

The Behavior Guide to African Mammals

Including Hoofed Mammals,
Carnivores, Primates

6640

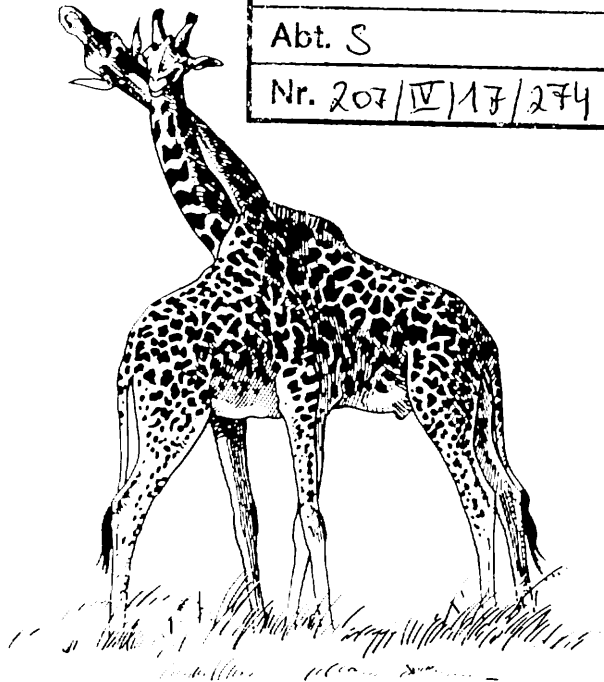
Richard Despard Estes

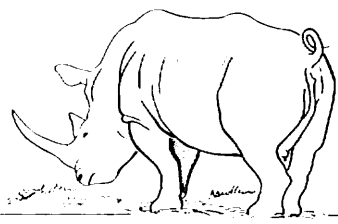
Drawings by Daniel Otte

Foreword by E. O. Wilson

Tiergarten Schönbrunn BÜCHEREI
Abt. S
Nr. 207/IV/17/274

1991





Rhinoceroses

Family Rhinocerotidae

African Species

Diceros bicornis, black rhinoceros
Ceratotherium simum, white rhinoceros

FAMILY TRAITS. Graviportal form typical of massive (and mostly extinct) mammals: vertebral column a girder balanced on the forelegs, with the head counterbalancing the body weight and the hindlimbs providing the main propelling force, the wide-set, pillarlike limbs and 3-toed feet making a firm foundation (6, 7). Head rather turtle-like, ending in beaklike snout (all except white rhino); small, puffy eyes low on the cheeks, and wrinkled skin. *Teeth:* massive molars and premolars adapted for grinding coarse vegetation, no incisors or canines in African species. *Horns:* not composed of modified hairlike fibers but of keratin, like true horn, though lacking a bony core and unattached to the skull, resting on nasal- and frontal-bone pedicels, continually growing (7). *Skin:* thick and hairless except for ear fringes and stiff bristles terminating the long, thin tail. *Coloration:* uniform gray to dark brown. Testes internal and penis recurved to rear (like hippos). *Scent glands:* none described in African species except possible preputial gland in white rhino (1). *Mammæ:* 2. Brain comparatively small; longevity 35–50 years.

Senses: weak eyesight, hearing and smell both acute.

ANCESTRY. The ponderous, armor-plated rhinoceroses look like relics of a bygone age. Of a diverse group once found throughout Eurasia, North America, and Africa, with over 30 different genera in the fossil record, only 3 genera and 5 species survived into modern times. All except the well-protected white rhino now face extinction because rhino horn is literally worth its weight in gold (5). Stemming from

small tapirlike ancestors, the first true rhinos appear in the Oligocene as already large but still hornless terrestrial browsers (2, 3, 4, 6). They reached their peak in the Miocene and Pliocene (table 1.1). The African rhinos belong in a separate subfamily of 2-horned rhinos, along with the Sumatran rhino (*Didermoceros sumatrensis*), the smallest and most primitive of the 3 Asian species. *Diceros*, the direct forerunner of the black rhino, is known from the early Pliocene of Europe, but the white rhino, *Ceratotherium*, the last and most specialized species, is wholly African and known only from the Pleistocene.

