

Connochaetes gnou. By Wolfgang von Richter

Published 28 June 1974 by The American Society of Mammalogists

***Connochaetes* Lichtenstein, 1812**

Connochaetes Lichtenstein, 1812:152. Proposed as a subgenus of *Antilope*. Type species *Antilope gnu* Gmelin.

Cemas Oken, 1816:727. Type species *Cemas gnu* Oken, 1816:728. Oken's work was ruled unavailable for purposes of zoological nomenclature because it is not consistently binomial (Opinion 417, Bull. Zool. Nomenclature, 14(1): 1-42, 1956).

Catablepas Gray, 1821:307. Type species *Antilope gnu* Gmelin. *Catablepas* H. Smith, 1827:366. Type species *Antilope gnu* Gmelin, by subsequent designation of later authors.

Gorgon Gray, 1850:20; 1851:139. Type species *Antilope gorgon* H. Smith, 1827, a synonym of *Antilope taurina* Burchell, 1823, now known as *Connochaetes taurinus*. *Gorgon* proposed as a subgenus of *Catablepas*, accepted as a genus by Roberts (1951:279), but generally recognized as a subgenus of *Connochaetes* (Ellerman *et al.*, 1953:204; Haltenorth, 1963:104; Ansell, 1968:129).

Butragus Gray, 1872:43. Type species *Butragus corniculatus* Blyth, in manuscript, a synonym of *Antilope taurina* Burchell, 1823.

CONTEXT AND CONTENT. Order Artiodactyla, Suborder Ruminantia, Infraorder Pecora, Family Bovidae, Subfamily Hippotraginae, Tribe Alcelaphini, Genus *Connochaetes* (with two subgenera, *Connochaetes* and *Gorgon*). Subgenus *Connochaetes* has one living and one extinct species.

***Connochaetes gnou* Zimmermann, 1780**

Black Wildebeest or White-tailed Gnu

Bos gnou Zimmerman, 1777:372. Type locality Cape of Good Hope. Ruled unavailable by the International Commission on Zoological Nomenclature (Opinion 257, Bull. Zool. Nomenclature, 5(18):231-244, 1954).

Antilope gnou Zimmerman, 1780:102. Type locality Cape of Good Hope; restricted to Colesberg, Cape Province, by Harper (1940:329).

Antilope capensis Gatterer, 1780:80. Type locality Cape of Good Hope.

Antilope gnu Gmelin, 1788:189. Type locality Great Namaqualand, Cape of Good Hope.

C [atablepas] Brooksii H. Smith, 1827:369, footnote. No type locality designated; based on horn of uncertain identity.

Catablepas operculatus Brookes, 1828:64. No type locality designated.

Bos connochaetes Forster, 1844:392. Type locality Cape of Good Hope.

CONTEXT AND CONTENT. Context noted above under genus. *Connochaetes gnou* has not been divided into subspecies. The synonymies above have been adapted from Ellerman *et al.* (1953) and not all original sources were seen by the author.

DIAGNOSIS. Horns are directed forward and downward before curving up. Back is straight, *tuber coxae* of ilium extends above the back. Color is dark brown to jet black in adult males; tail is long, black at the base, and distally pure



FIGURE 1. Female black wildebeest, age 31 months. Inset view of a head shows the more massive horns of a male, age 4 to 5 years. The facial tuft of the species also is conspicuous.

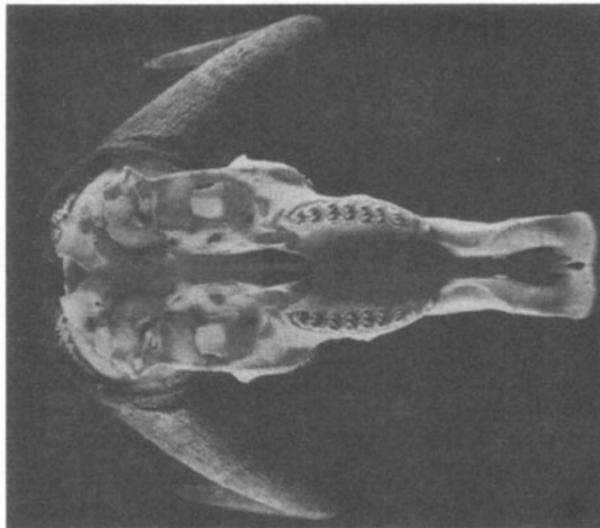
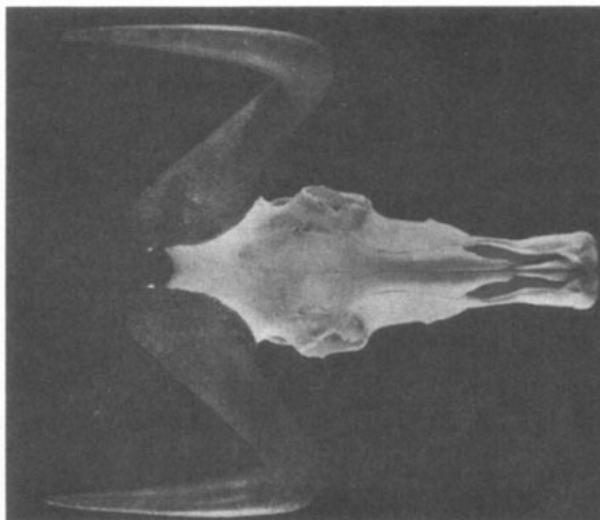


FIGURE 2. Skull of 3-year-old male in dorsal and ventral views. All photographs by T. Marais. Scales are different in the different views.

