

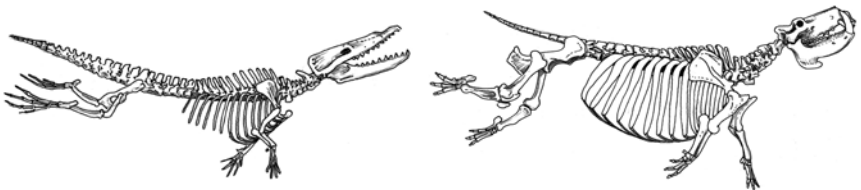
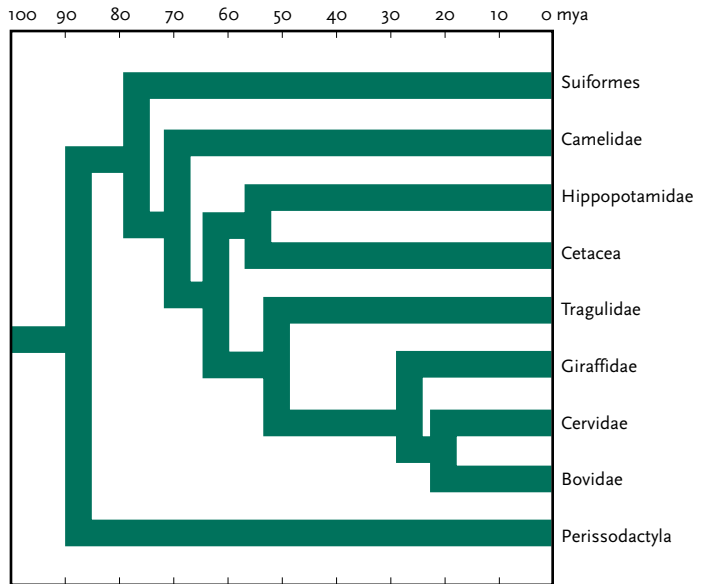
The cetartiodactyls embrace all the horned antelopes and cattle, deer, giraffes, camels, chevrotains, pigs, hippopotamuses and, surprisingly, whales (which are not profiled in this guide). They are one of the most important and successful of mammal lineages. The earliest types were not very different from carnivores, had prominent canine teeth and an omnivorous diet. A very small, but significant shift in how body weight was carried distinguished the cetartiodactyl ancestor. Instead of body weight being taken through the central toe (as in perissodactyls), weight was distributed between the third and fourth digits. This probably enhanced stability on many soft or uneven substrates.

The most significant feature of this group is the progressive improvement of their digestion through a system of storing, re-chewing and sifting of the food and a symbiosis with bacteria and protozoans living within the chambers of the stomach. These break down cellulose and release nutrients. Notably Giraffes and hippos excel in digestive efficiency and economy

The skulls of living cetartiodactyls have been adapted to specific modes of combat requiring elaboration of canines, incisors, horns or antlers. Cetartiodactyls also show very diverse social and ecological adaptations.

The principal threat to African cetartiodactyls is their continuing replacement by a few exotic domesticates. An ever-expanding and aggressive livestock industry is eroding and exterminating natural communities of animals and plants on a huge scale, at inordinate cost to the long-term health of African environments.

Tentative phylogenetic tree for Cetartiodactyla (after Bininda-Emonds *et al.* 2007 and Hassanin *et al.* 2012).



Left: Skeleton of *Rhodocetus*, an early fossil whale (after Gingerich *et al.* 2001). Right: Skeleton of Common Hippopotamus.

PIGS SUIDAE

Wild Boar	<i>Sus scrofa</i>
Bushpig	<i>Potamochoerus larvatus</i>
Giant Forest Hog	<i>Hylochoerus meinertzhageni</i>
Warthogs	<i>Phacochoerus</i> (2 species)

RECOGNITION Pigs are robust, large-headed animals with relatively short legs and a compact body build. They have wedge-shaped skulls, out-turned canine tusks and a barrel-like snout that is tipped with a very tough, mobile disc mounted on a well-reinforced prenasal bone. All have leathery, sparsely haired skin. Weight is taken on the two central toes of each foot but the side hooves splay out in soft ground. The skulls of African pigs show striking adaptations to their preferred foods and to modes of tusk- or snout-fighting that are unique to each species.

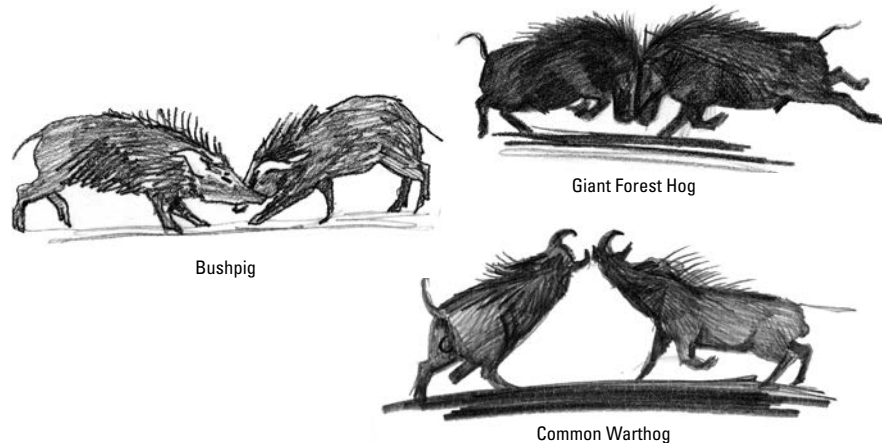
GENEALOGY Pig skulls are among the best preserved and most abundant of fossils in African deposits. Because morphological changes are rapid and reflect regional adaptation, they are excellent stratigraphic indicators. Originating in Asia about 30 mya, the ancestors of modern African species only appear about 4.6 mya in the form of *Kolpochoerus* from which first *Potamochoerus* and then *Hylochoerus* evolved within our continent. Warthogs have been thought to derive from *Metridiochoerus*, which entered Africa about 3.4 mya.

GEOGRAPHY An Old World group, pigs do best in moist areas with dense cover and soft soils, but the warthogs have adapted to arid Africa.

ECOLOGY Rootling is a primary adaptation in pigs. Wild Boar and bushpigs, the former in Eurasia and N Africa, the latter in Africa, are the most conservative in this respect. The bushpigs have branched into true forest and savanna-adapted species while the Giant Forest Hog has become a forest glade grazer. The warthogs have also become mainly grazers but have diverged into a mainline savanna species and a more specialised, arid-adapted form. The universal suid dependence on secure shelter or dens is met by self-dug or appropriated earth burrows.

NATURAL HISTORY Social animals for the most part, pigs communicate mainly through scent and sound. They are highly vocal and well supplied with glands around the genitalia and mouth. Competition, especially among males, is very intense and has led to elaborate threat and appeasement behaviour. They have short gestation periods, large litters, fast maturation rates and very high mortality in the young.

ADAPTATIONS The primacy of scent and ability to dig with the nose disc is manifested in well-reinforced skulls with long, tubular muzzles. The disproportionately large head is used as a lever for food and as a weapon in trials of power and weight during contests. Short, sharp tusks are typical of primitive lateral fighters and 'snout-boxers' while more elaborate 'antler tusks' have been developed by warthogs. These species derive from ancient stock that included near hippo-sized animals.

■ WILD BOAR *Sus scrofa*

OTHER NAMES Eurasian Wild Pig. Fr. *Sanglier*. Ger. *Wildschwein*. Swah. *Nguruwe mwitu*.

MEASUREMENTS HB 0.85–1.3m (♀), 1.0–1.6m (♂). T 150–210mm. Sh. ht 600–900mm. W 30–80kg (♀), 33–130kg (♂).

RECOGNITION A flat-sided and shaggy pig with a long snout, large, leaf-shaped ears and a short dorsal mane. Colour varies between dark grey-brown and a dirty tawny colour. Tracks reveal two oval hoof-marks (with side hooves only imprinting in mud).

GEOGRAPHIC VARIATION *S. s. algira* (often regarded as no more than a small, long-tusked variety of the European Wild Boar). Hybridises readily with bushpigs.

DISTRIBUTION Found over most of Eurasia. Originally the entire North African littoral but extinct in Egypt by 1902 and in Libya by 1890. Still occurs from the Atlas region to N Tunisia. In a feral state (derived from early domestic stock) in South Africa, Sudan, Pemba and Mafia and most recently introduced into Gabon and Burkina Faso.

HABITAT In North Africa mainly oakwoods and scrub; also in tamarisk groves on desert margins. Wild Boars make nests of gathered grass and branches or scrape a shallow depression in dense vegetation.

FOOD Omnivorous, with acorns the main seasonal staple in North Africa (at which time animals put on weight rapidly); also bulbs, roots, fallen fruits, snails, insect larvae and other invertebrates. Wild Boars occasionally scavenge and eat small vertebrates. The availability of food is the main determinant of their population cycles but climate, predation (in the past) and diseases such as hog cholera periodically kill large numbers of these pigs.

BEHAVIOUR Females and their young form associations with one or more other mother families. These have loose, temporary associations with adult males in the vicinity. The animals tend to be sedentary but are quick to respond to disturbance or hunting with rapid movement and changes in behaviour. Thus mainly diurnal habits can change to nocturnal habits and distances of 20–30km may be covered. Home-ranges are very variable, from 2–20km². Tusk glands, salivary secretions, genital scents and certain calls are all thought to facilitate courtship and mating. Three to 10 piglets are born after a gestation of 115 days. The mother gives birth in a nest of leaves, branches and grass, where she stays put for about a week before emerging, sometimes to rejoin other families in 'nursery groups'. The young grow rapidly and are sexually mature by about 1 year. They are annual breeders and have winter mating peaks. They live for up to 20 years in captivity, less in the wild.



Wild Boar



ADAPTATIONS Wild Boar males are unique in having dense dermal shields of protective tissue under the skin of the shoulders and on the barrel of the chest. This limits the damage from lacerating blows suffered during frequent fights between males during the winter rut. The side-curving tusks are very sharp and are wielded with a very fast and powerful sideways swipe of the head.

STATUS Wild Boars fluctuate in numbers but are common and widespread in Morocco and Algeria where they are not eaten and seldom hunted. Their recent introduction into hunting reserves in Gabon and elsewhere is highly irresponsible.

■ BUSHPIG *Potamochoerus larvatus*

OTHER NAMES Fr. *Potamochère*.

Ger. *Buschschwein*. Swah. *Nguruwe*.

MEASUREMENTS HB 1.00–1.77m. T 300–450mm.

H 550–1,000mm. W 45–150kg.

RECOGNITION Compact, with a slab-like, short-legged body, tapering into the head and snout with little indication of a neck. Extremely variable in colour, it is always covered in coarse, shaggy hair. The dorsal crest and face are often white or grey. The body colour varies from blonde or red to grey, brown or black. Colour varies with sex, age, region or individual; as a result 17 subspecies have been named.

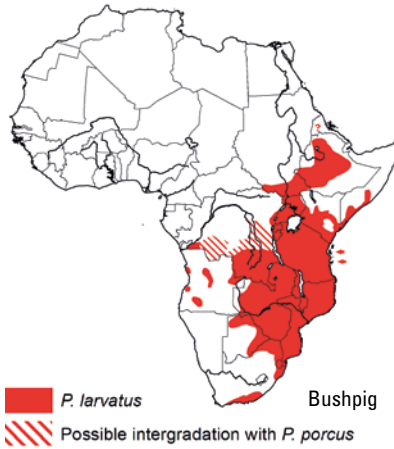
GEOGRAPHIC VARIATION Eastern Bushpig, *P. l. hassama* (uplands and eastern littoral); Southern Bushpig, *P. l. koiropotamus* (S and SE Africa). (Note: small pigs from the Horn of Africa have been called *P. l. somaliensis* but they appear to intergrade over a very broad front.)

DISTRIBUTION From the moister parts of southern Africa to the Congo R. and R. Kasai in the west. Likewise, the moister parts of East and NE Africa to the mountains of the central African Rift Valley. Bushpigs range up to 4,000m on Mt Kilimanjaro. They are thought to have been so recently introduced to Madagascar that early semi-domestication by Afro-Indonesian settlers on the mainland has been suggested as an explanation for their arrival on that island.

HABITAT A wide range of forested and woodland habitats, with a distinct preference for valley bottoms with dense vegetation and soft soils. Nest-making for raising young and in cold seasons is most prominent in the cooler parts of their range. More diurnal activity in the winter suggests that low temperatures are poorly tolerated.

FOOD Omnivorous and highly adaptive to local and seasonal conditions. Roots, tubers, bulbs and corms are the principal foods; also fallen fruits and herbage. In addition to fungi, Bushpigs take various animals, rooting for larvae and beetles, snails, amphibians and reptiles. They occasionally scavenge and a party has been seen to drive a Leopard off its kill. Seasonal changes in diet have been widely observed.

BEHAVIOUR A female and her young are often accompanied by an adult male within a restricted area where trunk-slashing along paths, rubbing posts and latrines suggest that males, and perhaps females too, are territorial, if only seasonally. Larger associations are seen



■ *P. larvatus*

▨ Possible intergradation with *P. porcus*

Bushpig



but only rarely. Home-ranges of up to 10km² have been estimated and nightly foraging walks of up to 6km. Contact grunts are common. Threats, assembly and alarm are all signalled by various grunts. Squeals and roars accompany fights in which contestants are sometimes lethally wounded or killed. Brow-to-brow pushing may be a preliminary to mating. Gestation (120 days) is followed by the female retiring into a nest or hollow to give birth to up to ten young. Piglets grow rapidly and slowly lose their brown and buff stripes over a period of months. They are sexually mature by about 18 months. Breeding is annual and seasonal, with most births at the end of the dry season (spring, i.e. September–November, in South Africa).

ADAPTATIONS Bushpigs occupy a wider range of habitats than the more specialised forest-dwelling Red River Hog. The relationship between these two species and the possibility of hybrid populations in Uganda and DR Congo await further study.

STATUS Bushpigs are a major pest for gardeners and farmers and are widely hunted for both control and meat. Without their natural predators they can become very abundant. They have been deliberately crossed with domestic pigs, and wild Bushpigs are reported to have hybridised with feral pigs in South Africa.

■ RED RIVER HOG *Potamochoerus porcus*

OTHER NAMES Fr. *Potamochère*.

Ger. *Flusschschwein*.

MEASUREMENTS HB 1.00–1.45m. T 300–450mm.

Sh. ht 550–800mm. W 45–115kg.

RECOGNITION A bright russet pig with a narrow white dorsal crest, white 'brows', cheek-tufts and jaw-line. The leaf-shaped ears end in a long white tassel. Muzzle and forehead are black and the fur is sleek and short over most of the body (except jaws and flanks which have longer hair).

GEOGRAPHIC VARIATION Subject to differences and gradients in size; six named subspecies but these are generally judged invalid.

DISTRIBUTION The main rainforest belt from Gambia to E DR Congo and south to the Congo R./R. Kasai. Also in galleries wherever permanent water and soft soils are maintained in valley bottoms.

HABITAT Rarely outside rainforest, with a marked preference for river courses and swamp-forest margins. Here it ploughs up extensive areas while excavating roots and invertebrates. The narrow extent and linearity of its habitat in some areas may force semi-nomadic circuits of movement.

FOOD Omnivorous but with underground roots and tubers the main staple. Fallen fruits are of great importance locally and seasonally, as are invertebrates. Finding fruit supplies is assisted by the noise made by primates, hornbills and other fruit-eaters.

BEHAVIOUR Often found in small groups of up to 15 animals,

the Red River Hog occasionally gathers in very large but temporary associations of up to 60 animals. During confrontations between males both animals strut broadside,

with bristling fur and erect crests.

They champ jaws, grunt, paw the soil and whip their slender tails back and forth. Champing clearly releases pheromones from the tusk and salivary glands while other secretions exude from the corners of the eyes, genitals and nape of the neck. Nothing is currently known of the nature of the information encoded in this

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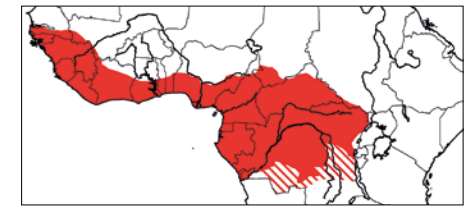
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■ *P. porcus*

▨ Possible intergradation with *P. larvatus*

Red River Hog



barrage of scents. Litters of very variable size are born, after a 4-month gestation, in a hollow tree or dense nest of gathered vegetation. For about 3 months the young are very prettily coloured in stripes of pale yellow and dark brown. At this time they crouch and 'play possum' when disturbed. As they age and their stripes fade, flight becomes the more normal response. Births have been recorded in February and March in Nigeria. Full grown at 2 years, captive specimens have lived for 20 years.

ADAPTATIONS Although the tusks of the male are short, they are very sharp and snout-boxing would tend to cut the large tendons and blood vessels that serve the rooting snout and its nostril disc. The Red River Hog has evolved knobbed, bony excrescences on the sides of the muzzle that appear to reduce the risk of such damage. The pocket behind this maxillary flange oozes a scented secretion. The facial pattern is well adapted for communicating contrasting signals relating to status. For example, horizontal ears signal aggression while vertically clamped ones indicate submission (see right).

STATUS One of the staple species pursued by commercial bushmeat hunters. Although its fecundity allows it to keep up with this attrition in some areas, many rarer mammals are soon eliminated. Wherever forests have disappeared this species becomes scarce and it is now rare outside protected areas in the most westerly parts of its range.



Red River Hog, frontal head signals: aggressive (above), submissive (below)

GIANT FOREST HOG

Hylochoerus meinertzhageni

OTHER NAMES Fr. *Hylochère*.

Ger. *Reisenwaldschwein*. Swah. *Senge*, *Nguruwe nyeusi*.

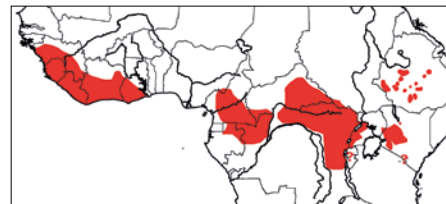
MEASUREMENTS HB 1.3–2.1m. T 250–450mm. Sh. ht 0.8–1.0m. W 100–200kg (♀), 140–275kg (♂).

RECOGNITION Heavily built pig covered in long black hair. Mature males are about 50kg heavier than females and have enormous, naked cheeks, a broad, flat muzzle and thick tusks of moderate length. The rhinarium, or snout disc, may be more than 500mm across and is very broad and swollen. Over the forehead is a dish-like depression surrounded by a circle of raised bone, tissue and bare skin. Mature males also have grotesquely swollen preorbital glands, which can exude copious secretions that spread over the face. Very young piglets are brown- or straw-coloured, with side-stripping most developed in the western parts of the range and mainly absent in the east.

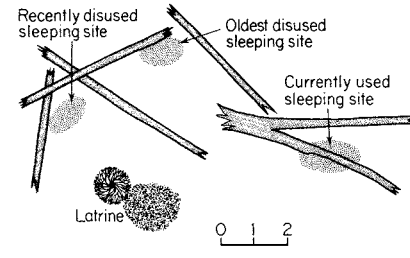
GEOGRAPHIC VARIATION Eastern Giant Forest Hog, *H. m. meinertzhageni* (east of Great Rift Valley); Congo Giant Forest Hog, *H. m. rimator* (W Nigeria to E DR Congo); Western Giant Forest Hog, *H. m. ivoriensis* (Upper Guinea).

DISTRIBUTION Scattered across tropical Africa in localised populations and in various vegetation types from sea level to 3,800m. They live in cold uplands as well as hot lowlands but do not tolerate low humidity or prolonged solar radiation. Their range resembles that of the Bongo antelope, which also exploits unstable forest-edge mosaics.

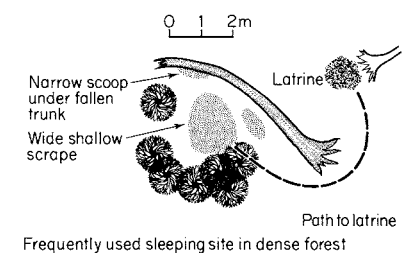
HABITAT Mainly forest/grassland mosaics but they range from subalpine areas and bamboo groves through montane to lowland and swamp forests, galleries, wooded savannas and post-cultivation thickets. A year-round and plentiful supply of green fodder and dense cover are found wherever these hogs occur. Their habitat is punctuated by sleeping sites, latrines, wallows, water holes, salt-licks and grazing meadows and is laced with a tracery of habitually used pathways.



Giant Forest Hog



Long-term sleeping sites in tangle of fallen timber



Frequently used sleeping site in dense forest

FOOD Many species of grasses, sedges and herbs, which are cropped at various stages of growth. In some montane areas herbaceous growth may also be very important. Giant Forest Hogs root very much less than other pigs and prefer to graze on mats of relatively short green grass. They masticate less thoroughly than warthogs (having lower-crowned molars) and differ in not selecting old or dry grasses. They seek salty earth which they excavate mainly using their lower incisors. After visits to salt-licks their dung may be mainly composed of earth. Latrines, usually sited very close to the temporary sleeping sites, are large and communally used.

BEHAVIOUR The basic social group is a mother and her offspring of up to three generations, but this unit may associate with a variety of neighbouring families. As sleeping-sites change frequently and are used by different permutations of neighbouring families, latrines may both advertise occupancy and help familiarise the changing sleeping partners with one another's scent. In Kenya the home-ranges of families probably comprise a series of overlapping foci but with each family having its own core area. In DR Congo males are thought to form more permanent bonds with particular families and core areas may have more of the character of defended territories. Males defend the females and young in their current family against other males and against predators (mainly Lions, Leopards and hyaenas).

They are often very vocal, using close-contact quiet grunts in thick cover and a louder barking call to establish contact over a distance. Males make an extended grunting call that builds up to a trumpeting crescendo and then dies away. Mating peaks are prominent but do not form a regular seasonal pattern in Kenya. In DR Congo mating peaks in March and in September, with births some 5 months later in August and February. Up to 11 piglets are born at a time and they remain in dense cover with their mother for about a week. The young are intensely playful and competitive, grow



rapidly and are weaned at 9 weeks and sexually mature by 18 months. In spite of very low survival rates, they can live for up to 18 years.

ADAPTATIONS Long sequences of fossil pigs that are immediate antecedents of *Hylochoerus* show that grazing was a relatively late development in this species. Grass-eating has involved the need for powerful lateral chewing. Developing the muscles and anchorage to support this has caused massive realignments in the skull and has led to unique forms of head-butting. The commonest contest, practised from an early age, is head-on snout-ramming. This form of contest is facilitated by the slightly bulbous, flat-fronted nasal disc which is not important for rooting. Most confrontations end in one male withdrawing but stalemate among larger, more evenly matched, mature males culminates in both backing off and charging from about 30m distance. When their massively reinforced foreheads meet in such clashes, the impact rocks one or the other back on its haunches. If the concave foreheads meet in exact opposition, a loud rifle-like report is produced by the escape of compressed air. Repeat charges may continue for up to 30 minutes with jaws champing, spittle flying and urine squirting every time. When the victorious male rejoins his group, preorbital secretions pour over his face, expressed from his grotesquely swollen glands. Submissive females gather to sniff him while adult males avoid him. Skulls are not infrequently broken but the 'false hull' structure of the skull (common to all pigs) protects the brain inside a well-insulated bony capsule. Broken skulls heal and their owners live to fight another day.

STATUS An easy target for hunters, especially those with dogs, which quickly bring them to bay, Giant Forest Hogs are threatened by commercial meat-hunting for urban markets. Unless such markets are prohibited it can be predicted that Giant Forest Hogs and many other species will disappear over most of their fragmented and declining range.

All populations are listed as rare and the most westerly ones (*H. m. ivoriensis*) as endangered (IUCN). They are nominally protected and are present in most forest parks and reserves within their ranges but are vulnerable even there because the grasslands and glades on which they depend are highly unstable. As a tractable grazing animal this species is a serious candidate for domestication or semi-domestication in equatorial Africa. Its potential needs investigation. Veterinary restrictions to protect domestic pigs from disease inhibit such initiatives and prohibit trade in any part of this animal.

WARTHOGS *Phacochoerus*

Survivors of a succession of now extinct African pigs, warthogs have become specialised grass eaters that have adapted their habits and diets to extreme seasonal and regional differences in grassland ecosystems.



Frontal views of Common Warthog (left) and Desert Warthog (right).

DESERT WARTHOG

Phacochoerus aethiopicus

OTHER NAMES Fr. *Phacochère du Cap*. Ger. *Desert Warzenschwein*. Swah. *Ngiri ya Somalia*.

MEASUREMENTS HB (est.) 1.0–1.5m. T (est.)

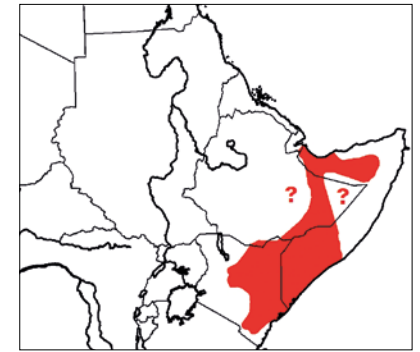
350–450mm. Sh. ht (est.) 500–750mm. W 45–100kg.

RECOGNITION Closely resembles the Common Warthog in size and general morphology but the dentition and the associated leverage for chewing have been modified and specialised, apparently towards more thorough mastication. The incisor teeth usually found at the front of both jaws are either totally absent or have become rudimentary and non-functional. The enlarged third molar is rootless and muscle attachments at the back of the palate are reorganised to allow greater lateral play. The head is relatively shorter and broader. The most obvious external differences are a more vertical snout, russet mane and 'droopy' sub-orbital warts.

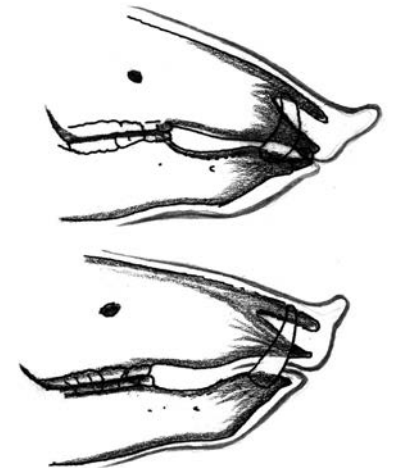
GEOGRAPHIC VARIATION *P. a. aethiopicus* (Cape and Karoo); extinct. *P. a. delamerei* (Horn of Africa).

HABITAT The now widely separate subspecies are known from recent fossils outside their present range. They are so similar it is likely that an 'arid corridor' linked them, perhaps during the last Ice Age (20,000 years ago). The extinct Cape Warthog would have had to tolerate exceptionally cold and arid climates on the Karoo, conditions that were much more extensive during glacial periods. In modern Somalia this species survives under conditions that are drier than any currently tolerated by the Common Warthog. Physiological adaptations are therefore likely to distinguish the two species.

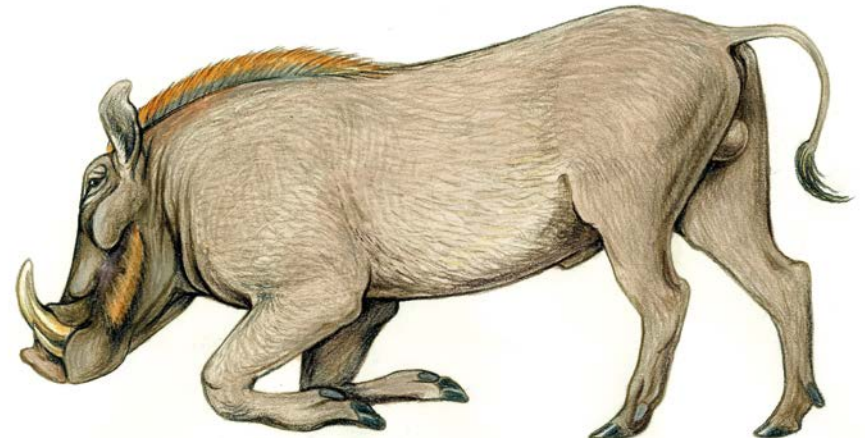
FOOD Desert Warthogs must graze and ingest excavated roots and rhizomes with their hard, sharp-edged lips. Common Warthogs only employ their incisors to wrench long tough grass or to



Desert Warthog



Above: Outlines of rhinarium (snout) and underlying nasal and mandibular occlusion in Common Warthog (top) and Desert Warthog (above).



excavate mineral-rich earth. Neither activity is possible for the Desert Warthog, which has possibly exchanged some minor dietary versatility for more thorough chewing and longer-lived molars.

STATUS After decimation by settlers and hunters in the Cape the remnant appears to have succumbed to the severe rinderpest epidemic of the 1890s. The Somali population is listed as vulnerable (IUCN). Its physiology and biology merit further study.

COMMON WARTHOG

Phacochoerus africanus

OTHER NAMES Fr. *Phacochère*.

Ger. *Warzenschwein*. Swah. *Ngiri, Mbango*.

MEASUREMENTS HB 1.05–1.52m. T 350–500mm.

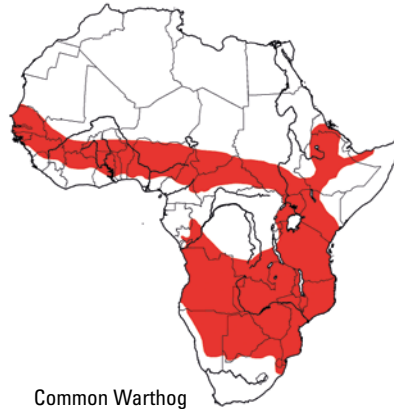
Sh. ht 550–850mm. W 45–75kg (♀), 60–150kg (♂).

RECOGNITION A relatively long-legged but short-necked pig with prominent, curved tusks. The nearly naked skin is grey. Lank black hair forms a dorsal crest that is longest over the neck and shoulders. Paler, often white bristles grow on the jaw-line callosity. The facial callosities, or 'warts', consist of three paired masses of thickened skin and connective tissue protecting the jaws, eyes and muzzle. Warthogs run at a high, jaunty trot, with back straight and the very narrow tail held vertically. The head, with its very protuberant eyes and ears, is held high. Feeding animals drop to their knees and commonly proceed to graze in this position, with their hindquarters raised.

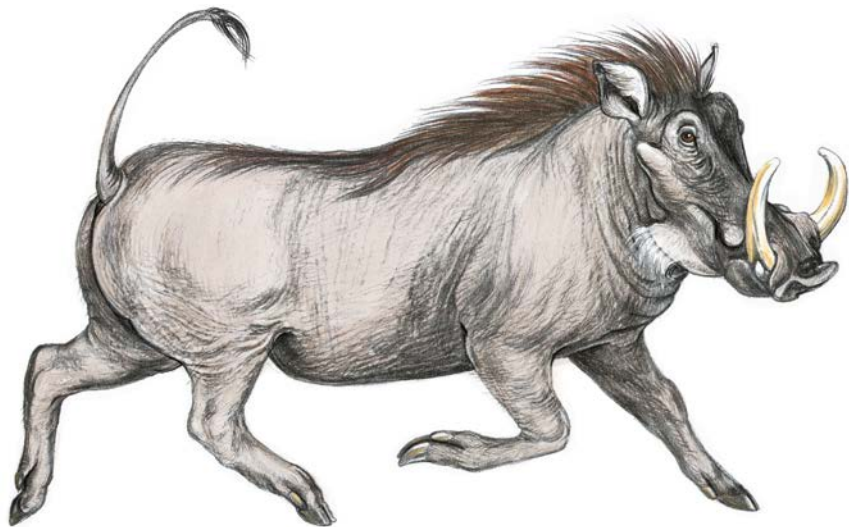
GEOGRAPHIC VARIATION *P. a. africanus* (Senegal to Ethiopia), *P. a. aeliani* (Eritrea), *P. a. massaicus* (E and central Africa), *P. a. sundevallii* (SW to SE Africa).

DISTRIBUTION Common Warthogs are unusual pigs in that they are able to live in arid and open areas. In spite of greater tolerance of heat and drought, animals depend upon natural or self-dug shelters to escape extremes of heat and cold. They range up to 3,000m in Ethiopia and on Mt Kilimanjaro.

HABITAT Commonest on alluvial soils in lightly wooded country with a mosaic of vegetation types but well distributed throughout savanna and open-woodland areas of tropical Africa. High densities



Common Warthog



are assisted by abundant Aardvark holes; deep burrows are essential to escape fluctuating temperatures and for protection from predators. Common Warthogs lack fur and surface fat and will insulate their burrows with grass, huddle together and bask in the sun to conserve heat.

FOOD Grazing throughout the rains, Common Warthogs favour mats of short species, such as *Sporobolus*, *Cynodon*, *Panicum* and *Brachiaria*. They also strip growing grasses of their seedheads. In the dry season they turn to leaf bases and rhizomes that store nutrients over that period. They unearth these with the sharp edge of the nose disc. In Zimbabwe preferred rhizomes are from species of *Digitaria* and *Tristachys*. Common Warthogs occasionally eat fallen fruits, faeces and animal foods. Soil is regularly eaten, presumably for minerals. Although they generally stay within walking distance of water, these animals can subsist for a while on succulents and other water-conserving plants.

