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Diceros bicornis. By A. K. Kes Hillman-Smith and Colin P. Groves

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Diceros Gray, 1821

Diceros Gray, 1821:306. Type species Rhinoceros bicornis Linnaeus, 1758, by monotypy.

Opisoceros Gloger, 1841:125, xix. Type species Rhinoceros bicornis Linnaeus, 1758, by subsequent designation (Thomas, 1911).


Colobognathus Brandt, 1878:51. Type species Rhinoceros bicornis Linnaeus, 1758. Proposed as a subspecies of Aetelodus Pocatell, 1853.

CONTEXT AND CONTENT. Order Perissodactyla, Suborder Ceratomorpha, Family Rhinocerotidae, Subfamily Rhinocerotinae, tribe Dicerotiini. The tribe contains one other genus, Ceratotherium. The genus contains one extant species, D. bicornis.

Diceros bicornis (Linnaeus, 1758)

Black Rhinoceros

Rhinoceros bicornis Linnaeus, 1758:56. Type locality “India”; corrected to the Cape of Good Hope, South Africa (Thomas, 1911:144).

Rhinoceros africanus Blumenbach, 1797:126. Type locality “Cape of Good Hope.”

Rhinoceros keelto Smith, 1836:44. Type locality “Mafeking, Transvaal.” South Africa; Stead (1973) says Zeerust District.

Rhinoceros gordoni Lesson, 1842:159. As “variety” of R. bicornis. Type locality, “Sources of Gamka River, Cape Province,” South Africa.

Rhinoceros bruci Lesson, 1842:159. Type locality “Bahr Homran, Ethiopia.”


Aetelodus bicornis, varieties plesioceros, porrhoceros and platyoceros Brandt, 1878:51. No localities given; discussed by Rookmaaker (1983b).

Rhinoceros bicornis holmwoodi Selater, 1893:517. Type locality “Chudula, situated at the N.E. point of Usukuma, 50 miles S. of Speke Gulf,” Tanzania.


Opisoceros occidentalis Zukowsky, 1922:162. Type locality “Kasokoveld, Namibia.”

Diceros bicornis punyana Potter, 1947:385. Type locality “Hluhluwe Game Reserve, Zululand, South Africa.” (Meester et al. 1986 attribute this name in error to “Potter & Mitchell.”)

Diceros bicornis longipes Zukowsky, 1949:16. Type locality “Mo- um, Chad.”

Diceros bicornis angolensis Zukowsky, 1965:73. Type locality “Virui Waterhole, Mossamedes District, Huila Province, Southern Angola.”

Diceros bicornis chobiensis Zukowsky, 1965:79. Type locality “Kunzi, sources of the Loma, right tributary of the Kuan- do,” Angola.

Diceros bicornis michaeli Zukowsky, 1965:115. Type locality “between Engaruka and Serengeti” [Tanzania].

Diceros bicornis rendili Zukowsky, 1965:122. Type locality “Northern Guaso Nyiro” [Kenya].


Diceros bicornis atabarensis Zukowsky, 1965:141. Type locality “Anseba Valley, Ethioaia” [=Eritrea].


CONTEXT AND CONTENT. Context as above. Recent works include 2–16 subspecies (Groves, 1967; Harper, 1945; Hop- wood, 1939; Zukowsky, 1965). The following seven subspecies are recognized by Groves (1967):

D. b. bicornis (Linnaeus, 1758:56, see above). (africanus Blumen- bach, campertii Schinz, gordoni Lesson, keelto Smith, niger Schinz, are synonyms.)

D. b. bruci (Lesson, 1840), see above. (atabarensis Zukowsky, palustris Benzon, somalensis Potocki are synonyms.)

D. b. chobiensis Zukowsky, 1965, see above.

D. b. ladosensis Zukowsky, 1965, see above.

D. b. longipes Zukowsky, 1949, see above.

D. b. michaeli Zukowsky, 1965, see above. (rendili Zukowsky is a synonym.)

D. b. minor (Drummond, 1876), see above. (angolensis Zukowsky, holmwoodi Selater, major Drummond, nyasae Zukowsky, occidentalibus Zukowsky, punyana Potter, roweae Zukowsky are synonyms.)