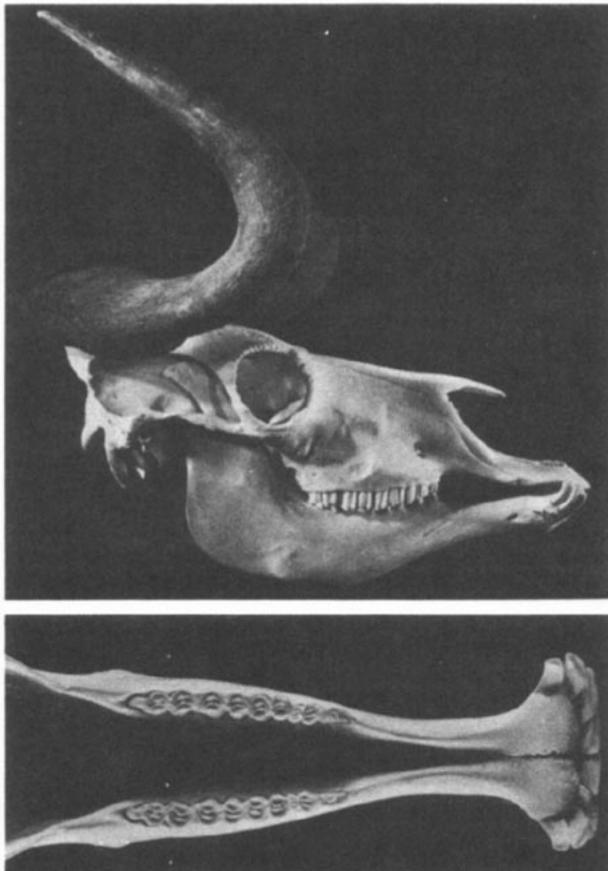


FIGURE 3. Skull of same specimen shown in Figure 3. Lateral view of skull with lower jaw in place, and enlarged view of part of the lower jaw showing well-developed incisors and incisorlike canines used in grazing.

white (figure 1). Face is covered with a large brush-like tuft of stiff hairs. Mouth and eyes are surrounded by long white hairs. Chest bears long mane, shorter at chin and throat. Profile of skull is concave. Nasals and muzzle are short, and orbital rings project prominently. Skull protrudes backward over the condyles. Incisors in their longitudinal axis slant forward (see figures 2 and 3).

There are normally 13 thoracic vertebrae as in *Connochaetes taurinus*. However, Lydekker and Blaine (1914:50) and Oboussier (1970:405) reported specimens with 14 thoracic vertebrae; the latter also collected a specimen with 13 vertebrae in the same population. The number of thoracic vertebrae therefore does not distinguish the two species.

GENERAL CHARACTERS. Detailed descriptions are in Haltenorth (1963:104) and Roberts (1951:278). Horns are present in both sexes; females are lighter and more slender than are males and have smaller horns that do not expand at the base so much as in males, in which they form a kind of massive shield. Calves are born with a shaggy, fawn-colored coat, and the tuft on the face is of soft, curling hair.

Measurements and weights for 17 animals (adults except for birth weights) are as follows (also see Roberts, 1951:579; Haltenorth, 1963:104; and Oboussier, 1970): over-all length, 2.12 to 2.42 m (five males), 2.13 to 2.23 (five females); tail length, .365 to .445 m (five males), .315 to .385 (five females); shoulder height, 1.11 to 1.21 m (five males), 1.06 to 1.16 (five females); weight in captivity, 140 to 157 kg (seven males), 110 to 122 (two females); birth weight, 14 kg (one male), 11 (two females).

DISTRIBUTION. The range of the species in historical times has been limited to the central inland plateau of South Africa, specifically in the present Orange Free State, the highveld regions of the southern, central, and northern Cape Province, the southern Transvaal, and marginally in the grassveld regions of Natal in the foothills of the Drakensberg Range (figure 4). The species also has been recorded from western Lesotho and northwestern Swaziland. The distribution coin-

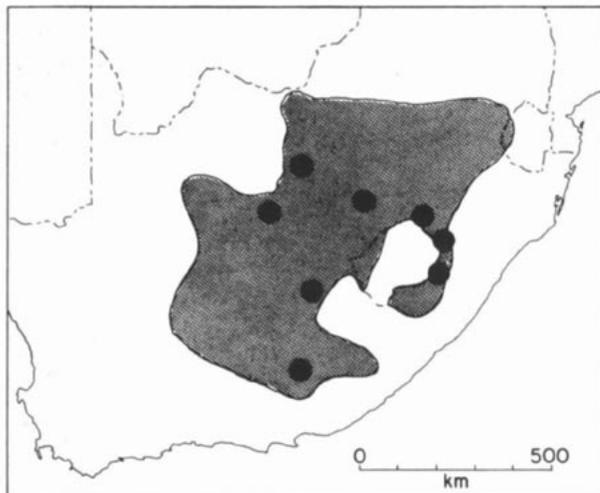


FIGURE 4. The documented historical distribution (stippled) of *Connochaetes gnou* in southern Africa. Major herds now present in National Parks and Game Reserves are shown with black symbols.

cides with the extension of the grassveld and Karoo vegetation types as delineated by Acocks (1953). Records (Sidney, 1965; Shortridge, 1934; du Plessis, 1969) indicating occurrence in bushveld vegetation are considered to be of migrating or wandering individuals and not resident populations, as Karoo or grassveld vegetation occurs adjacent to the reported localities or these are in pockets of Karoo vegetation within predominantly bushveld vegetation. No record of occurrence exists for the species in the Transvaal north of the open grassveld. A detailed discussion of the former range is in von Richter (1971a). By 1900, the species was nearly exterminated by hunting and the reduction of available habitat by European settlers. Through the efforts of some conservation-minded farmers in the Orange Free State and southwestern Transvaal, it was saved from extinction. Six farms in the Orange Free State and one in the Transvaal harbor herds descended from the last wild herds surviving into this century. Most restocking has been from those herds (von Richter, 1971a).

Some herds have been established in areas of ecologically marginal habitat or outside of the former range of the species. These include northern Transvaal and high-altitude reserves in the Drakensberg Range. An attempt at introduction into Zululand failed (Sidney, 1965).