BEHAVIORAL SUMMARY. Like other hairless mammals, rhinos are confirmed wallowers. They also dustbathe, rub and scratch themselves against objects, regularly visit salt licks, and readily enter swamps. They can cool off by sweating, too, thereby losing moisture which they have to make up by drinking or by browsing water-rich plants (4). The lips are used to gather browse and grass, taking the place of the incisors. Rhinos sleep soundly, lying on their briskets with legs gathered, sometimes on their sides, or while standing. They alternately feed and rest day and night, being least active and wallowing most often when it is hot. They are generally sedentary and solitary, but the white and also the black rhino are at least semisocial when young, and even territorial bulls tolerate subordinate males. Rhino home ranges are dissected by regularly used trails and scented with dung middens used by both sexes. Territorial bulls also mark by spraying urine (fig. 14.5). African rhinos have much the longest horns, which are employed as stabbing weapons against predators but usually only as staves in encounters with other rhinos (4). The white rhino is far less excitable and dangerous to man than the black rhino. Rhinos make a variety of sounds, from loud puffing snorts of alarm

to high-pitched squeals quite absurd for such behemoths. Both courtship and mating are remarkably prolonged. Gestation lasts 15–16 months and the single offspring remains with the mother 2–4 years.

References

1. Cave 1966.
2. Colbert 1969.
3. Hooijer 1978.
4. Kingdon 1979.
5. Martin and Martin 1987.
6. Romer 1955.
7. Young 1962.

Added Reference

8. Owen-Smith 1988.

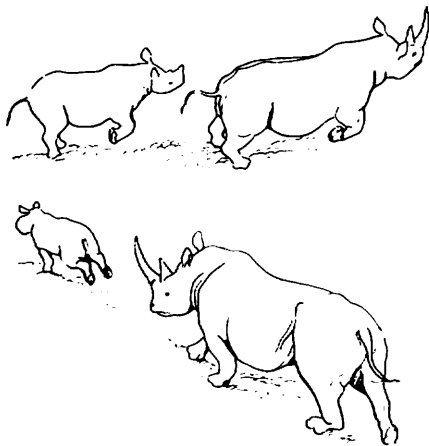


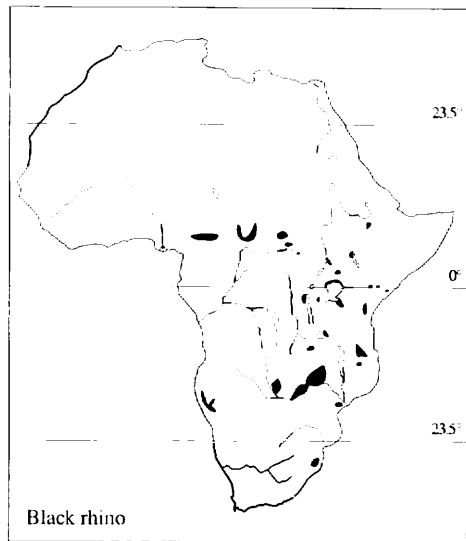
Fig. 14.1. Black rhino calves follow and white rhino calves lead their mothers during flight.

Black Rhinoceros

Diceros bicornis

TRAITS. No taller than a buffalo but twice as heavy: 1.7 m (1.4–1.8), 996–1362 kg (7); females as big but ± 100 kg lighter. **Coloration:** dark gray. **Horns:** extremely variable in shape and length, front horn up to 132 cm, rear horn shorter, more flattened sideways. Upper lip triangular and flexible, used as grasping organ.

DISTRIBUTION. Formerly the most widespread and numerous rhino and a notably successful member of the herbivore community. The range and number of *Diceros* dwindled steadily with the increasing human population. Its decline has been tremendously accelerated in the last decade by poaching to meet demand for rhino horn from Arab and Asian countries (8), and it is rapidly approaching extinction. Yet all it needs is protection: it is actually increasing in the same Zululand reserves where the white rhino lives.



ECOLOGY. A nearly pure browser with a marked preference for leguminous herbs and shrubs, the black rhino eats over 200 plants in 50 different families. Although they can go 4–5 days without drinking by chewing succulents (7, 9), rhinos may travel 8–25 km to water nearly every day (5), and dig for water in sandy riverbeds during droughts (7). When wetlands are available, rhinos frequent them in the dry season. The prehensile upper lip enables *Diceros* to browse selectively, but it uses its molars to take big bites and to eat woody or fibrous plants. The sound of munching carries up to 400 m. The horns are sometimes used as tools to remove bark, break off high branches, and excavate soil at salt licks.