DIAGNOSIS. Diceros bicornis (Fig. 1) is a dicerotine rhino- ceros with anterior dentition absent or rudimentary, and occipital crest protruding posteriorly. The jaws and nasals abruptly end not far in front of the level of the anterior premolars; the mandibular

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FIG. 1. Diceros bicornis in Nairobi National Park; subadult male and young.
has a broad, rounded basal portion and a comparatively slender, backcurved stem; the frontal horn is relatively large, its basal portion nearly or completely meeting that of the nasal horn. The black rhinoceros is easily distinguished in the field from Ceratotherium by its shorter head, pointed upper lip, sway-back, and absence of a nuchal hump (Fig. 1). The nasal horn is distinguishable from that of the white rhinoceros (Ceratotherium) by its more rounded anterior contour, especially at the base.

**General Characters.** Variation among subspecies exists for length of head and body, 280–290 cm; height of body, 132–180 cm; girth given in one specimen as 406 cm (Zukowsky, 1965); and body mass 2.199–2.896 kg (Guggisberg, 1966). However, von La Cheverrie (1970) gives means for body mass of 854.6 kg for eight males and 886.8 kg for six females from Hluhluwe, and 1,124.4 kg for 11 males and 1,080.5 kg for five females from Kenya. Denney (1969) gives similarly small body masses. The record length of the nose horn is 135.9 cm. Horns are longer in females in general with the posterior horn being relatively larger in females than in males in Kenya [length of nasal horn = 2.00 × length of frontal horn + 7.44 (r = 0.804) in males, but 0.98 × length of frontal horn + 14.34 (r = 0.655) in females (Freeman and King, 1969)]. The record length of the frontal horn is 81.6 cm obtained from a specimen of the common Kifia variety with the frontal horn longer than nasal (Best et al., 1962). Desert rhinoceroses, D. b. minor from northern Namibia, often have very long frontal horns, sometimes at least as long as the nasal (B. Loutit, pers. comm.). Occasional individuals with long horns, such as in Amboseli, Kenya, have horns in which the basal portion only is upright, the stem points forwards, and the tip turns slightly up again. Three-horned and fivehorned specimens are known (Guggisberg, 1966; Neville, 1927). Mean mass of horns collected in Tsavo, Kenya, between 1964 and 1973 was 1.84 kg giving a mean mass per rhinoceros of 3.68 kg (I. Parker, in litt.). The relations between various body measurements are: log body mass (kg) = 3.122 log body length (m) + 1.593, r = 0.966; log body mass = 3.87 log of the diameter of the forefoot (cm) + 1.61, r = 0.726 (Freeman and King, 1969).

**Distribution.** The black rhinoceros was originally distributed more or less continuously from Zululand to Somalia (Fig. 3; Sidney, 1965). In Angola D. bicoratus has always been restricted to the southern part; in Namibia it occurs from Kaokoveld and again (discontinuously) from Caprivii; it was once numerous in Ngamiland and the Shashi river district, but did not occur elsewhere in Botswana. In Tanzania, it was always absent from the high plateau and from the southern shores of Lake Tanganyika. In Somalia, it never occurred within 160 km of Berbera (Funaioli and Simonetta, 1966), although the neotype of D. b. somalensis supposedly comes from near Berbera (Zukowsky, 1965). In the Sudan, a century ago it lived on the Eritrean border and as far north as Roseires, Gallabat, and El Damer (7.35°N). In Zaire, it occurred in Shaba as far north as the Luulala–Luapula confluence and slightly to the north; until recently also in northeastern Uele district. It lived in eastern Rwanda, and in eastern and northern Uganda, but not in the west and south; it once occurred in Ankole (Guggisberg, 1966). The giant South African race, which became extinct 100 years ago, lived in southern and western Cape Province, and extended northward into Namibia. Beyond this continuous area of distribution, the black rhinoceros occurred west of the Nile River in suitable areas in the Sudan, in the Wau district (7.43°N, 28°E) and south of Lake Kieklale (100°N, 29°E); along the Bahar-al-Arab tributaries into the Central African Republic (Owen, 1947; Schomber, 1963) in 1915, in the Rumbeke District (Larken, 1947). The distinctive small, long-legged D. b. longipes occurred as far southeast as Fort Crampel, Central African Republic, and went into the Ngoundere District of Cameroon, north to the Lake Chad District and northeastern Nigeria. Further west, there are uncertain reports of black rhinoceroses from Niamey, the northern Ivory Coast, and northern Liberia. The species always may have been localized for habitat reasons: in Zimbabwe there are isolated populations in the Khyber, Mt. Darwin, and Save districts; and in Zambia (Ansell, 1959), there are no records of it in Kabompo, Mt. Mwinilunga, Solwezi, western Bulovale, or Kalabo. In part, some of the sporadic occurrence may reflect the former presence of white rhinoceroses, since in the Sudan the two species seem to be vicarious. Possibly this was the case in southern Africa also, according to dominant vegetation type. It now remains almost exclusively in conservation areas where the degree of protection has been sufficient to counteract a proportion of the poaching (Fig. 3).
FOSSIL RECORD. The genus Diceros is known from the upper Miocene of Europe (D. pachynathus or D. neumayrii) and North Africa (D. douaiensis, D. primaeus—Gerauds, 1966; Gue- rin, 1966; Thenius, 1952). Fossil remains of the extant species are known from Makapanagat (lower Pleistocene or upper Pliocene—Hooijer, 1958) and Hoppegeld (upper Pleistocene—Hooijer and Sing- er, 1960). A larger-toothed, less-hypsodont form occurs at Omo (upper Pliocene). The species does not appear at Olduvai until upper Bed II (ca. 1.2 × 10⁶ years ago), although Ceratotherium occurs throughout (Hooijer, 1969).