The altitudinal range is between 4000 and 5000 ft (1300 to 1650 m) on the central plateau and between 6400 and 8000 ft (2100 to 2600 m) in the Drakensberg Range. The latter area, however, did not previously support the species throughout the year as it does today, but only during seasonal migrations.

FOSSIL RECORD. *Connochaetes gnou* remains have been reported from the "younger gravels" of the Vaal River deposits (Cooke, 1964) but it is not certain whether they date back to the Cornelia stage (Wells, 1965) of the middle or late Pleistocene.

Connochaetes antiquus Broom, 1913, has been identified from the Florisbad stage (40,000 to 20,000 years BP according to radio-carbon age estimates—van Zinderen Bakker, 1957, as cited in Wells, 1965). The species has horn bases like those of the black wildebeest, but the distal part of the horn is intermediate in splay and curvature between the blue and black wildebeest (Wells, 1965).

Wells (1970) reported that a fragment of a horn core found in the Cradock district could be assigned either to *C. gnou* or *C. antiquus*. He stated that "the difference between these two is not certainly of specific value. A large number of teeth are in the size range of *C. gnou*, but some of these could equally well belong to the Cape Hartebeest (*Alcelaphus caama*)."

Péringuey (1918:3) mentioned finding horn cores of *C. gnou* in sand dunes near Hermanus in the southern Cape. The locality is well outside the recorded range of the species in historical times, and the dominant vegetation, Cape macchia, is quite unsuitable habitat for the species. There is no evidence that the vegetation in the area has changed drastically since the

Pleistocene. However, it is assumed that migrating animals from the Karoo might have wandered that far south.

FORM. Pre-orbital glands, present in both sexes, are simple and cannot be opened at will (Pocock, 1910). The glandular tissue is covered with tufts of long deep-rooted hair, along which the secretion works its way to the surface, impregnating the tufts. Interdigital glands, present only on the front feet, excrete a sticky substance. Inguinal glands are absent.

De Boom *et al.* (1953) picture a cross section of black wildebeest hair. Females possess two mammae. The milk was analyzed by van Zyl *et al.* (1970).

The deciduous dentition is di 0/3, dc 0/1, dp 3/3; permanent dentition is i 0/3, c 0/1, p 3/2, m 3/3; p2 (the first of three lower premolars) is normally absent; molariform teeth are hypsodont and selenodont; incisors are long and broad, the inner two pairs spadelike; the width of crowns decreases from il to c (Haltcnorth, 1963:103).

There are seven cervical, 13 thoracic, six lumbar, four fused sacral, and 16 caudal vertebrae (in five specimens, Department of Zoology, University of Pretoria, and Transvaal Museum, Pretoria). The number of thoracic vertebrae may be 13 or 14 (Lydekker *et al.* 1914; Oboussier, 1970).

Digits 3 and 4 are well developed, whereas digits 2 and 5 form well-developed false hoofs; metapodials 3 and 4 are united and form the "cannon-bone" as in all bovines.

Oboussier (1970) compared the skeleton of *C. gnou* with other Alcelaphini, giving skeletal measurements and proportions of the various regions of the spine and the extremities. The black wildebeest shows the tendency for elongation in the thoracic region. The form, build, and size of the brain as well as the *hypophysis cerebri* is discussed in detail by Oboussier (1970).

ONTOGENY AND REPRODUCTION. A gestation period of 250 to 260 days (being the time between the peak of observed copulation frequency and the peak of calving the next season) for 2 consecutive years corroborates the period of 8 to 8½ months given by Asdell (1964); the species is strictly seasonal in calving but the precise time varies in different localities from the middle of November to the end of December; peak calving takes place after the first rains and is usually completed in 2 to 3 weeks, although individual newborn calves have been observed outside the calving season (von Richter, 1971c). Dittlich (1970) also reported seasonal breeding in captive black wildebeest in European zoos. Twins have not been reported or observed by me. Parturition takes place within the female herds; females in labor do not separate from their herds or choose specific parturition sites; parturition takes place in short grass areas, the preferred habitat of the species. During labor the cows move restlessly around, alternately lying down and getting up. In the last stage of parturition the cow is lying down, but she rises immediately afterward, tearing the umbilical cord. In five observed births the duration varied from 25 to 196 minutes from the appearance of the allantoic sac to the complete parturition. The newborn calves started immediately after birth to get to their feet, an average of 9 minutes (range 6 to 14) elapsing before the calf would stand on its legs. Females occasionally chew on the after-birth but do not eat it. The calf follows its mother as soon as it is able to coordinate movements and stays close to the cow in the first few weeks ("follow-up type," Walther, 1966a). Calves start to nibble on grass blades after 4 weeks and are weaned between 6 to 9 months of age, depending on range condition.

A black wildebeest is born with dil, di2, dc, dp3, and dp4 just protruding through the gums; by the end of week 4 the four front teeth are fully erupted; by week 8 the deciduous dentition is complete; in month 6 the ml appears; and by year 3 all the molar teeth have erupted. The dil is replaced from month 12 onward; all incisors and the canine are replaced by about month 32; and p3 and p4 erupt between month 28 and 30 (von Richter, 1971b).

Calves are born without horns; small knobs appear by week 4 and grow into straight spikes, attaining a length of 200 to 250 mm by month 5; from about month 8 the horns begin to grow in a curve at the base and slightly sideward; in year 3, females nearly reach the final stage of their horn development, whereas males attain the final horn shape between years 4 and 5 (Blaauw, 1889; Mohr, 1965; von Richter, 1971b). Age is correlated with the growth of the mandible, mandibles of females stop growing by about month 30; those of males reach their ultimate length at approximately month 36.

Weight increases were recorded in captive animals in a

2-year period, but were influenced by the conditions of captivity (von Richter, 1971b).