BEHAVIOUR There are several social levels. Mothers and their female offspring retain the most enduring bonds. Thus a new family unit joins others that are probably also close relatives. These loose groupings live within 'clan areas' averaging about 4km². Any one family occupies one-eighth to the whole of this area, circulating between favourite burrows that are well spaced out among 100 or more (any one of which may serve as a refuge). Any one hole is never exclusive to an individual or group, and families seldom share holes, simply avoiding occupied ones. The size of the families varies with the number and fortunes of offspring (litters average two or three but can number up to eight).

Young males remain with their mothers until driven off or associate together very loosely while they slowly reach full size. Male mortality can be high, and by the time adult males mature at 4 years they are solitary; as few as one survives for every four females. Mature males circulate among females and fights are probably in defence of mating rights rather than clan 'territory'. Courtship is initiated by the male when he finds an oestrous female. He pursues her, champing, salivating and mumbling in an engine-like 'chug, chug, chug'. The female slows her flight and eventually acquiesces. The young are born in a burrow after a gestation of 160–170 days. They grow rapidly, beginning to graze within 3 weeks, and can be weaned at between 2 and 6 months. Piglets squeak and churr and tend to run for the nearest burrow at any disturbance. Warthogs are known to live for up to 18 years.

ADAPTATIONS A grass and grass-root diet has involved many dental adaptations centring on the elaboration of a 'heel' on the back molar that has tripled its length. The last molars are long, very deep and durable. The rest of the tooth-row is more shallow-rooted and wears away. This contraction is linked with Common Warthogs having a more downwardly depressed muzzle compared to other pigs. They employ their tusks in 'tusk-wrestling' and pushing duels. Pushing is interrupted by lightning disengagements to thump at the side of each other's faces. Both deaths and fractures are frequent and it is the hammering that their heads can expect which has selected for the huge 'warts' (that play a role comparable to the pads worn for American football).

STATUS Common Warthogs have been eliminated from all intensively farmed areas, both as a nuisance and as a reservoir of livestock diseases. They are well represented in numerous national parks and are listed by IUCN as widespread and abundant.



Individual and sexual differences in the flare of tusks and the shape of the Common Warthog's warts.

WHIPPOMORPHA

A clade created to embrace both wh(ales) and (h)ippos. That the two might share a close common ancestry was never anticipated by morphologists nor by biology as a whole. Yet genetics have shown many dimensions to the relationship – similarities in milk proteins and limb structure as well as at the molecular level.

The shift from herbivorous to carnivorous diets took place after the whales' ancestor had become amphibious, which makes the hippo an appropriate analogue for the very earliest whale ancestors.

HIPPOPOTAMUSES HIPPOPOTAMIDAE

Common Hippopotamus

Hippopotamus amphibius

Pygmy Hippopotamus

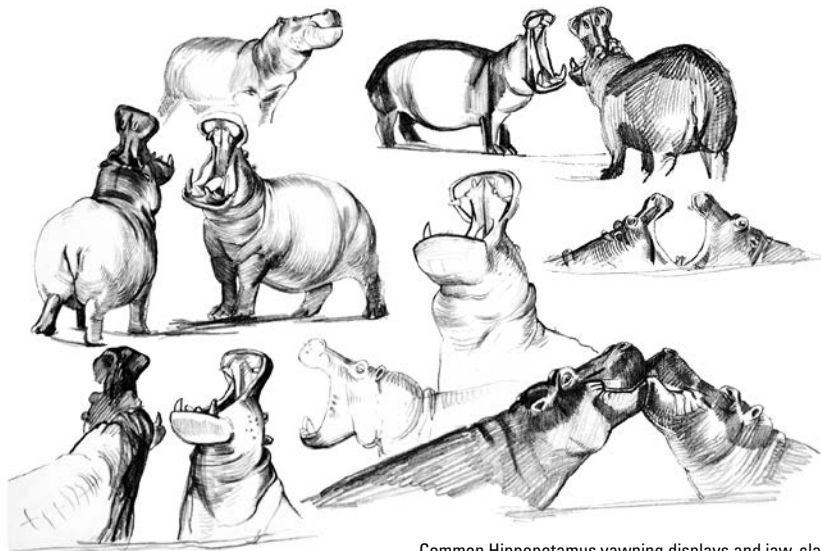
Choeropsis liberiensis

RECOGNITION Hippos resemble gigantic, amphibious pigs with enlarged lower jaw and canines, four large, blunt toes on each foot and a very rotund body build. Their shiny, naked skin is densely perforated by minute skin-conditioning mucus glands.

GENEALOGY Hippos were once thought to have evolved from, or shared an immediate common ancestry with, pigs. Instead, hippos seem to have derived from a primitive extinct group named ancodonts. Other likely members were anthracotheres, fossils of which disappeared just as the earliest fossil hippos appear. The living pygmy hippo clearly represents a more conservative type. In many respects it appears to be more primitive than any known fossil. As recently as one million years ago there were at least eight species of hippo in Africa and four of these are known to have co-existed in the L. Turkana basin. These differed in size, diet and aquatic niche. Other hippos have disappeared from India and at least three species have disappeared in historical times from Madagascar.

GEOGRAPHY Hippos of different species survived in India until recent prehistoric times. The group's origins are probably African.

ECOLOGY Hippos' use of swamps and waters as day-time refuges has allowed them to develop a particularly successful ecological strategy. Great economies in energy are made possible by secure resting places, a slow but efficient digestion, a modest appetite for their size and broad, lawn-mowing lips that can gather enough food in a short period of the night.



Common Hippopotamus yawning displays and jaw-clashing.

NATURAL HISTORY Although hippos inhabit very secure refuges in swamps or water, these tend to be overcrowded and the focus for much competition and fighting, especially among males. Bulky animals fighting in mud or water engage one another's teeth, after which the contest largely becomes a trial of weight and strength.

Hippos have evolved a number of ingenious solutions to the problems of their amphibious existence. The young can suckle under water, through their hard, grass-cropping lips, by folding their extruded tongue around the nipple. Their need to disperse scent-marks has led to the evolution of a muscular, flat-bladed tail which turns like a fan or propeller to disperse the faeces.

ADAPTATIONS Among the most extensive modifications are a reorganisation of the skull and jaws to allow the lower mandible, its canines and incisors to take the brunt of fighting. This makes the lower jaw more massively reinforced than the upper. Its hinging is also organised to jackknife the skull upwards and transfer the main force of impact from the lower jaw almost directly back to the neck and shoulders. While the skin is well adapted to continuous immersion it also renders hippos vulnerable to dehydration. They cannot survive long away from water and only graze at night or during rain.

STATUS Both hippo species are serious candidates for domestication or semi-domestic ranching beside waterways and in association with pisciculture. However, current international fashions in animal husbandry present major obstacles to indigenising Africa's natural resources. No living domestic animal can compete with hippos for the economy with which they convert vegetation into animal protein. Both species have been eliminated over much of their former range.

COMMON HIPPOPOTAMUS

Hippopotamus amphibius

OTHER NAMES Fr. *Hippopotame*.

Ger. *Grossflusspferd*. Swah. *Kiboko*.

MEASUREMENTS HB 2.59–3.50m. T 350–500mm. Sh. ht 1.30–1.65m. W 995–1,850kg (♀), 955–2,065kg (♂).

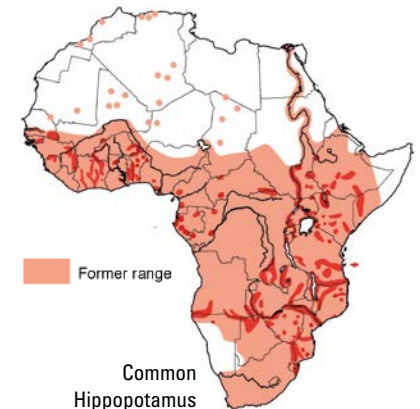
RECOGNITION Common Hippos have stumpy legs and splayed toes that are just adequate for carrying their vast rotund body on land and fold neatly away while resting or swimming. Eyes, ears and nostrils have migrated to the top of the head in this species. The main colour of the smooth, shiny hide is a deep purplish-grey to blue-black. The underside, eye rims, ears and mouth show very variable expanses of pink. The hide is peppered with glands that exude a blood-like fluid that spreads to form a flexible varnish (antiseptic, sunburn cream, water-loss sealant and social perfume are among the suggested functions for this secretion). The sexes are strikingly different in proportions, males having larger canines and incisor teeth set in massive jaws and skull. They have a correspondingly huge jowl and greatly thickened neck.

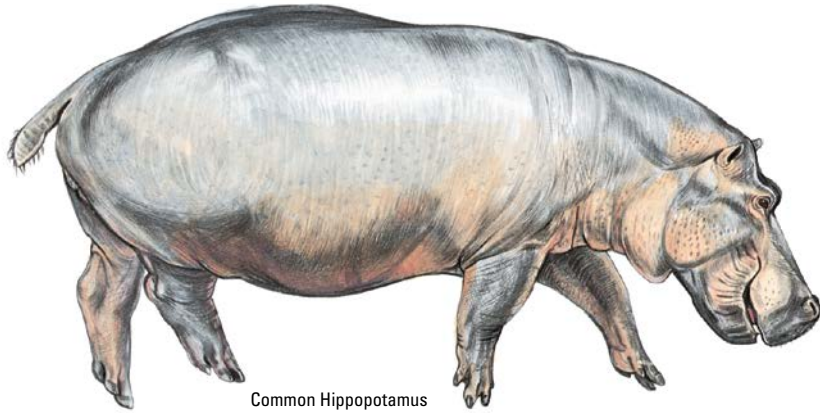
GEOGRAPHIC VARIATION Substantial regional variations in size but no subspecies recognised.

DISTRIBUTION Originally from the Nile delta to the Cape wherever the two requirements of permanent water and open grazing were met. Their upper altitude limit is about 2,000m. Present distribution is shrinking rapidly. Common Hippos aggregate in permanent water sources or wallows during the dry season and disperse very widely in the rains.

HABITAT A silent, solitary grazer on land by night, a vocal, densely social and sedentary wallower by day. The foreshore or bed of lakes and rivers influence Common Hippos, as does the depth and flow of water. Larger groups favour firm, gently sloping beaches and quiet waters, where they can stand or kneel on the bottom close to the surface. Large populations alter grass composition and inhibit fires by removing potential fuel. It is possible that such populations cause long-term vegetation cycles because their progressive degradation of the grazing increasingly encourages regeneration of thickets. Closely cropped lawns, paths radiating from the water and great accumulations of dung are characteristic signs of intensive use by Common Hippos.

FOOD Both creeping and tussock grasses are taken, notably *Cynodon* and *Panicum* species. *Brachiara*, *Themeda*, *Chloris* and *Setaria* are other important sources of grazing. The Common





Common Hippopotamus

Hippo crops grass entirely by means of its leathery (not muscular) lips. It walks slowly, closing its lips over mouthfuls of grass and wrenching them away with a regular swinging of the head. A Common Hippo can ingest up to 60kg in a night's grazing and seldom needs more than 5 hours out of the water. In Uganda, where pioneering studies of African ecology (and hippos) have taken place, fishermen and other villagers have been permitted to keep livestock inside national parks; as a consequence much disruption and erosion of Common Hippo habitat is taking place. **BEHAVIOUR** Common Hippos have a very hierarchical society in which individuals must advertise their status and condition, especially to superiors. Voiding urine or dung, and prostration in the face of a dominant individual are normal modes of appeasement.

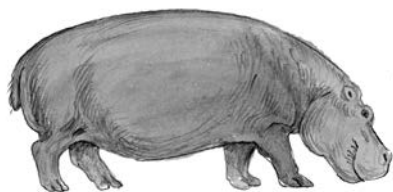
Females accompanied by up to four successive offspring are the only stable social unit. Individuals periodically change their resting sites but degrees of sedentariness or nomadism are highly variable. The largest males occupy narrow strips of water and land along the foreshore, the exact size of which can be quite variable. Here they defend exclusive mating rights but tolerate most subordinate males. Both female and bachelor associations are unstable in composition and vary a great deal in numbers. Aggregations range between 2 and 150.

Large groups are very vocal, the main call being a reverberating nasal wheeze followed by a series of guttural honks. In the early morning this is associated with the return to water. It is the response to all disturbances, particularly in the evenings as the hippos begin to move. Males also wheeze-honk while copulating (the female lies prostrate).

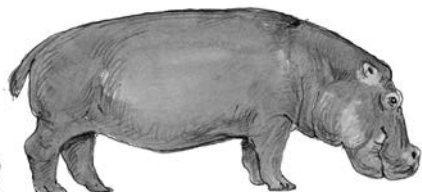
One young (very rarely two) is born after an 8-month gestation. The mother segregates herself for up to 2 weeks after a birth, during which time she is very alert and aggressive. The young begins to graze after some weeks but is suckled for 8 months or more. Calves are quite playful



Distribution of Common Hippopotamus groups along a stretch of the Nile (after Laws *et al.* 1975).



Common Hippopotamus, female

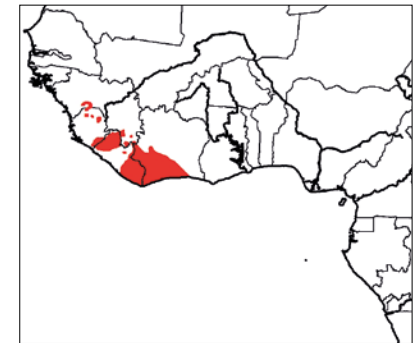
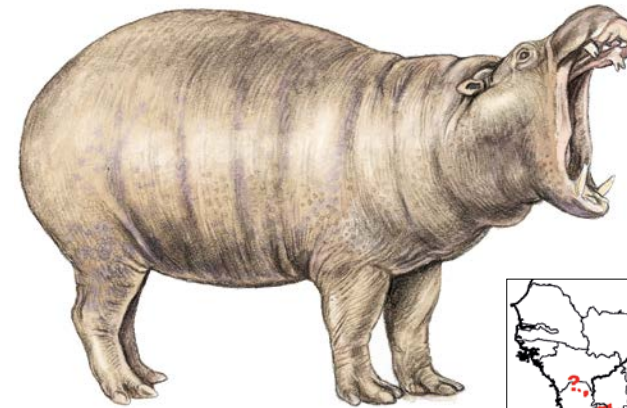


Common Hippopotamus, male

during this period. They continue to grow over 5 or 6 years and females become sexually mature between 7 and 15 years of age (males rather younger but they tend to be excluded from breeding for much longer by heavy dominant males). Births are spaced at about 2-year intervals. Common Hippos can live for up to 50 years in captivity, but probably do not survive as long in the wild.

ADAPTATIONS The body size and weight of adult females tends to stabilise at a regional norm, but males continue to grow, albeit very slowly, throughout life. This favours the oldest, heaviest males in their efforts to monopolise mating. A willingness to fight is advertised by yawning displays that are unique to the Common Hippo and contests are settled by clashing lower jaws together (which leads to much chipping of teeth). The incisors are modified to act like the antler tines of deer, allowing contestants to parry or get a purchase for a pushing contest. It is with the pushing contest that weight and jaw span are decisive. Younger males actively seek contests with frequent yawn displays that are preceded by a scooping up and violent tossing of waterweeds. Such rituals may be drawn out to last an hour or more, jaw to jaw, with occasional straining and weight-testing.

STATUS In spite of an extensive overall range, Common Hippos are very vulnerable to determined hunting. They are well represented in many national parks but suffer continuing local extinction. They are mainly hunted for their meat and in retaliation for the damage they cause to unfenced agriculture. They are readily re-introduced and can be controlled with fences and ditches. They have outstanding potential for domestication or ranching and make popular zoo exhibits.



Pygmy Hippopotamus

■ PYGMY HIPPOPOTAMUS

Choeropsis liberiensis

OTHER NAMES Fr. *Hippopotame nain*.

Ger. *Zwergflusspferd*.

MEASUREMENTS HB 1.42–1.77m. T 150–210mm.

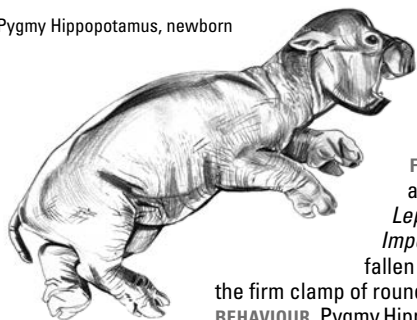
Sh. ht 700–920mm. W 179–273kg (sexes are of similar size).

RECOGNITION Rotund-bodied, thick-necked hippo with a similar rounded, toothy muzzle (but proportionately much smaller head) to the Common Hippo. Eyes, ears and nostrils do not protrude as much as in the Common Hippo. The body is naked, sepia-brown with lighter, more fleshy colouring on the throat and belly. The thin, sun-sensitive skin resembles that of the Common Hippo in its physiology and the secretions that give the animal's entire surface a glossy sheen. The toes, less webbed and more widely splayed than those of the Common Hippo, leave a distinctive 4-pronged spoor.

GEOGRAPHIC VARIATION *H. l. liberiensis* (Upper Guinea), *H. l. heslopi* (R. Niger and R. Cross deltas).

DISTRIBUTION In geologically recent times very similar species occurred in India, Madagascar, S Europe and E Africa. Until recently the African population has been divided into two separate populations. The western population is now fragmented into minuscule relicts, restricted to forests between the R. Corubal and R. Bandama. The Cross R. and R. Niger delta populations are now considered extinct.

Pygmy Hippopotamus, newborn



HABITAT Pygmy Hippos inhabit forested water-courses, where they shelter by day in ponds, rivers and swamps. At night they follow tunnel-like paths through dense riverine vegetation to graze in glades, clearings, chablis or along grassy margins of swamps and trails.

FOOD Graze consists of various green grasses and herbs, notably the main broad-leaf forest type, *Leptaspis*, species of *Andropogon*, *Hypparrhenia* and *Imperata*, various sedges, herbaceous shoots and fallen fruits. Food is cropped by tearing the plant between the firm clamp of rounded upper and shovel-shaped lower lips.

BEHAVIOUR Pygmy Hippos have only been recorded singly, in twos or, rarely, a mother and her offspring in temporary association with a male. They are normally very silent but captive specimens have been recorded snorting, grunting, squeaking and hissing. They also make a much quieter groaning equivalent of the Common Hippo's honking call. They bear one young after a 6–7-month gestation. The young is guarded by its mother who suckles it for up to 6 months, during which time it grows rapidly. The mother may have a second calf after 2 years, at which time previous young are likely to be repelled. The young are feeding on vegetation by 3 months and mature by 3 years. Captive specimens have lived for 30 years.

STATUS In spite of formal protection since 1933, Pygmy Hippos have declined drastically. This is partly due to extensive deforestation and to hunting. Although there are currently 350 animals held in 131 collections, they are mainly kept as pairs or singles for 'display' and mortality is high. Captive breeding is probably the only realistic hope for their survival in the short term because few, if any, of the relict populations are adequately protected. The Nigerian subspecies is critically endangered. IUCN rates the species as endangered.

RUMINANTS RUMINANTIA

In its contemporary meaning, Ruminantia describes and embraces most, but not all, two-toed herbivores and it subdivides into two main divisions (infraorders) that are based on the detailed structure of the stomach. One, the Tragulina, (or Traguloidea, sometimes described as Proto-Ruminants) lack an omasum, one of the sacculations of the stomach (thought to act as a sieve to hold back larger plant particles). The other division, Pecora, or 'true ruminants' comprises giraffes and two parallel lineages, deer and bovids. Both have made independent radiations to fill equivalent niches, one mainly in the northern hemisphere, the other with its greatest diversity among African antelopes.

CHEVROTAINS TRAGULIDAE

Chevrotains are small, spotted ungulates that superficially resemble duikers. They are the last relic of a family that diverged from the pecora some 51 mya and was widespread in the Old World from 40 to 25 million years ago. They share some features with pigs but, unlike them, have remained relatively generalised. The more recent evolution of bovids is thought to have preempted many or most avenues of specialisation. However, chevrotains had a head-start in adapting to the heavily shaded floor of equatorial forests. This appears to have favoured a versatile animal with a varied diet, living a solitary life at low densities.

Details of chevrotain anatomy, physiology and behaviour illuminate the progress of evolution, especially by illustrating early essays in ruminant existence.

There are other species of chevrotain in Asia, where the smallest are known as 'mouse-deer'.

■ WATER CHEVROTAIN *Hyemoschus aquaticus*

OTHER NAMES Fr. *Chevrotain aquatique*. Ger. *Hirschferkel*.

MEASUREMENTS HB 620–1,020mm. T 75–150mm. Sh. ht 300–400mm. W 7–16kg (av. 9.7kg ♂, 12kg ♀).

RECOGNITION A compactly built ungulate with a short, thick neck, small, narrow head, leathery nose, slit nostrils, canine tusks and inconspicuous ears. The hindquarters are powerfully muscled

but the lower limbs are short and delicate in relation to the length and bulk of the body. The feet resemble miniature pig's trotters; they have naked, shiny black skin behind the hocks. The sleek, reddish-brown coat is marked with longitudinal white stripes on the sides interspersed with bold dorsal spots. The throat and chin are covered in coarse hair boldly patterned in black and white. This coarse hair may act as a dispenser for scent secreted by chin glands unique to the chevrotains. When the tail is raised (or 'flashed') it reveals a vivid white underside.

GEOGRAPHIC VARIATION Three subspecies are named but not considered valid.

DISTRIBUTION From Guinea to W Uganda in well-watered equatorial lowlands.

HABITAT River valleys within lowland rain-forest, the margins of swamps or streams.

Never outside dense cover by day, it may forage in exposed clearings, floodplains, open riverbanks or sandy flats at night. It is reported to clamber into tangles of vegetation and up sloping tree trunks (perhaps to sunbathe). Water is a major refuge from predators but only for brief periods. Animals can dive and progress under water but quickly tire. Diving is a last resort after 'freezing', often in a shallow form or concealed refuge. Hollow trees or underground burrows may also be used during the day.

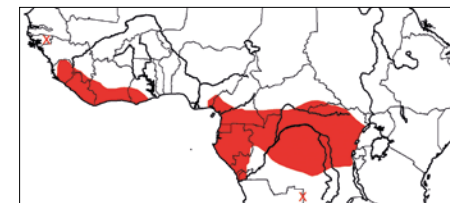
FOOD Mainly fallen fruits, notably figs (*Ficus*), *Pseudospondias*, palm nuts (*Elaeis*) and breadfruit (*Treculia*); also the fruits of gingers, arrowroots and many others. Insects, crabs, scavenged meat and fish have also been recorded. The Water Chevrotain relies mainly on scent in order to find food. Chemically protected plants that deter other herbivores are taken and the chevrotain digestive system is physiologically adapted to detoxify a wide range of plants.

BEHAVIOUR The social system resembles that of a solitary carnivore. Females are spaced out in isolated home-ranges with minimal overlap or contact. Related females occasionally share a range but without much contact. Male ranges overlap those of at least two females. Young males cluster around what are probably parental ranges but frequent wounding suggests that male competition, enforced with long, sabre-sharp canines, helps space out fully mature males so that they are up to several kilometres apart. Combatants rush forward with mouths wide open and make lateral swipes with their canines. Males are more aggressive and active than the larger females. When females fight (they possess shorter, blunter canines), they utter a high, pulsing chatter. They scream when wounded and bark in alarm. Weak bleats may be rare contact calls.

When a female is in oestrous the male follows, calling through closed mouth. At each cry the female stops, as if by reflex, whereupon the male licks her rump. After many repetitions she permits copulation. One young is born after a 4-month gestation. Females are reputed to defend their offspring. The young lie up and are relatively inactive during the first 3 months, nourished almost entirely on milk sucked during periodic visits by the mother. Weaning coincides with dispersal at 9 months, about the time of sexual maturity, although full size and full dentition is only reached at 2 years. Although few survive 8 years, Water Chevrotains are estimated to live for up to 13 years.

ADAPTATIONS Both rump and throat are well protected in both sexes by a dense, thick skin and deep dermal muscles. These undoubtedly mitigate the severe wounds inflicted by the males' sharp canines.

STATUS Naturally sparse and widely spaced, this species is known to suffer intensive hunting and has become rare in many parts of its range. It is also known to be susceptible to disturbance and animals leaving formerly well-known areas are unlikely to live long away from them. Their survival depends upon the continued existence of substantial areas of undisturbed primary and old secondary forest.



Water Chevrotain



Water Chevrotain

GIRAFFES GIRAFFIDAE

Giraffe	<i>Giraffa (camelopardalis)</i>
Okapi	<i>Okapia johnstoni</i>

RECOGNITION The two surviving giraffes are both tall, browsing animals whose long muscular tongue has been modified to serve as a plucking organ. They have 'horns' that begin as cartilaginous buds in the skin of the forehead. These become bony and eventually fuse to the skull below. Horns are covered throughout life with skin and fur. In males bone continues to build up over the horns, orbits, nape and nose. Eventually the cap of rugose bone and thickened skin dwarfs the features below. Both the Giraffe and the Okapi have tall shoulders and sloping hindquarters.

GENEALOGY Ancestral giraffes may represent one of the earliest cetartiodactyls to combine a shift out of the forest with enlarged body size. Thought to have derived from a long-legged, almost two-toed chevrotain-like ancestor about 24 mya, they diversified into many species, some becoming extinct quite recently. They included a grazing okapi (*Samotherium boissieri*), the giant-antlered *Sivatherium* and *Libytherium*. Recognisably true giraffes were the tall, heavy *Giraffa jumae* and the lightly built *G. gracilis*. Giraffes were widespread and diverse in Africa and S Eurasia between about 15 mya and 1 mya.

ECOLOGY Giraffes select very high-quality foliage and, in spite of being cud-chewing ruminants, rely less on mastication to release nutrients than on digestive efficiency. They have very large, tough, tongue-like papillae in the stomach which provide the largest absorptive surface area known in any ruminant. This very efficient stomach is half the size of that of a grass-eating African Buffalo. Long-necked Giraffes flourish where there is abundant, year-long browse above 2m and below 5.5m. Not only are they clumsy at lower levels but competition from antelopes makes low-level herbage a mere emergency food. The Okapi exploits a lower, narrower browsing zone but its forest competitors are shorter still in stature and fewer in number.

NATURAL HISTORY Female giraffes are both shorter and more lightly built than males and feed from a narrower stratum. To compensate, they eat a wider variety of food species over a larger area. Further specialisations of this sort may explain how several giraffe species could co-exist in the past.

ADAPTATIONS Apart from their long necks and legs, giraffes have unique gaits, a unique digestion and a unique circulatory system (with pressure-reducing valves). They also have unique shoulder-leaning modes of fighting in which the heavily reinforced, blunt-horned head is used somewhat like a club, augmented by an occasional kick.

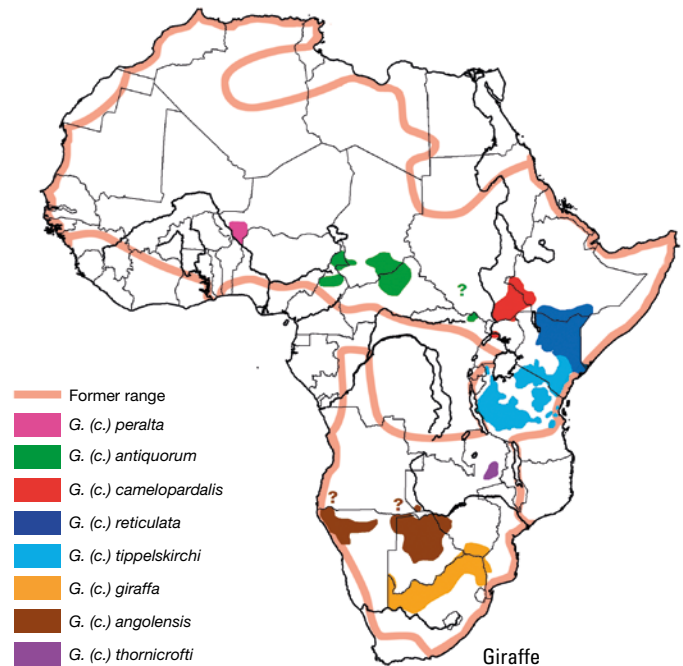
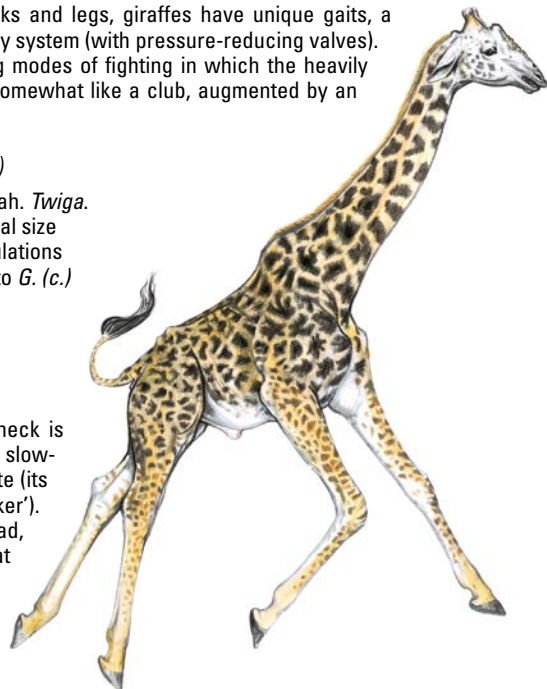
■ GIRAFFE *Giraffa (camelopardalis)*

OTHER NAMES Fr. *Girafe*. Ger. *Giraffe*. Swah. *Twiga*.

MEASUREMENTS Note that very substantial size differences exist between different populations and that the most reliable records refer to *G. (c.) giraffa*.

Total height 3.5–4.7m (♀), 3.9–5.2 (6.6?) m (♂). Sh. ht 2.72–2.92m (♀), 3.13–3.47m (♂). T 760–1,100mm. W 703–1,049kg (♀), 972–1,511(1,930?)kg (♂).

RECOGNITION The length of a Giraffe's neck is matched only by that of its legs, and its slow-motion lope covers ground at a great rate (its Arabic-derived name means 'fast walker'). The legs end in enlarged hocks and broad, rounded hooves. Giraffes can run at 60kph, at which rate the hoof may pivot forward so that the animal's weight is borne directly on the hock. Both young and old are able to outstrip



most predators. The neck is fringed with a short, thick mane and both sexes develop 'horns' above the eyes. Bony protuberances above the eyes preclude the Giraffe from being able to see upward. The face is strongly tapered and a 450mm tongue is the principal means of gathering foliage in to the large, elastic mouth and lips.

Given the familiarity of Giraffes in zoos and parks and their images in media, biologists, like most of the public, generally thought of the Giraffe as a single species. Two major genetic studies have challenged this assumption and demanded a re-assessment of Giraffe taxonomy and nomenclature. A major conclusion to emerge has been recognition that Giraffes from the centre–west realm have been genetically separate from Giraffes in the south–east realm for some 1.5 million years. Excepting small Reticulated Giraffes from the Horn of Africa (which probably deserve to be treated as a third major population), subpopulations within each of these realms are much younger.

Because no known fossils of modern Giraffes pre-date the Pleistocene, it is likely that the Giraffes' common ancestral population began to diverge not long after its initial spread through all African savannas. When populations, such as those of Giraffes, are more distinctive genetically than their appearance and anatomy suggests, grouping species into a super-species offers a useful naming system and that course is followed in this revised edition. While the two or three geographic mega-units (centre–west, south–east and Horn of Africa) clearly exist at a higher level of distinctness than do the regional subpopulations, the Giraffe species-groups presented here follow precedent in accepting a total of eight members. Colours vary greatly between individuals and occasional 'sports' have bizarre patterns, from uniform fawn or black to various blotchy permutations. In spite of this variation, all the populations listed below are morphologically distinct. The ranges cited here are historic because most Giraffe distributions are now vestigial.

Centre–west realm

West African Giraffe, *G. (c.) peralta* (includes *renatae*): W of L. Chad to Senegal.

Kordofan Giraffe, *G. (c.) antiquorum* (includes *congoensis*): W of R. Nile to L. Chad between 2° N and 14° N.

Nubian Giraffe, *Giraffa (c.) camelopardalis* (includes *rothschildi* and *cottoni*): E of R. Nile and W of Ethiopian dome, from Equator to 16° N.

Horn of Africa arid focus

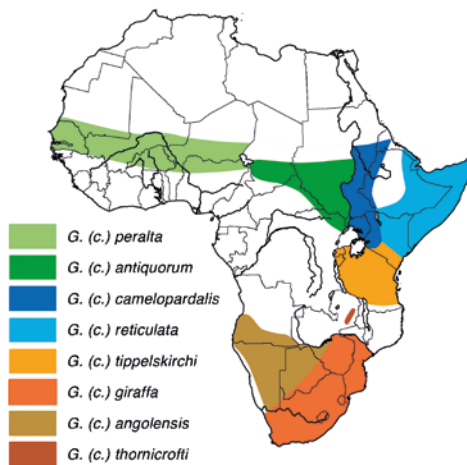
Reticulated Giraffe, *Giraffa (c.) reticulata*: Horn of Africa E of Ethiopian dome to R. Tana. Thought to hybridise with Masai Giraffe between R. Tana and R. Galana. Also to hybridise with Nubian Giraffe along the Lorogi plateau to Samburu Hills (possibly further west too).

