp *et al.* (1997) updated the lists with their own studies and recorded eight ixodid tick species known to infect White Rhinos in South Africa and seven in Zimbabwe, including *Amblyomma hebraeum*, *A. sparsum*, *Hyalomma marginatum*, *H. truncatum*, *Rhipicephalus maculatus* and *R. simus*. Walker (1991) mentioned that the adults of two species, *Amblyomma rhinocerotis* and *Dermacentor rhinocerotinus*, feed primarily on African rhinos. Penzhorn *et al.* (1994) provide a checklist of the helminths of White Rhinos. Ciliated intestinal protozoa are reported on by Van Hoven *et al.* (1988) and Obanda *et al.* (2008).

Conservation IUCN Category: Near Threatened (*Ceratotherium simum cottoni* – Critically Endangered A2abcd; B2ab(i,ii,iii,v); C1+2a(i,ii)b; D; E). CITES: Appendix I (excluding populations from South Africa and Swaziland, which are on Appendix II).

White Rhinos lived in abundance alongside indigenous peoples in southern Africa. The Zulus did not regard their flesh as edible and so did not hunt them. Only when white adventurers arrived with guns, and rhino hide and horns became a trade commodity, did the situation change. Animals were easily found by waiting at waterholes in the dry season, so that some hunters killed nearly 100 within a single year. Within about 50 years the southern subspecies was reduced to the verge of extinction. The last animals were shot in Botswana during the late 1870s and in Zimbabwe in 1893 (see Rookmaaker 2003b). A remnant pocket of White Rhinos surviving near the Umfolozi R. in South Africa was given legal protection when the Umfolozi G. R. was

proclaimed in 1897. A few individuals persisted in a remote region of Mozambique until the 1930s, when the last individuals were shot.

The first conservator claimed that only 20 White Rhinos remained in the then Umfolozi G. R. when he arrived in 1911. This was almost certainly an underestimate, because the first counts made around 1930 indicated a total population of over 200. Rookmaaker (2002) suggests that there were never less than 200 White Rhinos in Zululand before 1929. However, a founding remnant of 20–50 animals at the beginning of the twentieth century would be consistent with the subsequent population increase (Emslie & Brooks 2002b).

All surviving White Rhinos of the southern subspecies are derived from this remnant. Under protection the White Rhino population grew to reach about 550 in 1948, and about 1800 by 1968 (Emslie & Brooks 1999). Concerned by the risks associated with this single population, the then Natal Parks Board began trials on live capture using drugged darts in 1961. By 1970 a total of 730 White Rhino had been translocated to other parks, but 2000 animals still remained within the enlarged Hluhluwe–iMfolozi complex. The new concern was overpopulation within the now fenced confines of the protected area, which led to the study by Owen-Smith (1973). The immediate management response was an accelerated capture and removal programme, aimed at reducing the population below this high level, restocking the species through its former range, and supplying animals to various zoos (and see Player 1972).

The ecological recommendation from this research was to restrict White Rhino removals to designated dispersal sinks, or vacuum zones (Owen-Smith 1973, 1974, 1981). The aim was to allow the core population to adjust naturally to changing food resources while providing a safety outlet within the fenced area. This policy was eventually put into effect in 1985, but following several adjustments to the sink locations only became properly effective in 1998. Animals of suitable age classes and reproductive status settling within the sink areas are captured and offered for sale annually.

By December 2010, Southern White Rhino numbers stood at an estimated 20,160 (Emslie 2011), up from 6784 in 1993, 7532 in 1995, 8441 in 1997, 10,377 in 1999, 11,640 in 2001, 11,320 in 2003, 14,550 in 2005 and 17,475 in 2007 (Emslie & Brooks 1999, Emslie 2004a, Emslie *et al.* 2007, Milliken *et al.* 2009). The small drop between 2001 and 2003 does not reflect an actual decline in numbers as the difference is due to a lower population estimate for the biggest population (Kruger N. P.). There is no evidence of any actual decline in this park, and the difference is almost certainly an artefact of the sampling variability inherent in the method used to estimate numbers for this large population. Kruger's rhinos are descendants of just 336 founder animals (D. Pienaar pers. comm.). As of December 2010, South Africa held 93% (18,796) of the wild White Rhino population, predominantly in Kruger N. P. (10,500 animals) and Hluhluwe–iMfolozi Park (2312). While the state-run conservation agencies continue to manage most of the White Rhinos in Africa (72%), the private sector also manages a significant proportion (5504, 27%) with likely in excess of 5000 White Rhinos on private land in South Africa (AFRSG data unpubl.).

Around 1960–62, Garamba N. P. and surrounding reserves in NE DR Congo contained more than 1200 Northern White Rhinos, before armed rebels and others reduced the population to 100–200 during the rebellion following independence (Bourliere 1965, Curry-Lindahl 1972, K. Hillman Smith pers. comm.). White Rhinos increased again to about 500 in 1976 (Savidge *et al.* 1976), but between then and

1984 poaching for rhino horn reduced the population by 97% to just 15 animals (five adult ♀♀, six adult and one subadult ♂, and three juveniles) in the southern third of the park (Hillman Smith 2006). The Garamba Project was started in 1984, supported by a coalition of donors, and under protection the remnant population doubled to 30 by 1992 (0.015/km²), but following an upsurge in poaching from mid-2003 (11 carcasses were found in a three-month period between Mar and May 2004 alone), surveys counted only four individuals in the park and up to another four in an adjoining hunting area (Hillman Smith *et al.* 2003, Hillman Smith & Ndey 2005). Given the critical situation and unsustainable levels of poaching, an emergency plan to temporarily translocate five animals to a Kenyan sanctuary was developed, but this was not implemented due to internal political reasons. A survey in 2006 (Emslie *et al.* 2006) only counted two rhinos with another two different animals being seen subsequently. In recent years, there have been no signs or sightings of animals (one carcass was found in 2008), and it is feared this population is now extinct. Until the 1970s, White Rhinos were reportedly seen by hunters in E Central African Republic and S Chad, but their continued existence there seems unlikely. Fewer than 300 were estimated to occur in S Sudan in 1981, but this population also seems now extirpated (Hillman Smith 1981). The species became extinct in Uganda by 1982 (Edroma 1982).