Females may reach sexual maturity between months 16 and 18 and give birth the first time when they are 2 years old. The majority, however, conceive the first time when they are about 28 months old and give birth when 3 years old. Males probably reach sexual maturity at 3 years of age, but only males of 4 years and older can procure a territory and partake in the rut. Under captive conditions a male might mature much earlier as indicated by a reliable report of a 16-month old male serving a cow successfully.

Crandall (1965) recorded a captive black wildebeest as old as 19 years and 7 months, and M. T. Mentis (1972) reported 15 years. Mortality is highest in calves and decreases substantially with age. As all black wildebeest herds are kept in game reserves with no large predators and only a small number of black-backed jackals (*Canis mesomelas*), mortality due to predation is negligible. The observed mortality of 5.3% in one reserve is attributable to separation of cows and calves and is directly related to the size of female herds (von Richter, 1971c).

ECOLOGY. The species was probably preyed upon by all the larger carnivores that once occurred on the highveld: lion, leopard, cheetah, wild dog, spotted hyaena, and probably to a lesser extent also black-backed jackal. Inasmuch as the blue wildebeest is similar in its habitat requirements and behavior, it seems permissible to apply blue wildebeest studies to the black wildebeest as well. Spotted hyaenas (*Crocuta crocuta*) are the chief predators of newly born calves, whereas lions (*Panthera leo*) are the main predators of adult wildebeest (Wright, 1960; Talbot *et al.*, 1963; Estes, 1966; Kruuk *et al.*, 1967; Pienaar, 1969).

In most reserves, the species shares the habitat with blesbok (*Damaliscus dorcas phillipsi*) and springbok (*Antidorcas marsupialis*). These species graze to a large extent on the same plants, but otherwise no interaction was observed. Cattle egrets (*Bubulcus ibis*) sometimes accompany black wildebeest herds. Egrets catch insects disturbed by the movement of the herds and pick insects from the bodies of black wildebeest. Occasionally egrets will perch on an animal and scrutinize the coat for food.

Sporadic outbreaks of anthrax in black wildebeest have been recorded up to 1943 and proved to be fatal (Neitz, 1965). Bovine malignant catarrh causes no apparent symptoms in the species and may be transmitted to domestic cattle. Cumming (1850, as cited in du Plessis, 1969) described the disease in his oxen, when they grazed in close contact with black wildebeest. Black wildebeest have been shown to be susceptible to heartwater (*Rickettsia ruminantium*) but the infection is inapparent (Neitz, 1965). In recent years, however, black wildebeest have succumbed to heartwater in a small reserve in Northern Transvaal (Visagie, personal communication). Rinderpest and foot-and-mouth disease seriously affect blue wildebeest, and probably the black wildebeest also would succumb to those diseases, if infected. Cumming (1850, as cited in du Plessis, 1969) reported the repeated outbreaks of scab or mange in black wildebeest populations, which resulted in large scale die-offs. Bedford (1932), Theiler (1962), Neitz (1965) and Levine *et al.* (1970) list ectoparasites and endoparasites and the incidence of zoonoses in the species.

Brand (1963) reported sex ratio at birth as 103 males to 100 females (63 births), whereas 17 calves out of a total calf-crop of 19 in a reserve resulted in a ratio of 42 males to 100 females in 1963. The sex ratios of adults in the various reserves always favor females, because more males than females have been removed. In one reserve where no animals are being caught, the sex ratio of adults is nearing parity. In the reserves with suitable habitat, the annual calving rate of adult females varies between 75 and 85%; two records indicate an even higher calving success of 92 and 100%. In expanding populations, yearlings and calves amounted to from 41.6 to 44.7% of the total. Three reserves show expanding populations, whereas the populations protected on marginal habitats are at best stable (von Richter, 1971c).

Black wildebeest are predominantly grazers, although they also make use of karoo shrubs; van Zyl (1965) recorded 41 species, which represented 16% of all occurring vegetation; 10 grass species and six karoo shrubs were taken 3 months or more of the year. The preferred habitat is the treeless sweet grassveld savanna and Karoo of the central South African plateau; sour grass species, which mature quickly and become unpalatable are taken only when fresh; short-grass veld is preferred and areas of long mature grass are avoided. The species conditions its own preferred habitat by the ten-

dency of herds to stay for prolonged periods in the same areas, thereby keeping grass in the preferred short stage (von Richter, 1971c).

Prior to European settlement of the range of the species, black wildebeest migrated in both east-west and north-south directions, probably following the onset of the rains and the changing vegetation cycles. Black wildebeest at one time crossed the Drakensberg Range in an easterly direction in autumn in search of better pastures, returning to the highveld regions in early spring and moving westward as far as sweet-grass and Karoo vegetation prevailed. The north-south migration also was induced by the maturing of sour grass species beyond the Vaal River in the north; a detailed account is given in von Richter (1971a). The species is now confined to game reserves and farms and no migration takes place. The tendency of the species to stay for long periods in the same area presents a serious management problem as trampling and overgrazing of the range is common.

Adult males (4 years and older) display territoriality throughout the year and show a strong and lasting attachment to their territories. The territories are smaller when population density is greater. The number of territorial males varies from population to population and is dependent on the available habitat and number of males in the population. The spacing of territorial bulls varies from 180 to 450 m in densely populated areas but can be as much as 1 km in less populated areas.

Female herds occupy home ranges to which they show strong attachment. Home ranges averaged 1 km² in one population. The size of home range is greater when the number of females in a herd is greater, when the quality of range is poorer, or when suitable habitat is readily available (von Richter, 1972).

Only approximately 600 animals survived in 1900. The first census was taken in 1945 (Bigalke, 1947) and yielded 1048 animals; 20 years later numbers had increased to 1808 (Brand, 1967); the most recent survey (in 1970) yielded 3100 animals (von Richter, 1971a). The survival of the species is safe; the black wildebeest is protected in 10 major reserves, most of which are optimal in terms of size and suitable habitat. An increasing number of private individuals, especially in the Orange Free State, keep the species on farmlands. However, few farms harbor reasonably large and healthy populations. A number of animals are kept in small reserves outside the former range of the species or on marginal habitat, resulting in declining populations.