South-east realm

Masai Giraffe, *Giraffa (c.) tippelskirchi* (includes *schillingsi*). Tanzania and S Kenya from Galana R. south to Rufiji R. Thought to hybridise with *reticulata* between R. Galana and R. Tana.

Cape Giraffe, *G. (c.) giraffa*: southern Africa. Angola Giraffe, *G. (c.) angolensis*: Kalahari and neighbouring *Acacia* country in SW Africa.

Luangwa Giraffe, *G. (c.) thornicrofti*: isolate in Luangwa valley.



Historic Giraffe ranges interpreted as three major populations with mixed or intermediate types along boundaries.

On present genetic evidence the eight forms listed above are claimed to be discrete, with each population behaving like an isolated species. In at least one instance where the range of a long-established regional population abuts that of its neighbour (the 'Galana hybrid zone' between *reticulata* and *tippelskirchi*) many observers have pointed out that most individual Galana Giraffes exhibit permutations of coat pattern that strongly suggest widespread hybridisation (one example is pictured here). Other apparent overlap zones have been suggested in the past but, with all ranges shrunk and so many Giraffe populations facing extermination, the argument may never be settled.

DISTRIBUTION Formerly widespread throughout the drier savannas of Africa (including the Sahara and Atlas Mts during the wetter conditions of about 7,000 years ago). They range up to 2,000m but are rare in precipitous hilly country.

HABITAT Present situations are a poor guide because most Giraffe habitats are now under agriculture. They remain mostly in savannas, open woodlands and seasonal floodplains (with abundant raised, thicketed tertiary islets). Commonest in areas where rainfall, soils, wind, fire, elephants or flooding favour scattered low and medium-height woody growth. They are especially associated with savannas where *Acacia*, *Commiphora* and *Terminalia* are abundant trees.

FOOD Known to feed from more than 100 species of plant but *Acacia*, *Commiphora* and *Terminalia* species are major staples. Feeding and movement patterns differ from wet to dry seasons. The wet season is a period of abundant, green deciduous growth, during which time the Giraffes are widely dispersed. During the dry season they concentrate where evergreens survive. Sustained pruning of scattered bushes maintains a sort of acacia lawn. Irregular firing forces medium-term rotations by burning off light twig growth and removing browse for one or more years.

Giraffes, their extinct relatives and other browsers are thought to have shaped the biology of their food trees, including the evolution of thorns and galls, and the growth form of branches. Persistent and heavy browsing not only shapes the trees' form but can either delay or stimulate further growth.

The amount that Giraffes eat in a day varies but is less than half the intake of typical grazers. It is the concentrated nutritional value of the foliage they select and super-efficient digestion that makes modest feeding possible.

BEHAVIOUR All social units are temporary. Adult male Giraffes may be vestigially territorial because mature bulls monopolise all matings and tend to be intolerant of other large males at the cores of their very variably sized home-ranges (cores may be as large as 80km² but year-long movements are known to range from 5 to 654km² or more). Females have very unstable home ranges that may drift from year to year. These overlap those of very many other females, with which they may associate (in mixed-sex groups of up to 50 animals). Such associations are temporary. The only



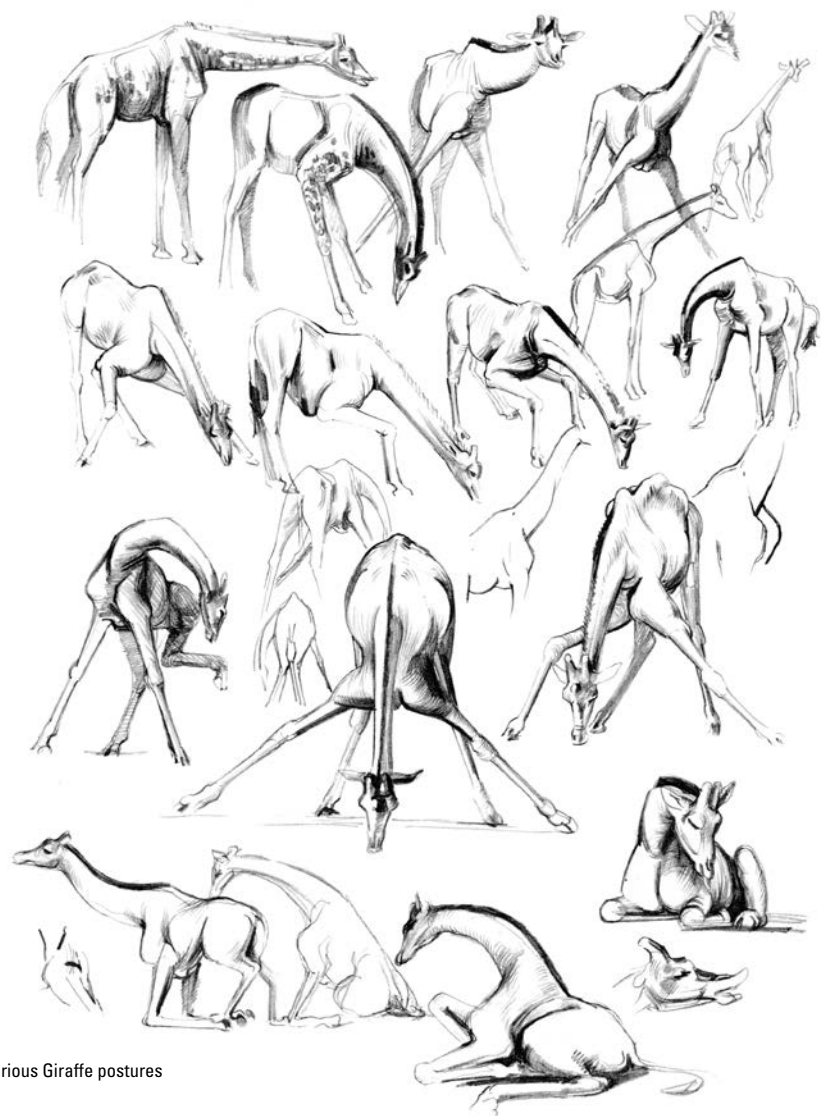
Giraffe patterns display both regional characteristics as well as individual variation. Patterns shown above come from localities indicated on the map (opposite) and correspond to the key (below).

Key to Giraffe patterns:

- | | |
|---|--|
| 1. Nubian Giraffe <i>G. (c.) camelopardalis</i> | 6. Masai Giraffe <i>G. (c.) tippelskirchi</i> (light morph) |
| 2. Reticulated Giraffe <i>G. (c.) reticulata</i> (dark morph) | 7. Nubian Giraffe <i>G. (c.) camelopardalis</i> (dark morph) 'cottoni' |
| 3. Reticulated Giraffe <i>G. (c.) reticulata</i> (light morph) | 8. Nubian Giraffe <i>G. (c.) camelopardalis</i> 'rothschildi' |
| 4. West African Giraffe <i>G. (c.) peralta</i> | 9. Masai Giraffe <i>G. (c.) tippelskirchi</i> (dark morph) |
| 5. Hybrid Reticulated Giraffe <i>G. (c.) reticulata</i> × Masai Giraffe <i>G. (c.) tippelskirchi</i> (between Tana and Galana Rivers) | 10. Angola Giraffe <i>G. (c.) angolensis</i> |
| | 11. Cape Giraffe <i>G. (c.) giraffa</i> |
| | 12. Masai Giraffe <i>G. (c.) tippelskirchi</i> |

stable associations of a female Giraffe's life are the year-long periods of motherhood and the traditional, highly localised, calving area to which she returns again and again to give birth.

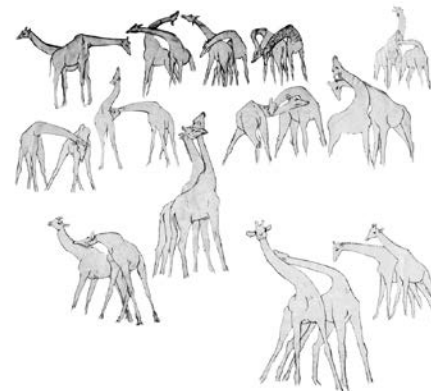
Gestation lasts 14 months. An oestrous female may attract close attention from many males but the majority of matings are with one or other of a few very large males. These tend to be spaced



various Giraffe postures

out within her current range. Newborn calves rise to their feet within 5 minutes and after a week or so may join up to nine other very young calves also born in the vicinity. One or more mothers are often nearby, although they tend to leave the 'crèche' of youngsters on their own during the middle of the day (the time of day when they feed most intensively and when most predators are inactive). Lactation lasts from 6 to 12 months and the young remain close to the crèche for 3–4 months, after which they begin to accompany their mothers for gradually increasing periods of time. By 6 months a calf is moving independently with adults.

Between half and three-quarters of all Giraffes fail to survive their first year. The main cause of death is predation from Lions, hyaenas, Leopards, crocodiles and humans. Their fearlessness and independence render them easy prey. Male calves are especially vulnerable because they remain in groups for 3–4 years before gradually becoming more solitary and localised. Their preoccupation



Neck sparring and fighting in male Giraffes.

with 'necking' may prejudice their survival still further.

Necking behaviour in young males tends to result in some sort of hierarchy or *modus vivendi* being established among them. These contests of strength involve rival males standing shoulder to shoulder, straining against each other, seeking to gain purchase in order to deliver and counter periodic arching blows of the head. The apparently languid pace is misleading – the necks and jaws of adult giraffes are occasionally broken in such contests and one blow has been seen to launch an adult eland into the air. By the time survivors are fully mature (at about 10 years) they are likely to have become more residential and reduced their range. Ranges narrow especially in the dry season, the peak season for conceptions.

ADAPTATIONS The long neck of the Giraffe has involved a number of physiological and anatomical changes. The shoulders are deep and muscular, the thoracic vertebrae are exceptionally long in order to carry strong ligaments and the circulatory system has had to evolve very elastic vessels as well as valves to offset the sudden build-up of blood pressure whenever the head swings.

The exceptionally fast growth of Giraffes (animals double their height in 12 months) probably represents an early evolutionary strategy whereby very large, but relatively defenceless, animals were able to mitigate predation by growing too large for predators to overpower. A vast and nutritious food supply and the ability to sustain high levels of predation from carnivores was probably shared with those other giraffe species that became extinct in relatively recent eras.

STATUS Giraffes are now restricted to protected conservation areas and a few sparsely populated regions and their range continues to contract. Giraffe densities and biomass vary but, in optimal habitats, densities of up to two Giraffes per km² (a biomass of 2,000kg per km²) are sustainable without prejudicing the much higher densities of other grazers on the same land. This resource could be returned to many regions if more rational patterns of land-use were devised than those imposed by currently blinkered pastoral and livestock interests. While some southern and eastern Giraffe taxa are not yet threatened, all Sahelian forms face extinction.

■ OKAPI *Okapia johnstoni*

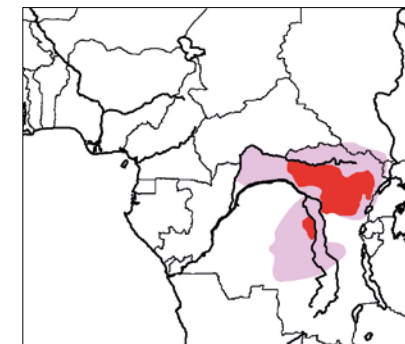
OTHER NAMES Fr. *Okapi*. Ger. *Okapi*.

MEASUREMENTS HB 1.90–2.15m. T 300–560mm.

W 210–356kg.

RECOGNITION A rotund, tall-shouldered ungulate with robust legs, a thick neck, large ears and an exceptionally long, mobile tongue. The hornless females are chocolate to chestnut-brown with bold black-and-white markings on the legs and white stripes radiating out from the genital area across the rump. Males are similarly marked but smaller and darker, some almost purplish black. They have swept-back, skin-covered 'horns' above the eyes. A mane, prominent in juveniles, is reduced or absent in most adults.

DISTRIBUTION NE DR Congo and (formerly) Bwamba, Uganda. Mainly associated with minor tributaries of the NE DR Congo river basin at altitudes above 500m. It is absent from lower-lying parts of the basin and prefers firm ground. Fossils suggest that Okapis or close relatives were formerly more widespread. The spread of fire, antelopes and prehistoric hunting may have combined to extirpate them.



Possible recent range

Okapi



Okapi

HABITAT Dense, low undergrowth within the rainforest belt in river valleys, chablis and on higher ground in the wet season.

FOOD Shade-loving plants in the undergrowth; also fruits, ferns and fungi. Violet-shrubs (*Rinorea*) and *Drypetes* (a common tree) are reported favourite foods. Single leaves or entire twigs are plucked with the long, muscular, blue-black tongue. The Okapi maintains a very consistent diet and browsing routine throughout the year.

BEHAVIOUR Although of a restricted distribution and scarce over most of its range, the Okapi is common in some localities, reaching 1–2.5 per km². Female home-ranges average 5km². Males range over a much wider area and some male territorial behaviour is suspected. They snort loudly when disturbed and make coughs and a piping sound. A female remains in oestrus for as long as a month, during which time she is closely attended by a male. Both show frequent aggression, interrupted by much rubbing, circling and head-tossing. There is an oestrus want call. Fighting males wrestle with their necks but also charge and butt one another. One precocious young is born after a 427–457-day gestation. The calf maintains contact with the mother by coughs, bleats and whistles but remains hidden; the mother goes to suckle it when called. Calves are weaned by 6 months. Male horns develop at between 1 and 5 years. Females are sexually mature at 3 years. The Okapi lives for 15–20 years.

ADAPTATIONS The disposition of pattern differs fundamentally from that found in many bovids. The Okapi has neutrally coloured ears and neck, dark fronts to the forelegs and is rather dull and inconspicuous from the front. In contrast, the tail view is truly startling. Infancy and courtship (both involving close following) are the only major departures from a mainly solitary existence. Conditioning in infancy may serve to make the optical impression created by the stripes powerfully attractive, thus offsetting aggressive or anti-social behaviour.

STATUS The Okapi has enjoyed absolute protection since 1933. The emergence of a massive commercial bushmeat trade in DR Congo now threatens it in all parts of its range. Reintroduction to Uganda's national parks should be considered if the government can be persuaded to take conservation more seriously.

DEER Cervidae

Deer are a non-African line of ruminants that resembles antelopes very closely in body proportions and ecological niches. The most primitive species have sharp tusks like chevrotains. More advanced forms have tusks and small antlers that serve as defensive weapons against wounding by canines. In other species antlers have acquired elaborate branched structures and secondary uses in head-to-head clashes and 'wrestling'. Unlike the fixed horns of bovids, antlers are shed each year (their fast annual growth has physiological resemblances to forms of wound-healing processes, which suggests that antlers may have evolved from a type of scar-tissue). Species vary in the degree to which the side-toes have been reduced.

Deer digestive systems parallel those of bovids in having diverged in order to cope with difficult diets, but differ in structural details. Both cervids and bovids are the most recently evolved of ungulates. The former are widely distributed over Eurasia and the Americas but are most diverse in South-East Asia and South America. Red Deer have been in North Africa no more than 1 million years and there is no evidence to suggest that other species colonised any other part of Africa.

RED DEER *Cervus elaphus*

OTHER NAMES Fr. *Cerf élaphe*. Ger. *Hirsch*.

MEASUREMENTS HB 1.6–2.5m. T 120–150mm. Sh. ht 0.9–1.4m. W 100–150kg (♀), 150–225kg (♂).

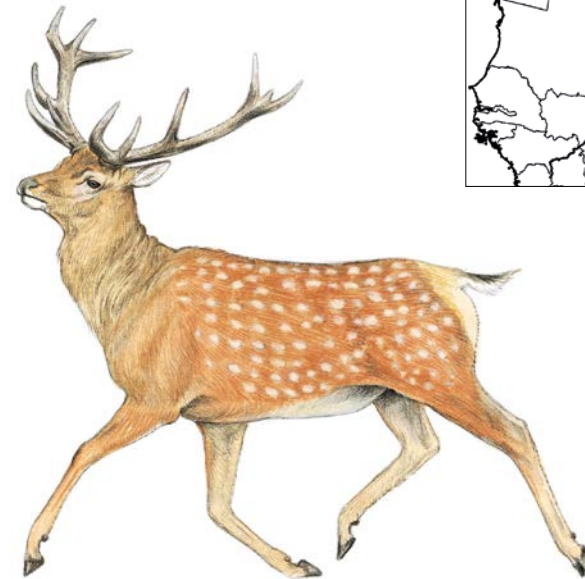
RECOGNITION A large, long-legged antelope-like ungulate. Females are without head weapons. The larger males also lack them, briefly, in spring but grow prolonged bone-like 'antlers' over the summer months. Antler 'velvet' is shed in late summer and the antlers are used as weapons only in the short autumn 'rut' or mating season. The winter coat is dark brown with longish hair. After the spring moult the shorter summer coat is lighter reddish with pale spots. The rump is yellowish. There are scent glands in front of the eyes, under the tail, between the hooves and behind the hocks.

GEOGRAPHIC VARIATION Barbary Red Deer, *C. e. barbarus*, is the only race in Africa.

DISTRIBUTION Known as fossils from Morocco to Tunisia for nearly 1 million years. Probable relicts of that population are now only found in the Medjerda Mts on the Algeria–Tunisia border. Their greatest resemblance appears to be to Corsican deer.



Red Deer



HABITAT Cork oak and wild olive forests growing on sandy mountain soils. Red Deer remain in the woods during the day, only emerging into the open at night. The habitat is a mosaic of oak woodland, maquis and grassy meadows. Wallows are used in the summer, while moulting and during the rut (males).

FOOD Shoots of trees and shrubs, bark, young twigs, grasses, sedges and herbs; also fungi and cultivated crops. In spring and summer Red Deer enter fields and vineyards (at night or in the early morning). They are most active around dawn and dusk.

BEHAVIOUR Males and females live largely separate existences outside the rutting season. Females tend to be very residential. Male gatherings are strongly hierarchical, even for the period the animals are without antlers. The rut, which is noisy and conspicuous in many parts of their range, tends to be more cryptic in North Africa, possibly as a response to hunting. All copulations are monopolised by dominant males. After a gestation of 235 days, young are born in May and June. They tend to 'freeze' or hide when disturbed during the first 2 months. After moulting an infant coat they grow and develop rapidly, moult again into their winter coat and continue taking milk for about 7 months. They are sexually mature at 18 months (but males can seldom win mates while still young). They live for about 15 years (rarely up to 25 years).

ADAPTATIONS Long-term studies on Red Deer have shown that fewer than five surviving calves are the average lifetime offspring for each sex. However, males that win more fights get more mates and have been found to sire up to 24 offspring (about twice the maximum for females). This massive success of the winning stags is the outcome of intense male competition squeezed into the few weeks of the rut. It is antlers (backed up by brawn and drive) that allow stags to win fights but outside the rut antlers have limited use. Were antlers permanent, frequent damage would eliminate otherwise healthy contestants. Each year's regrowth progressively enlarges and adds more branches to the antlers, thereby improving the chances of their owner winning fights and siring more offspring. It is therefore likely that large antlers were elaborated in the context of strongly seasonal breeding.

STATUS Although deer have been introduced from Europe to both Morocco and South Africa, the Medjerda population is the only one thought to represent a stock that has occupied NW Africa uninterrupted since the Pleistocene. They are protected on both sides of the border, in the El Kala NP in Algeria and the Feijja NP in Tunisia.

BOVIDS, HORNED UNGULATES BOVIDAE

Bovines Bovinae
Antelopes, goats and sheep Antilopinae

RECOGNITION Horned ungulates are long-legged, hooved herbivores that range in size from the 2kg Pygmy Antelope to the 1,000kg elands. The males of most species are horned with true keratinous horn sheaths over bony cores. In some species, females are hornless; in others, females also have horns (but never as heavy as in males). Most antelopes have a variety of scent glands. Most have horizontally oriented pupils. They come in a great variety of coat colours and patterns. All horned ungulates ruminate but food preferences vary widely: green-leaf-eating and dry-grass-eating are extremes (with fruit-eating duikers a specialised offshoot).

GENEALOGY Of Eurasian origin, both conservative Asian and African spiral-horned bovines are less well adapted to very dry habitats than the more arid-adapted true antelopes, or Antilopinae, which are now mainly African (although of ultimate Asian origin). Antilopinae have evolved a highly efficient water-saving and cooling mechanism in the nose while the more conservative bovines rely on water-wasting sweat to cool down.

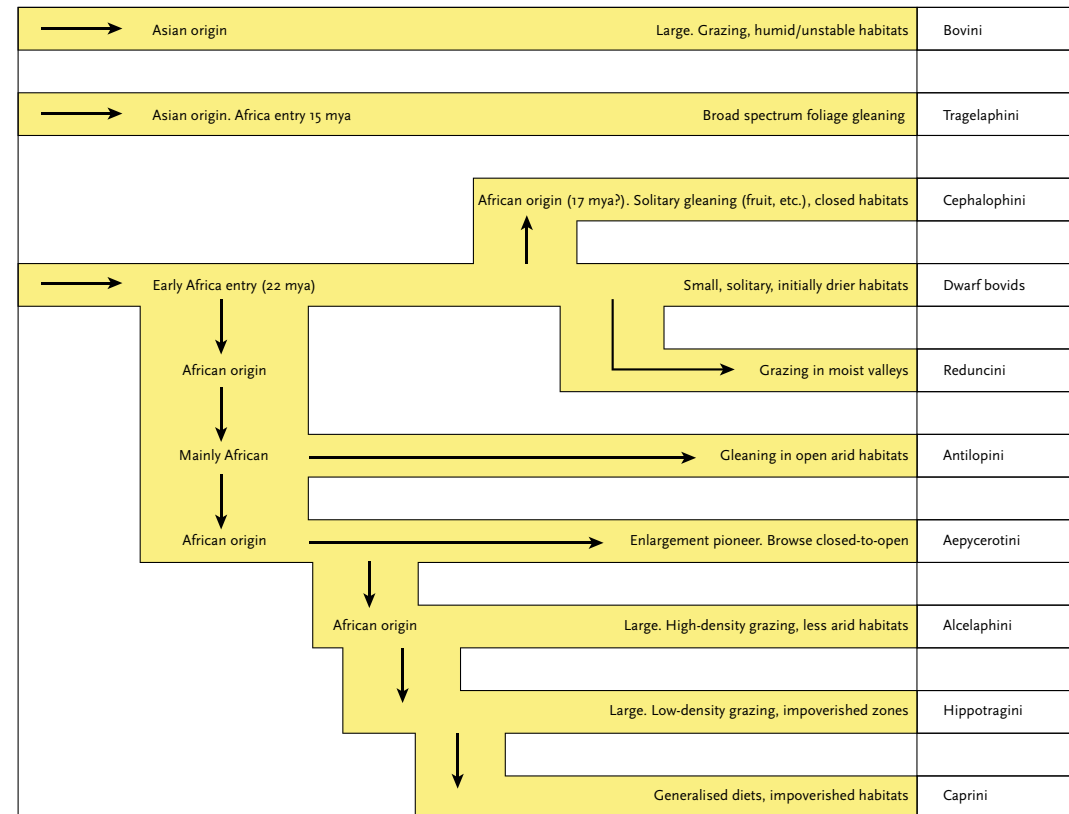
GEOGRAPHY While Eurasia was home to the most primitive living bovids (called the boselaphines) and to the earliest fossils, bovids entered Africa more than once. Thus a small ancestral antelope was the earliest immigrant (more than 20 mya); an ancestral spiral-horned bovine came next (about 15–18 mya) while buffalo and caprines were still later (about 6 mya and 1.5 mya respectively) immigrants from Eurasia. The latter, sheep and goats, derived from an early African antelope but returned to Asia where, in the face of much competition from deer, they became mountain-dwelling specialists. The other antelope tribes are mostly African. The more arid-adapted groups have been better able to move between continents because corridors were usually relatively dry.

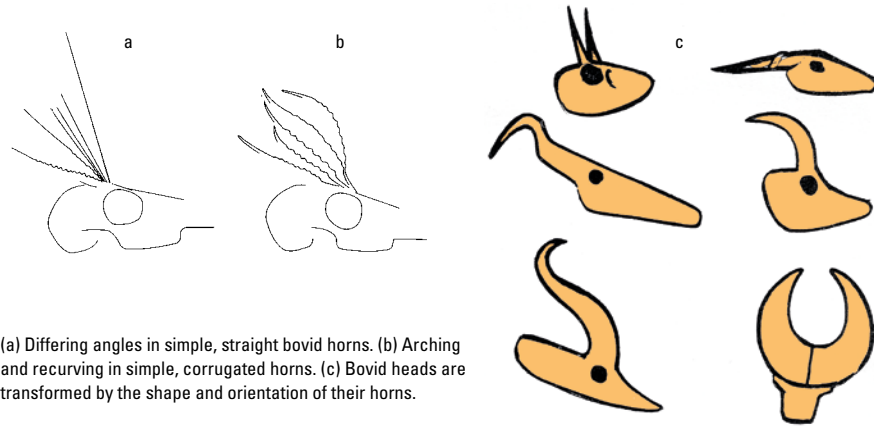
ECOLOGY Advanced rumination is the central adaptation of bovids. It could not have developed in very active animals forced to make frequent and varied demands on their metabolism. The more conservative species live solitarily in small, well-known territories where they can pick food, swallow it and then retire to chew the cud. This ecological strategy would have typified the earliest bovids. Specialisation in grass-eating came much later and developed in parallel among several bovine and antilopine lineages.

NATURAL HISTORY The need for more efficient weapons helps to explain the development of horns. A most important difference between chevrotains and bovids is the loss of tusks in the latter, leaving the mouth wholly devoted to food-gathering. In the male, simple, short, sharp 'head spikes' replaced tusks as weapons and helped protect his exclusive access to one or more females. Subsequently horns have elaborated until they have totally transformed the architecture of bovid heads. Every type of horn is wielded according to appropriate fighting and defensive techniques. Most species are annual breeders with births tending to peak in the wet season. Bovids produce well-developed young that may remain hidden for a while or, in advanced species, are sufficiently strong to run after their mothers within hours of their birth.

ADAPTATIONS The grosser differences between bovines and antelopes concern thermoregulation, gland structures and horn types. The divergence probably began with a basal bovine stock in cooler Eurasia responding to unstable seasonal habitats by enlarging its body size and becoming nomadic. In Africa improved heat and drought resistance was linked at first with small body sizes. These features permitted stable home-ranges and year-round territories.

Diversification by habitat of Bovinae and Antilopinae.





(a) Differing angles in simple, straight bovid horns. (b) Arching and recurving in simple, straight horns. (c) Bovid heads are transformed by the shape and orientation of their horns.

Scent signals are augmented by a variety of loud barks, whistles, moos and trumpeting. Visual signals are also important, with heads, ears, legs and rumps marked with various contrasting patches which are flagged or flashed in appropriate contexts.

The development of hard cellulose digestion (grass-eating) from the universal 'nitrogen-metabolism' type of digestion (leaf-eating), has taken place independently in at least six of the 10 main bovid tribes.

BOVINES Bovinae

Oxen	Bovini
Spiral-horned bovines	Tragelaphini

These animals are distinguished from antelopes by their generally larger size, an absence of facial or pedal glands, and smooth or keeled rather than annulated horns. Most are mobile and tend to form hierarchies in which males generally avoid direct confrontation. Hierarchy encourages sexual selection in favour of larger males. Females are smaller, hornless or less heavily horned than males in all bovines. The development or suppression of horns in females is neither primitive nor advanced, rather both horns and hornlessness involve different mechanisms for getting at resources. Horned females tend to resemble males in establishing hierarchies. They are also active in defending their young.

OXEN Bovini

African Buffalo	<i>Syncerus caffer</i>
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Characterised by low, wide skulls with a short face and smooth horns that splay out sideways from the skull, oxen are large, heavy and short-legged, needing long periods for rumination. Old males tend to become slow and placid.

The living African Buffalo evolved from a smaller ancestral type that entered Africa 5–6 mya. Possibly aided by human predation, African Buffalo had effectively replaced a giant and very wide-horned type which was abundant and widespread from about 4 million to a few thousand years ago. It is now being replaced by domestic cattle.

Although some traditional pastoral societies were quite tolerant of wild animals and co-existed with antelopes, the modern take-over and conversion of land for livestock and the direct competition from cattle now threaten the existence of many wild animals right across Africa. Rapidly accelerating exploitation of exotic oxen and grasslands continues to raise major social, economic and political issues in Africa.

AFRICAN BUFFALO *Syncerus caffer*

OTHER NAMES Fr. *Buffle d'Afrique*. Ger. *Büffel*. Swah. *Nyati, Mbogo*.

MEASUREMENTS HB 2.25–3.40m. T 670–900mm. Sh. ht 1.0–1.7m. W 425–850kg.

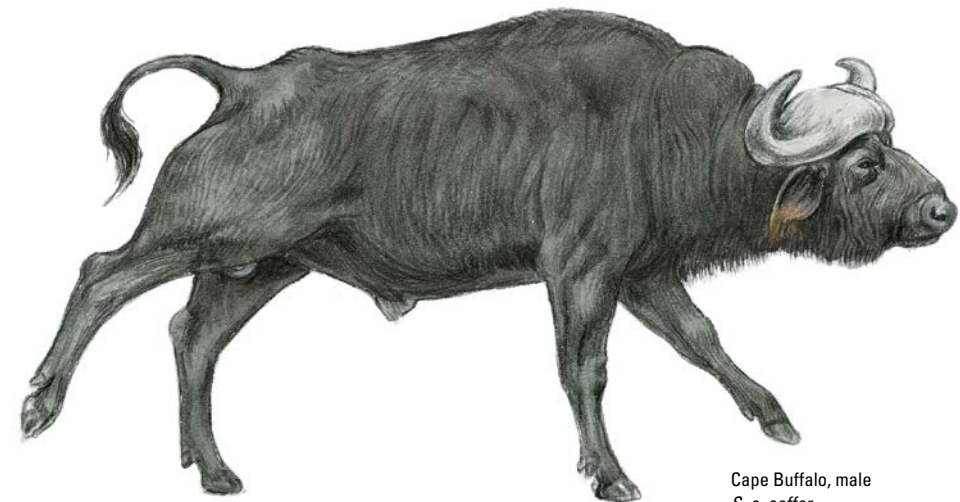
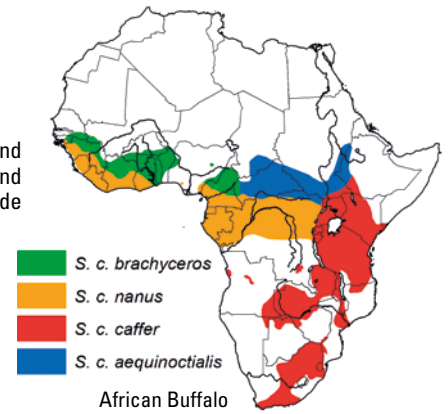
RECOGNITION Large ox with thick, bossed horns and tasselled ears. The coat is short, often sparse and coloured from a rich red to black. The underside and chin is often pale (even creamy white) and patches of contrasting colour appear on the face and legs. The differences between forest and savanna forms are substantial but there are intermediate and mixed types.

GEOGRAPHIC VARIATION Western Buffalo, *S. c. brachyceros*; Forest Buffalo, *S. c. nanus*; Cape Buffalo, *S. c. caffer*; Sudanic Buffalo, *S. c. aequinoctialis*; plus the possible relict 'Mountain Buffalo', *S. c. mathewsi* (N of L. Tanganyika).

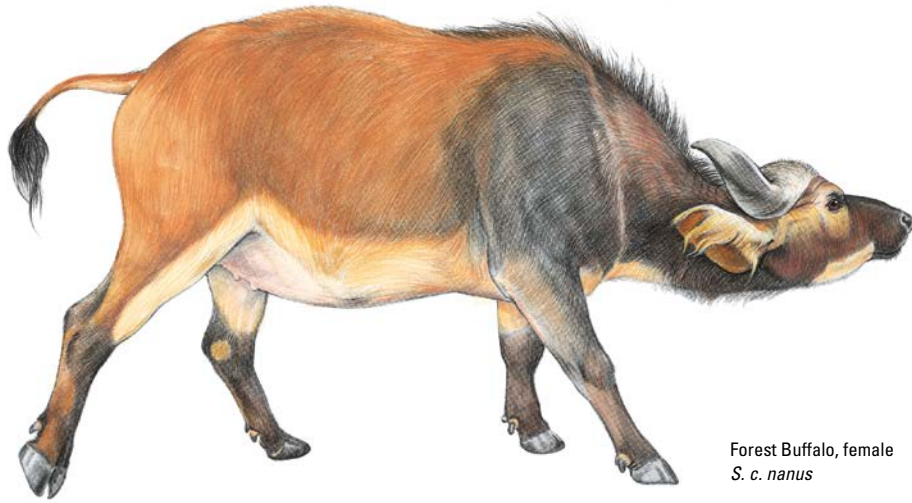
Forest Buffalo are generally below 1.2m in height and 320kg in weight while the savanna forms tend to exceed these measures.

DISTRIBUTION The larger savanna forms are thought to represent recent expansion and evolution of the smaller and more conservative forest form. Until recently they ranged across all but the driest parts of sub-Saharan Africa, their local range being limited to about 20km from water. Greatly reduced by hunting and habitat loss, some populations may never have recovered from the rinderpest epidemic of the 1890s.