SOCIAL ORGANIZATION: sedentary, overlapping home ranges, females rarely alone, adult males usually solitary and possibly territorial.

This animal is not as solitary and antisocial as commonly portrayed, but instead rather similar to the white rhino. Thus, bulls may tolerate male acquaintances as long as they remain submissive (6). Although cows with calves tend to stay alone, they sometimes allow an unrelated immature male or female to attach itself following rejection by its own mother. Such an attachment may continue to maturity (4). In Ngorongoro, 2 cows associated together for 13 months, and after mating, an adult male and female, her calf, and a subadult male

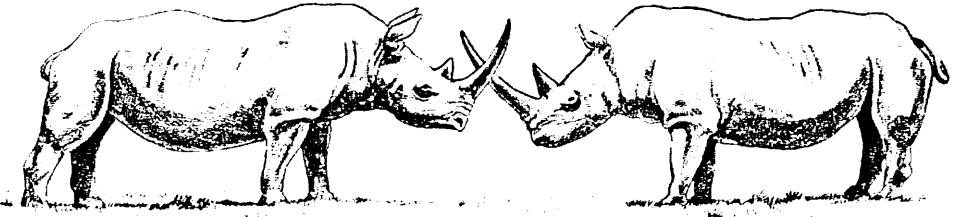


Fig. 14.2. Male black rhinos confronting horn to horn.

stayed together for 4 months (4). Rhinos often associate briefly but amicably when they meet at water holes and salt licks. Up to 13 have been seen in a group (4).

Yet displays of bluff and bluster are typical of black rhino meetings, indicating a degree of tension. An encounter between a bull and a cow is usually marked by *puffing snorts* from either or both. The bull then approaches with cautious steps, head lowered and ears forward, thrashing his head from side to side or rooting the air with his horns. This is pure bluff, for if the cow advances in turn or lunges at him, he wheels and gallops off, only to circle and make another cautious approach. As the preliminary to courtship, this performance may continue for hours and lead to the formation of a tending bond if the female is nearing estrus. Females also approach each other cautiously though less aggressively. They usually end up horn to horn (fig. 14.2) and gingerly nudge heads or joust with their spears, finally separating with evident indifference. Male encounters may be aggressive or peaceful. At least some bulls have overlapping home ranges; meetings on their common ground tend to be peaceful, including gentle head and horn nudging and resting side by side. More often bulls avoid one another after establishing identity through an approach that may include dominance and threat displays. But a resident bull "invariably attacks" when he meets a stranger in his home range (4)—or is it a territory? The question is still unresolved. Black rhinos studied in Natal seemed to be very similar to white rhinos (q.v.): radio-tracked bulls had territories of 3.9–4.7 km², and female ranges were 5.8–7.7 km² (6).

Home range size varies greatly, depending on the habitat and to some extent on sex and age. The average in Ngorongoro was 16 km² (2.6–44) for both sexes (4). But Serengeti rhinos had ranges of 43–133 km² (2). Subadult males wander most widely.

ACTIVITY. Most of the time rhinos do little more than sleep and eat. Like other

wildlife, they tend to be most active early and late in the day and least active at midday. They move about and feed more but also spend time sleeping at night (4, 10). Although they will lie out in hot sunlight, they tend to wallow during the hottest part of the day, smearing mud on both sides and sometimes rolling on their backs.

POSTURES AND LOCOMOTION.
See Antipredator Behavior.

SOCIAL BEHAVIOR COMMUNICATION

Olfactory Communication: scent-marking by *dung-scattering*, *urine-spraying*.

Rhino dung middens are scattered seemingly at random and used by all passersby. The depositor sniffs the pile of dung intently, and may sweep and root it with the forehorn (especially males), then *shuffles* through it stiff-legged before defecating on the same spot. After or less often during the act, the animal scatters its dung by kicking backward in slow motion. Calves have been known to defecate in imitation of their mothers (12). Dung middens undoubtedly serve as message stations, and the odor of the individual's dung is also dispersed on its feet (5). In addition, adult males perform a *urine-marking ceremony*. Using a bush or shrub as a target, the bull backs up and sprays it 2–4 times (fig. 14.5). Sometimes one attacks and demolishes bushes after *urine-spraying* or *dunging* (4, 10).