FORM. The skin is 13-mm thick on the hind parts, where thickest, but is harder and more callous on the soles than elsewhere (de Bougainville, 1953). The skin is hairless externally in adults, but rudimentary hairs are present in foetuses. Areolae pilosae in absent and large apocrine sweat glands are present (Cave and Am- monier, 1965). There are hairs on the penis skin, but none on the shoulder skin of a fetus and abdominal skin of a juvenile. The abundant apocrine glands are surrounded by highly vascularized myoepithelial cells. The stratum corneum of a juvenile was 100-μ thick and the stratum Malpighi was 18.5-μ thick (Cave, 1969).

The anterior horn may be wrenched off, wholly or partially; if partially, a new horn begins to grow (after ca. 5 weeks), underneath, and the older fibers are not naturally severed (Jacobi, 1957). In the completely shed horn, regrowth occurs at a rate of about 5 cm/year, always with a clear demarcation between inner and outer sets of fibers (Bignall, 1945).

There are two inguinal mammae. Fat content of milk remains at 0.45% throughout, but other elements change from celostrom to milk proper: lactose increases from 4.38 to 6.90%; protein decreases from 6.4 to 1.65%; biotin, vitamin B12, and pantothenate vary; riboflavin decreases; vitamin B6 and thiamine decrease at first, then increase (Greed, 1960; Gregory et al., 1965). At 19 months after birth, the milk contains (in percent) only a trace of fat, 8.10 solids, 1.11 casein, 0.34 ash, 0.06 calcium, 0.04 phosphorus, 0.04 sodium, 0.09 potassium, 0.08 chlorides, and trace amounts of vitamins (Greed, 1960).

The skull is less markedly dolichocranial than Ceratotherium, but the occipital crown is still markedly produced backwards (Fig. 2). The nasals are steep, humped, and abbreviated in front like the premaxillae. There is a broad rugose area on the frontals for support of the posterior horn. The subaural channel remains open throughout life. The mandible has an abbreviated, narrow symphysis; the corpus is robust and heavy; there is no angular prominence; and the ascending ramus is somewhat flattened. The infra-orbital foramen, situated over P3, is often bifid in southern populations, and sometimes in D. b. bruchi and D. b. longipes, but never in East Africa. The articular process is mastoid in form; the lacrimal bridge is osseous in 77% of skulls (Cave, 1965).

The premolar row occupies 39-45% of the whole toothrow. The height of unworn molar crowns is 45-55 mm; a crista is nearly always absent from the molars, but is present on the premolars (especially P3 and P4) in D. b. bicorius, D. b. bruchi, and D. b. longipes, but not in other subspecies. The crocuta is often bifid in D. b. minor and other eastern and southern subspecies; mediofossitess tend to form on those teeth with cristae; the protoloph and metalopli are at right angles to the ectoloph; the parastylo processes but little; the paracone bulge is less prominent; post flossettes become isolated only late in wear (Rookmaaker and Groves, 1978). The metafossil is small, its anterior and antero-external walls forming an angle of 100° (Cook, 1950). Deciduous dentition is described by Hooijer (1958): on DM3 and DM4 the ectoloph has a paracone style, which is absent from DM2, but the metacone is slight; there is no metacone style; the anterior lingulina is strong and horizontal, forming a ledge at the base of the protocone; the postmolar is shallower than the medianus. Permanent P1 typically exists, but may be suppressed by eruption of P2 too far forward. Occasionally, the reverse is true (Schauerte, 1966). Forty percent of a Huilhui sample lack P1; almost all the other East and South African skulls lack it, only D. b. bruchi and D. b. longipes characteristically retain it (Rookmaaker and Groves, 1978). Occasionally skulls are found with small, cylin- drical incisors (Anderson, 1966). Rudimentary mandibular D1 (can- ines?) occasionally occur (a case is figured by Schauerte, 1966), but not as deciduous incisors. deciduous or permanent. Enamel hardness is greater than Ceratotherium, 281 kg/mm² (Schauerte, 1966). Vialli (1955) records a skull with a right DP4, slightly compressed, rotated through 80°.