HABITAT The Forest Buffalo depends on low-level browse and an undetermined minimum of grass in its diet, limiting it to grassy glades, watercourses and waterlogged basins. The humid climate ensures continuous plant growth which ensures that small areas will support buffalo throughout the year. Heavy browsing and grazing in 'buffalo glades' helps to limit or delay plant growth. Savanna buffalo (*brachyceros* and *caffer*) also seek out forests and valley bottoms, where possible, but can stay in the open and resist overheating and desiccation by becoming immobile or by lying in wallows. Their need for water and dense cover, as well as grass, makes them favour mosaics and savannas with patches of thicket, reeds or forest. They retain strong attachments to traditional ranges even when conditions change.



Cape Buffalo, male
S. c. caffer



Forest Buffalo, female
S. c. nanus

FOOD Grazing, breaking and trampling by buffalo favours rapid grass regrowth which encourages intense and repeated foraging. Particularly favoured grasses are *Cynodon*, *Sporobolus*, *Digitaria*, *Panicum*, *Heteropogon* and *Cenchrus* species but a wide choice of swamp vegetation is eaten. Grazing is quickly influenced by disturbance or human predation, with animals switching from continuous grazing to dawn, dusk and night-time grazing.

BEHAVIOUR The Forest Buffalo forms small groups of up to 12 animals with related females and their offspring as the core and one or more attendant males. Other males are solitary or form small bachelor parties. Savanna buffalo can assemble in much larger aggregations but similar 'family' clusters amplified into regular clan-like associations are also attended by bulls. Within these clans adults of both sexes develop hierarchical rank orders. They have well-marked seasonal breeding peaks and the dry 'off-season' sees many males breaking away from female families or clans. Gatherings of as many as 2,000 animals are only possible during the rains or on major patches of rich pasture.

Female receptivity is preceded by signs of oestrus that attract many bulls. Here the effects of male rank come into play, with the top bull or bulls having priority. Nonetheless fights are common and collisions after head-to-head charges have ended in one bull cartwheeling into the air to land on his back. Gestation lasts about 11 months and birth intervals of 2 years are normal. The cow-calf bond is very strong and exclusive but the female's attachment to her herd is also close. Thus, all adults respond to distress calls and even bulls wounded by other bulls seek refuge in the herd. Blind or three-legged animals are known to be healthy members of their family or clan. African Buffalo have been known to live for 26 years.

ADAPTATIONS The Forest Buffalo lives in habitats that do not suit large carnivores and offer easy retreat into cover. A heavy build, short legs and slow pace are therefore no disadvantage. Food is in limited, patchy but reliable supply, leading to scattered, small, resident herds. The small, back-swept horns of the Forest Buffalo reflect the infrequency of fighting and head-to-head weight-testing engagements. Increase in the frequency of fights and ever-greater selection for larger males has contributed to the rapid evolution of enormous horn bosses. When the field is free from obstruction to movement or vision, challenges are taken up from a distance and end in a full-tilt charge.

Savanna buffalo betray recent forest origins in other ways. Vision, a dominant sense in most open-country animals, is less important than sound. Quiet lowing is the preferred way of keeping in touch, especially in dark forests. This allows even blind animals to remain safe in the herd.

STATUS While this species as a whole is in no danger of extinction, its western and central African mountain forms are declining fast. Nonetheless it is well represented in numerous national parks and reserves. Not endangered.

SPIRAL-HORNED BOVINES *Tragelaphini*

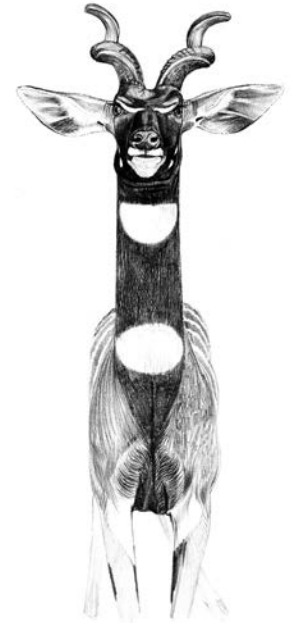
Nyalas, kudus and bushbucks *Tragelaphus* (7 species)

Elands *Taurotragus* (2 species)

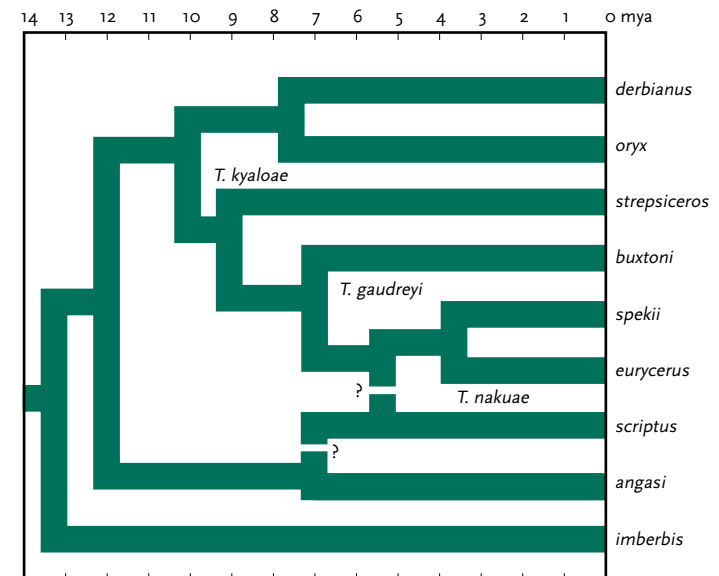
Medium-sized to large bovines with a deep body and a narrow head with big ears and twisted or spiral horns in the males. Teeth are low-crowned and, like the digestion, adapted to a diet of young, nutritious vegetation. Glandular secretions are mostly diffuse (rather than from facial or pedal pockets). The hornless females of most species have more of a generic resemblance than the larger males, which have distinctive horn shapes and darker, more contrasting coat patterns. The elands and the Bongo are 'giant' forms, with horned females.

Some zoologists used to make no distinction between tragelaphines, oxen and an Asiatic animal that resembles both, the Indian Nilghai (*Boselaphus*). Fossils suggest a common Asian origin for all three bovine groups but their African branch has been distinct for at least 15–18 million years.

In the past tragelaphines were often subdivided into various genera or sub-genera. With the advent of molecular phylogeny the consensus has been to group all tragelaphines in *Tragelaphus*. All species derive from a single immigrant ancestral type of which the earliest derivatives are the Lesser Kudu and Nyala (*T. imberbis* and *T. angasi*), both confined to dense thicket habitats. At about 10 mya a split developed between a gracile but still conservative, thicket-loving lineage and a lineage of larger size, adapted to more open habitats. Greater Kudu and the elands are descendants of this adaptive phase. The Mountain Nyala, *T. buxtoni*, is the relict of a large type sharing origins with the Greater Kudu. Still later, a forest lineage emerged giving rise to three surviving species: Bongos



Lesser Kudu, frontal view



Tentative phylogenetic tree of tragelaphine radiation (in part after Willows-Munro *et al.* 2005 and Hassanin *et al.* 2012). Note that SE and centre-west *Tragelaphus scriptus* might have separate or genetically mixed origins.

(large forest-edge descendants), Sitatunga (swamp refugees) and Bushbucks ('dwarf' morphs). Bushbucks have very complex genetics and, possibly, might represent an amalgam between an early Nyala-like descendant and a dwarfed Bongo-like lineage.

Fossil relatives (or parallel cousins) of this now exclusively African group are known from south Asia. There is still a strong eastern and southern African bias in their distribution (typical of other organisms with 'immigrant' origins).

All species are gleaners of green foliage in a wide variety of mostly unstable habitats. None tolerates true desert. Herding in the larger tragelaphines is not induced by the habitat (as it appears to be among the kobs, Reduncini) but is the defensive strategy of females and young.

Their social structures tend to be rudimentary. Vulnerability of the young is a major incentive for forming herds among the largest, most mobile species. Females are the more ready to associate, and the need to defend the young (as well as enforce rank) has influenced the development of horns in female Bongos and elands.

Males also show rank orders and sometimes live at very high densities. Rank is assessed through size-enlarging displays and may be partly cyclical. Periodic testosterone 'surges' are signalled by aggression, or *ukali*. This deters confrontations. Rare instances of all-out fighting and death may result from confrontations between well-matched males who are both in their *ukali* phase. Males of all species horn the soil, or vegetation. These are not territorial beacons but more general advertisement of status and presence.

In marked contrast to buffalo and other bovines, tragelaphines are alert and highly visual animals and visual signals are both subtle and highly structured. All species begin as striped and blotched infants that 'freeze' or hide to escape detection. They have conspicuous white flashes on ears, muzzle and lips. These function most obviously when mothers approach hidden young, at which time they bob or flag their heads up and down, sometimes calling very softly at the same time. Adult males develop ritualised broadside displays to impose upon other animals. Manes, crests, black-and-white markings and rangy, flat-sided figures all serve to enhance male displays during courtship but more especially in rank contests.

Another clue to rank is the loudness and timbre of the male barks. Visual and vocal signals appear in different permutations in four closely related species. The flamboyant Nyalas, living in mosaics of thickets laced with open corridors, valleys and glades, silently strut their frills and crests. Lesser Kudu, risking ambush in denser, drier bush, have subtle, close-contact patterns on legs, face and throat and bark sparingly. The Sitatunga, submerged in thick grass, mud or water, has vestigial or muted patterns but barks frequently, loudly and persistently. The Bushbuck is the most versatile: colourful, contrasty and Bongo-like in the forested west, it is more discretely Nyala-like in the drier, more open (and dangerous) south and east. Both sexes can be voluble.

Spiral horns have variable functions but are particularly well suited to defensive horn-wrestling. The differential growth mechanisms determining spirals are so simple that much variation is possible. Individual variations are common in some species but nonetheless the trajectory of spirals is highly species-specific.

Studies of tragelaphine brains have revealed that the Nyala (*T. angasi*) and Lesser Kudu (*T. imberbis*) have much the smallest (and presumably most primitive) brains, confirming their conservative status.



Sitatunga male head, frontal view.

■ LESSER KUDU *Tragelaphus imberbis*

OTHER NAMES Fr. *Petit koudou*. Ger. *Kleinkudu*. Swah. *Tandala ndogo*.

MEASUREMENTS HB 1.10–1.75m. T 250–400mm. Sh. ht 0.9–1.1m. W 56–70kg. (♀), 92–108kg (♂).

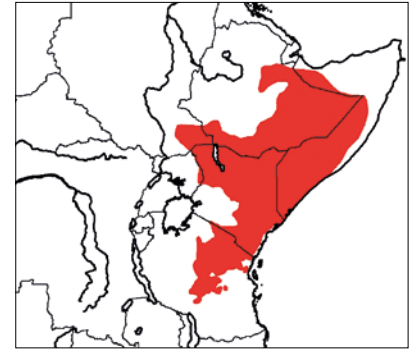
RECOGNITION Females and young are bright russet, with 11–15 vertical white stripes. They have a long, narrow head and resemble the Nyala very closely, except for slightly longer legs and neck. Yearling males acquire sandy-grey colouring that is almost identical to that of similarly aged Nyala males. The black-and-white markings on face, tail and tawny-orange legs are also extremely similar in both species, with the greatest contrast in males. Although the males of both species darken with age, Lesser Kudu remain well-camouflaged by their colouring. The short and sparsely haired neck has geometric white markings on throat and chest. There are inguinal glands in the groin and secretions around the false hooves.

GEOGRAPHIC VARIATION Two subspecies described, *T. i. imberbis* (Horn of Africa), *T. i. australis* (E Africa), but apparently a continuum. A distinct form might have occurred in Arabia.

DISTRIBUTION Horn of Africa, E Ethiopia (up to 1,300m) and the drier, lower regions of Kenya and Tanzania. Formerly in S Arabia.

HABITAT Deciduous bushlands and thickets dominated by *Acacia* and *Commiphora*. Resident Lesser Kudus display some seasonal movement from the more deciduous upper slopes in the wet season to low-lying evergreen belts in the dry season.

FOOD Browsers of foliage and herbage with a strong reliance on a few evergreen species during the dry season, notably the succulents (*Calyptrotheca* and *Euphorbia*) and the Toothbrush Tree (*Salvadora persica*). Nonetheless, more than 100 species of plants have been recorded from a single locality, including sprouts (especially *Combretum* and *Cordia*), buds, leaves and pods of various *Acacia* species, flowers and fruits. Grasses are



Lesser Kudu



Lesser Kudu tail flash



Lesser Kudu, male

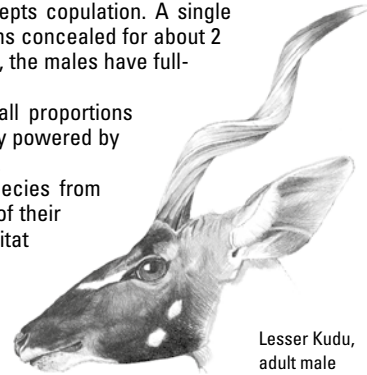
taken sparingly while green and fresh. Lesser Kudus are able to extract sufficient moisture from their food but visit water-holes or rivers where they can.

BEHAVIOUR Highly residential but non-territorial animals. Females tend to aggregate most (up to 24 in a group) and occasionally two or three females (presumably close relatives) sustain long-term companionships. Hierarchies have not been observed and all classes meet and part casually. Older males actively avoid each other except in the presence of oestrous females. Females are the most residential, with home-ranges of about 60–500ha. Newly independent males move over a larger area (up to 670ha) but gradually settle into a smaller home-range.

The normal gait is a level walk but animals can leap 2m when fleeing, throwing tail and hindquarters in the air and sometimes uttering a harsh bark as they go. Both sexes bark but this mainly serves avoidance and orientation rather than signalling alarm. There is no observable breeding peak. The male courts the female with a hicking, gasping call and whines, continually following her while rubbing and nibbling until she accepts copulation. A single young is born after about 222 days' gestation and remains concealed for about 2 weeks. Sexually mature between 18 months and 2 years, the males have full-length horns by 4 years. Lesser Kudus live for 15 years.

ADAPTATIONS Males strut and spar but their slender, tall proportions favour a form of see-sawing horn wrestling that is mainly powered by the neck and designed to bring opponents to their knees.

STATUS Extreme alertness and shyness protect this species from predators (and conceal them from would-be assessors of their status). Animals are wholly dependent on their habitat remaining relatively closed and may even benefit from overgrazing that suppresses fire. As a widespread but patchily distributed species it is not yet endangered. Nonetheless it has disappeared from a large part of its former range in Somalia.



Lesser Kudu, adult male

■ NYALA *Tragelaphus angasi*

OTHER NAMES Fr. *Nyala*. Ger. *Tieflandnyala*.

MEASUREMENTS HB 1.32–1.46m (♀), 1.60–1.98m (♂).

T 360–550mm. Sh. ht 0.8–1.05m (♀), 1.0–1.21m (♂).

W 55–68kg (♀), 92–126 (140?)kg (♂).

RECOGNITION Females are slender and russet with up to 18 bold white stripes down their sides. Males begin with similar colouring but pass through a prolonged metamorphosis as they mature. First they turn sandy grey and grow tufts on the chin, throat and belly. As the horns lengthen, the dorsal crest and continuous fringes of hair also grow in length. The colour darkens and the pale vertical stripes fade and may disappear altogether. The timing of all these developments varies individually and in some cases crests and colours remain relatively or absolutely undeveloped. The 'false' or side hooves are fringed with glands but Nyala lack inguinal glands in the groin. Male horns range from 400 to 835mm in length. Chunky hooves leave a distinctive spoor, with a compact, rounded margin.

DISTRIBUTION The Nyala occupies a highly anomalous region in SE Africa where Kalahari-type sands outcrop near the east coast. The low-lying Limpopo basin, with appreciably lower rainfall than its surroundings, forms the heart of its distribution but even outside this core area well-drained soils support a similar 'lowveld' vegetation unique to the region. It does not occur above 1,400m.

HABITAT A mosaic of dense Mopane (*Colophospermum mopane*) thickets and more open woodlands, pans and scrub. Grass in the open areas tends to be ephemeral growth during the summer rains. Patchy fires help to maintain this very unstable mosaic. The Nyala uses the thickets for browsing and shelter but emerges into more open areas at night, especially during the wet season. The denser areas of its habitat resemble those in NE Africa, with bush-willows (*Combretum*), Shepherd's Tree

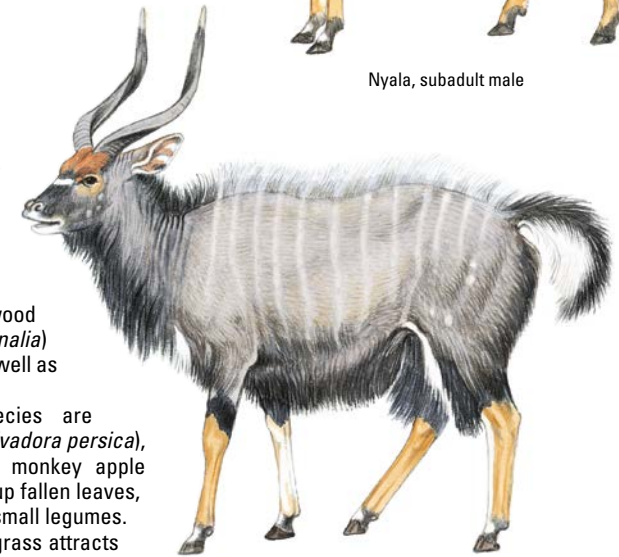


Nyala



Nyala, female

Nyala, subadult male



Nyala, adult male

(*Boscia albitrunca*), torchwood (*Balanites*), myrobalan (*Terminalia*) and baobabs (*Adansonia*), as well as acacias.

FOOD Favoured browse species are *Acacia*, Toothbrush Trees (*Salvadora persica*), buffalo thorn (*Ziziphus*) and monkey apple (*Strychnos*). The Nyala picks up fallen leaves, herbs, cucurbits and various small legumes. During the rains fresh green grass attracts it into open areas.

BEHAVIOUR Up to 50 animals can gather on a flush of fresh growth while oestrous females can attract much smaller aggregations. Essentially independent, animals will readily meet and part with a frequency that depends on local Nyala densities. Home-ranges vary from 33 to 360ha, with an average of about 75ha. There are two slight breeding peaks but births can occur in any month. Gestation exceeds 7 months (about 220 days) and the young remain concealed for nearly 3 weeks before emerging to follow their mother and join other females for variable periods. They are sexually mature by 18 months but males are unlikely to breed until they have long horns, dark colouring and fully developed crests and tassels (at about 3 years). They live for at least 16 years.

ADAPTATIONS Among bovids, Nyala males are the most extreme specialists in advertisement through visual display. Their fringes enlarge the body boundaries and dark colour increases the impression of weight and solidity. Strutting displays generally result in the subordinate male lowering his head and crest as he quietly withdraws. Rare fights with the horns are all-out and can cause death or serious wounding.

STATUS Currently satisfactory, as it is represented in good numbers in many parks and reserves. The Nyala is also a common zoo animal. Its habitat has rather low agricultural value although this could change with the provision of irrigation. Not endangered.

■ MOUNTAIN NYALA *Tragelaphus buxtoni*

OTHER NAMES Gedemsa. Fr. *Nyala de montagne*. Ger. *Bergnyala*.

MEASUREMENTS HB 1.9–2.0m (♀), 2.4–2.6m (♂). T 200–250mm. Sh. ht 0.9–1.0m (♀), 1.20–1.35m (♂). W 150–200kg (♀), 180–300kg (♂).

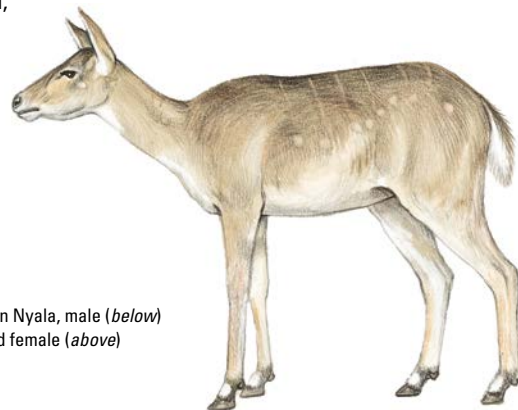
RECOGNITION In general proportions and size, the hornless female Mountain Nyala resembles a Red Deer hind. The females are of a pale liver colour, with paler undersides and a scatter of vestigial spots and stripes. The horned adult males can be nearly twice as heavy, with deep chests, a dorsal crest and body colour of sepia brown that slowly gets darker with age. This throws white markings on the ears, face, throat, chest and forelegs into strong relief. The males can be smooth and glossy or can become quite shaggy during the cold season. The tightness of the horns' spiral, and their thickness and length, vary; they can measure up to 1.18m along the curve.

DISTRIBUTION Formerly ranging all over the SE highlands of Ethiopia from Ch'erch'er Mts to Sidamo before being exterminated; now limited to the Bale massif. Ranges from 3,000 up to 4,200m but stragglers occur as low as 1,800m.

HABITAT Until very recently it flourished best in a mosaic of high-altitude woodland, bush, heath, moorland and valley-bottom grassland. The woodlands (mostly juniper and *Hagenia*), heath and bush (dominated by sage brush,



Mountain Nyala



Mountain Nyala, male (below) and female (above)



Artemesia and everlasting, *Helichrysum*) provide dry-season refuge. With the rains there is a greater choice of pasture at lower levels (a similar pattern found with the Bongo in mountains). The sedgy grasslands tend to be waterlogged and animals have even been seen eating water-plants.

FOOD Herbs and shrubs with occasional grass, lichens and ferns. The most frequent browse is plants of the tomato family (Solanaceae), St John's wort (*Hypericum*), lady's mantle (*Alchemilla*) and goosegrass (*Galium*). The Mountain Nyala eats fallen leaves of *Hagenia* during the dry season.

BEHAVIOUR Females accompanied by one or two generations of young form very frequent but essentially impermanent associations with other mother–young groups. These are regularly joined or monitored by adult males. Numbering up to 13, such groupings tend to be smaller in the dry season when they range very widely. Females restrict their movements in the rains to about 5km². Males, instead, range as widely as 20km². Young males are more mobile and less solitary than the older males and determine local hierarchies with frequent horn-wrestling contests. Older males are more prone to slow, circling displays with raised crests. Once one male begins to drop his head the engagement is broken off and the subordinate departs. There is a mating peak in about December and single young are born after an 8–9-month gestation, at the end of the wet season. The ochre-coloured young lie up for a couple of weeks and then stay closely attached to their mother for as long as 2 years, by which time female calves are themselves pregnant and males have long horns and join bachelor groups.

ADAPTATIONS The lowlands surrounding the Bale massif are inhabited by Greater Kudu and it is very likely that this more arid-adapted and more agile species outcompetes the Mountain Nyala in these habitats. Adaptation to extreme temperature oscillations and a more limited diet of specialised montane vegetation is probably the product of their prior occupation (by some millions of years) in the region. While their ancestors had a wider span of habitats (before the evolution of Greater Kudu) they have now become montane specialists in their diet and physiology.

STATUS On present showing, this pivotal species in tragelaphine evolution faces extinction. A total population estimated at 12,500 in the 1960s was reduced by 1988 to 2,000–4,000 animals, but at least half this population was restricted to a small part of Bale NP (where they reached densities of more than 20 animals per km²). From 1991, two decades of official folly have combined with gross environmental mismanagement to shatter Ethiopia's conservation estate. While licences to kill Mountain Nyalas and other 'game' animals are still easily available, study of and education about the country's natural resources and their maintenance are neglected. Export of live animals is forbidden, yet sustained captive breeding by responsible agencies has become the last best hope for this and other Ethiopian species. In the face of appalling official inertia, past proposals for the establishment of protected satellite populations in the Arssi and Harerghe Mts and elsewhere have become inconsequential. IUCN rates the species as endangered.

■ GREATER KUDU *Tragelaphus strepsiceros*

OTHER NAMES Fr. *Grand koudou*. Ger. *Grosskudu*. Swah. *Tandala*.

MEASUREMENTS HB 1.85–2.35m (♀), 1.95–2.45m (♂). T 300–550mm. Sh. ht 1.0–1.4m (♀), 1.22–1.50m (♂). W 120–215kg (♀); 190–315kg (♂).

RECOGNITION A tall dun-coloured bovine with 4–12 pale stripes on the body and spiral horns reaching a record length of 1.81m (along the curve) in males. Both sexes have a crest down the middle of the back and a mane. Males have a tessellated dewlap. Females vary in colour from sandy yellowish-grey to russet, males tend to be greyer. Females are normally hornless. Both sexes have very large, rounded ears. All living forms are substantially smaller than Pleistocene Greater Kudus.

GEOGRAPHIC VARIATION *T. s. strepsiceros* (S and E Africa), *T. s. chora* (NE Africa), *T. s. cottoni* (Chad to W Sudan).

DISTRIBUTION Originally from the mountains of SE Chad to Ethiopia and throughout the drier areas of East and southern Africa, wherever there were thickets and dense woodlands to provide



Greater Kudu



Greater Kudu, male in strutting posture

browse and shelter. Greater Kudus are increasingly restricted to stony, hilly country by expanding settlement. They can survive without water if browse is sufficiently moist.

HABITAT Thickets and evergreen forests along watercourses and on cloudy heights provide dry-season refuges. In the wet season they disperse through deciduous woodlands and may emerge at night to graze off herbs and grass on open *Acacia/Commiphora* pans. Their long legs and necks allow them to browse to greater heights, exceeded only by the giraffe.

FOOD A very wide range of foliage, herbs, vines, flowers, fruits, succulents and grass. There are striking seasonal changes in diet, with trailing morning glory (*Ipomoea*), vines (*Vigna*), firebush (*Hymenodictyon*), lucky bean (*Abrus*) and bean trees (*Markhamia*) being typical wet-season browse. Choice is much more restricted in the dry season but Sodom Apple (*Calotropis procera*), buffalo thorn (*Ziziphus*), *Acacia*, *Aloe*, *Cassia* and *Cadaba* are staples, while the slow leaf-fall of bush-willows (*Combretum*) provides browse well into the dry season.

BEHAVIOUR Wide dispersion during the rains tends to separate the sexes and there is a mating peak during the dry season when animals return to the core of their range in valley thickets. Groups of 2–25 typically include several adult females with offspring of both sexes. Although parties mingle and separate frequently, some individuals form loose associations that last from one year to the next. Males also return to the same refuges every dry season. Here several clusters of females regularly share the home-range of a dominant bull (which averages about 10km²). Such males are not territorial but they drive off any males attempting to consort with their current female companions.

Adults utter very loud and startling barks; males grunt when fighting or during confrontations. A hooting bleat signifies distress and a courting male makes a strangulated whimper as he persistently follows and nudges the female. Gestation lasts 9 months; the young lies up for about 3 weeks and is weaned and fairly independent by 6 months but remains in touch for up to 2 years. Females are sexually mature by 3 years, males by 5 years (their horns reach full length by 6 years). Greater Kudus have lived for 23 years in captivity.

ADAPTATIONS There is a relationship between the Greater Kudu's height and the great length of its horns because they have to shield the body of a sparring male. Contestants engage their spirals in order to make a firm link-up before pushing and trying to throw one another off balance. The spiral structure relates to this wrestling technique but the horns are also visual symbols of rank that may influence female preferences or choice for mating.

STATUS The Greater Kudu is rare in some peripheral parts of its range. It is endangered in Somalia and Uganda and is thought to be vulnerable in Chad and Kenya. Its overall range in Tanzania continues to contract, but Greater Kudus are still widespread and well represented in national parks and reserves, especially in southern Africa. Not endangered.

■ BUSHBUCK *Tragelaphus scriptus*

OTHER NAMES Fr. *Guib harnaché*, *Guib*.

Ger. *Schirrantilope*. Swah. *Mbawala*, *Pongo*.

MEASUREMENTS HB 1.14–1.50m. T 190–250mm. Sh. ht 0.61–1.00m. W 24–60kg (♀); 30–54 (80?)kg (♂).

RECOGNITION A small bovine, the Bushbuck converges with many antelope and deer in having average proportions. Females and young are mainly red and males become progressively darker with sexual maturity and age. Both sexes and all ages have a white underside to the broad, woolly tail, white flashes above black hooves and white markings on face and ears. Western forest forms are 'harnessed', with both vertical and horizontal white body stripes and numerous spots on the haunches. Eastern and southern 'sylvan' populations are sometimes plain and often sparsely marked with a few light spots or streaks on flanks or haunches.

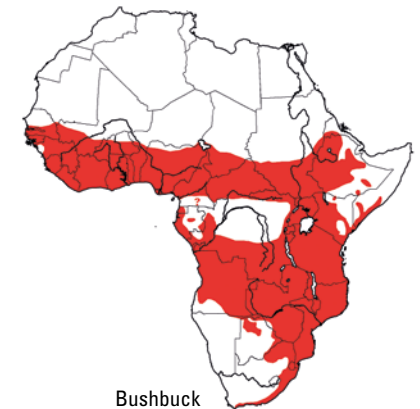
In central Africa there is a broad polymorphic belt. Genetic studies have opened the possibility of one ancestral source (*scriptus*) in the west, another (*sylvaticus*) in the south, in which case at least two species (and perhaps a hybrid swarm, too) would be called for. Much more research is needed before any informed taxonomy can emerge.

The male's horns are 250–570mm long and vary from being very short, thick and nearly straight to longer and thinner with two marked kinks in the spiral. Montane and forest forms are blacker and/or redder while those from the driest areas are yellower. In between are intermediate tints. Pale dorsal crests are present in most populations. Necks and faces are short-haired in most areas but hairy in some montane populations.

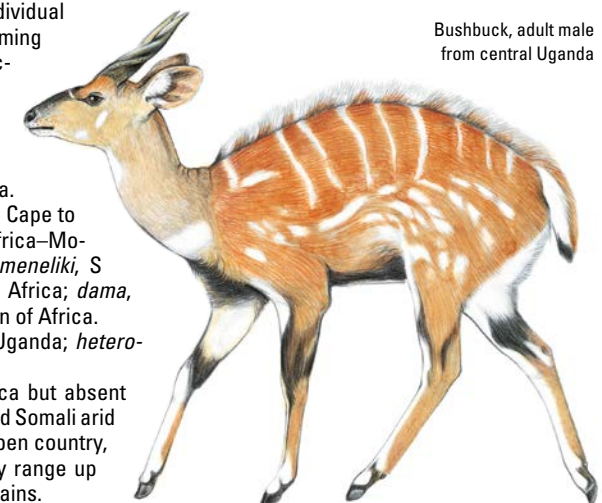
GEOGRAPHIC VARIATION Much individual variation has influenced the naming of some 27 subspecies; a selection is listed below:

Harnessed antelopes: *scriptus*, Upper Guinea; *phaleratus*, Bight of Benin; *bor*, east-central Africa; *decula*, N Ethiopia. Bushbuck antelopes: *sylvaticus*, Cape to KwaZulu-Natal; *roualeyni*, SE Africa–Mozambique; *delameri*, E Africa; *meneliki*, S Ethiopia; *ornatus*, south-central Africa; *dama*, L. Victoria region; *fasciatus*, Horn of Africa. Montane isolates: *barkeri*, NE Uganda; *heterochrous*, Mt Elgon.

DISTRIBUTION Sub-Saharan Africa but absent from the south-west, Kalahari and Somali arid regions. Locally absent in dry, open country, they are water-dependent. They range up to 3,000m on East African mountains.



Bushbuck



Bushbuck, adult male from central Uganda



Bushbuck polymorphism.

Key:

- | | | | |
|---|---|----|--|
| 1 | A dark morph of West African <i>scriptus</i> male | 8 | Pale male from Ujiji, Tanzania (<i>dama</i>) |
| 2 | West African <i>scriptus</i> male | 9 | Ethiopian Mts male (<i>menelik</i>) |
| 3 | West African <i>scriptus</i> female | 10 | Pale male from Moyale, North Kenya |
| 4 | A light morph of West African <i>scriptus</i> male | 11 | Four animals from a single high-altitude locality (Mt Elgon) (11 and 11.2: female and her young) (<i>heterochrous</i>) |
| 5 | Three males from a single locality (Kasulu, Tanzania) to show variation in pattern and colour (<i>dama</i>) | 12 | |
| 6 | | 13 | |
| 7 | | 14 | Male from Fort Portal, Uganda (<i>dama</i>) |

HABITAT Essentially dependent on thick cover, even if this is no more than small thickets centring on termite mounds. They need water but can subsist on dew. They sometimes live in reedbeds.

FOOD Largely shrubs, leguminous herbs and growing grass (often a nocturnal preference); also pods, fruits of many species. Feeding patterns are strongly influenced by disturbance and predators. Frequently resting and ruminating, Bushbucks are strictly solitary, even if they feed close to other Bushbucks.

BEHAVIOUR Living at very variable densities, the males appear to maintain linear hierarchies where both colour-coded age grades and *ukali* (testosterone surges) may influence individual status. Although normally very residential they are not territorial, even at densities of up to 26 per km² (on a fertile bushy peninsula). Deaths, the incursion of immigrants, maturation of males and coming into season of females are potentially disruptive. Females form regular associations with other females and a smaller number of males that live in the same area (and are likely to be close relatives).