The black wildebeest has bred successfully in various zoological gardens throughout the world. In 1968, 155 black wildebeest were being kept in 36 zoological gardens (Lucas, 1969). In two large reserves, a number of animals are caught annually and distributed to interested persons. The aims of the policy are to establish breeding herds outside the game reserves and to relieve the grazing pressure on the reserves. More males than females are regularly removed, on the assumption that single or bachelor males are excessive and can be removed without harm to the population. The removal is limited and so far no adverse effect on the populations has been observed. Animals are caught either from a vehicle, by hand, or chased into nets where they are then selected and removed. The procedure sometimes involves heavy losses. Pienaar (1968) reported the use of Etorphine hydrochloride (M-99 Reckitt) in combination with a tranquilizer in wild animals, whereas Gauckler *et al.* (1970) successfully used xylazine (Bya Va 1470) in captive animals.

The economic value of sport-hunting or cropping is gradually being developed, especially because numbers are now high enough to allow a controlled exploitation. Individual farmers sell males on a small scale for hunting purposes or shoot them themselves to sell the meat. The Nature Conservation Department of the Orange Free State has created a hunting reserve where at present only bulls can be hunted for sport. When the herd is sufficiently established, hunting will be used as a management tool.

The best method found for marking animals so far is collars of a nylon weave material covered with polyvinyl plastic. Double strips have so far lasted 2 years without undue wear.

In the middle of the last century, the black wildebeest was hunted primarily for meat and skins; the latter were used by early settlers for all kinds of domestic purposes or were exported as hides.

BEHAVIOR. Three social units can be differentiated in a black wildebeest population: (1) female herds, consisting of adult females, their calves and yearlings (mostly females);

(2) bachelor herds consisting exclusively of males of all ages; (3) territorial bulls.

The number of females per herd varies from population to population (11 to 32 in four populations) and is greatest in the densest populations. Large herds will break up into smaller herds, which have a survival value as the risk of separation of cow and calf is reduced. Members of a female herd show a strong attachment to each other. Strange individuals are only reluctantly accepted into a herd. Lactating females, non-lactating females, and female yearlings tend to form groups of their own within the herd. Small calves stay with their cows. Later calves form small aggregations within the herd. Male yearlings are expelled during the calving season as a result of their getting between the cow and the new born calf. Some individual male yearlings stay with the female herd; the others join bachelor herds. By removing the male yearlings from the female herd, one cause of separation of cow and calf and the consequent increase in mortality is eliminated (von Richter, 1971c).

Bachelor herds are loose aggregations, which roam freely throughout the available habitat and show no particular attachment either to specific areas or to each other. Sexual-territorial behavior is dormant and males are extremely tolerant of each other. Bachelor herds act as a reservoir for future territorial males, as a challenge to established territorial owners thus ensuring that only the fittest males hold a territory and can reproduce, and as a refuge for males unable to procure and hold a territory.

Territorial bulls are spaced out throughout available habitat forming a mosaic of territories. The center of the territory is a patch of bare ground covered with dung, where the bull performs most of his advertising displays. Estes (1969) first reported that the black wildebeest is territorial and drew the attention to the close similarity of the social and territorial behavior of the two species of wildebeest.

Evidence of territorialism throughout the year and the social organization result from a sedentary mode of life as opposed to a migratory one, as in the blue wildebeest where territoriality is confined to the time of rut (Estes, 1969; Watson, 1969). The management of the black wildebeest herds also affects their social organization.

Territorial males advertise by means of demonstrative-threat displays such as pawing, horning the ground, and rolling; by static-optic advertising such as the mere presence of a territorial bull on his stamping ground and the head-high posture; and by a loud call, best described as "Ge-nu," uttered through the mouth. Territorial males do not defecate at random and defecation is always linked with pawing; defecation combined with pawing, rolling, and horning serves as advertising and threat. The feces and the secretions of the interdigital glands do not seem to influence other bulls. However, particles of the secretion and of the feces adhere to the male's coat and the bouquet may give him self-assurance. Territorial bulls defend their property against other intruding territorial bulls; herding of females and chasing of bachelor herds are only done by territorial bulls.

The encounters between territorial males are highly ritualized and have been termed "Challenge Ritual" by Estes (1969) for the blue wildebeest. This terminology is used for the black wildebeest also because the ritual in both species is nearly identical. The ritual may include the following steps, although not necessarily as in the sequence below (von Richter, 1972): (1) approach by one or both contestants in the Grazing Attitude (head at the ground, sometimes actually grazing); (2) next, both animals move into Reverse-parallel Position; (3) while in this position Head-head Rubbing or licking each others' face seldom occurs, Head-rump Rubbing was never observed; (4) in Reverse-parallel Position usually one male urinates and the other bends down to smell and perform Flehmen (Urination-flehmen Sequence), the opponents may reverse the procedure; (5) while in the Reverse-parallel Position and during the Urination-flehmen Sequence, one or both contestants tilt their heads sideways, aiming the "nearer" horn at themselves and at the hindquarter of the opponent (Angle-horn); (6) in the Parallel or Reverse-parallel Position, or when facing each other, the animals may turn their heads sideways and ostensibly look away from each other (Head Flagging); (7) the animals circle each other in the Grazing Attitude; (8) the climax of an encounter between two bulls is combat. In low intensity combat, they interlock horns and push each other in a standing position; in high intensity combat, they drop to their "knees," pushing vigorously, foreheads flat on the ground, always trying to avoid losing proper contact. No resulting injuries were observed.