The brachial index is 84.9; the length of the tibia is 75% of the femur, that of the humerus 96.7% of femur; the length of the tibia is 91.7% of the radius, the length of the forearm is 103.9% of the hindlimb; the length of humerus is 82.8% of the basal skill length, metacarpal III is 46.5% of the radius length; there are subspecies differences in these ratios (Rookmaaker and Groves, 1978). The vertebral formula is 7C, 19–21T, 2–5L (thoracolumbar total 23– 24, 4–5S, 21–22Ca (13 skeletons); but an embryo of this species from Punda Milia, Kenya, had 18T, thoracolumbar total 22 (Davies, 1952). Spines of 7C and 1T are elongated, gradually reducing in height from 1T to 7T; spines of 19T to 3L slightly raised; no anteciliar vertebra.

In a female from Zambia, the heart weighed 6 kg and measured 305 by 280 mm (Wilson and Edwards, 1965); in two specimens of the nominotypical race it was 460 mm long by 460 mm wide and 340 mm by 340 mm (Rookmaaker and Groves, 1978). The brain of a specimen of D. b. bicorius was 16 cm long, 10 cm deep; its volume about one quart (de Bougainville, 1953). The spleen measured 118–120 by 21–45 cm (Rookmaaker and Groves, 1978). Lungs of a Zambian female weighed 7.3 kg (Wilson and Edwards, 1965); in the Cape specimen they were 61 cm long, and both lobes were subdivided, the right one incompletely (de Bougainville, 1953). Nasal cavity is large; its membranes very extensive, covering the whole body when unfolded (de Bougainville, 1953). Viscera amount to 27% of total body mass (Talbot and Talbot, 1964) in an East African specimen and 3.05% when empty, 18.87% when full, in a Zambian animal (Wilson and Edwards, 1965). The esophagus was 91 cm long, the stomach 78.5 by 60.9 cm, the small intestine 11.1 m, the large intestine and cecum 4.5 m, the total being 7 times the head and body length (Wilson and Edwards, 1965) in the Zambian female; in the Cape specimen, the following measurements are quoted by de Bougainville (1953): stomach, 1.2 by 0.61 m; small intestine, 8.03 m long, 15 cm in diameter; cecum, 1.05 m long, 61 cm at base; colon, 2.44 m long, following course of spine then contracting into a rectum 46 cm long and 15 cm thick. The liver in the Zambian animal (Wilson and Edwards, 1965) weighed 14.5 kg and was 5-lobed, measuring 75 by 50 cm, with no gall bladder; in two Cape animals (de Bougainville, 1953; Rookmaaker and Groves, 1978) the liver measured 105 by 75 cm and 78 by 60 cm, with three large lobes and one small lobe which was 30 cm long. These rather remarkable differences may reflect adaptations to different environ- ments, or may be purely individual; further studies should be un- dertaken to estimate ranges of variation in the living populations.

The prepuce is dark; there are no ecrine glands on the penis.
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The basal length of young skulls, with full deciduous complement (hence, presumably about 1 year old), is 40–47% of the adult length when measured by the time M3 begins to erupt. M4 is not until M3 is in wear. Occipital basin length increases with the gradual posterior growth, in normal feral population, being shorter than 10% of the female and 10% in the male; symmetric breadth decreases through the growth phase from 63% of basal length when in deciduous dentition to 58% as M1 begins to erupt, then increases again to 60–61% nasal breadth increases steadily throughout growth period.

Age at first mating in captive specimens varies from 4.5 to 9 years, but age at first fertile copulation is from 6 to 9 years (Jarvis, 1967). In the wild, ages at first copulation along with gestation length vary between populations, tending to increase in higher densities, or under poor conditions: 3.5–5.7 years in East Africa (Goddard, 1970a); 3.5–4 years in Zimbabwe (Thompson, 1971), but from 3 years 10 months to 9 years 1 month in the high density (introduced) population in Addo National Park, Cape Province: the records for the three oldest ages of first calving (mean, 8 years 11 months) were from the time they were at highest density (Hall-Martin, 1986).