Vocal Communication: *puffing snorts*, *squealing*, *shrieking*, *grunting*, *groaning*, *mewing*.

Black rhinos produce *puffing snorts* during tense encounters with conspecifics and other species. They also *shriek* like pigs and *grunt* and *groan* when fighting, and females *squeal* while mating. A cow separated from her calf calls it with a high, thin *mewing*. The calf's distress cry, a throaty *squeal*, summons not only the mother but other rhinos on the double.

AGONISTIC BEHAVIOR

Dominance/Threat Displays: *stiff-legged walk* with *lateral presentation*,

dunging ceremony with horn-sweeping, approach with head lowered, ears flattened, eyes rolling, and tail raised, giving puffing shrieks, feinted attack with puffing shrieks and empty horn thrusts.

Defensive/Submissive Displays: confronting aggressor silently in *head-low* (combat) posture, *backing away*, slow or rapid retreat.

Fighting: *jousting* (horn-clubbing) or *stabbing* (rare), with vocalizations [see Vocal Communication].

A resident bull approaching a stranger produces a *screaming groan* with the upper lip curled [3]. Meanwhile the intruder faces him silently with head lowered to defend himself should the other attempt to club or gore him. A bull that turns tail and runs for it is immediately pursued, often for over 2 km. Usually the outsider withdraws slowly and deliberately. The other dominance and threat behaviors appear during encounters between equals, which may lead to or include *jousting*. Fights are likeliest to occur in the presence of an estrous female, but seem rarely to result in serious injury [6].

REPRODUCTION. The black rhino has no strict breeding season. Females mature at c. 7 years, but individuals of 3.8–5.7 years have been known to conceive; males are mature probably by 10, but one 4.3 years of age was seen mating. Gestation is 15–16 months, lactation continues for 1–2 years, and calving intervals range from 2¼–4 years [7, 9].

SEXUAL BEHAVIOR. Male: cautious approach and *urine-testing*, *retreat* and *circling*, dominance and threat displays (*rubbing, jabbing, horn-clubbing, puffing, dunging ceremony*), *nudging* with horn and head, *rubbing muzzle on female's sides and shoulders*, *resting chin on croup*. Estrous female: threat and feinted or real attack, frequent *spray-urination*, *mouthing, squealing*.

A bull that detects a female approaching estrus—by sampling her urine with a pronounced *grimace* (fig. 14.3)—becomes her consort and begins the time-consuming process of conditioning her to accept contact and eventually copulation (see white rhino account, fig. 14.7). When a cow is finally in full estrus, the bull begins a series of *preliminary mounts without erection* which may be repeated for several hours, interspersed with bouts of feeding and walking. Copulation lasts for about ½ hour, during which the cow stands quietly, sometimes emitting a *low-pitched squeal* and



Fig. 14.3. Male black rhino *testing* female's urine.

making *mouthing expressions*. A female may mate with several different bulls during a 3-day estrus.

PARENT/OFFSPRING BEHAVIOR.

In the 1 published observation of a wild birth, the calf was dropped within 10 minutes of becoming visible, while the mother stood [7]. She then removed the birth sac and the calf stood within 10 minutes. Before and after calving, females are particularly irritable, and at this stage the previous offspring, by now 2½–3½ years old, is driven away and may seek a substitute companion. Calves follow very closely (fig. 14.1) (cf. white rhino) and in case of alarm companions press their rumps together and face outward. Calves rarely have peers to play with, but have been seen tossing vegetation and picking up sticks [1].

ANTIPREDATOR BEHAVIOR: *puffing snorts, distress squealing*, mock and real charges with *stabbing, flight with tail raised*

A mother has been seen to kill a lion that tried to take her small calf, but mothers may also ignore attacks on their offspring until alerted by the calf's squeals. Despite their bulk, rhinos can gallop at 50 kph and turn in their own length [7]. When given advance warning of danger—by the chirring of attendant oxpeckers, scent, or noisy movement—rhinos will usually make off at a fast trot, tail curled over the back and head high.