One young is born after a gestation of about 6 months. Infants keep well hidden for up to 4 months and mature by 1 year, although male horns reach adult size only at about 3 years (at which time colouring and behaviour also change). They live for 12 years or more.

ADAPTATIONS The survival of Bushbucks in settled, agricultural areas and their very wide distribution imply that their smaller size and 'freezing' and crouching strategy help conceal them from both humans and carnivores. A versatile diet and ability to subsist on both grass and browse also contribute to their success. Males have a very loud, deep, roaring bark that serves to mob or even intimidate predators, as well as to challenge or alert other Bushbucks. Females also bark but less loudly and less frequently. When uttered repeatedly by a moving animal, barks indicate change and movement. Neighbouring Bushbucks scarcely ever bark in response but usually change direction or seek shelter. Males utter a twittering call while courting.

STATUS Isolated mountain morphs, such as the Mt Elgon and N Uganda forms (*T. s. heterochrous* and *T. s. barkeri*), are locally vulnerable but overall Bushbucks remain common and widespread.

■ SITATUNGA *Tragelaphus speki*

OTHER NAMES Fr. *Sitatunga*. Ger. *Sumpfantilope*. Swah. *Nzoho*.

MEASUREMENTS HB 1.04–1.46m (♀), 1.36–1.77m (♂). T 140–370mm. Sh. ht 0.75–1.05m (♀), 0.85–1.25m (♂). W 24–57kg (♀), 76–119 (130?)kg (♂).

RECOGNITION A shaggy, long-legged bovine distinguished by its long, splayed hooves and somewhat spread-eagled stance (both adaptations to living on boggy ground). The hornless females resemble other tragelaphines and are rufous with eight or ten white dorsal stripes. Males are larger and darker, with heavy, sharply keeled horns measuring 450–920mm. They describe a shallow spiral with one and a half twists. Deep, muscled cheeks contrast with a relatively short and slender muzzle.

GEOGRAPHIC VARIATION Nile Sitatunga – *T. speki* (*speki*) (Nile watershed); Congo Sitatunga – *T. s. gratus* (W and central Africa); Southern Sitatunga – *T. s. selousi* (southern Africa). **DISTRIBUTION** The primary habitat and centre of Sitatunga distribution is the Congo basin (where the ancestral population probably adapted to the shores and tributaries of the former Congo Lake). Populations in the Niger and other river basins west of this region have been allocated to the same subspecies (*T. s. gratus*). Distinct populations inhabit swamps, lakeshores and valley bottoms centred on the R. Nile and R. Zambezi/R. Bangweulu drainage basins. **HABITAT** Adaptation to a grassy diet and open swamps is secondary to inhabiting the more complex communities of shrubby growth, herbs, sedges, grasses and palms that border forest waterways.



Sitatunga



female

Eastern, southern and far western parts of their range are dominated by extensive beds of reeds (*Echinochloa*), bullrushes (*Typha*) and sedge or papyrus (*Cyperus*).

FOOD Shrubs, herbs and grasses with strong regional biases; *Monodora*, *Uvaria*, *Xylopia* and *Alchornia* species are favourite browse in Uganda, swamp grasses and sedges in Bangweulu, Okavango and the Sudd. Some flowering plants are especially favoured. Sitatungas often feed very intensively in a small area for some days or even weeks and then desert it. They are most active from 18.00 to 10.00, but are less restricted in undisturbed swamps.

BEHAVIOUR A rich, year-round supply of greenery permits exceptionally small home-ranges and potentially high densities. On Nkosi, a small, wooded island in L. Victoria, densities once reached about 200 per km² and 55 per km² have been reported elsewhere. Temporary aggregations gather for a few hours on favourite pastures only to disperse. Females are especially prone to gather in high-density areas and may be accompanied by more than one generation of calves. They have a clumsy gait but are quiet and deliberate in their movements. They avoid attention by cautiously entering thick vegetation and sink down into water very slowly, leaving only the snout and part of the head above the surface.

Crescendos of barking are common at night in high-density areas, especially after a disturbance, and sometimes stimulate more than one barker. If listening males can discern age and vigour from the timbre of a bark, such calling could reduce the likelihood of lethal fights. Courtship resembles that of other tragelaphines. Gestation lasts more than 7 months, with birth peaks noted in the dry season (July in E and SE Africa). One young is born on a trampled resting platform or in a 'form' in thick vegetation. It is then left on its own, except for quick visits by the mother. The female keeps hiding and suckling places separate by leading the young into dense vegetation to nurse. The young are independent and playful from an early age.

Resting and ruminating are invariably solitary. Sitatunga mature by about 4 years and captive specimens have lived for up to 20 years.

ADAPTATIONS The most striking adaptation is elongation of the hooves, which renders animals particularly clumsy on dry or broken terrain. Sitatungas emerge from swamps to wander more widely in the wet season. In the Sudd this represents a modest but discernible shift from deep permanent swamp onto the margins of a seasonal floodplain with different food plants.

STATUS Hunting may threaten Sitatungas in some marginal areas of their range. They are particularly vulnerable to persistent snaring, because they use paths and tunnels, and to wholesale burning or drainage of their habitat. However, they can withstand heavy and persistent hunting if the swamps remain intact. They are rare or endangered locally, i.e. in Kenya, L. Chad, Zimbabwe, but substantial populations of all three subspecies remain. Possibly the best suited of all tragelaphines to intensive domestication or semi-domestication. Not endangered.



Sitatunga, male (above) and female (right)

■ BONGO *Tragelaphus eurycerus*

OTHER NAMES Fr. Bongo. Ger. Bongo. Swah. Bongo, Ndongoro.

MEASUREMENTS HB 1.7–2.5m. T 450–650mm. Sh. ht 1.1–1.3m. W 182–276kg (♀), 240–405kg (♂).

RECOGNITION Long-bodied, muscular bovine, coloured deep russet red, with 10–16 vivid white stripes on each side. Both sexes are spiral-horned with deep, flat flanks. Males have a vestigial dorsal crest and bold, black-and-white markings on the extremities. Males continue to put on weight with age and slowly darken until they are nearly black. Body proportions vary, with W African Lowland Bongo consistently smaller and shorter-legged. The Kenya Mountain Bongo is taller and much heavier. Glandular secretions appear to be dispersed over the body and are not restricted to discrete sacs or tracts.

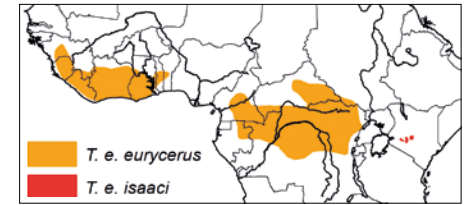
GEOGRAPHIC VARIATION Lowland Bongo, *T. e. eurycerus* (W and central African lowlands); Mountain Bongo, *T. e. isaaci* (Kenya highlands only).

DISTRIBUTION Restricted to forest mosaics on or north of the Equator. Bongos occur patchily from Sierra Leone to Mt Kenya. Like all tragelaphines, they are adapted to unstable habitats. In Kenya they prefer slopes between 2,000 and 3,000m, ranging (in larger groups) above 2,500m up to 4,000m in the dry season and dispersing at mainly lower altitudes in the rains.

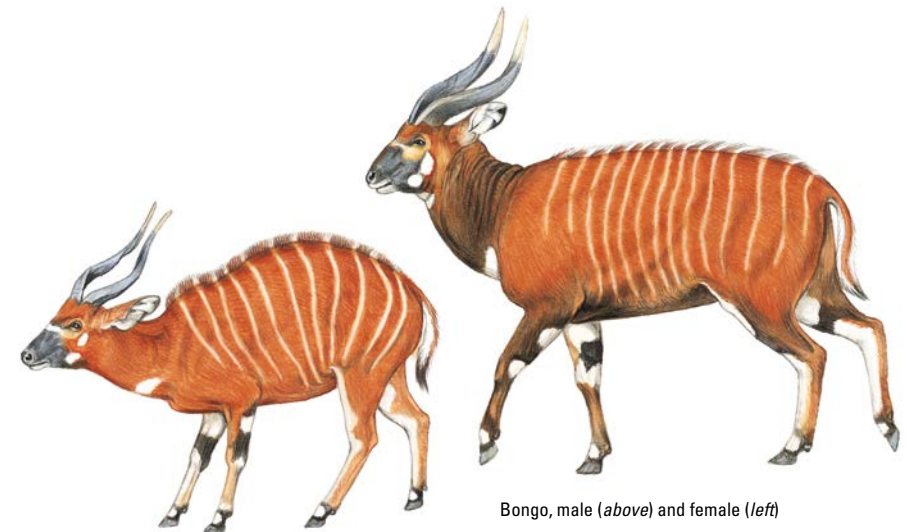
HABITAT Landslides, floods, fires, treefalls, heavy elephant-browsing, logging and fallow all favour regrowth of the low-level fresh greenery that Bongos need and they only occur in such disturbed forest mosaics. In montane areas mass die-offs of bamboo suit them. They remain relatively inactive in dense cover during the day and tend to move at night, but are always close to refuges in undergrowth or thickets.

FOOD More than 80 food plants have been recorded from a single locality. These include the foliage of shrubs and young trees, herbs, young grass and especially vines that are dragged down off trees or pulled up from the ground. Occasionally particular species become favourites: young *Albizia* seedlings, the herbs *Acalypha* and *Rinorea*, balsam (*Impatiens*) and wild yam vines (*Dioscorea*) have been noted.

BEHAVIOUR Individuals (of both sexes) do not form permanent links with others beyond the mother-young bond. Nonetheless, mothers suckling young after the latter's concealment phase seek one another out. Three months after the July–September birth peak in Kenya all lactating females are in large nursery herds where their behaviour is more confident and relaxed than when single (and



Bongo



Bongo, male (above) and female (left)

typically alert and timid). They range widely (possibly 120–300km²) and all classes have overlapping home-ranges.

Males do not herd females nor coerce them, nor do they influence their movements or groupings. Typically scattered dispersal favours efficient tracking and testing of females rather than direct competition for isolated, unpredictable mating opportunities. Body odours may assist this trailing process. Animals grunt and snort, females have a weak mooing contact call and all classes bleat in distress. Like other tragelaphines, males 'click' while courting the female. Gestation lasts about 284 days and the newborn young remains concealed until, with its mother, it joins a nursery group. Sexually mature after 2 years, males are unlikely to mate successfully until they reach their prime at about 4 or 5 years. They live up to 20 years.

ADAPTATIONS Bongos differ from elands in being shorter-legged, shorter-winded and water-dependent, but resemble them in having to range widely in search of concentrated nutritious herbage. They are vulnerable to predators and so stay in, or close to, thick cover where they can hide or defend themselves. Males resemble Nyalas in parading their age and status in strutting displays, but depend less upon visual illusion of mass than real mass. Displays are commonly performed at very close quarters at night.

STATUS Still common in parts of Cameroon, DR Congo and central Africa, the Bongo is in danger of extinction in Sierra Leone and Ghana. It has become rare or vulnerable in Côte d'Ivoire, Gabon and Liberia. The Mountain Bongo has become a 'flagship species' for conservation in Kenya. Conservation plans must take account of its need for unstable habitats. Widespread in moderate numbers and currently not endangered overall. IUCN classifies the species as near-threatened, but the Mountain Bongo *T. e. isaaci* is critically endangered.

■ GIANT ELAND *Taurotragus derbianus*

OTHER NAMES Lord Derby's Eland. Fr. *Élan de Derby*. Ger. *Riesenelantilope*.

MEASUREMENTS HB 2.62–3.20m. T 550–700mm. Sh. ht 1.65–1.78m. W (est. ave.) 450kg (♀), (est. ave.) 900kg (♂).

RECOGNITION A very large bovine with 8–12 vertical white stripes on a sandy grey or rufous body. Both sexes have horns; those of the male are longer (up to 1.23m), more widely splayed and have a looser spiral than in the Common Eland. Mature males also have a black neck and pendulous dewlap from chin to chest. The ears are broad, rounded and prominently marked, as are the hocks.

GEOGRAPHIC VARIATION *T. d. derbianus* (west of R. Niger): rufous, average 15 stripes. *T. d. gigas* (east of R. Niger): sandy-grey, average 12 stripes.

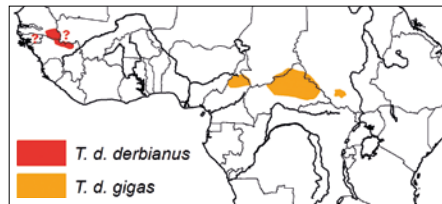
DISTRIBUTION A narrow and increasingly fragmented belt of *Isoberlinia* woodland stretching from Senegal to the Nile and sandwiched between the dry but heavily cultivated wooded savannas of the Sudanian zone and wetter mosaics of forests and grasslands to the south.

HABITAT Quite strictly confined to the *Isoberlinia doka* woodlands where herds (sometimes numbering up to 60) are highly mobile. Occasional vagrants into the wetter savannas to the south of this region have given a misleading impression of the total range. They move long distances to drink but can do without water for some time.

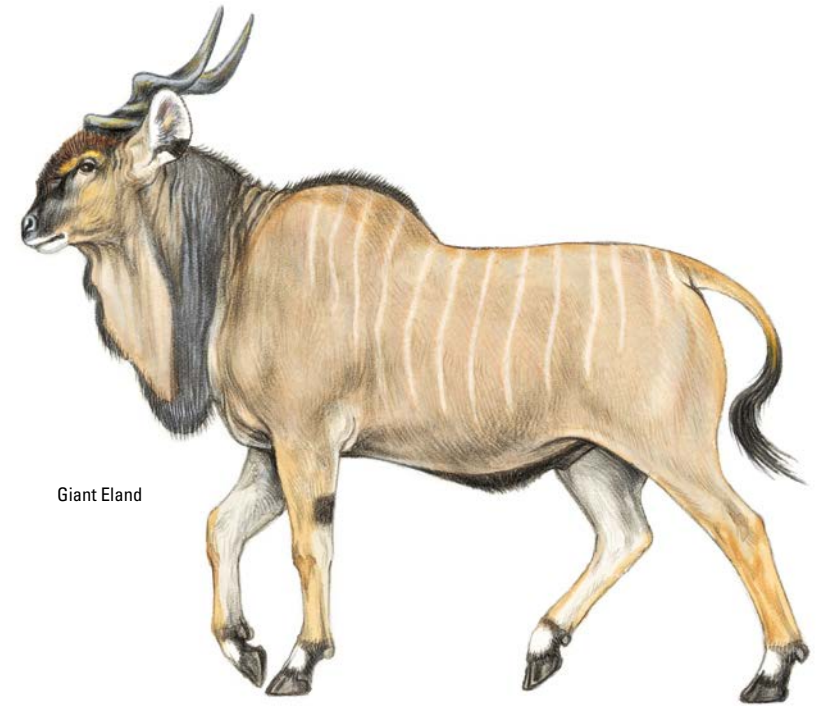
FOOD Browse consists of the dominant leguminous trees, notably *Isoberlinia*, *Julbernardia* and some young grasses and herbs early in the wet season. They will break branches with their horns to get at green leaves.

BEHAVIOUR Highly nomadic, with very large ranges and distinct seasonal movements. Males are often solitary and their contact with females ranges from a few hours to several weeks. Large herds in both wet and dry seasons suggest that security of the young, or social rather than ecological factors, influence female gregariousness. Males have been reported absent from some of these aggregations. Breeding patterns are likely to resemble those of Common Eland or kudu with a 9-month gestation and a brief lying-up period.

ADAPTATIONS Head carriage, horn and dewlap shape and neck colouring suggest that the Giant Eland is intermediate between the 'horn exhibitionist' Greater Kudu and the 'parade bull' Common



Giant Eland



Giant Eland

Eland (which displays its body and bulk as a single mass). Both kudu and Giant Elands emphasise height in their strutting displays. Markings serve to focus attention on the head, ears and neck. Of course, large ears are more important for an animal living in thick woodland.

STATUS Giant Elands have been totally or virtually exterminated over a large part of their former range. They remain common in parts of Senegal, Central African Republic, Cameroon and S Sudan, where they are nominally protected in national parks. Their wanderings render them vulnerable to hunting and they are exceptionally susceptible to rinderpest, which hit them very hard in 1983. Listed as threatened (IUCN). Niokola Koba NP in Senegal now supports the only secure population of the western race.

■ COMMON ELAND *Taurotragus oryx*

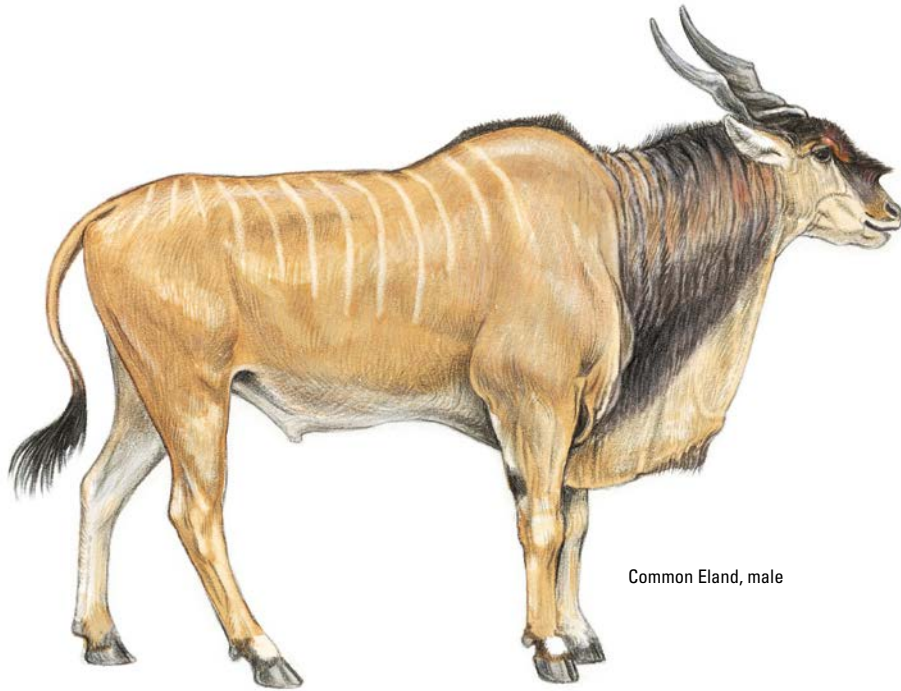
OTHER NAMES Fr. *Élan du Cap*. Ger. *Elantilope*. Swah. *Pofu*.

MEASUREMENTS HB 2.0–2.8m (♀), 2.4–3.45m (♂). T 500–720mm. Sh. ht 1.25–1.60m (♀), 1.35–1.78m (♂). W 300–600kg (♀), 400–942kg (♂).

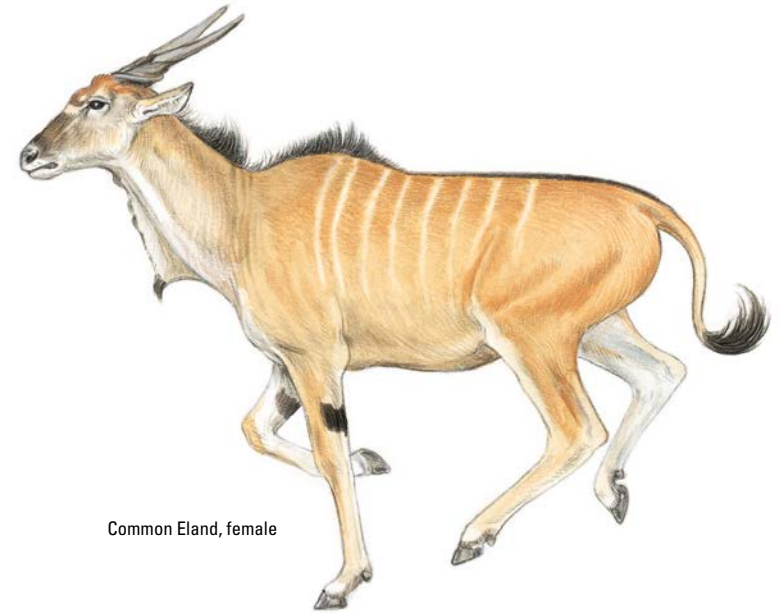
RECOGNITION A very large, tan bovine in which both sexes have horns and a dewlap, a long tail with a tufted tip and narrow, relatively small ears. Males tend to increase in weight throughout their life, neck and shoulders darken from tan to grey and the dewlap enlarges until it hangs like a curtain to below the level of the knees. Hair on the male's forehead also changes with time, becoming more and more bushy (but it can decline in size, suggesting hormonal control). The mouth and muzzle are small and pointed in comparison to those of African



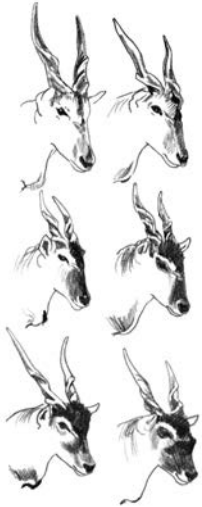
Common Eland



Common Eland, male



Common Eland, female



Variations in frontal tuft colouring and horn shape of male Common Eland.

Buffalo and cattle. Teeth, jaw muscles and stomach physiology are all adapted to a high-protein, low-fibre diet. The side, or 'false', hooves on the hindlegs are embedded in glandular patches, which presumably leave scent trails.

GEOGRAPHIC VARIATION Cape Eland, *T. o. oryx* (S and SW Africa): tawny, adults lose stripes. Livingstone's Eland, *T. o. livingstonii* (central woodlands): brown, up to 12 stripes. East African Eland, *T. o. pattersoni* (E Africa): rufous tinge, up to 12 stripes.

DISTRIBUTION Originally from the Cape to forest margins in the Congo basin, the R. Katonga, to south of the Nile floodplain and arid N Kenya.

HABITAT Primarily animals of the woodlands and woodland-savanna. In South Africa they had extended their range into temperate Highveldt and the Karoo. Common Elands gather into larger herds during and after the rains and scatter into smaller groups in the dry season. For the females this corresponds with a shift into more open country during the rains and into thickets and woodlands in the dry season. Mature males move much less and venture less into the plains. In effect, large female groups form primarily as a defence and for protection of the young.

FOOD Browse consists of foliage and herbs. They can tolerate tougher and more aromatic foods than other tragelaphines. In the dry season, myrrh (*Commiphora*) and bush-willows (*Combretum*) become the major foods in many localities. Marula fruit, acacia seeds and reed syringa (*Burkea*) are other favoured dry-season foods; these are sometimes browsed in poor-quality scrub dominated by *Protea* or hemp

(*Diplorhynchus*). Early flushes of grass and herbs attract the elands (notably females more than males). Acacia pods are eaten in quantities during the dry season.

BEHAVIOUR Common Elands are gregarious but have a fluid and open system. Intense mutual attraction among calves leads to temporary isolated groups of up to 50 animals, all juvenile.

These calf assemblies provide the nucleus for female herds (in which mothers are to some extent interchangeable). Hierarchies form within these juvenile herds and the principle of 'rank by age and size' remains typical of all ages of these elands and both sexes. The expedient of defensive bunching in open habitats allows independent animals the benefits of herd life without forming ties. Thus no energy is expended seeking lost partners. On the other hand, every animal is alert to local events, such as fires, showers and thunderclouds, thereby causing temporary congregations of up to 1,000 head to form on flushes of green growth. Young animals, especially females, are highly nomadic; older animals, especially males, are more residential. Thus, home-ranges have been found to vary from 1,400 to 1,500km². Neighbouring males may be in one another's company with some frequency but seldom number more than six or seven. Larger male assemblies are very temporary and tend to disperse rapidly. More matings have been recorded in the rains, leading to birth peaks nearly 9 months later at the end of the dry season. The young have a brief lying-out period before joining the 'crèches'. Growth rates are exceptionally fast, due in part to the extreme richness of eland milk. In spite of female defence, mortality is high, with predators, disease and accidents all taking their toll. Animals are known to have lived for up to 25 years.

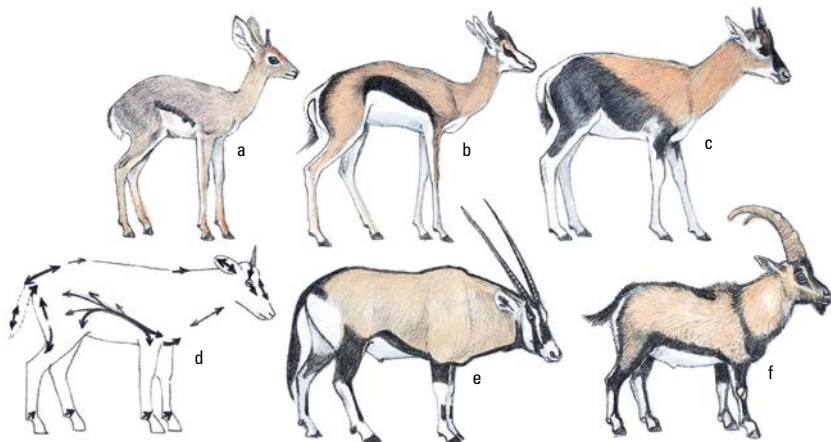
ADAPTATIONS The huge size of males is the most distinctive peculiarity of Common Elands. Continuous enlargement of neck, shoulders, dewlap and facial brush ensures that most of the males within a locality are strung out along a size gradient. This seems to be an extension of the hierarchy formed by very fast-growing calves. The only modification of this strictly linear rank order may be the outbursts of male aggression, known as *ukali*, which may serve as a dispersal mechanism and is typical of most, if not all, tragelaphines.

STATUS Common Elands are hunted over much of their range and have disappeared from most farmed areas. Nonetheless they are still widely distributed and well represented in national parks. They are semi-domesticated as exotics in several countries. Locally vulnerable or endangered (e.g. in Uganda and Rwanda, where, until very recently, they were locally abundant), but overall not endangered.

ANTELOPES, SHEEP AND GOATS Antilopinae

Dwarf antelopes	Neotragini
Duikers	Cephalophini
Grysboks	Raphicerini
Dikdiks	Madoquini
Gazelline antelopes	Antilopini
Oribi	Ourebiini
Reduncines, kobs	Reduncini
Klipspringer	Oreotragini
Impala	Aepycerotini
Alcelaphines, topi and allies	Alcelaphini
Horse-like antelopes	Hippotragini
Sheep and goats	Caprini

Of all the radiations of animals in Africa, from tree frogs to turacos, guenons to mongooses, the radiation of antelopes is the most celebrated and well known. Ranging in size from less than 2kg to more than 300kg, the very diversity of antelopes typifies them. They began as the newly separate African branch of a common bovid stock some 20–23 mya. A divergence based initially on a separation between bovids on a cooler, mainly temperate, continent and those in a hot, dry, mainly tropical continent selected for opposite traits. Movement between seasonal pastures favoured herding among larger-bodied animals in Eurasia. In Africa, year-round residence on territories favoured spatial intolerance among small-bodied animals. Where the niches of those first pioneers have remained relatively unchanged, small size and territorial behaviour are still favoured, as is evident in dikdiks and other dry-country dwarf antelopes. Whatever morphological changes have taken place over the last 12–18 million years are relatively subtle, thus dikdiks have modified their noses, Klipspringers the structure of their hooves and hairs, while a scarcity of green growth in forest territories selected for shrinkage in the pygmy antelopes. Modest but high-quality diets permitted the early antelopes to live in small territories (some even without water). Recent studies on small, conservative antelopes have shown that home-ranges are generally shared by a pair but marked and defended by the male only. Secretions, notably those from preorbital face glands, are probably just as important for sustaining the cohesion of a pair (or a family) as for land-labelling. Each sex transmits signals that attract the other and the scents, calls and postures of adult females generally provoke the close attention and interest of their male partner several times a day.



Coat patterns in Antilopinae. (a) Beira. (b) Springbok. (c) Bontebok. (d) Diagram of attention-guiding visual foci common to many antelopes. (e) Gemsbok. (f) Goat.

Tentative phylogenetic tree for Bovidae (modified from Hassanin & Douzery 2003, Hernández Fernández & Vrba 2005 and Hassanin *et al.* 2012).



Females show less overt interest in males but are exposed to almost continuous reminders of the male, either by his actual presence or through trails left by his pedal glands, landmarks demarcated by excreta or secretions, or whiffs of scent wafted from the male's sacs, brushes or patches.

Intimate and up-to-date knowledge of a small home-range and its occupants ensures exclusive (and efficient) breeding for both partners. When their offspring are born and inducted into this universe of scents, they too benefit from this shared security.

'Nasal panting', a method of cooling blood in the nose with minimal water loss, is most likely to have begun in small, arid-adapted antelopes because small bodies in hot climates must conserve water and avoid overheating (they cannot afford to waste water through sweating). Being small is therefore functionally linked with this and other conservative habits, such as the possession and use of glands.

Antelopes that do not grow heavier than 16–20kg can survive in territories where exposure to danger is greatly reduced by familiarity with both its food resources and its refuges. They need not enlarge their range, lengthen their legs nor elaborate their horns. This very durable strategy for survival is common, in one form or another, to all small-scale niches. In little modified form, the small antelopes represent descendants from the root stock of all antelopes and present a miniature model for the whole antelope radiation. Thus the dynamics of evolution, the process that has given

us life, are writ large in the living diversity of antelopes, linking their survival with our own (but only when we acknowledge the ancient ecological and continental contexts of our own origins).

A long history of mainly solitary animals attached to defended territories is still evident in a strong bias towards territorial behaviour, even among larger species that have become nomadic. Strong glandular and excretory scents are characteristic of all species. Some glands extrude solid secretions, others disperse aerosols. Horns, often of complex shape, are generally annulated on their forward surfaces, except for a smooth tip (small conservative species sometimes have short, smooth spikes). Noisy gratings of the horns on branches or soil is closely associated with deposition of dung and glandular scents in territorial behaviour. Conspicuously bruised plants help to mark out territory and broadcast scents. Annulated horns assist this function, as well as being able to inflict damage on rivals and trespassers. The evolution of antelope horns has centred on the development of defensive sparring or wrestling and the elaboration of hooks, twists and rams, all of which features are linked with the irregular growth patterns typical of annulated horns.

Their coat patterns are often idiosyncratic but many share a common format that focuses attention on the rump, flanks and head, which suggests a common origin or common mode of elaboration for their patterns. They have various permutations of face, skin and foot glands and, usually, one pair of mammae.

Geographic settings for the very earliest divergences among antelopes can only be guessed at but the equatorial centre–west was clearly the main region of emergence for dwarf antelopes (Neotragini) and duikers (Cephalophini). The south–east realm, instead, was where small antelopes first increased body size, manifest today in the Impala. Klipspringers probably evolved on the Ethiopian massifs and dikdiks in dry piedmonts in north–eastern Africa. Gazelles, horse-like antelopes and proto-caprines probably emerged in North Africa but spread to Eurasia early on. Reduncine reedbuck and lechwe originated in a vast string of flats and wetlands running from Okavango and Zambezia through the L. Victoria basin to the Sudd. Compare the phylogenetic trees on pp.501 and 523 for some current thinking about the antelope radiation.

DWARF ANTELOPES *Neotragini*

Dwarf antelopes	<i>Neotragus</i> (2 species)
Suni	<i>Nesotragus moschatus</i>

Dwarf antelopes have slender legs, large eyes, a rounded head with a small mouth and muzzle, large preorbital glands and simple spike horns in males. Until recently, and in the first edition of this guide, all small, conservative antelopes were grouped as Neotragini (*sensu lato*). However, molecular genetics has shown that many of these superficially similar little antelopes have long been separate and, in several cases, are linked with the emergence of even more distinctive lineages.

With the Royal Antelope the already small size of conservative species actually declines to an absolute minimum of 1.5kg. *Neotragus* therefore represents dwarfing as an adaptation to living under shade in the equatorial forests of the centre–west. *Nesotragus*, on the other hand, is a larger, and probably older, form occupying the south–east realm where droughts and predation are more frequent. Somehow, the constraints imposed by small size were circumvented by a very early antelope that was more likely to have resembled *Nesotragus* than any other type of small antelope. Once its proportions and body size were free to enlarge, the potential for a much larger, Impala-like antelope became possible.

ROYAL ANTELOPE *Neotragus pygmaeus*

OTHER NAMES Fr. *Antilope royale*. Ger. *Kleinstbockchen*.

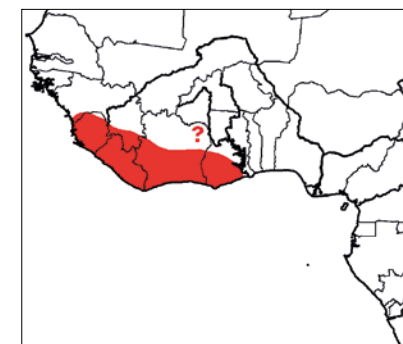
MEASUREMENTS HB 380–510mm. T 50–80mm. Sh. ht 240–260mm. W 1.5–3.0kg.

RECOGNITION A tiny antelope with very thin, long legs, a small muzzle, large eyes, relatively small, flesh-coloured ears and a diminutive tail with a white underside. Body colour is reddish or golden brown, with a white belly, chin and chest, and a rufous brown collar. Only males have tiny, conical horns. Its gait is high-stepping under a bunched, compact body but it can slip away in a ground-hugging scamper, or with fast, high jumps powered by disproportionately muscular upper hindlegs.