Extreme inter-cal intervals recorded were 24–30 months (Thompson, 1971) and 38–39 months (Mukinya, 1975). The longest intervals in Addo are from the time of poorest conditions; the extremes are 2 years, and 9 years 6 months (Hall-Martin, 1986). The captive longevity record is 34 years 14 days. Two others survived 30 years, and several survived >20 years in captivity (Reynolds, 1965).

ECOLOGY. Black rhinoceroses are found in a wide range of habitats from montane forest, through savanna woodland, bush and thicket, medium grassland–woodland ecotones, scattered tree grassland, and semi-desert to desert. Medium to dense cover generally is selected, however, especially during the day. In a mixed habitat, A. K. Hillman (pers. comm.) found that 60% of daytime locations of black rhinoceroses were in areas typified by lateral cover of 50% or more. Hitchins (1969) in Hluhluwe Reserve and Thompson (1971) in Zimbabwe found a direct relationship between density of rhinoceroses and density of habitat, with densities ≤1.7 km² in the thickest habitat in Hluhluwe, which supported 25.7% more black rhinos than the savanna. Goddard (1967) found local densities varying from 0.03 to 1.5 km² in Tsavo depending on habitat and 0.2 km² in Okuavi with 0.3 km² in mixed habitat of Ngorororo. In the open Serengeti, Frame (1980) found densities from 0.02 to 0.05 km².

Black rhinoceroses are browsers on woody shrubs, small trees and certain forbs. Some grass is taken with other things and succulent plants are often selected in the dry season (Mukinya, 1973). Black rhinoceroses have even been observed to approach and feed on a burn (P. M. Hitchins, pers. comm.). In feeding trials, adult intake averaged 23.6 kg of mixed browse per day (A. K. Hillman, pers. comm.).

Goddard (1968, 1970b) recorded 191 species of plants in Ngorororo (Tanzania) and 102 in Tsavo (Kenya) eaten by black rhinoceroses, while Hall-Martin et al. (1982) recorded 111 species consumed in Addo (South Africa). Species used vary with area and season, but certain species of Acacia and Dichrostachys commonly are selected as are nitrogen-fixing legumes. In the extremely arid Damalander in northern Namibia, Loutit et al. (1987) recorded 74 species of plants browsed by black rhinoceroses, concluding that they use a wide variety of available species and shift food selected according to circumstances, and that they are able to use plants that have heavy chemical defenses against most herbivores.

Black rhinoceroses are predominantly solitary, the most commonly observed groups being lone males, and adult females with young. Females without young usually are alone, but may associate with others. Subadults frequently associate with other black rhinoceroses. An adult male and female, with the latter's young if she has one, form temporary associations for mating during the female's estrus. Other aggregations of various ages and genders occur, but usually are temporary. The largest temporary group reported by Goddard (1970a) was of 13.
Hyenas (Crocuta crocuta) and lions (Panthera leo) are known to prey on young black rhinoceroses and some instances of lions attacking black rhinoceroses have been reported (Richards, 1973; Thompson, 1973). Goddard (1970a) reports threat behavior by adults towards lions, and an adult killing a lion in defense of her young, but the main predators of adult black rhinoceroses are humans.

Black rhinoceroses often have a symbiotic relationship with oxpeckers (Buphagus africanus and B. erythrorhynchus). The birds feed on external parasites of the rhinoceroses and by the bird’s more acute eyesight give warning of potential danger. Important and more temporary and associated sometimes occur with cattle egrets (Bubulcus ibis), starlings (Lamprotornis), and drongos (Dicrurus). Black rhinoceroses occasionally have been observed to associate temporarily with buffalo (Syncerus caffer) profiting from the buffalo’s more acute vision (Thompson, 1971).

In many areas black rhinoceroses have skin lesions behind the forelegs caused by filarial parasites carried by the fly Rhinoceros brucei (Richards and Keep, 1970; Sheidrick, 1980). Ticks are common in skin folds, around the anus, eyes, and ears. Many black rhinoceroses also have intestinal infestations of the larvae of Gyrnostoma (C. Dewhurst, pers. comm.). Black rhinoceroses also have blood parasites to which they may succumb if stressed. Anthrax and parasitic anemia have caused deaths, particularly when black rhinoceroses have been moved to other areas or to captivity (Hillman-Smith, pers. comm.).