References

1. Frame 1971.
2. ——— 1980.
3. Goddard 1966.
4. ——— 1967.
5. ——— 1970.
6. Hitchens 1968, 1969.
7. Kingdon 1979.
8. Martin and Martin 1987.
9. Owen-Smith 1984b.
10. Schenkel 1966b.
11. Schenkel and Schenkel-Hulliger 1969.
12. Spinage 1962.

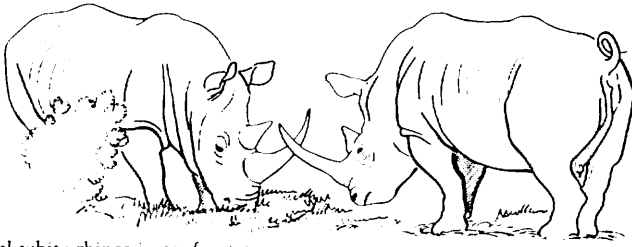


Fig. 14.4. Territorial white rhinos in confrontation

White Rhinoceros

Ceratotherium simum

TRAITS. The biggest land mammal after the elephant (but outweighed by hippo). *Height and weight:* 171–183 cm; males 2040–2260 kg, females average 1600 kg (4). Twice the bulk of the black rhino with proportionally longer, larger head, wide, square mouth, large ears, and pronounced hump. *Horns:* average c. 60, maximum 150 cm. *Coloration:* slate gray to yellow brown. *Scent glands:* preputial papillae with possible olfactory function (1).

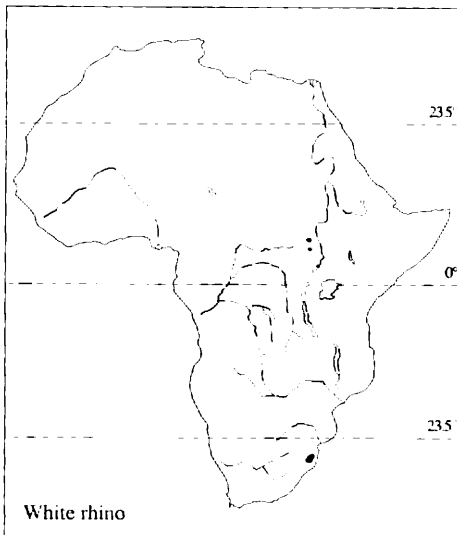
DISTRIBUTION. Widely distributed in the Northern and Southern Savanna within human memory (cave paintings), this species has been in decline for centuries because of failure to adapt to human predation and space competition (see black rhino, map). The southern population was wiped out by early in this century except for a few hundred in Natal. The northern

population (*C. s. cottoni*), which ranged west of the White Nile in Uganda, Zaire, Central African Republic, and southwestern Sudan, has been virtually exterminated within the last few years, following civil wars and general chaos in these countries. Fortunately the approximately 2000 white rhinos in Natal's Umfuluzi and Hluhluwe Game Reserves have produced a surplus, which has gone to restock parks within (and outside) the species' former range (7).

ECOLOGY. Possibly the largest pure grazer that ever lived, this bulk feeder has a wide, square mouth which enables it to graze most efficiently in dense swards of short, green grass (cf. hippo) (4, 8). Good habitat includes trees and ample water as well as open grassland. It often drinks twice daily but can go 2–4 days without drinking if water is distant. White rhinos near the White Nile used to concentrate in wetlands during the dry season and migrate at least 10 km inland to higher ground during the rains (2).

SOCIAL ORGANIZATION: sedentary, semisocial, territorial and satellite males.

Adult females live in overlapping home ranges which encompass 6–7 territories averaging 1.65 km² (0.8–2.6). Females and subadults are rarely solitary. They associate in pairs, typically a female with her most recent offspring. A juvenile rejected at 2–3 years when the mother calves again seeks another companion, preferably of the same age and sex, but may attach itself transiently to another cow with calf. A calfless cow will tolerate 1 or more juvenile substitutes, and 2 calfless cows may join forces. Stable herds of up to 6 head can be formed in this way; larger groups, of up to a dozen, represent temporary aggregations, especially during midday heat when white rhinos sleep on breezy ridges. Adult females rarely permit any individual except their partners to come closer than several meters, but the



young are less standoffish and often engage in horn-wrestling.