Demonstrative-threat displays (as noted above), cavorting, head-shaking, head-throwing, and various displacement activities occur during a Challenge Ritual. Nonterritorial animals also display cavorting when grossly disturbed, and head-shaking and head-throwing are almost invariably addressed to inferior conspecifics by territorial and nonterritorial animals alike. Standing behind a lying conspecific is a mild threat, usually resorted to by inferior animals, as a lying animal temporarily loses his social status (Walther, 1966b).

Nonterritorial black wildebeest display stereotyped submissive behavior in four steps if molested by conspecific (Walther, 1966b; von Richter, 1971b).

Males in bachelor herds may perform the various steps of the Challenge Ritual; cavorting and chasing each other in large circles is common; and occasionally interlocking of horns can be observed. Adult males in the bachelor herd sometimes display sexual interest and occasionally will try to mount a cow if the territorial bull is distracted. Calves and yearlings chase each other in play, and interlock horns and push each other, sometimes on the "knees." Mounting between animals of the same sex also has been observed.

Black wildebeest have two gaits; pacing and galloping. Herds graze either in line or in loose aggregation. When moving, a herd normally proceeds single file. Walther (1966b) discussed the resting formations and positions of a captive black wildebeest herd.

Social grooming was reported by Walther (1966b) but was rarely observed in the field. Cows lick their newborn calves, especially the anal region, and remove any remnants of the fetal membrane and amniotic fluid. No drinking or eating of the calf's urine or feces has been observed. Grooming of the calf is only prevalent during the first month. Zannier-Tanner (1965) and Walther (1966b) described the lying down behavior of the species.

When sucking, the calf stands with its hindquarters toward the head of the cow; in the beginning it will stand, later on it goes down on the "knees." Sucking is accompanied by strong head movements (Euterstoss) and tail-wagging.

Mating is confined to a short period from mid-March to mid-April. Female herds that wander into a territory are herded by the male; the bull tries to keep them within his territory but will not follow them outside his territory. While females are in his territory, he pays attention not only to them but engages also in Challenge Rituals; neighboring bulls will take advantage of this and attempt to herd females away. The movements of a female herd through a series of territories ensures that all females in estrus are served.

Precopulatory behavior is not well developed. A male approaches a female with neck stretched long horizontally and sniffs either at the vagina or butts with the snout at the tail root, hindquarters, or shoulder of the female. The male usually approaches the female from behind, but may also approach from the front or side. Female and male may move into Parallel or Reverse-parallel Positions. On several occasions, the bull approaching from the side or front hooked the female under the neck, jerking his head upward, or pushing and butting the female. Before mounting, the male rests its head on the female's rump or, when approaching from the side, on the withers. The mounting male stands rather erect, frontlegs clamping the flanks of the female in front of the croup, the head resting on the female's back. The receptive female holds her tail raised; when the male approaches and sniffs, the tail will be raised even higher and swished across the male's face. Hindlegs of the female are set apart and slightly under the body, the back is slightly arched. While mating, the female's tail is raised almost vertically and the head lowered to the ground (see drawing in Walther, 1965:32). After successful mountings the animals separate; on some occasions the female follows the male with raised tail and butts him with the snout at his tail's root. All observed matings were in the late afternoon.

Most action occurs early in the morning or in the late afternoon. During the height of summer, activity ceases almost completely during the hours 1000 to 1600, when the animals rest and chew the cud. Black wildebeest have been observed drinking in early morning and late afternoon, more frequently during the hot summer than during the cool winter. When fresh sprouting grass is available, the animals are less dependent on surface water because of moisture content of the fodder.

Black wildebeest are one of the most vociferous of antelope species. The call of the territorial bull is a means of accoustical advertising. Once one bull starts calling, others call also. Whether calls attract female herds or intimidate other males is not clear. Males returning to a female herd after a Challenge

Ritual or having chased an intruder will call often. Calves utter a bleating sound (mû-ô), similar to domestic stock, when separated from their cows; the same sound, only fuller, is the distress call. Snorting through the nose denotes alarm in both sexes; when approached by a human, a territorial bull will stand on his stamping ground, stamp with the front legs and snort, facing intruder.

REMARKS. Zimmermann based the first scientific description on an article by Allamand (1776) that appeared as an addition to Tome XV (1771) of the Amsterdam Buffon edition (Tuijn *et al.*, 1969). Allamand took measurements from a specimen that lived in the menagerie of the Prince of Orange. Tuijn *et al.* (1969) reproduced an Indian ink painting of the black wildebeest, dated 1774, which served Allamand for his account.

Sidney (1965) recorded hybrids between *C. gnou* and *C. taurinus* in the Orange Free State. Several other hybrids were brought to the author's attention by persons who kept both species in captivity. It could not be ascertained whether the hybrids are fertile.

The colloquial name gnu originates from the Hottentot name T'gnu, which is an onomatopoeic description of the bull's advertising call.

The South African postal authorities issued several stamps depicting a black wildebeest; the South African Mint struck a 2c piece with a cavorting black wildebeest. The coat of arms of the Province of Natal also depicts the species.

A number of the original works cited in the synonymies were not seen by the author. The author is grateful for comments made on the manuscript by Dr. J. Meester.