As sedentary, easy to stalk animals, populations of black rhinoceroses were severely reduced in the south of the range by early colonialists, and the nomotrophic species eliminated; their numbers were also reduced to some extent by conflict with agriculture and loss of habitat. But conservation measures in the 1930s to 1950s, such as the creation of national parks, gave them adequate suitable habitat to support large numbers, until poaching became a major problem. Few indigenous people of Africa placed much traditional value on parts of black rhinoceroses, but a strong pressure to kill them for their horns developed from a demand in the Far and Middle East. Rhinoceros horns were used principally as fever-reducing medicinal agents in the Far East and as a prestigious traditional dagger (Jambii) handle in North Yemen (Martin, 1985). Poaching escalated in the early 1970s, concurrent with, but slightly later than, the rise in ivory poaching. The price of rhinoceros horns rose 2,000% between 1975 and 1979 and the world market then averaged 8 metric tons/year (E. B. Martin, pers. comm., equivalent to over 2,100 black rhinoceroses/year (A. K. Hillman, pers. comm.).

Experiments have shown that injection of aqueous extract of rhinoceros horn (species not stated) in laboratory rats does, in fact, produce a short-lived antipyretic effect; but horn of cattle and buffalo (Bovidae) gives a reaction equal to that of rhinoceroses (But et al., 1962).

In 1969, the black rhinoceros population of Kenya was probably 15,000-20,000 animals. By 1977 there were ca. 2,000-4,000 and in 1979 <1,500, a reduction of 90% in 10 years (Hillman and Martin, 1979), by 1985 the numbers was 500 (according to the African Elephant and Rhino Specialist Group in 1987). In Tsavo National Park alone, between 1969 and 1979 the black rhinoceros population went from approximately 7,000 to 150 (Hillman, 1983). In 1981, there were estimated to be 10,000-15,000 black rhinoceroses in 18 countries in Africa, but of these only five countries had >1,000 individuals (Hillman-Smith, pers. comm.). All black rhinoceroses were distributed in about 78 populations, but 55% of those contained <50 individuals, a situation where loss of genetic heterozygosity could become a problem. Seventy-four percent of the populations (representing 84% of individuals) were decreasing (Hillman, 1983). In 1984 the estimate was down to 8,800 (Western and Vigne, 1985) and in 1987 to around 3,800 in ca. 69 locations (Cumming and Du Toit, 1989). Black rhinoceroses were known to be present in Tanzania, Zambia, Kenya, Zimbabwe, South Africa, Namibia, Botswana, and Botswana (listed in descending order of their 1980 population sizes), while their numbers or even continued existence in Central African Republic, Sudan, Somalia, Angola, Mozambique, Cameroon, Ethiopia, and Chad were in doubt. (Since then a small population has been reported from Somalia: J. Sale, pers. comm.)

The only countries reporting increases in black rhinoceroses since 1980 were South Africa, Zimbabwe, and Namibia. Since 1971 South Africa has been successfully transplanting black rhinoceroses from a high density and increasing population in Umfolozi-Hluhluwe Game Reserve to other protected areas within their range (Brock, 1983). In 1987 Zimbabwe contained 1,760 black rhinoceroses, at that time the largest in any one country, but since then the black rhinoceros in the Zambezi Valley have been subject to severe poaching. In Namibia, poaching of black rhinoceroses in Damaraland in 1989 prompted the first application of the conservation measure of de-horning (Hillman-Smith, pers. comm.).

Since 1979 there has been continual international action to try to slow decline. These have largely been coordinated through Conservation Action Plans drawn up by the African Rhino Specialist Group of the IUCN/SSC (Hillman, pers. comm.), which then became the African Elephant and Rhino Specialist Group (Cumming and Du Toit, 1989). Cumming and Jackson, 1984), and through National Rhino Conservation Strategies, such as those of Kenya and South Africa. In Kenya this has had to include moving black rhinoceroses into fenced and intensively protected sanctuaries, either within existing national parks or on private land. In South Africa most protected areas are already fenced and controlled and detailed plans for management of populations of black rhinoceroses, with strict criteria for movements, are possible (M. Brooks, pers. comm.).

Most countries that traded in rhinoceros horns have now signed the Convention on International Trade in Endangered Species (CITES) and have been taking steps to implement bans on trading (Martin, 1985). However, since 1986, Taiwan, which, through China, is party to CITES, has emerged as a major entrepot with escalating prices and volumes of traded rhinoceros horns (Vigne and Martin, 1989).