Unlike cows and adolescents, adult bulls are basically solitary. Except to check the females' urine, they associate only with those in estrus. In Natal, all available range is partitioned into territories held by only $\frac{1}{3}$ of the mature bulls, whose average tenure is 3 years. Perhaps because dispersal is prevented by fences, the other $\frac{2}{3}$ live as satellites on the territories. One or occasionally 2–3 satellite bulls reside within a particular territory whose owner becomes conditioned to their presence to the point of ignoring them, as long as they behave submissively (cf. black rhino, waterbuck). The fact that territorial bulls treat nonresident intruders far more aggressively promotes the residency arrangement.

SOCIAL BEHAVIOR COMMUNICATION

Olfactory Communication: *dunging ceremony, urine-spraying, scraping.*

A territorial male maintains 20–30 dung middens where he always defecates, scattering and excavating the pile with slow, ritualized kicks before and after. Females and young, and nonterritorial males, add their deposits but without kicking. Only territorial males spray urine and only while on territory. First the bull *horn-wipes* a bush or the ground, then *scrapes* with all 4 feet, then *sprays* this spot 3–5 times (fig. 14.5). Patrolling bulls *urine-mark* about 10 times an hour. They also pause to *scrape-mark* their paths every 30 m or so. Marking is most concentrated along territorial boundaries (4, 5, 6).

Vocal Communication. These are sounds commonly made by the white rhino.

Panting: a contact call common in groups, for example, by a calf that has lost visual contact with its mother.

Whining: juvenile begging call.

Squeaking: calf in distress.

Gruff squealing: chasing.

Snarling: defensive/submissive, grades into a shriek at highest intensity.

Chirping: a peculiar sound made by a rhino fleeing from an aggressor.

Hic-throb: male lovesong.

Loud wailing: by a courting male trying to prevent a female's departure.

Gasp-puffing: fright (alarm).

AGONISTIC BEHAVIOR

Dominance/Threat Displays: *silent approach with head raised and ears cocked, standing horn to horn and staring at opponent, horn-to-horn blow, feinted attack, wip-wip horn on ground.*

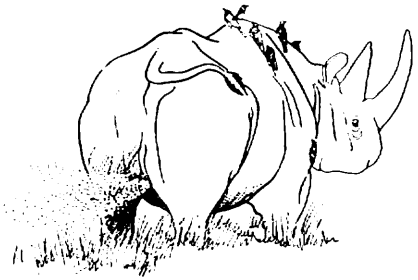


Fig. 14.5. Territorial male white rhino *spraying urine.*

Defensive/Submissive Displays: *head down and forward with ears back, snarl-threat/shrieking, feinted attack, backing away, flight.*

Fighting: *horn-fencing, shouldering, horn-thrusting (very rare).*

Aggression is rare and mild except on the part of territorial males. The owner examines the credentials of every rhino he meets on his land, approaching in the dominant manner described until within olfactory and visual range. Except for small calves, all—including passing territorial males forced to go to distant water holes—respond with defensive/submissive behavior (fig. 14.6). Females and adolescent males are seldom molested, but older males, particularly nonsatellites, often have to sue loudly for peace. The territorial bull continues his approach until he is *standing horn to horn* with the interloper and may then simply *stand staring* at him. Or he may *bang horns*, which the latter parries to the accompaniment of *trumpeting shrieks*, while *backing away*. Sometimes subadult and young adult bulls will make a break for it, but slower adults thereby invite pursuit and expose their rears to a stab from the extremely dangerous front horn. It is safer to face the danger and even to bluff an attack, but meanwhile screaming for mercy.

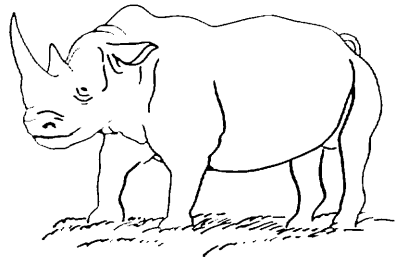


Fig. 14.6. Submissive posture (with ears back) of a male white rhino responding to threat behavior of a territorial male.