LITERATURE CITED

- Acocks, J. P. H. 1953. Veld types of South Africa. Bot Surv. Mem. 28, Government Printer, Pretoria.
- Allamand, J. N. S. 1776. Histoire naturelle du gnou, du grand gerbo et de l'hippopotame. Amsterdam.
- Ansell, W. F. H. 1968. 8. Artiodactyla (excluding the genus *Gazella*). Preliminary identification manual for African mammals (J. A. J. Meester, ed.), Smithsonian Inst., Washington, D.C.
- Asdell, S. A. 1964. Patterns of mammalian reproduction. Constable & Co., London, 2nd ed., 437 pp.
- Bedford, G. A. H. 1932. A synoptic checklist and hostlist of ectoparasites found in South African Mammalia, Aves and Reptilia. 18th Rep. Dir. Vet. Serv. Anim. Ind., pp. 223-522.
- Bigalke, R. 1947. The status of the black wildebeest *Connochaetes gnou* (Zimm.) in the Union of South Africa. S. African Jour. Sci. 43:213-220.
- Blaauw, F. E. 1889. Development of the horns of the white-tailed gnu (*Catoblepas gnu*). Proc. Zool. Soc. London, pp. 2-5.
- Boom, H. P. A. de, and J. H. Dreyer. 1953. Identifying hair from South African game for forensic purposes. S. African Jour. Sci. 49:233-234.
- Brand, D. J. 1963. Records of mammals bred in the National Zoological Gardens of South Africa during the period 1908-1960. Proc. Zool. Soc. London 140:617-659.
- 1967. Numerical status of the white-tailed gnu *Connochaetes gnou*. Internat. Zoo Yearbook 7:188-189.
- Brookes, J. 1828. Catalogue of the Anatomical and Zoological Museum of Josiah Brookes.
- Burchell, W. J. Travels in the interior of Southern Africa, Longman and Co., London, vol. 2, 473 pp., map.
- Cooke, H. B. S. 1964. Pleistocene mammal faunas of Africa, with particular reference to Southern Africa. Pp. 65-116, in African ecology and human evolution (Howell and Bourlière, eds.), Viking Publications in Anthropology.
- Crandall, L. S. 1965. Record of African antelopes in the New York Zoological Park. Internat. Zoo Yearbook 5: 52-55.
- Cumming, R. G. 1850. Five years of a hunters life in the far interior of South Africa. J. Murray, London, 2 vols., 769 pp.
- Dittrich, L. 1970. Beitrag zur Fortpflanzungsbiologie afrikanischer Antilopen im Zoologischen Garten. Der Zool. Garten, N.F. 39:16-40.
- Ellerman, J. R., T. C. S. Morrison-Scott, and R. W. Hayman. 1953. Southern African mammals, 1758 to 1951. A reclassification. British Museum (Nat. Hist.), London, 363 pp.
- Estes, R. D. 1966. Behaviour and life history of the wildebeest (*Connochaetes taurinus* Burchell). Nature 5066: 999-1000.