It is unlikely that the black rhinoceros will go totally extinct, but their recent decline has been one of the most precipitous of any large mammal. Many populations have been and are being lost as is much of the previous subspecific variation.

In 1981 there were about 169 black rhinoceroses in captivity, with a sex ratio of 1:1.3, but their numbers were declining at about 7%/year (Lindemann, 1983). Steps have been taken toward interacting the decline and securing back-up populations in captivity. Following the relocation from the Natal Parks Board to zoos and institutions in the USA since 1983, the world captive population was 87 males (38 wild caught, 20 captive born) and 103 females (55 wild, 48 captive born; Lacey, 1987). There were 82 identifiable founders and 49.6 effective founders. Rookmaker (1983a) attempted to estimate the numbers of each subspecies in the captive stock; only D. b. minor, D. b. michaeli, and perhaps D. b. labiatus are represented.

**BEHAVIOR.** Black rhinoceroses are sedentary, remaining largely within their own home ranges. Ranges overlap for all except dominant males, and vary in size with habitat and possibly population density. Goddard (1967) found ranges (in km2) of 1.5 (Tanzania) of: adult males 15.6, females 14.9, immature males 35.9, and immature females 27.4, but with ranges as small as 2.6 in forest with water. In poorer habitat at Olduvai (Tanzania), home ranges were larger: 21.8 for males, and 35.1 for females. Home ranges in Mara (Kenya) were 5.6-22.7 (Mukinya, 1973), and were 43-133 in Serengeti (Tanzania - Frame, 1980). In medium to dense habitat black rhinoceroses adopt ranges of 2-17 after introduction, despite the availability of more unoccupied habitat (Hillman-Smith, pers. comm.). In desert habitat, Loutit et al. (1987) found large ranges shared by a number of individuals, for example, 500 used by two females with young and one mature male. Within overall ranges certain areas may be more frequently used (core areas) and there may be differential use of parts of the range seasonally. Subadults generally have larger ranges than adults, probably as a means of dispersal (Frame, 1986; Goddard, 1967; Loutit et al., 1987; Mukinya, 1973).

As home ranges, even of males, overlap, Goddard (1967) did not recognize territoriality, although he described behavior patterns indicative of territorial defense. P. M. Hitchins (pers. comm.) and Hillman-Smith (pers. comm.) found evidence of similar territoriality to that of the white rhinoceros (Ceratotherium simum), that is, dominant alpha males maintaining territories against other dominant males, but allowing overlap by subordinate males and females and subadults. In excessively arid areas, Schenkkel and Schenkkel-Hulliger (1969) claimed that black rhinoceroses are capable of crossing any trace of territoriality or even regular home ranges. Overlapping, but distinct, home ranges were recognized in arid desert of northern Namibia (Loutit et al., 1987).
Black rhinoceroses are more active, both feeding and walking, in early morning and late afternoon to evening. Although Goddard (1967) reported a rise in activity in the middle of the day, the authors observed that at 1200 h, 70% of the rhinoceroses were inactive (sleeping or standing). His observations and those of Hillman-Smith (pers. comm.) using radiotelemetry indicate that black rhinoceroses usually are active at night, often feeding, drinking, and walking outside their core areas and in more open habitat than during the day. Resting black rhinoceroses usually lie on the sterrum with tails prevailing wind, but stand now and then.

A semi-prehensile upper lip is used to twist round twigs in feeding. Hillman (pers. comm.) found the usual feeding height is 0–1 m, though they can reach >2 m. Small trees are sometimes pushed down by walking over them to make high branches available. Diameter of twigs bitten off were mainly in the range 3–10 mm, but could be ≤30 mm. This gives a high proportion of woody to green material in the diet (Hillman-Smith, pers. comm.).

Offactory communication is important. Like other rhinoceros species, black rhinoceroses frequently defecate in dung piles, and the presence of fresh dung on the piles is thought to indicate to other rhinoceroses who was in the area and when. Adults, particularly males, scrape hind feet in dung which may leave scent on their feet. Goddard (1967) found that a male closely followed a dragged trail of his own dung, and on releases of translocated black rhinoceroses it was found that the spreading of its own dung helped to localize a rhinoceros in an area (Hillman, pers. comm.). Adults, particularly males, spray/urinate on bushes and rocks, scrape hind feet in earth, and rub horns in bushes (complex bull ceremony—Schenkel and Schenkel-Hulliger, 1969).