HABITAT Lives in spaced-out singles or pairs within very small territories, apparently signposted with dung. It prefers dense undergrowth at ground level along forest edges, in clearings, road



Royal Antelope



Royal Antelope

verges and cultivation, both within the moist forest belt and in galleries in drier forest–savanna mosaics. It takes more than a year to mature and can live for 6 years.

FOOD Fresh greenery, buds, leaves, shoots and, less frequently, fruits and fungi. These are plucked with the very small mouth and long tongue. The Royal Antelope feeds during the day but is most often seen by torchlight when it visits verges or farms.

STATUS Still widespread and abundant. Listed by IUCN as not threatened overall but its survival outside parks and reserves could become threatened. It is a major item on West African bushmeat stalls.

DWARF ANTELOPE *Neotragus batesi*

OTHER NAMES Bates's Pygmy Antelope, Bates's Dwarf Antelope. Fr. *Antilope de Bates*. Ger. *Batesbockchen*.

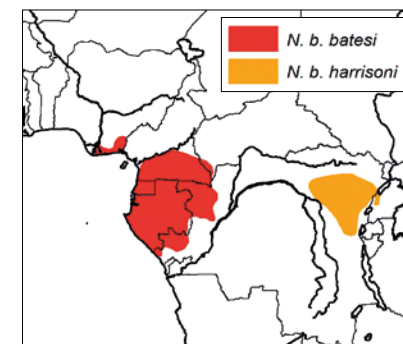
MEASUREMENTS HB 500–575mm. T 45–80mm. Sh. ht 240–330mm. W 2.0–5.5kg (♀ ave. 0.6kg heavier).

RECOGNITION A small, extremely slender-legged, forest antelope with a short muzzle, large eyes and moderately small ears. The soft mahogany-brown fur has a shiny gloss. White markings in the ears and on the chin and throat are conspicuous. The belly is white and the short tail has a lighter underside. The smaller male has very short conical horns.

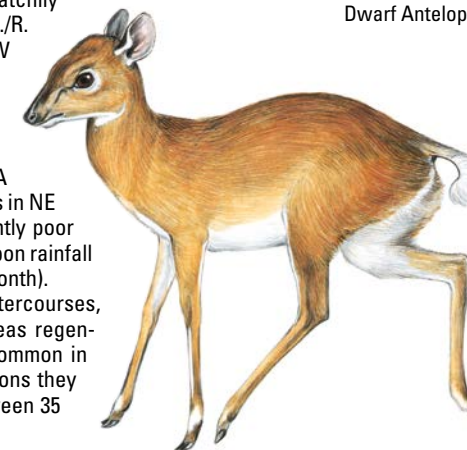
GEOGRAPHIC VARIATION *N. b. batesi* (very patchily distributed between R. Niger and Congo R./R. Sangha), *N. b. harrisoni* (NE DR Congo, W Uganda). A third subspecies might exist in the S Ogooué basin.

DISTRIBUTION Found in discrete pockets in SE Nigeria, parts of SE Cameroon, Gabon and Congo-Brazzaville to R. Sangha. A distinct and equally patchy population occurs in NE DR Congo and W Uganda. They are apparently poor colonists or recolonists and are dependent upon rainfall minima in the dry season (about 50mm per month).

HABITAT Dense, low undergrowth near watercourses, roads, gardens, chablis (tree falls) or in areas regenerating after logging. They are especially common in cocoa plantations. Under favourable conditions they have been known to reach densities of between 35 and 75 per km².



Dwarf Antelope

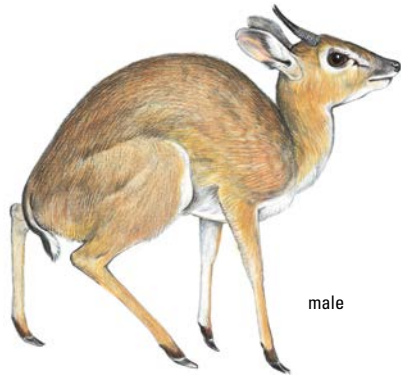


FOOD A browser of leaves and shoots, rather selective by species and for fresh growth. Recorded preferences are the acanthus *Brillantaisia* and *Phaulopsis*, Bitter Cucumber (*Momordica charantia*) and many cultivars, notably yams, sweet potatoes and peppers.

BEHAVIOUR Males mark their home-ranges with the copious secretions of their facial glands, and torn ears suggest that males fight for territories. They do not seem to make middens, nor to ritualise defecation. Panting raucous barks while fleeing may alert neighbours to a disturbance as well as to the runner's position. Nasal moans are a common contact call. Gestation is thought to be in the region of 6 months, possibly with biannual birth peaks at the end of the rains. Maturation times are not known.

ADAPTATIONS Rapid closure of forest canopies may render this species very dependent on unpredictable tree-fall areas and make its home-ranges less permanent. Periodic rotations of pastures have been observed and greater mobility might explain why overt territorial behaviour is not obvious in this species.

STATUS In spite of its very sporadic occurrence over a vast range, it appears to be common where it is found. It is so marginal as to be very vulnerable in Uganda but is less endangered elsewhere.



Suni

■ SUNI *Nesotragus moschatus*

OTHER NAMES Fr. *Antilope musquée*. Ger. *Moschusbockchen*. Swah. *Suni*, *Paa mwekundu*.

MEASUREMENTS HB 570–620mm. T 80–130mm. Sh. ht 300–410mm. W 4–6kg.

RECOGNITION A small antelope with long, slender legs, a typically compact stance and a disproportionately broad head on a short neck. Males have finely annulated horns that reach a maximum of 13mm. The facial glands are enormous, especially in males. The sleek, shiny fur is freckled dark brown with regional and individual differences in the tints of rufous or grey to body colour or legs. The underside is white or very pale grey. The tail has a white underside and is flashed from side to side (rather than flipped up and down, as is the case with the Blue Duiker).

GEOGRAPHIC VARIATION *N. m. moschatus* (N of Zambezi), *N. m. livingstonianus* (S of Zambezi).

DISTRIBUTION A fragmented range from Somalia to Zululand east of the Great Rift Valley.

HABITAT Coastal forests and thickets wherever there is thick undergrowth and regenerating fallow. They are commonest in the broken forests skirting the foothills of large mountain massifs, especially along watercourses, margins and fertile pockets. They have favourite spots within tangles to lie up in. Both visible and invisible scented pathways are regularly followed. Individual and communal dung middens tend to be on the peripheries of a territory.

FOOD Browsers with a varied diet of leaves, shoots and herbs and, more rarely, grass, roots and mushrooms. Among the commonest food plants are Sunn Hemp (*Crotalaria juncea*), *Commelina*, *Acacia* and brandybush (*Grewia*), which are all eaten off the plant. Sunis prefer false nettles (*Fleurya*) and morning glories (*Ipomoea*) that are wilted and pick up various dry fallen leaves. They gather under feeding colobus monkeys to pick up dropped leaves and shoots of brittlewood (*Nuxia*). They feed in short bursts interspersed with rests and are most active after rainstorms or spells of dense mist, especially between nightfall and 22.00 and after 04.00. They rest during the heat of the day.

BEHAVIOUR Mainly pairs on territories of approximately 3ha. Where larger numbers of females (up to four) share a male home-range he associates more closely with just one female. Incursions into territories by other males are met with energetic grating of the horns and chases in which the aggressor champs his jaws while trying to strike glancing blows or parry horn jabs. A higher ratio of females in most populations is probably due to deaths following the fierce contests of territorial males. Males do not acquire full adult characteristics before 14 months of age but females are thought able to breed by about 6 months. One, very rarely two, young are born after a gestation of 180 days. There is a birth peak just before the rains in February–March. Young keep hidden and make a soft, bird-like contact call that resembles grating marbles. They begin browsing within days of birth and the suckling period is very brief. Animals are known to live for at least 6 years.

ADAPTATIONS Well named the 'musk antelope', the Suni has a strong body odour (in addition to more specific preorbital and pedal gland scents). These smells demarcate territory and identify the sex and status of individuals, but also appear to act as insect repellants.

STATUS Although very localised in an environment subject to much depletion (for wood, charcoal and farmland), Sunis remain common and widespread through parts of their total range. Sold in bushmeat markets (sometimes deliberately maimed), they are subjected to unconscionable cruelty.

DUICKERS *Cephalophini*

Blue duikers

Philantomba (3 species)

Bush Duiker

Sylvicapra grimmia

Forest duikers

Cephalophus (16 species)



Bush duiker



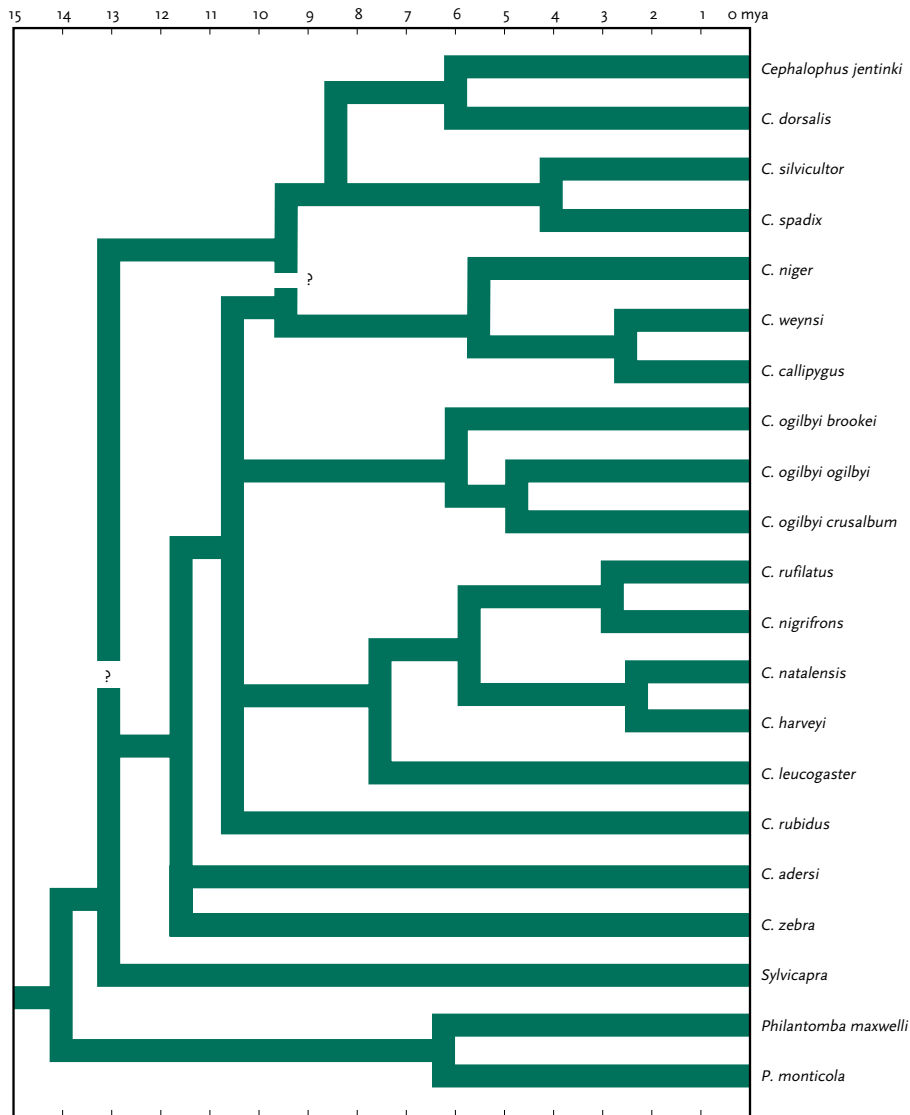
Black-fronted Duiker

RECOGNITION Duikers are antelopes with a compact body and a short, wedge-shaped head, with horns normal for both sexes (except female bush duikers). The mouth is large, with a wide maw. All species have 'smear-type' facial glands on the sides of their muzzle; some have glands in the groin, under tufts of hair on the legs or between the hooves. They range in size from 3.5 to 80kg. Legs vary in length from species to species but none can compare with open-country, running antelopes. Intensely territorial, the males of most species can be called up by imitating the duiker's bleat.

GENEALOGY Duikers follow a broad progression in which the smallest belong to more conservative lineages while the largest are the more advanced. Dwarfing is one mechanism whereby leaf-eating herbivores can first adapt to the scarcity of herbage on the forest floor. Only after initial dwarfing could the ancestral duikers make a dietary reversal back to more frugivorous, even omnivorous, diets. Duikers are rare in the fossil record. However, their brain morphology is consistent with their being advanced derivatives of the dwarf antelopes. They have among the largest and most complex brains of all bovids.

GEOGRAPHY Most duikers live only in forest but some have adapted to more open, swampy or montane environments. They are exclusively African and there are no fossils to suggest they ever crossed the Sahara.

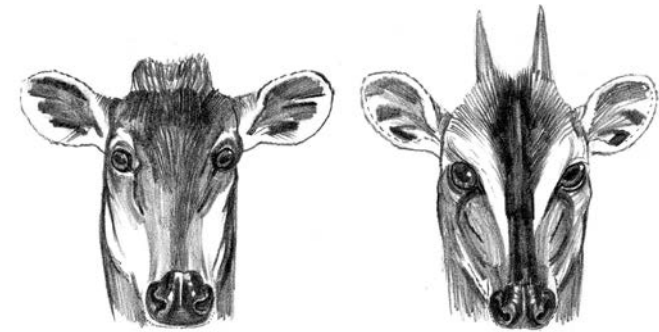
ECOLOGY The ecological partitioning of forest duikers is summarised later (see p.534). The duiker radiation involves isolation, regional specialisation, partitioning of the habitat by food type, by



Phylogenetic tree for Cephalophini (adapted from Jansen van Vuuren & Robinson 2001 and Hassanin *et al.* 2012).

activity (diurnal, nocturnal) and, above all, size differences. All duikers are to a greater or lesser extent dependent upon monkeys, squirrels, birds and fruit bats to dislodge the fruits, flowers and leaves on which they feed. Part of their alertness and 'strategic intelligence' is linked with this sensitivity to what is happening in the canopy. Some duikers can clamber up sloping trunks or dense tangles, some are specialised in skilled concealment (mostly during the day), relying on a short fast dash to escape if found. All can make prodigious leaps when pursued.

NATURAL HISTORY All species are thought to be territorial and most form close associations between the sexes, each excluding others of their own sex. The size of territories and degree of exclusivity (particularly along margins) probably varies greatly. Well-trodden paths connect habitual feeding,



Bay Duiker (*right*), Yellow-backed Duiker (*left*) to show former's larger eyes, broader face and shorter muzzle.

ruminating, sleeping and refuge areas. All species use scents and vocalisations to regulate social contacts. Precocious young are born after a relatively long gestation. All are slow to reach full maturity, suggesting that prolonged learning may be necessary for successful exploitation of a difficult environment.

ADAPTATIONS Duikers have thickened and enlarged frontal bones and their short, sometimes vestigial, horns grow from further back on the skull than in other antelopes. This can be correlated with hard head-butting in many species, directed at rivals and (less commonly) predators, hard fruits and crashing through undergrowth. Their reduced horns and other neotenus features are further indications of dwarfed origins.

The tentative phylogenetic tree opposite summarises current knowledge of duiker relationships.

BLUE DUIKERS *Philantomba*

Blue Duiker	<i>Philantomba monticola</i>
Maxwell's Duiker	<i>Philantomba maxwelli</i>
Walter's Duiker	<i>Philantomba walteri</i>

Blue duikers are small, greyish, brown or fawn animals that have retained many of the original adaptive traits of the duiker tribe but clearly refined their own niche at an early date. Formerly considered to be two species, but a third is profiled here. *P. monticola* occupies a wide range in central and southern Africa, and breaks down into two major divisions (N and S of the Congo R.). *P. maxwelli* occurs in West Africa and its easternmost population (in the Dahomey Gap) has recently been described as a third, previously overlooked species, *P. walteri*. Blue duikers have become a very successful and widely distributed group.



Philantomba spp. frontal views of Maxwell's Duiker (*left*); Blue Duiker *P. monticola congicus* (*centre*); and Blue Duiker *P. m. monticola* (*right*). Several current subspecies may well prove to be full species.

■ BLUE DUIKER *Philantomba monticola*

OTHER NAMES Fr. *Céphalophe bleu*.

Ger. *Blauducker*. Swah. *Ndimba*, *Chesi*.

MEASUREMENTS HB 550–900mm. T 70–130mm.

Sh. ht 320–410mm. W 3.5–9.0kg.

RECOGNITION A small, grey or brown antelope that has differentiated into a large number of regional and insular species. Populations living in very wet areas tend to be much darker than those in drier areas. It has large eyes, rather small ears and a very wide, flexible mouth. The tail has a narrow midline of black but the underside and fringe has white, crinkled hairs that reflect light so well that the flickering tail resembles a small flashlight going on and off along the dark forest floor.

GEOGRAPHIC VARIATION 26 subspecies named. Two main divisions. Also montane and insular races.

South–east division – russet legs: *P. m. monticola* (southern Africa, eastern littoral), *P. m. bicolor* (KwaZulu to R. Zambezi), *P. m. hecki* (east coast littoral), *P. m. defriesi* (central Africa), *P. m. anchietae* (Angola), *P. m. simpsoni* (S Congo basin).

Centre–west division – grey legs: *P. m. congicus* (Cross R. to Congo R.), *P. m. aequatorialis* (R. Uelle to W Kenya).

Dark montane isolates: *P. m. lugens* (southern highlands, Tanzania), *P. m. schusteri* (Eastern Arc Mts, Tanzania), *P. m. fuscicolor* (Manica highlands).

Insular forms: *P. m. sudevalli* (Zanzibar I.), *P. m. pembae* (Pemba I.), *P. m. melanorheus* (Bioko I.).

DISTRIBUTION Forest and forest mosaics from the R. Niger to W Kenya, and from Angola to the east coast (Cape to R. Tana).

HABITAT Lowland and montane rainforests, riverine and littoral forests and moist thickets. Patchily distributed and at variable densities because of its dependence upon a year-round supply of fruits. The animals normally rest all night, under cover from rain or beside tree trunks. In disturbed areas they may become more nocturnal.

FOOD Where fruiting trees and shrubs are abundant, up to 80% of the diet may be fruits, otherwise foliage with traces of flowers, gum and animal matter is taken. Preferred fruits are the abundant small berries or seeds that are often typical of dominant trees in secondary or colonising forest. Dry fallen leaves are commonly eaten. Blue Duikers have been seen to follow below monkeys and birds to pick up fallen fruits.

BEHAVIOUR Bonded pairs are formed on a small and regularly traversed territory (as little as 2.5–4.0ha in rich W African forests). Such territories are saturated with scent clues emanating from a continuous flow from pedal glands

(between the hooves), frequent

rubbings from the face

glands, and from faeces,

urine and horn-gratings.

Both sexes chase off

intruding duikers but tol-

erate their own offspring

for up to 18 months. Forays

outside the territory are made to

temporary food sources (and by the

male while the female has her newborn

lying-up). Gestation has been reported as 5

months, but 4 months is a more likely esti-

mate. The mother and young make contact

through soft, groaning calls and both freeze

at the slightest alarm, only running if encoun-

tered unexpectedly. At such times a male may



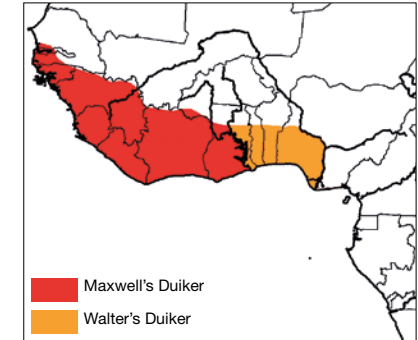
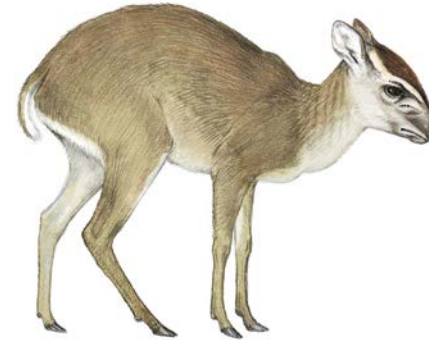
Blue Duiker



utter a whistle or sneezing call that both signifies alarm and advertises movement and position to its mate and neighbours. Young mature slowly (i.e. 2 years) and are known to live for 10 years.

ADAPTATIONS Densities of up to 62–78 per km² have been recorded in the fruit-rich forests of Gabon. This implies that this species is particularly efficient at picking up the ephemeral resources that fall from the trees above. It is very likely that such densities are only possible where there are very large numbers of monkeys and birds displacing and ‘wasting’ a super-abundant fruit supply. Close bonding of a pair may assist this strategy by reducing danger from predators and increasing the thoroughness with which the ground is covered.

STATUS In spite of heavy hunting pressure all over its range, this duiker is still widespread and common. However, felling of fruit trees and killing of monkeys degrades their habitat and food supply.



Maxwell's and Walter's Duikers

■ MAXWELL'S DUIKER *Philantomba maxwelli*

OTHER NAMES Fr. *Céphalophe de Maxwell*. Ger. *Maxwellducker*.

MEASUREMENTS HB 630–760mm. T 120–150mm. Sh. ht 350–420mm. W 6–10kg.

RECOGNITION The Upper Guinea counterpart of the Blue Duiker, distinguished by its strongly marked and more angular head, clearly demarcated facial glands and deeply pocketed pedal glands. It is grey-brown with paler neck, chest and undersides but without white markings. Both sexes are normally horned but some females lack horns.

GEOGRAPHIC VARIATION Six named subspecies (two from mid-river islands).

DISTRIBUTION Intermittently from Senegal to the Dahomey Gap.

HABITAT Rainforest galleries and relicts, in moist or derived savannas with abundant fruiting trees and shrubs.

FOOD Fallen fruits, herbs, shrubs and new growth; probably some animal matter.

BEHAVIOUR Generally resembles the Blue Duiker, i.e. pairs share a small common territory defended against others of the same sex. The territory is incidentally marked by the pedal glands, faeces and urine, more deliberately marked with facial glands. Gestation is reported to be 120 days. The young of captive specimens maintain tranquil relations with parents for more than a year. They are fully mature by 2 years.

ADAPTATIONS Face glands are used to mark not only surroundings but also companions within the territory. Both sexes mark and both also solicit and receive grooming, in which face, ears and neck are licked vigorously. Gestures of appeasement are also linked with face-licking and suggest that close family bonds are continually maintained.

STATUS Maxwell's Duiker has lost much habitat and is hunted intensively, often excessively. In spite of this it is still widespread and common.

■ WALTER'S DUIKER *Philantomba walteri* (not illustrated)

OTHER NAMES Fr. *Céphalophe de Walter*. Ger. *Walterducker*.

MEASUREMENTS No data. Likely to be slightly smaller than Maxwell's Duiker.

RECOGNITION Newly described species based on morphology and genetic data. Formerly considered to be the easternmost population of Maxwell's Duiker. Intermediate in size between the larger Maxwell's Duiker to the west and the smaller Blue Duiker to the east. Morphologically

similar to Maxwell's Duiker with a relatively long tail, large pedal glands and striking superciliary line, but differs from the other two species in the genus in cranial measurements, having a smaller nasal constriction and cranial height.

GEOGRAPHIC VARIATION None known.

DISTRIBUTION Occurs from the Dahomey Gap (Togo and Benin) to the R. Niger in Nigeria.

HABITAT As Maxwell's Duiker.

FOOD Presumably similar to other species in the genus.

BEHAVIOUR Presumably as Maxwell's Duiker.

STATUS Populations in Togo and Nigeria are considered to be vulnerable and those in Benin are probably threatened. The species is clearly at risk from deforestation and considerable hunting pressure – the first specimens of this new taxon, which led to recognition of its distinctness, were discovered in a bushmeat market.

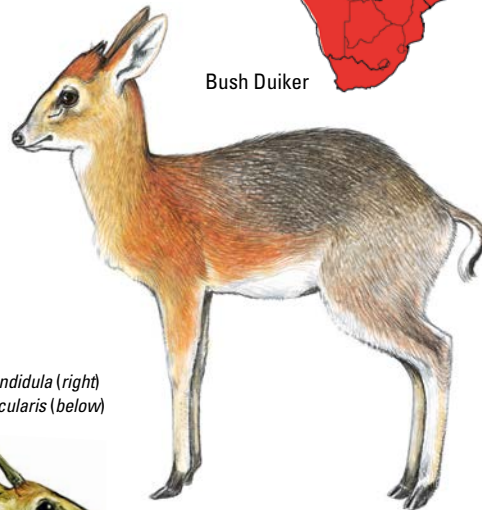
■ BUSH DUIKER *Sylvicapra grimmia*

OTHER NAMES Common Duiker, Grey Duiker, Grimm's Duiker. Fr. *Céphalophe couronné*. Ger. *Knonenducker*. Swah. *Nsya*.

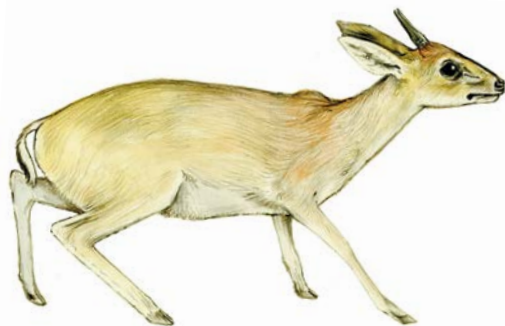
MEASUREMENTS HB 900–1,115mm (♀), 700–1,050mm (♂). T 70–195mm. Sh. ht 450–700mm. W 10.0–22.4kg (♀), 10–26kg (♂).

RECOGNITION The long but typical duiker face has swollen face glands and a black facial midline, ending in a rounded, leathery black nose. The Bush Duiker is longer legged and larger eared than the forest duikers. Colouring varies from region to region, with plain tawny animals in the far east and west and heavily grizzled, grey or brown animals in the central part of its range. The short tail is black above, white below. Straight, upright horns, only in the male, measure up to 180mm.

GEOGRAPHIC VARIATION More than 40 races listed but regional groupings can be recognised: *S. g. grimmia* group (S Africa); *S. g. steinhardtii* group (Kalahari region); *S. g. orbicularis* group (E Africa); *S. g. splendidula* group (S Congo basin); *S.*



S. g. splendidula (right)
S. g. orbicularis (below)



g. rosevelti group (Niger to Nile savannas); *S. g. abyssinica* group (Uganda to Eritrea); *S. g. deserti* (Somali–Kenya littoral); *S. g. coronata* (Upper Guinea savannas). They are darker in moist habitats and lighter in drier habitats.

DISTRIBUTION Savannas and woodlands of sub-Saharan Africa. They are absent from forests, open plains, deserts and subdeserts but live in various mountain areas up to the coldest alpine zones.

HABITAT They flourish in a wide range of habitats where their need for shelter and suitable food can be met. They benefit from reduced predation and patches of low secondary growth in settled areas, including suburbia. They avoid the heat of the day and also rest up for a large part of the night.

FOOD Leaves and shoots of numerous dominant bush plants, such as *Acacia*, bush-willow (*Combretum*), myrobalan (*Terminalia*) and morning glories (*Ipomoea*). Fruits are also very important seasonally, notably the pods of leguminous trees and shrubs, figs and the fruit of the Duiker Tree (*Sapium integerrimum*) and Kudu Berry (*Pseudolachnostylis maprouneifolia*). Flowers, bark, resin, roots, bulbs, tubers and fungi are also eaten; also traces of grass. Animal foods are rarer but not infrequent. Bush Duikers do not need water.

BEHAVIOUR Males defend territories with little or no overlap in range. Female home-ranges are also discrete but may be based more on avoidance. Male territories can enclose more than one female range. Lying up is solitary and females prefer lower, denser refuges while males select higher, more open vantage points at which to rest or ruminate. Both sexes are active during courtship, with much chasing and play. Gestation is thought to last about 6 months. The young lie up in dense cover for several weeks and mature very rapidly. Reaching near adult size in 6 months, some females drop their first calf at 1 year of age. They live for at least 12 years.

ADAPTATIONS In spite of being hornless, females are larger than males and capable of butting both other duikers and small predators approaching the young. Juveniles bleat very loudly if caught and both parents converge at once. This behaviour is exploited by hunters who imitate the bleat to call duikers within range.

STATUS Still widespread and common.

FOREST DUIKERS *Cephalophus*

Zebra Duiker	<i>Cephalophus zebra</i>
Aders's Duiker	<i>Cephalophus adersi</i>
Rwenzori Red Duiker	<i>Cephalophus rubidus</i>
White-bellied Duiker	<i>Cephalophus leucogaster</i>
Natal Red Duiker	<i>Cephalophus natalensis</i>
Harvey's Duiker	<i>Cephalophus harveyi</i>
Red-flanked Duiker	<i>Cephalophus rufiflatus</i>
Black-fronted Duiker	<i>Cephalophus nigrifrons</i>
Ogilby's Duiker	<i>Cephalophus ogilbyi</i>
Weyns's Duiker	<i>Cephalophus weynsi</i>
Peters's Duiker	<i>Cephalophus callipygus</i>
Black Duiker	<i>Cephalophus niger</i>
Abbott's Duiker	<i>Cephalophus spadix</i>
Yellow-backed Duiker	<i>Cephalophus silvicultor</i>
Bay Duiker	<i>Cephalophus dorsalis</i>
Jentink's Duiker	<i>Cephalophus jentinki</i>

There are at least 16 species of forest duikers and one or more of them once occupied virtually every type of forest in Africa. Supposed relationships within this enormous radiation are summarised in the tentative phylogenetic tree on p.528.

Cephalophus is the most diverse duiker group. The smaller ones are conservatives, occupying peripheries or islands that are marginal to their central habitat – equatorial forest. The Zebra Duiker, *C. zebra*, would seem to derive from the earliest beginnings of this radiation. Genetically, its closest affinities are with Aders's Duiker, *C. adersi*, a relict 'dwarf red' confined to coral rag and other coastal forests along the Kenya/Tanzania coast and to Zanzibar I. The Rwenzori Red Duiker,

Forest type	Lowland forest: closed, high canopy, thin undergrowth	Lowland and montane forest: broken canopy, dense undergrowth	Alpine and subalpine habitats	Swamp forest	Gallery, riverine and drier, low-canopy forests	Forest edge and secondary growth
Main food resources for duikers in possible order of importance	Fruit, shoots and seedlings, leaves, flowers, bark and fungi	Fruit and herbaceous growth, leaves, shoots and seedlings, fungi	Herbaceous growth, leaves, fruit, moss, young grass	Fruit, herbaceous growth, fungi, bark, semi-aquatic vegetation	Fruit, leaves, seasonal shoots, seedlings and herbaceous growth	Fruit, herbaceous growth, shoots and seedlings
Species (<i>Cephalopus</i> and <i>Philantomba</i>)						
<i>C. silvicultor</i> 68 (45–80)kg	mainly nocturnal (in Gabon 71% fruit, 29% leaves)					
<i>C. spadix</i> 55 (52–60)kg	allopatric sibling sp. of above (montane only)					
<i>C. dorsalis</i> 22 (14.5–24)kg	nocturnal (in Gabon 73% fruit, 27% leaves)					
<i>C. callipygus</i> 20 (16–23)kg	diurnal (in Gabon 83% fruit, 16% leaves)					
<i>C. nigrifrons</i> 17 (13–18)kg	diurnal (in Gabon 72% fruit, 28% leaves)					
<i>C. harveyi</i> 15 (13–16)kg	diurnal and nocturnal				diurnal and nocturnal	
<i>C. rubidus</i> 15kg	diurnal					
<i>C. leucogaster</i> 13 (12–18)kg	in Gabon 73% fruit, 27% leaves and flowers				diurnal	
<i>C. rufilatus</i> 13 (12–14)kg					diurnal and nocturnal	
<i>C. natalensis</i> 13 (12–14)kg					diurnal and nocturnal	
<i>C. adersi</i> 8 (6.5–12)kg					diurnal	
<i>P. monticola</i> 5 (3.5–9)kg	in Gabon 78% fruit, 20% leaves				mainly diurnal	

Food and habitats of duikers (dietary data from Gautier-Hion, Emmons and Dubost 1980).

C. rubidus, lives at the highest altitudes on the very wet, cold Rwenzori Mts. (On drier peaks the Bush Duiker, *Sylvicapra*, has moved into this niche.) The White-bellied Duiker, *C. leucogaster*, seems to derive from an earlier population that has only survived competition with its near-descendants by becoming a semi-nomadic inhabitant of mono-dominant zones such as Limbali (*Gilbertiodendron*) forests. It belongs to a branch of adaptable species that includes the Natal Red and Harvey's Duikers, *C. natalensis* and *C. harveyi*, generalised south-eastern duikers. Two other members of this branch have adapted to marginal environments within the forest. The Black-fronted Duiker, *C. nigrifrons*, has become a swamp specialist while the Red-flanked Duiker, *C. rufilatus*, is a small, generalist in literally 'marginal' habitats along the northern edges of the rainforest belt.