- 1969. Territorial behavior of the wildebeest (*Connochaetes taurinus* Burchell, 1823). *Z. Tierpsychol.* 26:284-370.
- Forster, J. R. 1844. *Descriptio Animalium quae in itinere ad Maris Australis terras per annos 1772-74 suscepto collegit, observavit et delineavit J. R. Forster, etc. Königlich-preussische Akademie der Wissenschaften, Berlin.*
- Gatterer, C. W. J. 1780. C. W. J. Gattereri breviarium zoologiae. Pars 1, Mammalia, Gottingae, xvi + 227 pp.
- Gauckler, A., and M. Kraus. 1970. Zur Immobilisierung von Wildwiederkäuern mit Xylazin (Bya Va 1470). *Der Zool. Garten, N.F.* 38:37-46.
- Gmelin, J. F. (ed.) 1778. C. a Linné. . . Systema naturae. . . ed. 13, tom 1, pt. 1, Mammalia, Lipsiae, x + 232 pp.
- Gray, J. E. 1821. On the natural arrangement of vertebrate animals. *London Med. Repos.* 15:296-310.
- 1850. Cleanings from the menagerie and aviary at Knowsley Hall. Hoofed quadrupeds. Knowsley, iv + 76 pp., 62 pls. col. fol.
- 1851. Synopsis of the species of antelopes and strepsicerus, with descriptions of some new species. *Proc. Zool. Soc. London*, pp. 111-146.
- 1872. Catalogue of ruminant Mammalia (*Pecora*, Linnaeus) in the . . . Museum. *British Museum (Nat. Hist.)*, London, viii + 102 pp., 4 pls.
- Haltenorth, Th. 1963. Klassifikation der Säugetiere: Artiodactyla 1(18): Handbuch der Zoologie. 8(32):1-167.
- Harper, F. 1940. The nomenclature and type localities of certain Old World mammals. II. *J. Mammal.* 21:322-332.
- Kruuk, H., and M. Turner. 1967. Comparative notes on predation by lion, leopard, cheetah and wilddog in the Serengeti area, East Africa. *Mammalia* 31:1-27.
- Levine, N. D., and V. Ivens. 1970. The coccidian parasites (protozoa, sporozoa) of ruminants. *Illinois Biol. Monogr.* 4:1-278.
- Lichtenstein, M. H. C. 1812. Die Gattung Antilope. *Mag. Ges. Naturf. Freunde Berlin* 6:147-160, 164-182 (not seen).
- Lucas, J. (ed.) 1969. *Internat. Zoo Yearbook* 8:1-295.
- Lydekker, R., and G. Blaine. 1914. *Catalogue of ungulate mammals in the British Museum (Natural History)* 4 vols.
- Mentis, M. T. 1972. A review of some life history features pertinent to the productivity of the large herbivores in Africa. *Lammergeyer* 16:1-89.
- Mohr, E. 1965. Besonderheiten an Cavicornier—Hörnern. *Milu* 2:21-47.
- Neitz, W. O. 1965. A checklist and hostlist of the zoonoses occurring in mammals and birds in South and South West Africa. *Onderstepoort J. Vet. Res.* 32:189-376.
- Oboussier, H. 1970. Beiträge zur Kenntnis der Alcelaphini (Bovidae—Mammalia) unter besonderer Berücksichtigung von Hirn und Hypophyse. *Morph. Jb.* 114:393-435.
- Oken, L. 1816. *Okens Lehrbuch der Naturgeschichte*. C. H. Reclam, Leipzig, pt. 3, zool., sect. 2, pp. xvi, 1270. (not seen).
- Opinion 257. 1954. Opinions and declarations rendered by the International Commission on Zoological Nomenclature 5(18):231-244.
- Opinion 417. 1956. Opinions and declarations rendered by the International Commission on Zoological Nomenclature 14(1):1-42.
- Péringuey, L. 1918. Report of the South African Museum for 1917. p. 3.
- Pienaar, U. de V. 1968. Handling of wild herbivores. Pp. 125-132, in *A practical guide to the study of the productivity of large herbivores* (F. B. Golley and H. K. Buechner, eds.), IBP Handbook no. 7, Blackwell, Oxford and Edinburgh.
- 1969. Predator-prey relationships amongst the larger mammals of the Kruger National Park. *Koedoe* 12:108-176.
- Plessis, S. F. du. 1969. The past and present distribution of the Perissodactyla and Artiodactyla in Southern Africa. M. Sc. thesis, Univ. Pretoria.
- Pocock, R. I. 1910. On the specialised cutaneous glands of ruminants. *Proc. Zool. Soc. London*, pp. 840-986.
- Richter, W. von. 1971a. Past and present distribution of the black wildebeest, *Connochaetes gnou* Zimmermann (Artiodactyla: Bovidae) with special reference to the history of some herds in South Africa. *Ann. Transvaal Mus.* 27:35-57.
- 1971b. The Black Wildebeest (*Connochaetes gnou*). *Dept. Nature Conserv. Orange Free State, Misc. Publ.* 2:1-30.
- 1971c. Observations on the biology and ecology of the black wildebeest (*Connochaetes gnou*). *Jour. Southern African Wildlife Mgt. Assoc.* 1:3-16.
- 1972. Territorial behaviour of the black wildebeest *Connochaetes gnou*. *Zool. Africana* 7:207-232.
- Roberts, A. 1951. The mammals of South Africa. Johannesburg, xlviii + 700 pp.
- Sc Slater, P. L., and O. Thomas, 1895. *The Book of antilopes*. R. H. Porter, London, vol. 1, 220 pp.
- Shortridge, G. C. 1934. *The mammals of South West Africa*. W. Heinemann, London, vol. 2, 340 pp.
- Sidney, J. 1965. The past and present distribution of some African ungulates. *Trans. Zool. Soc. London* 30:1-396.
- Smith, H. 1827a. *Mammalia. . . with specific descriptions by E. Griffith, C. H. Smith and E. Pidgeon. Vol. 4, in The Animal Kingdom . . . by the Baron Cuvier with additional description of . . . species . . . by E. Griffith and others.* 16 vols.
- 1827b. *The Ruminantia. In vol. 5 [Synopsis of the species of the class Mammalia, by J. E. Gray], The animal kingdom . . . by the Baron Cuvier with additional descriptions of . . . species . . . by E. Griffith and others.* 16 vols.
- Talbot, L. M., and M. H. Talbot. 1963. The wildebeest in western Masailand, East Africa. *Wildlife Monogr.* 12:1-88.
- Theiler, G. 1962. The ixodoidea parasites of vertebrates in Africa south of the Sahara. *Project S. 9958, Rept. Dir. Vet. Serv. Onderstepoort, cyclostyled*, 260 pp.
- Tuijn, P., and P. J. van der Feen. 1969. On some eighteenth century animal portraits of interest for systematic zoology. *Bijdr. tot de Dierkde* 39:69-80.
- Walther, F. 1965. Psychologische Beobachtungen zur Gesellschaftshaltung von Oryx-Antilopen. *Der Zool. Garten, N.F.* 31:1-58.
- 1966a. *Mit Horn und Huf*. Paul Parey, Berlin und Hamburg, 171 pp.
- 1966b. Zum Liegeverhalten des Weiszschwanzgnus (*Connochaetes gnou* Zimmermann, 1780.). *Z. Säugetierk.* 31:1-16.
- Watson, R. M. 1969. Reproduction of wildebeest, *Connochaetes taurinus albojubatus* Thomas, in the Serengeti Region, and its significance to conservation. *J. Reprod. Fert., Suppl.* 6:287-310.
- Wells, L. H. 1965. Antelopes in the Pleistocene of South Africa. *Zool. Africana* 1:115-120.
- 1970. A late Pleistocene faunal assemblage from Driefontein, Cradock District, C. P. S. *African Jour. Sci.* 66:59-61.
- Wright, B. S. 1960. Predation on big game in East Africa. *Jour. Wildlife Mgt.* 24:1-15.
- Zannier-Tanner, E. 1965. Vergleichende Verhaltensuntersuchung über das Hinlegen und Aufstehen bei Huftieren. *Z. Tierpsychol.* 22:696-723.
- Zimmermann, E. A. G. 1777. *Specimen zoologiae geographicae, quadrupedum domicilia et migrationes sistens. Lugduni Batavorum, Apud Theodorum Haak, et Socios*, xiv + 686 pp., 1 tab.
- 1780. *Geographische Geschichte des Menschen und der vierfüssige Thiere. In der Weygands Buchhandlung, Leipzig*, vol. 2, 432 pp.
- Zinderen Bakker, E. M. van. 1957. A pollen analytical investigation of the Florisbad deposits (S. Afr.). *Proc. Pan African Congr. Prehist.*, 3:56-67.
- Zyl, J. H. M. van. 1965. The vegetation of the S. A. Lombard Nature Reserve and its utilization by certain antelope. *Zool. Africana* 1:55-71.
- Zyl, J. H. M. van, and A. S. Wehmeyer. 1970. The composition of the milk of springbok (*Antidorcas marsupialis*), eland (*Taurotragus oryx*) and black wildebeest (*Connochaetes gnou*). *Zool. Africana* 5:131-134.

Primary editor of this account was SYDNEY ANDERSON.

WOLFGANG VON RICHTER, MAMMAL RESEARCH UNIT, UNIVERSITY OF PRETORIA, SOUTH AFRICA; PRESENT ADDRESS F.A.O. WILDLIFE ECOLOGIST, DEPARTMENT OF WILDLIFE AND NATIONAL PARKS, P. O. BOX 131, GABORONE, BOTSWANA.