Ritualized postures are part of direct interactions and sounds vary from the quiet mew between mother and young to loud roars and snorts of aggression (Hillman-Smith, pers. comm.). The female—young bond is strong and the young lies or feeds close to its mother. There are instances of mothers leaving young in hiding when they go to waterholes at night (Thompson, 1971). The young follows close behind its mother when she moves off, unlike the white rhinoceros where the young runs in front. If separated, each calls to the other with high-pitched mews and if the young squeals in distress it may attract other black rhinoceroses as well as its mother. The young usually is forced to leave its mother after 2 or 3 years when she has another calf, or sometimes when she is mated. The subadult may, however, later rejoin its mother for temporary periods of association, especially if it is a female.

Two females usually approach each other cautiously, but with little aggression. On contact they may nudge another with the sides of the head or horn, then usually walk away. The meeting of a male with a female or another male is more likely to be accompanied by aggression, with a stiff-legged, short-step approach, snorting and occasionally pawing or rearing to the front; sometimes attacked by males, particularly at mating (Hillman-Smith, pers. comm.).

When males meet, aggression may be violent but usually the subordinate or visitor to a territory retreats. The resident may attack with head lowered and ears flattened emitting a snarling groan. The anterior horn is used for clubbing or goring the other animal (Goddard, 1967). Ritualized behavior and knowledge of the social hierarchy usually prevents physical conflict, but during translocations where the social order is disrupted aggression may lead to fighting and deaths. This occurred even between females at Addo National Park (South Africa) and in a holding paddock in Etoha National Park (Namibia), where densities through introductions became too high (Hill-Martin and Penson, 1977).

An association between male and female for mating may continue over several days while the female is in estrus. It may be associated with some aggression and chasing, but fights with other males may occur. The male usually trails the female at first,continually testing her urine. Approaches before the female is ready are usually rebuffed with short charges that send the male off in a tight circle. The male may then approach the female in a stiff-legged shuffle and may sweep the ground with his horn. In instances where the female is lying down he may prod her with his horn until she gets up. He may attempt to mount frequently, but she will not stand still until she is ready. They may remain in copula for 30 min or longer, with a number of ejaculations during that time. Mating may be repeated several times a day during the period they are together (Hillman-Smith, pers. comm.).

When alarmed, a black rhinoceros will usually run off with its tail curled, sometimes emitting a series of snorts. If, however, it is only mildly disturbed and cannot identify the disturbance, it may approach, either cautiously or in a rush. Despite their reputation for aggression, most charges by black rhinos are investigatory or a mild threat which is not carried through into an attack. However, if harassed too much, a rhino may charge and inflict damage.

GENETICS. A female that died in Philadelphia zoo had a diploid chromosome number of 84, one of the highest recorded in any mammal. There were 1 pair of large and 3 pairs of small metacentrics; 9 pairs of large submetacentrics; and 13 pairs of longer, 16 pairs of shorter acrocentrics. A small pair of acrocentrics had satellites on the long arms. The X chromosome was not identified (Hungerford et al., 1967). Heinichen (1969) and Ryder et al. (1987) confirm the chromosome number. There is some variation in the number of chromosome arms in D. b. michaeli due to the presence or absence of heterochromatic small arms, revealed under G-banding. A single individual of D. b. minor had heterochromatic small arms of appreciable size only on four chromosomes, a pattern more similar to that of the white rhinoceros (Ryder et al., 1987).

A recurring syndrome seems to be absence of ear pinnae combined with an underdeveloped ear (Guggisberg, 1966). Goddard (1969) records seven males, only one female, with bilateral absence of ear pinnae; the female may have been sired by one of the earless males, whose mother was not earless. Goddard suggests a sex-linked condition. Conversely, an earless calf was seen by Goddard (1969) in Ouduavi, where this character had not been previously recorded. Hitchins (1986) reports that of 21 earless black rhinoceroses examined in Hluhluwe and the Hluhluwe-Umfolozi corridor, only one had no ears and so could have inherited the condition; he attributed the other cases to attempted predation on calves, especially by hyaenas. The three-horned tendency also appears to be genetic, being localized in different parts of Africa (Guggisberg, 1966).

REMARKS. In light of the current threat to the species as a whole, it is considered appropriate to reexamine Groves' (1967) arrangement, which was based on an admittedly small sample, using as many specimens as become available. This is now underway on a cooperative basis by the African Elephant and Rhino Specialist Group (Du Toit, 1987).

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