The prime forest niche for medium-sized duikers living in territories and feeding on rich nutritious foods such as fallen fruits is occupied by 4–6 species, three of which are recently evolved (*C. weynsi*, *C. callipygus* and *C. niger*) and appear to be in the process of replacing their precursors (*C. ogilbyi* group). Sharing the smooth, short neck hair, robust, long skull and broad noses that typify the 'giant' Black Duiker, *C. niger*, there is some uncertainty as to whether the giant duikers emerged out of this lineage or share common origins with *Silvicapra*.

The origins of two so-called 'fibre duikers', *C. dorsalis* and *C. jentinki*, are equally uncertain but they probably originated in Upper Guinea, where they are mainly confined to primary rainforest. The widely distributed Bay Duiker, *C. dorsalis*, is the most advanced in its adaption to hard, fibrous foods. Molecular clocks have suggested that the *Cephalopus* radiation has taken place within the last 14 million years and in response to repeated fragmentation of forest blocs as climates fluctuated. This helps to explain the survival of relict or specialised forms in marginal or isolated localities.

ZEBRA DUIKER *Cephalopus zebra*

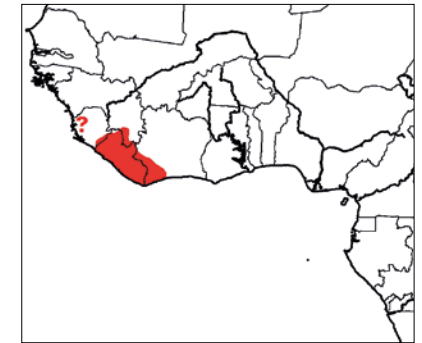
OTHER NAMES Banded Duiker. Fr. *Céphalophe zébré*. Ger. *Zebra duiker*.

MEASUREMENTS HB 700–900mm. T 100–150mm. Sh. ht 400–500mm. W 15–20kg.

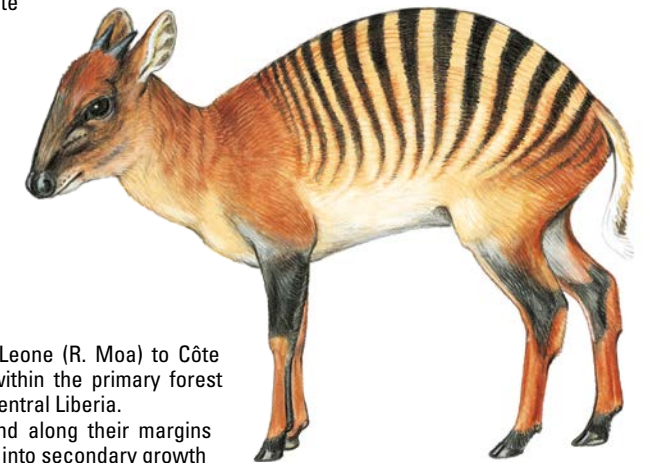
RECOGNITION As its name suggests this duiker has a panel of vertical, vivid black-and-cream stripes from behind the shoulder to the tail. The head, shoulders and lower legs are russet red, with hocks, muzzle and leg joints nearly black. Both sexes have robust, conical and very sharply pointed horns above a forehead and nasal area where the bone is massively thick and reinforced. They have prominent tufted glands just below the heels of the back legs and glandular pockets in the groin.

GEOGRAPHIC VARIATION None.

Alternative and now obsolete scientific names are: *C. zebra*, *C. doria* and *C. doriae*.



Zebra Duiker



DISTRIBUTION From Sierra Leone (R. Moya) to Côte d'Ivoire (R. Niouniourou) within the primary forest zone. Commonest in east-central Liberia.

HABITAT Primary forests and along their margins and in clearings, extending into secondary growth and swidden cultivation. It favours lowland forest (notably the Sinoe and other river valleys in Liberia) but may also live in low montane and hill forests.

FOOD Fruits and foliage. Details are unknown but the Zebra Duiker does not appear to have specialised teeth or diet. It may use its head to break open the shells of larger fruits.

BEHAVIOUR Friendly relations between captive pairs involve mutual rubbing and licking, suggesting that breeding pairs are the normal social unit (as they are in most duikers). Because both sexes have horns and a thickened skull (which do not appear to correlate with a specialisation in ecology or diet), it seems likely that bonded pairs share defence of their home-range against intruding duikers. Scarred heads suggest that the collisions that are normal in duiker confrontations are particularly vigorous and uninhibited in these exceptionally stocky and muscular antelopes.

ADAPTATIONS Known to be a strong stimulus to the eye/brain sensory system, stripes may serve as a focus for social attraction (in which case the resemblance of these duikers to zebras may be more than superficial). An advantage of stripes in this species could be to inhibit goring of the soft abdomen during aggressive encounters. Thus, while other animals shield themselves from the worst effects of aggressive rivalry with thickened skin, bony plates, etc., these duikers may have a subtler strategy for reducing damage during excessive aggression.

STATUS Formerly widespread over much of Liberia and Sierra Leone, Zebra Duikers are declining fast as their habitat is being destroyed and commercial bushmeat hunting becomes more entrenched and appallingly comprehensive in its onslaughts. Listed as threatened (IUCN) in Liberia but in danger of extinction in Sierra Leone and Côte d'Ivoire.



Aders's Duiker

■ ADERS'S DUIKER *Cephalophus adersi*

OTHER NAMES Fr. *Céphalophe d'Aders*. Ger. *Adersducker*. Swah. *Paa nunga*.

MEASUREMENTS HB 660–720mm. T 90–120mm. Sh. ht 300–320mm. W 6.5–12kg.

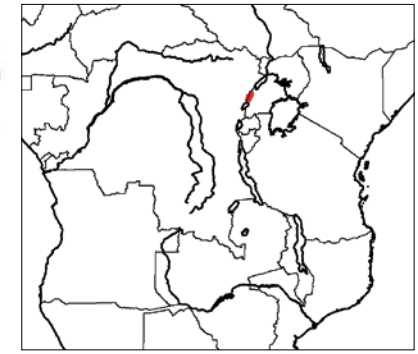
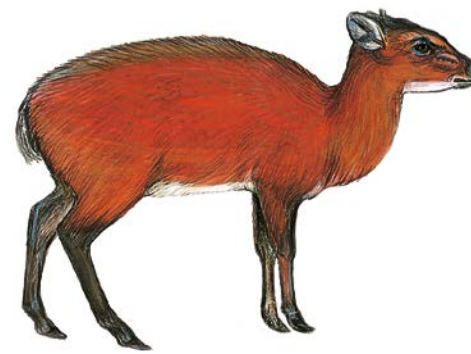
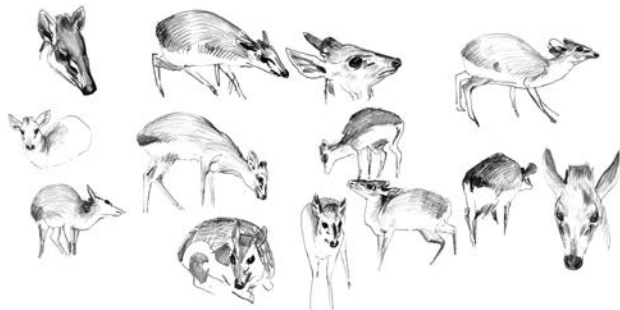
RECOGNITION A small duiker of a washed-out, tawny-red ground colour with a bold white band across the buttocks and white freckling on the red legs. The neck is greyish and there is a red tufted crest. Fur is particularly soft and silky. The muzzle is pointed, with a rather flat front to the nose.

HABITAT In Zanzibar this species has become almost entirely restricted to tall thicket forest growing on waterless coral rag. Its survival is influenced by all the commonest trees and shrubs bearing prolific crops of flowers and berries. Dominant tree species are Ebony (*Diospyros consolatae*), Kooboo-berry (*Cassine aethiopica*) and Bush Guarri (*Euclea schimperi*), with an understorey of turkey berries (*Canthium* spp.) and *Polyspheria*.

Pairs live in territories and breed throughout the year. They feed from dawn to about 11.00, after which they rest and ruminate before becoming active again from 15.00 to nightfall. Aders's Duiker is extremely alert and sensitive to sound so that driving with nets and dogs or silent ambush at a feeding tree are the main methods of hunting it.

FOOD Fallen flowers, fruits and leaves, often picked up beneath foraging monkeys and birds; also sprouts, buds and fresh growth.

STATUS In danger of extinction along the Kenya and Tanzania coasts, the main hope for this duiker's survival lies in Zanzibar (Nguja) I., but this requires the declaration and protection of national parks. Regulation of hunting, formerly exerted by both central administration and by village elders, has been scrapped since the 1962 revolution and local hunters describe a reduction in their harvest of antelopes of 20–30% in recent years. This may be partly due to felling and charcoal-burning in the remaining areas of tall coral thicket. Hunters will travel as far as 30km on foot in order to obtain duikers from well-known 'hot spots', such as Michamvi and Mamboiya. At Mtende Aders's Duiker has been estimated to form 70% of the hunters' antelope kills. As its habitat becomes more fragmented, free-ranging or feral dogs become a major menace. Dogs are known to have eliminated the entire population of Aders's Duikers on Funzi I. (where it had been reintroduced and flourished). Listed as threatened (IUCN).



Rwenzori Red Duiker

■ RWENZORI RED DUIKER *Cephalophus rubidus*

OTHER NAMES Fr. *Céphalophe du Ruwenzori*. Ger. *Ruwenzoriducker*. Konjo dialect *Isuku*.

MEASUREMENTS HB 750mm. T (ave.) 100mm. Sh. ht (ave.) 450mm. W (est.) 15kg.

RECOGNITION A stocky duiker with a dense, glossy rufous coat with long, coarse hair on the neck, changing to dense, soft fur over the hindquarters. The belly is white, hindlegs are almost black and there are dark-brown markings on the joints of the forelegs. A black or dark-brown blaze stretches from the nose to the crown. Down the midline of the back and neck there is a zone of dark grey underlying the uniform red tips of the fur. The underfur of the flanks is cream.

GEOGRAPHIC VARIATION The lower slopes of the Rwenzori Mts are inhabited by a race of the Black-fronted Duiker, which has a thinner, harsher, grizzled coat. Nonetheless, it is possible that the two are actively hybridising in a region of overlap at about 3,000m.

HABITAT Afroalpine and subalpine zones, *Hagenia* woodland and bamboo zones of Rwenzori.

FOOD Browse in a rich and continuous pasture of herbs, notably wild parsleys, balsams, violets, sorrels and *Galium*, a scrambling herb much favoured by all high-altitude herbivores. The Rwenzori Red Duiker is mainly diurnal but activity periods could be strongly influenced by rain.

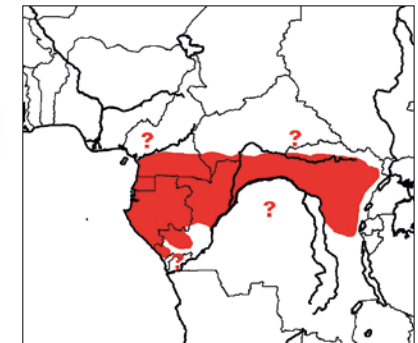
STATUS Heavily snared. Climbers have reported a substantial decline or disappearance along the Bujuku and Kitandara routes to the peaks. Vulnerable.

■ WHITE-BELLIED DUIKER *Cephalophus leucogaster*

OTHER NAMES Fr. *Céphalophe à ventre blanc*. Ger. *Weissbauchducker*.

MEASUREMENTS HB 780–1,000mm. T 80–150mm. Sh. ht 420–510mm. W 15–20kg.

RECOGNITION A pale forest duiker with warm, sandy-brown forequarters, graduating towards grey near the black dorsal line. The rump has a rufous flush and the crest is orange. The front, heels and hocks are black. The underside is white. The nape is short-furred but the rest of the neck has long,



White-bellied Duiker

coarse hair. The tail has a fluffy, black-and-white tip. It appears to have a deeper jaw, a wider gape and a stronger bite than other duikers with coarse neck fur.

HABITAT A very sparsely and intermittently distributed duiker ranging from the R. Sanaga to Rwenzori and the West Rift, but only north of the Congo R. It does not occur in extensively flooded forests and is known to be common in only a few highly localised places (notably N Gabon and Congo).

FOOD A ratio of 73% fruits to 25% foliage (and a marked taste for flowers) has been recorded in Gabon. Hard-shelled fruits (among them Mututu, *Klainedoxa*) in the diet implies that this duiker might smash them open (probably with the forehead).

STATUS A sample of hunters' bags in DR Congo showed this species to be the least frequently caught duiker (thought to be a measure of low density and elusiveness). It is found in several reserves but is likely to be one of the earliest animals eliminated as the commercial bushmeat trade gathers momentum. Widespread but locally vulnerable. Currently not endangered overall.



Natal Red Duiker

■ NATAL RED DUIKER *Cephalopus natalensis*

OTHER NAMES Fr. *Céphalophe du Natal*. Ger. *Rotducker*. Swah. *Funo*, *Ngarombwi*.

MEASUREMENTS HB 750–870mm. T 90–140mm. Sh. ht 400–430mm. W 12–14kg.

RECOGNITION A small duiker with red body, legs and frontal tuft. The neck may be red or pale grey. Margins of the ears, chin, throat and underside of the tail are white. The upperside of the tail, ears and muzzle are black.

GEOGRAPHIC VARIATION Four subspecies have been named, some of which may be invalid. Southern populations tend to be red overall (*C. n. natalensis*). Northern populations often have grey on the upper neck (*C. n. robertsi*).

HABITAT From central Natal to the R. Rufiji valley, inhabiting coastal forests and thickets, low-lying riverine growth, escarpment and montane forests east of L. Malawi (L. Nyasa) and the R. Shire. A diversity of trees that may flower and fruit through most of the year are prerequisites for its presence.

FOOD Opportunistic; fruits, flowers and foliage. All feeding is normally diurnal but the animal may become nocturnal in very disturbed areas.

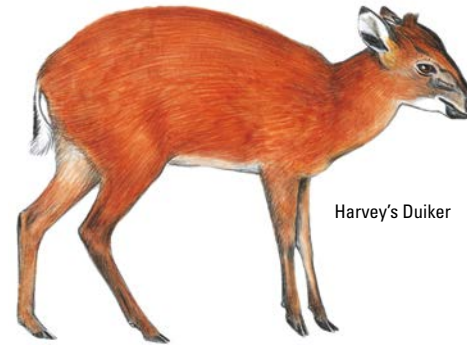
STATUS The Natal Red Duiker is still widespread and common, but rarely seen, in spite of intensive hunting and trapping over most of its range. Conversion of its habitat for settlement and agriculture is proceeding rapidly in many parts of its extensive but already fragmented range. Not yet endangered.

■ HARVEY'S DUIKER *Cephalopus harveyi*

OTHER NAMES Fr. *Céphalophe de Harvey*. Ger. *Harveyducker*. Swah. *Funo*.

MEASUREMENTS HB 850–950mm. T 110–150mm. Sh. ht 440–500mm. W 13–16kg.

RECOGNITION A rich red duiker with a black line down the centre of the face and nape. In most parts of its range it has dark legs and a black-and-white chin. The white-lined, tufted ears are black-tipped.



Harvey's Duiker



Harvey's Duiker

GEOGRAPHIC VARIATION This species appears to hybridise with *C. natalensis* in the region of Dar es Salaam and with *C. weynsi* in the Mau, central Kenya. *C. h. bottegoi* has been named from the coast in the Somali–Kenya border area.

HABITAT From coastal thickets to montane forests, riverine gallery and secondary forests wherever there is a variety of fruiting and flowering trees and shrubs. It ranges from the south Somali coast to the mainland opposite Zanzibar I. and across the mountains of E Kenya and Tanzania to Malawi and Nyika Mt.

FOOD Fruits, flowers and foliage from the forest floor. Diurnal.

STATUS Widespread and common but declining as its habitats become degraded or destroyed for charcoal or agricultural land.

■ RED-FLANKED DUIKER *Cephalopus rufilatus*

OTHER NAMES Fr. *Céphalophe à flancs roux*. Ger. *Rotflanken ducker*.

MEASUREMENTS HB 600–800mm. T 70–100mm. H 300–38mm. W 6–14kg.

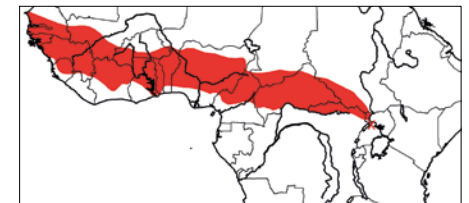
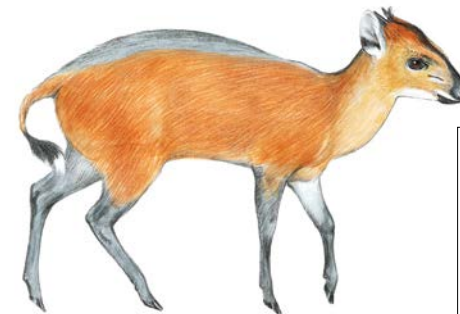
RECOGNITION Prettily coloured with bright orange-red on the face, neck and flanks, brown or blue-grey gauntlets on the limbs and a brown or grey dorsal patch which has pale grey underfur. The black nose and lower lip contrast strongly with white jaws and upper lip. The ears have black and white flashes. The nose is straight and the skull narrow. Relative to its size it has the largest preorbital glands of any duiker. This indicates exceptionally active marking behaviour.

GEOGRAPHIC VARIATION *C. r. rufilatus* (Senegal to the Chari and Benue valleys), *C. r. rubidior* (Chari to Nile valleys).

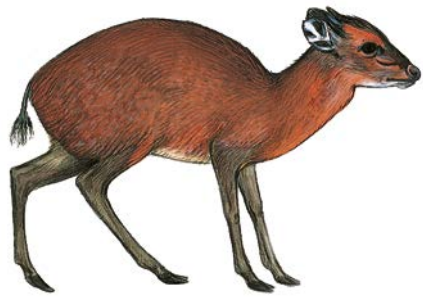
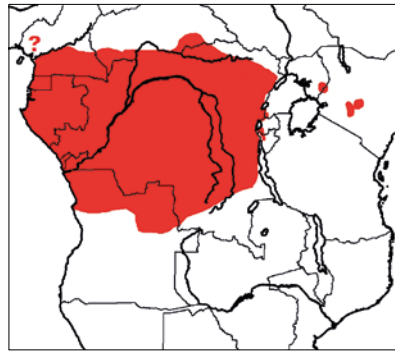
HABITAT A resident, territorial species living in forest relicts and riverine thickets within the savanna along a broad band of country from Senegal to NW Uganda.

FOOD Fruits, flowers and foliage from numerous riverine species of trees, shrubs and herbs.

STATUS This species can withstand considerable hunting pressure as long as enough suitable habitat remains available. It is in decline in very heavily settled areas but is still widely distributed. Listed as not endangered (IUCN).



Red-flanked Duiker

Mt Kenya Black-fronted Duiker *C. n. hooki*

Black-fronted Duiker

BLACK-FRONTED DUIKER

Cephalophus nigrifrons

OTHER NAMES Fr.

Céphalophe à front noir.

Ger. *Schwarzstirnducker.*

MEASUREMENTS HB 800–1,070mm. T 75–150mm.

Sh. ht 450–580mm. W 14–18kg.

RECOGNITION A long-legged, long-hoofed duiker with glossy red coat that is plain and thin in lowland forms and thicker, darker and more grizzled in montane forest forms. The legs, darker than the body, are almost black at the hocks and thinly haired. There is a distinct pale 'brow' below the black forehead blaze that gives it its name.

GEOGRAPHIC VARIATION *C. n. nigrifrons* (lowland forest from Cameroon to E DR Congo), *C. n. kivuensis* (W Rift mountains and volcanoes), *C. n. fosteri* (Mt Elgon), *C. n. hooki* (Mt Kenya).

HABITAT From Cameroon to Mt Kenya, where they are adapted to swamp forest and marshes at both low and high altitudes (up to 3,500m.). Like other duikers, they have territories marked out with face glands and a loud whistling call. They also make a loud thumping sound in the chest (the vocal equivalent of a typical bovid foot-stamp?). They follow regular paths from night shelters to day-time feeding grounds in swamp.

FOOD A variety of fruits and succulent vegetation, including balsam (*Impatiens*), Wild Coffee and other Rubiaceae. A ratio of 72% fruits to 28% foliage has been recorded in a fruit-rich Gabonese forest.

STATUS Widely distributed but in Kenya appears to have been hunted-out in the Aberdare Mts, and also vulnerable to intensive hunting on Mt Elgon.

OGILBY'S DUIKER *Cephalophus ogilbyi*

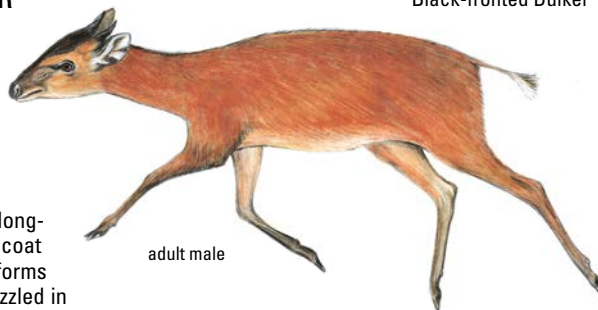
OTHER NAMES Fr. *Céphalophe d'Ogilby.* Ger. *Ogilbyducker.*

MEASUREMENTS HB 850–1,150mm. T 120–150mm. Sh. ht 550–560mm. W 14–20kg.

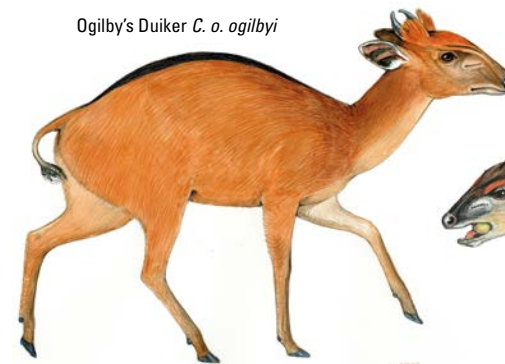
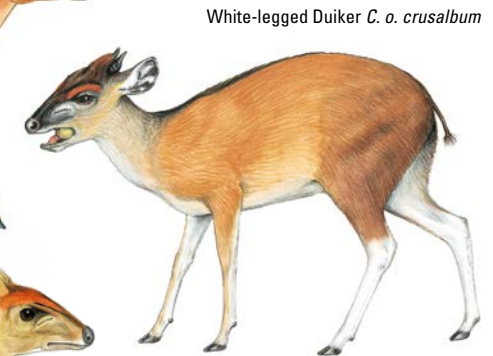
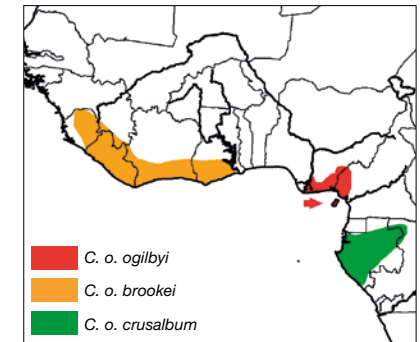
RECOGNITION Orange to mahogany-coloured duiker with a very red rump, a paler underside, and a black dorsal line (of variable extent). The face has marked brows and short but peculiarly curved horns with strong corrugations (in both sexes). Legs vary in colour. The tail is short and tufted. This species has massive hindquarters, a deep, slab-sided body and long, slender legs.

GEOGRAPHIC VARIATION Ogilby's Duiker *C. o. ogilbyi* (Bioko I. and Cameroon/Nigeria borderlands), Brooke's Duiker *C. o. brookei* (Sierra Leone to Ghana), White-legged Duiker *C. o. crusalburn* (Gabon). These forms might merit species status.

HABITAT Primarily forests close to the West African coast, where it is now rare and patchily distributed. On Bioko I., it was a common and dominant species, notably on the less disturbed upper slopes of the mountains. The absence of other large duikers is clearly a factor in this.



adult male

Ogilby's Duiker *C. o. ogilbyi*White-legged Duiker *C. o. crusalburn*Brooke's Duiker *C. o. brookei*

■ *C. o. ogilbyi*
■ *C. o. brookei*
■ *C. o. crusalburn*

FOOD Mainly fallen fruits, with the large, hard fruits of mututu (*Klainedoxa*) noted. The distribution of this species might be influenced by a super-abundance of fibrous fruits and numerous primates that contribute to the fruit-fall.

STATUS Habitat destruction and degradation threatens *C. o. brookei* with extinction everywhere, except in the Korup NP. *C. o. crusalburn* will only be secure if logging is stopped in the Lopé Reserve. *C. o. ogilbyi* is not currently endangered but requires the implementation of national park status for the Caldera de Luba on Bioko I. and control of the burgeoning urban bushmeat trade.

Ogilby's Duiker

WEYNS'S DUIKER *Cephalophus weynsi*

OTHER NAMES Fr. *Céphalophe de Weyns.*

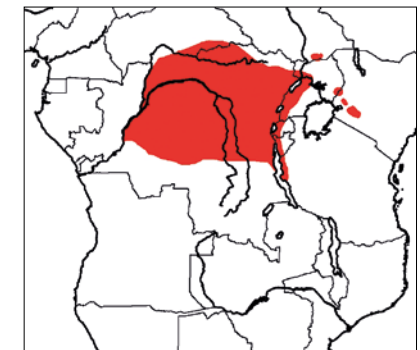
Ger. *Weynsducker.*

MEASUREMENTS HB 800–1,150mm. T 80–160mm.

Sh. ht 450–600mm. W 15.5–20kg.

RECOGNITION A fairly large duiker of very variable colouring. The main body colouring can range from pale tawny to rich russet or dark brown. The dark brown may be confined only to the legs or tint the shoulders, neck and face. The frontal tuft is russet in all subspecies. The forehead is among the most heavily reinforced of any duiker, with the dense bone of the frontal up to 13mm thick in some males.

GEOGRAPHIC VARIATION *C. c. weynsi* (R. Ubangi to Victoria Nile), *C. c. barbertoni* (E Uganda, W



Weyns's Duiker



Weyns's Duiker

Kenya), *C. c. lestradei* (north end of L. Tanganyika). (Supposed hybrids with *C. harveyi* on Mau, Kenya.)

HABITAT Ranges from R. Ubangi to W Kenya in both lowland and montane areas. This diurnal and territorial species flourishes in regenerating patches after logging but is not found in outlying riverine strips and galleries. **FOOD** About 70% of the diet consists of both ripe and unripe fruits. Fallen foliage made up most of the balance. **STATUS** A preferred prey of forest hunters but, in the absence of serious forest degradation, it seems able to withstand light but regular hunting. It is now rare or vulnerable in Burundi, Rwanda, Kenya and Uganda.

■ PETERS'S DUIKER *Cephalopus callipygus*

OTHER NAMES Fr. *Céphalophe de Peters*. Ger. *Petersducker*.

MEASUREMENTS HB 940–1,090mm. T 80–150mm. Sh. ht 450–600mm. W 17.5–25.2kg.

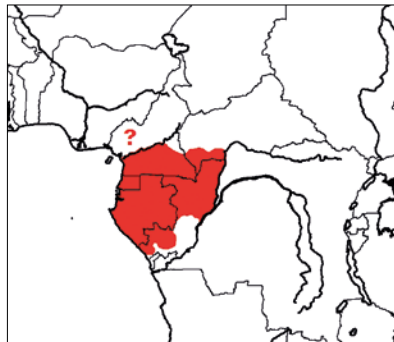
RECOGNITION A fairly large duiker with a rich-red rump graduating into tawny flanks, neck and cheeks. Bright russet frontal tuft. A black mid-dorsal stripe widens over the hindquarters. The belly has a sepia midline that broadens on the chest. White flashes on ears, chin and lips. Like *C. weynsi*, the forehead is reinforced with a dense bony frontal.

GEOGRAPHIC VARIATION None, but individuals have been photographed that appear to have hybridised with *C. ogilbyi*. If so, it is possible that *callipygus* is actively replacing and interbreeding with *C. ogilbyi*.

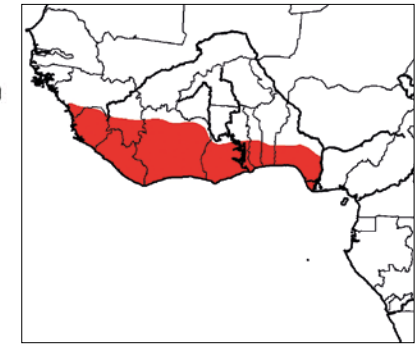
HABITAT Ranges through the moist equatorial forest zone from the R. Sanaga in Cameroon to the R. Ubangui. A diurnal and territorial species that even occurs in regenerating patches after logging so long as fruit and monkeys remain, but not in outlying mosaics or galleries. It occasionally survives in farm-bush.

FOOD Recorded as taking 83% fruits and only 16% leaves (at Makoku, Gabon). This was the most completely frugivorous of all the duikers studied there.

STATUS Can withstand regular hunting and is known to exist at densities of up to 20 per km² in Gabon. As a preferred species for commercial bushmeat trade, offtake levels are unsustainable in more settled areas.



Peters's Duiker



Black Duiker

■ BLACK DUIKER *Cephalopus niger*

OTHER NAMES Fr. *Céphalophe noir*. Ger. *Schwarzducker*.

MEASUREMENTS HB 800–1,000mm. T 70–140mm. Sh. ht 450–550mm. W 16–24kg.

RECOGNITION A heavily built, long-bodied, long-headed, glossy black duiker with swollen nostrils and short, stocky legs. The coat pales to light grey around the throat and chin and the lining of the ears. The tail shows some white hairs. Short horns, normally present in both sexes, are largely hidden in a coronal tuft of dense reddish hair.

HABITAT Rainforest from Sierra Leone to SW Nigeria, also survives in some riverine galleries, isolated patches and semi-deciduous forests on the margins of its range. It can also survive in regeneration areas after logging. It is mainly diurnal and territorial and is thought to fill a similar niche in Upper Guinea to Peters's Duiker, *C. callipygus*, in central Africa.

FOOD Fallen fruits and flowers, leaves and herbs. The Black Duiker is presumed to be as dependent on year-round fruit fall as other largish duikers.

STATUS This species suffers from overhunting throughout its range, except in some remote or better-protected localities in Liberia, Ivory Coast and Ghana. It is rare and endangered in Sierra Leone, Togo and Nigeria. Still widespread, its supposedly 'satisfactory' IUCN status will change unless curbs are put on the ever more voracious and cruel bushmeat trade.

■ ABBOTT'S DUIKER *Cephalopus spadix*

OTHER NAMES Fr. *Céphalophe d'Abbott*. Ger. *Abbottducker*. Swah. *Minde*.

MEASUREMENTS HB 970–1,400mm. T 80–130mm. Sh. ht 660–740mm. W 50–60kg.

RECOGNITION A large, glossy, nearly black duiker with a paler grey face, a very prominent russet tuft between the horns and a reddish tinge to the belly and lower flanks. The wedge-shaped head ends with a broad, flat-fronted nostril pad that overhangs the mouth (as with Yellow-backed Duikers). Overall, this is a stocky duiker with rather short, thick legs and a thick neck.

HABITAT Montane forest duiker restricted to the wetter (and therefore mainly eastern) sides of a few isolated massifs in E and S Tanzania. It is commonest in the Kilimanjaro NP and Forest Reserve between 1,300 and 2,700m in forest and high-altitude swamps, but is said to range up to 4,000m and has been seen in high-altitude scrub and moorland. It formerly



occurred above L. Manyara, in the Uluguru and Usambara Mts. It just survives on Mt Rungwe and in the Uzungwa mountain range. Disturbance may drive this species into more nocturnal activity but its preference for dense cover and its alertness keep it from view.

FOOD Fruits, flowers, green shoots and herbage; recorded browsing Balsam (*Impatiens*).

STATUS Although Abbot's Duiker is protected by law and occurs in the Kilimanjaro NP, this species is acutely threatened by poaching and the destruction of its habitat for charcoal, logs and potato fields. The Udzungwa and proposed Chita National Parks will be essential for the long-term survival of this forest endemic.



Abbott's Duiker

■ YELLOW-BACKED DUIKER

Cephalophus silvicultor

OTHER NAMES Fr. *Céphalophe à dos jaune*.

Ger. *Riesenducker*. Swah. *Kipoke*.

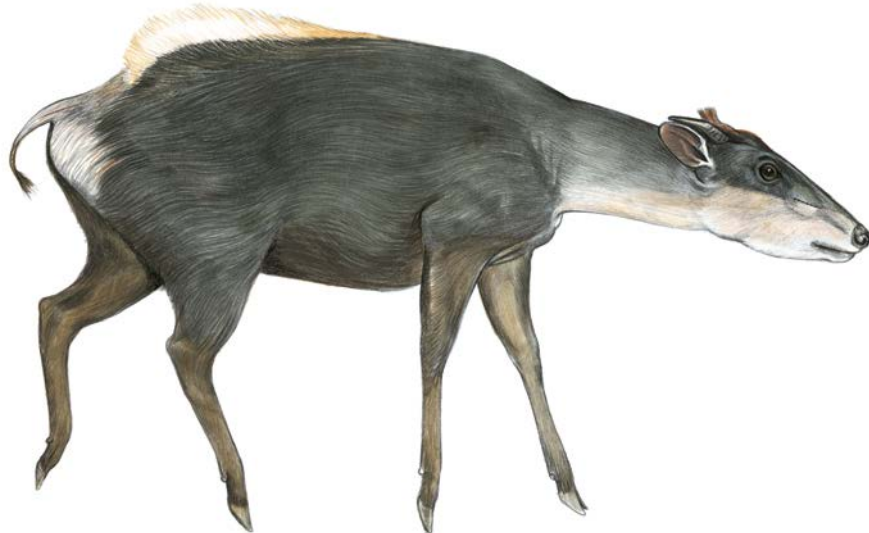
MEASUREMENTS HB 1.25–1.90m. T 110–200mm.