CITES has downlisted South Africa's, and more recently Swaziland's, White Rhinos from Appendix I to Appendix II, allowing limited trade in live animals although not in products like horns. Hunting is permitted under strictly controlled conditions. Whether international trade in rhino horns should be allowed in order to generate funds to conserve this and other rhinoceros species effectively remains highly contentious, especially in the context of the hugely escalated illegal trade through 2009–12, due to rising demand particularly in Vietnam. In 2011 alone, around 450 individuals were killed by poachers, about half in Kruger N. P. Unless effective counteraction is implemented, further escalation of the killings could lead to a down-turn in the population trend of the species and reverse the conservation gains of the past.

Although captive breeding of Southern White Rhinos has been successful (but see Swaisgood *et al.* 2006), especially where a number of animals were held in large enclosures, captive reproduction of Northern White Rhinos has been less so. Emslie & Brooks (1999) noted the last birth among nine individuals held in two zoos had taken place in 1989 (Dvur Kralova in the Czech Republic, and at San Diego Zoo in the USA). At the time of going to press, the last four potential breeding animals from Dvur Kralove Zoo in Czech Republic had been introduced to a private reserve in Kenya. The animals are all related and the ♂♂ are very old, and the best that probably can be hoped for is to conserve some adaptive Northern White Rhino genes by inter-crossing with the southern subspecies. As of December 2005, there were more than 750 of the southern subspecies in zoos worldwide (Emslie *et al.* 2007).

Measurements

Ceratotherium simum simum

HB (♂♂): 3710 (3620–3800) mm, n = 3
 HB (♀♀): 3480 (3370–3630) mm, n = 5
 T (♂♂): 870 (700–1200) mm, n = 3
 HF: n. d.
 E: 250 mm*
 Sh. ht (♂): 1740–1850 mm*

Sh. ht (♀): 1710–1770 mm*
 WT (♂): max. 2300 kg*
 WT (♀): max. 1700 kg*
 KwaZulu–Natal, South Africa (Owen-Smith 1973)
 *Sample number and range not given

Ceratotherium simum cottoni

HB (♂♂): 3660 (3590–3750) mm, n = 4
 HB (♀♀): 3120 (2990–3220) mm, n = 4
 T: 670 (610–740) mm, n = 5**
 E (♂♂): 320 (280–340) mm, n = 3
 E (♀♀): 300 (270–340) mm, n = 7
 HF: n. d.
 Sh. ht (♂♂): 1730 (1630–1820) mm, n = 3
 Sh. ht (♀♀): 1530–1770 mm, n = 3
 WT: n. d.
 Garamba N. P., DR Congo (K. Hillman Smith pers. comm.)
 **Sexes combined

Body length increases with age and approaches an asymptote at around 14 years, but chest girth only attains an asymptote at around 20 years (Rachlow 1997)

Skull and horn measurements:

Ceratotherium simum simum

Anterior basal circumference (♂♂): 730.4 ± 65.0 mm, n = 65
 Anterior basal circumference (♀♀): 610.0 ± 34.4 mm, n = 39
 Anterior horn length (♂♂): 583.4 ± 141.9 mm, n = 72
 Anterior horn length (♀♀): 589.4 ± 98.0 mm, n = 107
 Anterior horn WT (♂♂): 6.1 ± 1.8 kg, n = 91
 Anterior horn WT (♀♀): 4.0 ± 1.5 kg, n = 33
 Posterior horn WT (♂♂): 2.2 ± 1.1 kg (n = 69)
 Posterior horn WT (♀♀): 1.2 ± 0.7 kg (n = 19)
 Kruger N. P., South Africa (Pienaar *et al.* 1991, Pienaar 1993)
 Anterior horn length (♂♂): 640 (620–660) mm, n = 4
 Anterior horn length (♀♀): 720 (620–820) mm, n = 5
 Posterior horn length (♂♂): 310 (270–390) mm, n = 3
 Posterior horn length (♀♀): 200 (160–260) mm, n = 5
 KwaZulu–Natal, South Africa (Owen-Smith 1973)

Ceratotherium simum cottoni

Anterior horn length (♂♂): 650 (560–740) mm, n = 4
 Anterior horn length (♀♀): 540 (480–590) mm, n = 4
 Posterior horn length (♂♂): 195 (143–235) mm, n = 4
 Posterior horn length (♀♀): 194 (180–210) mm, n = 4
 Garamba N. P., DR Congo (K. Hillman Smith pers. comm.)

The record length for the Southern White Rhino is an animal from South Africa which had a front horn measuring 1581 mm; its accompanying rear horn was 566 mm. For the Northern White Rhino, the record front horn length is 1273 mm and 559 mm for the rear, for an animal from East Africa (Selous 1899).

Key References Emslie & Brooks 1999, 2002a, b; Meister & Owen-Smith 1998; Owen-Smith 1973, 1975, 1988; Pienaar *et al.* 1991, 1993a, b; Rachlow *et al.* 1999; Shrader & Owen-Smith 2002; White *et al.* 2007.