When territorial bulls meet at the border, both assert dominance (fig. 14.4). One may fake a charge by trotting up with lowered head, checking at the last moment, but usually they both walk up with heads raised and *stand horn to horn staring at each other*. Next they *back away* and *ground-wipe* with the front horn, *readvance*, *back up*, and so on. Sometimes they *clash horns* briefly. After interacting for anywhere from a few minutes to over an hour, both bulls *back off* one last time, turn, and go their separate ways, often after *scraping* and *urine-spraying*. A territorial bull that is caught trespassing lets himself be walked backwards by the owner until he reaches the boundary, whereupon he asserts his rights in the usual way. One of 2 serious fights that were seen in a 3-year study occurred when the trespassing neighbor refused to kowtow but chose to fight his way home across the owner's whole territory. Most of the time the combatants fenced slowly with raised heads, but occasionally one tried to get under the other's guard by suddenly dropping his head and *stabbing* upward. The resident bull succeeded several times in *goring* his rival in the head, shoulders, and body (5). Attempts to take over a territory or to head off an estrous female as she is about to enter a rival's land are likeliest to provoke serious fights. However, 2 of 3 observed changeovers came about without a long fight. Interestingly enough, each of the defeated bulls remained on his property, simply changing to the status of satellite male.

REPRODUCTION. Females calve for the first time at 6½–7 years, after a 16-month gestation. There is a conception peak early and a calving peak late in the rains in Natal (4). Estrus cycles occur at monthly intervals.

SEXUAL BEHAVIOR: *hic-throbbing* call, *urine-testing*, *following*, *chin-on-rump resting*, *preliminary mounting*. Estrous female: frequent urination, *mock charges* and *threat-snarls*, *curling tail* and *standing* for copulation.

Bulls make *hic-throbbing* sounds when approaching cows, only to be driven backward by *mock attacks*. When the urine test reveals a cow approaching estrus, the territorial bull begins a protracted courtship lasting from 5 to 20 days, during which he shows remarkable restraint. Apart from heading off any attempt to quit the premises (blocking the way and *chasing*, while *squealing*), he keeps the distance set by the female (5–30 m) until she comes into full estrus. Stimulated

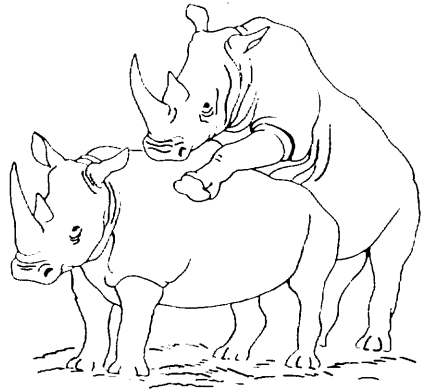


Fig. 14.7. Male white rhino mounting female.

by her urine, he comes closer, crooning his lovesong, but retreats each time she threatens and even puts up with interference by her calf or juvenile companion. Eventually the cow allows him to *rest his chin on her rump*, followed a little later by *attempted mounting*. Finally, after 15–20 hours of persistent approaches, the female *stands with tail curled* during the half-hour copulation (fig. 14.7). The consortship usually continues another 2–5 days, even though repeat copulations are the exception (5).

PARENT/OFFSPRING BEHAVIOR.

Cows seek seclusion in dense cover before and for several weeks after calving. Calves can stand within an hour but remain wobbly for a couple of days. Within a month the cow resumes her normal routine and range, always closely accompanied by the calf, which moves in front but responds immediately to the mother's changes of direction. During flight the calf gallops ahead and the mother follows close on its heels (up to 40 kph) (fig. 14.1). The calf suckles on demand for 2–3 minutes or until satisfied, and begins grazing at 2 months. Weaning occurs at 1 year (4, 7).

ANTIPREDATOR BEHAVIOR. There are few reports of predation on the white rhino. Only calves are vulnerable to hyenas and lions, and the close maternal bond insures that the young are well-protected. When alarmed, companions press their hindquarters together and face in different directions. The white rhino has only 1 enemy: man. Unfortunately that is 1 too many.

References

1. Cave 1966.
2. Foster 1967.
3. Kingdon 1979.
4. Owen-Smith 1973.
5. ——— 1974.
6. ——— 1975.
7. ——— 1984b.
8. ——— 1988.