Sh. ht 650–870mm. W 45–80kg.

RECOGNITION A large, greyish-brown duiker with a vivid cream-coloured patch on the back. The long, wedge-shaped head has a light grey muzzle and cheeks ending in a shiny black rhinarium. Eyes and ears are small. The horns can be as long as 210mm. Newborn calves are dark umber, with freckled sides and a deep reddish tinge all over the underparts. The centre of the back is all jet black and only changes to adult colouring by 9 months of age. Juveniles at intermediate stages of growth can be difficult to identify.



Yellow-backed Duiker



GEOGRAPHIC VARIATION Nine subspecies are described but some are likely to be within the normal range of variation. Four subspecies are provisionally recognised here: *C. s. silvicultor* (Senegal to Niger delta), *C. s. longiceps* (Niger delta to Nile headwaters), *C. s. curticeps* (mainly eastern and central African montane form), *C. s. ruficrista* (south of Congo R. basin). **DISTRIBUTION** Senegal to SW Sudan and discontinuously to W Kenya. Angolan littoral to western shores of L. Tanganyika.



Yellow-backed Duiker

HABITAT Rainforest, montane forests and many permutations of forest-savanna mosaics, from narrow riverine strips to fragmented woods. It is often found close to deep swamps. It lies up singly in characteristic 'forms' at the base of large trees, under fallen trunks or in dense tangles. It likes to shelter from rain (and may even use the remnants of a pit-sawer's or hunter's lean-to). As many as six such resting places can be found within 1km². Throughout its range it lives only in pockets of suitable habitat where it can be quite numerous. It is attracted to salt-licks.

FOOD Fallen seeds, fruits, berries and the bark of shrubs, fungi, ground moss and many herbs. In montane areas, Waterberry (*Syzygium*), Dog Plum (*Ekebergia*) and Yellowwood (*Podocarpus*) are favoured fruits. In lowland forests Stem-fruit (*Chrysophyllum*), African Mangosteen (*Garcinia*) and Duiker Tree (*Sapium integerrimum*) have been recorded. Kudu Berry (*Pseudolachnostylis maprouneifolia*), raisin trees (*Canthium*), and snake beans (*Swartzia*) are savanna or forest-edge plants taken in the south of its range.

BEHAVIOUR This duiker is mainly solitary and spaced out in territories (probably shared by a male and female). Lying up on 'observation posts' on termite mounds suggests that surroundings are regularly monitored and broken male horns could indicate active defence of territory by males.

One, rarely two, young are born after a 151-day gestation. The newborn lies tight for a week or more but starts to nibble vegetation almost at once. It grows rapidly and is weaned by 6 weeks. The horn buds appear after about a month, when light hairs begin to show in the black back. Animals reach adult proportions and colouring by 9 months and are sexually mature by 1 year. Adults communicate with resonant grunts and a shrill bleat.

ADAPTATIONS The yellow back is not as conspicuous in the field as one might suppose because the hair lies close, reducing the pale colour to no more than a streak. The hair can be erected in display but this has only been observed in captivity in response to disturbance. It is probable that the yellow back has a social function. It may cover glandular skin, but this has yet to be verified.

STATUS Widespread and common in many parts of its range, recent reports from Kenya suggest that it may have become endangered there, as it has in Gambia. Over much of the rest of its range it is declining but not yet endangered.

■ BAY DUIKER *Cephalophus dorsalis*

OTHER NAMES Fr. *Céphalophe bai*.

Ger. *Schwarzruckenducker*.

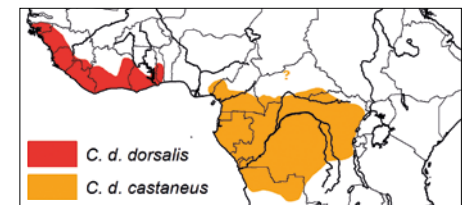
MEASUREMENTS HB 700–1,000mm. T 80–

150mm. Sh. ht 400–560mm. W 15.0–24.5kg.

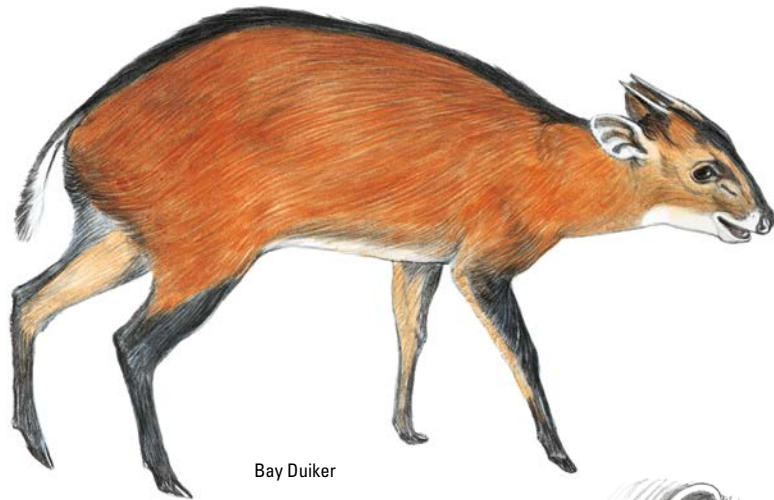
RECOGNITION Heavily built duiker with a red or yellowish-brown coat, black or dark-brown legs and a black midline along back and belly (definition varies individually). The fur is coarsely textured. The muzzle is extremely reduced and strongly tapered. The eyes are larger and higher in the head and the entire head is broader and flatter than in any other duiker, due to its enlarged cheek muscles (for lateral chewing action).

GEOGRAPHIC VARIATION *C. d. dorsalis* (Senegal to Togo), *C. d. castaneus* (E Nigeria to E DR Congo).

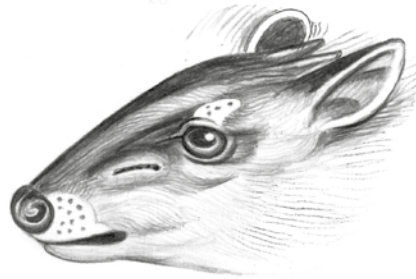
HABITAT The entire equatorial lowland rainforest block from Senegal to L. Tanganyika, with a preference for high primary rainforest. Also patches within savanna mosaics (if undisturbed).



Bay Duiker



Bay Duiker



Head of Bay Duiker female indicating vibrissae embedded in white 'signal' patches above eye and behind rhinarium.

Within the rainforest zone they may visit edges of clearings and prefer well-diversified zones with both dry and waterlogged areas. They shelter in hollow trees, between buttresses, under fallen trunks and in dark, dense thickets, only emerging to feed at night. They live at a lower density than other duikers and even in the richest habitats it has been estimated that two or three animals inhabit 12–20ha.

FOOD Hard or fibrous fruits, such as wild mango (*Irvingia*), mututu apples (*Klainedoxa*), African Breadfruit (*Treculia africana*), and white star apple (*Chrysophyllum*), have been recorded; also less difficult fruits, such as monkey orange (*Strychnos*) and yellow mulberry (*Myrianthus*).

Bay Duikers are also known to stalk, kill and eat birds but fruits accounted for 73%, and foliage 27%, in a Gabon sample.

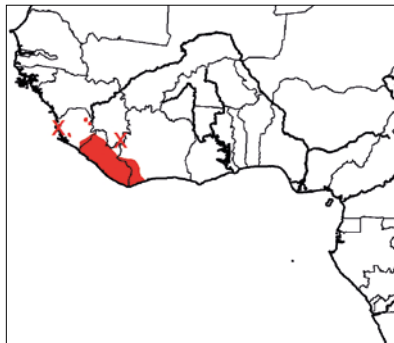
STATUS A very widespread species but a popular quarry for hunters. Declining in many West African countries, this species is now rare in Nigeria and Sierra Leone and extinct in Uganda. Overall not yet endangered.

■ JENTINK'S DUIKER *Cephalophus jentinki*

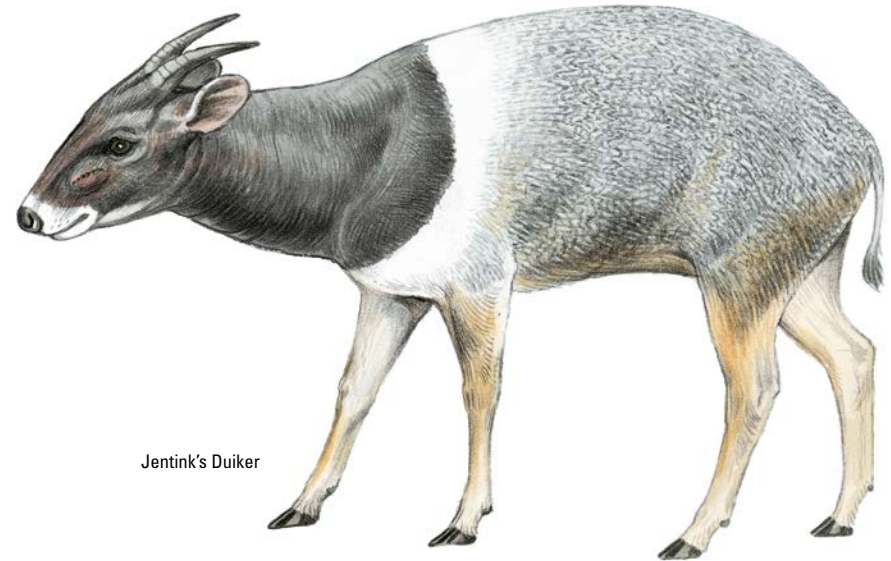
OTHER NAMES Fr. *Céphalophe de Jentink*.
Ger. *Jentinkducker*.

MEASUREMENTS HB (est.) 1.3–1.5m. T (est.) 120–160mm. Sh. ht (est.) 0.75–1.0m. W (est.) 50–80kg.

RECOGNITION A long-horned (up to 170mm), very robust, short-legged duiker with a bold pattern of black, white and grey (its early name of 'forest goat' was not entirely inappropriate). The nearly black head and neck are offset by a vivid white halter over the shoulders and lower chest and a white border surrounds the mouth and nose. This presents a symmetrical oval when viewed from in front. The colouring involves both skin and fur, the latter being



Jentink's Duiker



Jentink's Duiker

extremely short and fine. In contrast to the fore-end the hindquarters are grey agouti (this grizzled fur giving it a local name of 'squirrel-duiker').

HABITAT Only found in the high primary forest zone between Sierra Leone and the R. Niouniourou, a distribution that broadly coincides with many monkey populations and also that of the Zebra Duiker (see map, p.535). Within this zone, it enters secondary growth, scrub, farms, plantations and is even known to visit the seashore, presumably for salt. It is a 'hider', choosing hollow trees, fallen trunks and the buttress bays of Kapok (*Ceiba*), *Bombax* and Mututu Trees (*Klainedoxa*) for shelter. Unusually for duikers, it sometimes lies up in pairs. Like the Bay Duiker, it bolts from these day-time refuges with great speed if discovered, but has no stamina and does not go far. It is very residential and supposedly territorial but makes nocturnal forays out of thick forest, especially during periods when fruit is scarce. It is so secretive that it continued to survive less than 30km from Freetown, a city of half a million people, hiding on steep, densely forested slopes in the city's water catchment area. Its most basic requirements appear to be a diversity of fruiting trees and very dense shelter rather than a specific forest type.

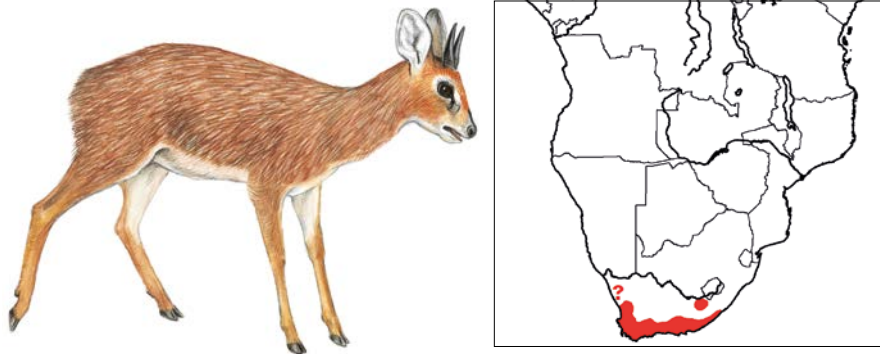
FOOD Known to enter plantations to eat palm nuts, mangoes and cocoa pods. The growing stems of tree seedlings are eaten (African Teak, *Chlorophora excelsa*, has been identified). Hunters familiar with the duiker's habits have identified many fruits with hard seeds or shells, notably kola nuts, erimado (*Ricinodendron*), Cherry Mahogany (*Tieghemella heckelii*), sand apples (*Parinari*) and Tallow Tree (*Pentadesma butyracea*). Jentink's Duiker has also been reported chewing roots after exposing them with its hooves.

STATUS Reportedly common in Sierra Leone at the turn of the century (before commercial loggers stripped the forests), it is now found only in the few remaining areas of undisturbed forest where hunting is now intensifying. Likewise, in Liberia, a new generation of commercial bushmeat hunters is now entering formerly remote areas to take out meat (mostly smoked in situ). This form of asset-stripping is nominally prohibited in Sierra Leone and Côte d'Ivoire but is legal in Liberia, the centre of the duiker's range, and still its main stronghold. Listed as endangered (IUCN) in Sierra Leone and Côte d'Ivoire. It is endangered by new hunting and snaring practices in Liberia.

GRYSBOKS Raphicerini

Cape Grysbok	<i>Raphicerus melanotis</i>
Sharpe's Grysbok	<i>Raphicerus sharpei</i>
Steenbok	<i>Raphicerus campestris</i>
Beira	<i>Dorcatragus megalotis</i>

Of all living antelopes, the Cape Grysbok, *Raphicerus melanotis*, provides the closest approximation to an ancestral type. It also resembles the earliest currently known antelope fossil, the 16-million-year-old *Eotragus* (from Eurasia).



Cape Grysbok

■ CAPE GRYSBOK *Raphicerus melanotis*

OTHER NAMES Fr. *Grysbok du Cap*. Ger. *Kaapgreisbock*.

MEASUREMENTS HB 650–800mm. T 40–80mm. Sh. ht 450–550mm. W 8–12kg. (♀ 0.5kg heavier).

RECOGNITION A thick-coated, chunky little antelope with russet-brown fur densely interspersed with white hairs to give a 'strawberry roan' colour to the body. There is less white flecking on the head, neck and legs, which are yellowish in tint. The ears are very large and lined with white hair. The short, blunt muzzle has a black bridge to the nose and a shiny black nostril pad and lips. Males have short, sharp and smooth horns (normally about 80mm long) which are widely spaced. Rump fur can be fluffed out to increase the impression of size. The tail is short and inconspicuous.

HABITAT A Cape relict species found between Albany and the Cedarberg Mts. It lives in scrub-covered sand dunes and thickets bordering rocky hills and steep gorges but also shelters in reedbeds or along riverbeds along the southern margins of the Karoo. It is probably territorial and is usually seen singly. The young, born after a 6-month gestation, are hidiers and grow fast. Most young are born between September and December (summer).

FOOD Browser of thicket and shrubby growth. Although the Cape Grysbok is active during the morning and late afternoon during winter, it is mainly nocturnal (possibly influenced by disturbance).

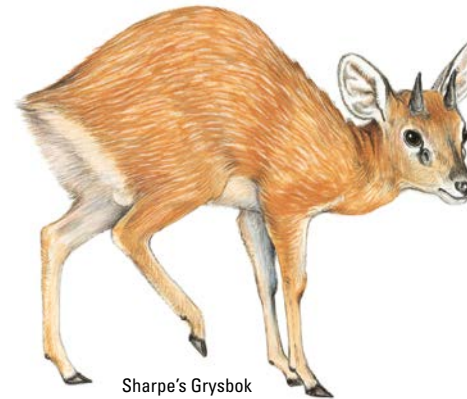
STATUS As the closest approximation to the model of an antelope ancestor, the survival and study of this species is of great importance. In spite of greatly retracted habitats it is still common within its localised range and in numerous parks and reserves. Listed as not endangered (IUCN).

■ SHARPE'S GRYSBOK *Raphicerus sharpei*

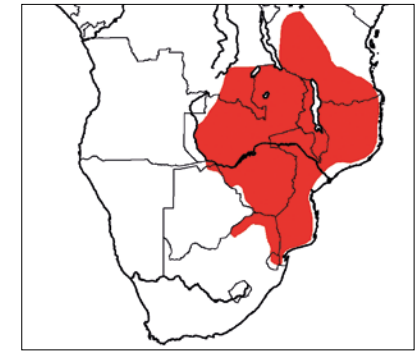
OTHER NAMES Fr. *Grysbok de Sharpe*. Ger. *Sharpegreisbock*.

MEASUREMENTS HB 610–750mm. T 50–70mm. H 450–600mm. W 7.0–11.5kg.

RECOGNITION A small antelope with a 'skirt' of elongated fur over the hindquarters. The reddish-fawn fur is densely interspersed with white hairs. The face, throat and undersides are much paler, even off-white. Horns (present in males only) and eyes are widely spaced and the muzzle is short but deep, with a large mouth and robust cheek teeth. The moderately large ears are mounted on a



Sharpe's Grysbok



Sharpe's Grysbok

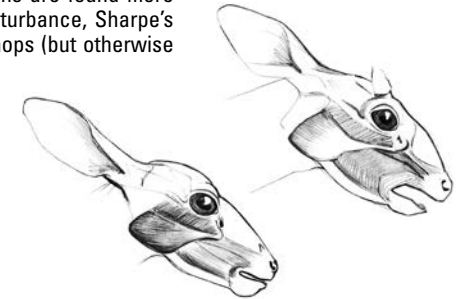
thick base (resembling the Klipspringer in this respect). Its 'tipped-up' rump posture while grazing herbs results from a short neck and face on a relatively long-legged body.

GEOGRAPHIC VARIATION Two subspecies have been named but are probably invalid.

HABITAT Ranging from L. Victoria to the Transvaal, the Zambezi watershed approximates to its western limits. Within this extensive area it is generally scarce and localised, preferring low thicket and secondary growth, stony outcrops and broken uplands, where it favours fertile zones on the lower foothills. It is predominantly nocturnal and lives in territories where pairs may form a loose association but are usually seen singly. Middens are found more easily than the animals themselves. At any disturbance, Sharpe's Grysbok departs rapidly, with short, stamping hops (but otherwise silently). It has been reported hiding in Aardvark burrows. In southern Africa a birth peak during the summer rains has been suggested.

FOOD Browses leaves, buds, herbs and fruits in a habitat where dry-season vegetation is generally tough. The teeth and jaw are well suited to such a diet and *Acacia*, raisin bush (*Grewia*), buffalo thorn (*Ziziphus*), ebony (*Diospyros*), and various fruits and berries have been recorded, along with grass (about 30%).

STATUS Probably declining generally but impossible to assess accurately because of its extreme shyness. Not endangered overall but locally rare.



Facial myology of *Raphicerus* spp. compared, showing mouths predominantly adapted to browsing, Sharpe's Grysbok *R. sharpei* (above) and to grazing, Steenbok *R. campestris* (below).

■ STEENBOK *Raphicerus campestris*

OTHER NAMES Steenbok, Steinbuck. Fr. *Steenbok*. Ger. *Steinbockchen*. Swah. *Isha*, *Dondor*.

MEASUREMENTS HB 700–950mm. T 40–60mm. H 450–600mm. W 7–16kg.

RECOGNITION More slender than a Bush Duiker, less so than an Oribi, the Steenbok can be mistaken for either but has characteristically rounded haunches without visible tail, very large, white-lined ears, a retroussé, black-bridged nose and big, black-rimmed eyes encircled by white. The males have very upright, polished spike horns. Colour ranges from pale brown to fawn or bright rufous.

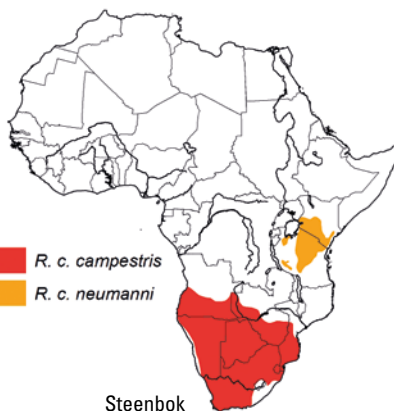
GEOGRAPHIC VARIATION *R. c. campestris* (southern Africa, 24 listed), *R. c. neumanni* (East Africa).

DISTRIBUTION All of southern Africa from Angola to near the mouth of the R. Zambezi. East Africa on both the Kenya coast and open plateaus and savannas inland up to 4,750m. Scarce or absent in most Miombo (*Brachystegia*) woodland areas.

HABITAT In southern Africa they are mainly open-plains animals. In East Africa they are common in stony savannas and among *Acacia*-grassland mosaics. Steenbok favour transitional and unstable conditions, following bush-clearance by cultivation, roads or elephants, often under a very dry



Steenbok



■ *R. c. campestris*
■ *R. c. neumanni*

Steenbok

climate. In open plains they tend to focus on riverbeds or belts of thicket where they can find well-hidden, regularly used resting places or refuges.

FOOD Browsers at or near ground level and adept at scraping up selected roots and tubers with hard, sharp hooves. Steenbok favour shoots of dominant shrub and tree species, such as *Acacia*, Leadwood (*Combretum imberbe*), buffalo thorn (*Ziziphus*), *Bridelia* and Mopane (*Colophospermum mopane*). They also take fruits and, during periods of early growth, may graze almost wholly on sprouting grass. They can survive without water and may live as far as 80km from water in the Kalahari subdesert.

BEHAVIOUR Pairs are thought to live for long periods with the same partner on the same territory (4ha to 1km²). Members of such pairs appear to move and rest independently but observers have suggested that routines and scent cues could keep such pairs mutually aware of one another's movements and position much of the time. In the absence of territory-marking with face glands (which are very small in Steenbok) the principal scent beacons are dung middens. These are connected by trails laid by secretions that ooze from glands between the hooves. Middens are scraped following defecation (by both sexes). It is possible that this associates individual 'signatures' in dung and urine with less specific food scents. The reception of such subtle clues is enhanced by the fact that most of the Steenbok's foraging is on or just above the soil surface.

A territorial male becomes very aggressive during his female's oestrus. Following a gestation of about 170 days a precocious fawn is born which remains well hidden for 2 weeks (in spite of being able to walk in 5 minutes) before joining its mother foraging. Lactation lasts 3 months and by 6–8 months female offspring are fertile. Some males are thought to breed twice a year, and this fecundity may explain their persistence in parts of South Africa in spite of sustained persecution. Animals live for at least 7 years.

ADAPTATIONS As a first line of defence Steenbok resort to the infantile strategy of sinking to the ground and freezing, ears retracted, while attentively watching any approaching danger. Their second strategy is to flee if the danger draws too close. Fast, zigzag flight alternates with repeated attempts at prostrate concealment. Both are compromise defences in a small conservative antelope that has invaded environments very different from those to which other *Raphicerus* are adapted.

STATUS Although this species has been exterminated from many small localities, it is still common in suitable habitats. Overall status, not endangered.



Steenbok, male

■ BEIRA *Dorcatragus megalotis*

OTHER NAMES Fr. *Beira*. Ger. *Beira*.

MEASUREMENTS HB 760–870mm. T 50–80mm. H 500–760mm. W 9–12kg.

RECOGNITION A very long-legged, long-necked antelope with enormous ears, vertical, upright horns (90–130mm) in the male only, and goat-like hooves which have rubbery centres and are especially rounded on the hindlegs. The coarse, thick fur is grey on the back and neck, graduating into a broad, oblique stripe of very dark grey from elbow to thigh. The underparts, throat and inner limbs are cream while the outer limbs and cheeks are ochre yellow. The forehead and nose (with hairy, slit nostrils) are covered in short, bright russet fur. The lids of the eyes are intensely black, contrasting strongly with their surround of brilliant white fur. The ears are also made conspicuous by dense white hair tracts.

DISTRIBUTION Confined to hills and mountains in N Somalia, notably the Migiurtina, Warsengeli Xadeed, Buuraha and Marmar ranges where it favours loose rubble screes.

HABITAT Usually close to stony ridges, gorges and plateau margins (where the Beira can make a quick get-away and break contact with potential predators). The extensive fields of finely fragmented stone in which it lives support scattered bushes but most plant growth is dwarfed or stunted. Some dominant plants in the preferred habitat are *Acokanthera*, *Buxus*, *Cadaba*, *Cadia*, *Carissa*, *Dodonaea* and various succulents, such as aloes, euphorbias and *Sansevieria*.

FOOD Beira have been observed feeding on the very common shrimp plant, *Justicia*. The Beira presumably browses the scattered shrubs, notably *Acacia etbaica*, while there is fresh growth on them but relies for its staple food on very small herbs growing among the pebbles. *Solanum*, *Cordia* and *Hibiscus* species have all been recorded.

BEHAVIOUR Usually seen in pairs or parties with a single male. Larger groups, up to 12, are possibly temporary associations of two neighbouring families. Such aggregations are rarely seen and may include two adult males. Each group is intensely attached to its own hillside or plateau. Gestation is estimated to last about 6 months and births have only been recorded in April (the peak of the rains).

ADAPTATIONS Exposure to predators in an open environment demands speed. Stamina is less critical where any pursuer is less well adapted to the terrain than the pursued. Extensive home-ranges and a scarcity of prominent landmarks help to explain the Beira's suppression of scent glands and overt marking behaviour. However, its ground-level foraging might have favoured the retention of pedal glands between the hooves. The raised rubbery cushions behind the hoof's margins are specifically adapted to walking and running on its very difficult terrain. The Beira's huge ears allow it to hear any approach across the loose stones, a capacity confirmed by its celebrated wariness and its survival in a region where many other species have become extinct.

STATUS The Beira's limited range, the absence of any protected areas within it, uncontrolled hunting, habitat degradation and competition from goats must all prejudice its long-term survival. It was thought to have made a slow recovery after dying in large numbers during the very severe 1975 drought. Nonetheless, its extreme specialisation for a very difficult and marginal habitat should continue to favour its survival for some time. The only viable captive breeding group is currently held in a private collection at Al Wabra (Qatar). Listed as threatened with extinction (IUCN).



Beira



DIKDIKS *Madoquini*

Formerly included within the Neotragini (when that taxon embraced all the dwarfed antelopes). Contemporary genetic research has demanded the disaggregation of Neotragini and the recognition that the dikdiks represent a lineage that has been distinct for more than 10 million years.

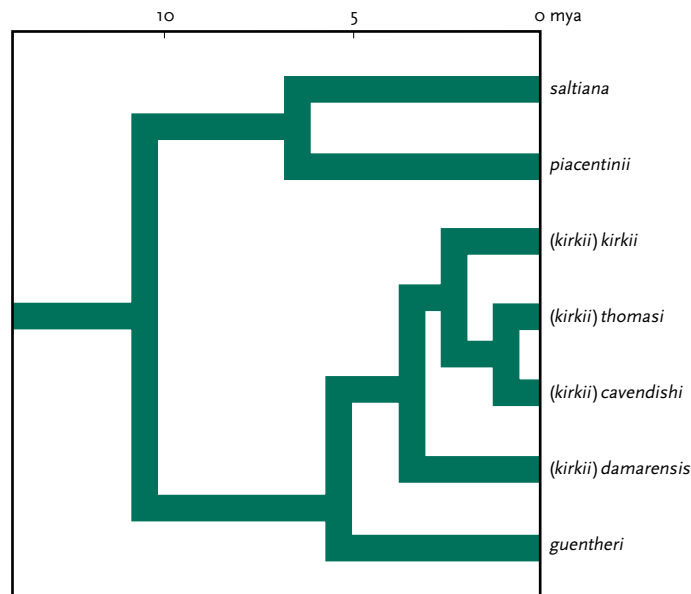
DIKDIKS *Madoqua*

Salt's Dikdik	<i>Madoqua saltiana</i>
Silver Dikdik	<i>Madoqua piacentinii</i>
Kirk's Dikdik species group	<i>Madoqua (kirkii)</i> (4 species)
Günther's Dikdik	<i>Madoqua guentheri</i>

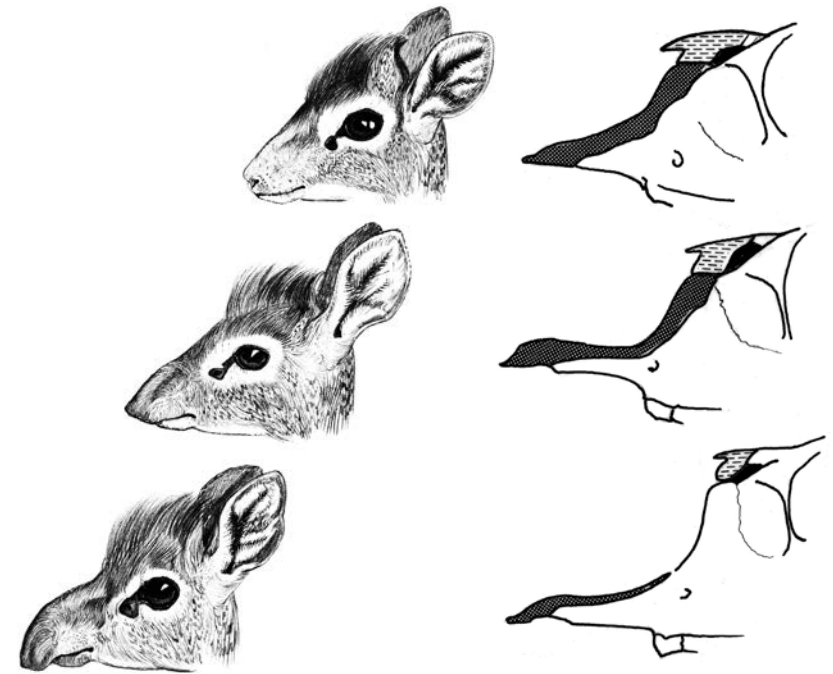
RECOGNITION Very small, long-legged antelopes with a fine, soft, grizzled (sometimes colourful) coat. They have relatively large eyes and ears, a prominent crest and a fur-covered nose that extends into a proboscis in several species. Probosces are the visible sign of a technique of temperature control that is more developed in dikdiks than in any other antelope. The nose of each species shows a different degree of elaboration and specialisation. The tail is vestigial but the pale underfur of the buttocks can be fanned into discs that are more conspicuous than any tail signal.

GENEALOGY Dikdik fossils are only known for some 4 million years (possibly 7 million years) but are likely to have begun as a distinct lineage (in the Horn of Africa) at a much earlier date. The distribution of living forms is some guide to the progress of evolution. Thus, the most conservative, least specialised forms, notably Salt's Dikdik, remain confined to the evergreen thickets that fringe the Ethiopian plateau and the Somali coast. The most advanced and most heat-tolerant species lives in the driest deserts and subdeserts of the region. Intermediate types, of the *M. kirkii* complex, occupy a much broader range of habitats in East and SW Africa.

GEOGRAPHY Essentially a group of small, arid-adapted antelopes endemic to the Horn of Africa, with a single outlying and isolated population in SW Africa. An arid corridor has clearly connected the two regions many times in the past, as is clear from other organisms with a similar pattern of



Tentative phylogenetic tree for *Madoqua* radiation (adapted from Hernández Fernández & Vrba 2005).



Left, top to bottom: Salt's Dikdik; Kirk's Dikdik; Günther's Dikdik.

Right, top to bottom: Diagram of nasals and premaxilla in the same three species.

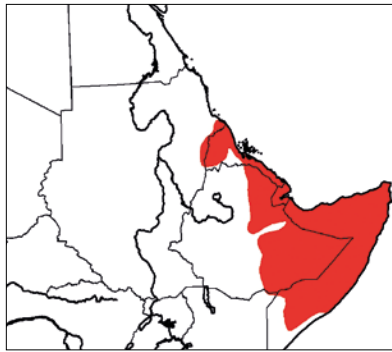
distribution. Although Kirk's Dikdik lives under a wide range of conditions in East Africa, its relative in Namibia is confined to warmer areas with less than 500mm annual rainfall.

ECOLOGY The more primitive species minimise the effects of high temperatures by being very largely nocturnal. The long-nosed Günther's Dikdik, with the greatest tolerance of heat, is more diurnal. All species depend upon low-level thickets and succulents growing on well-drained soils where there is little grass growth. If local changes allow patches of dense, tall grass to colonise their home-ranges, animals shift to another area.

NATURAL HISTORY Dung, urine and face-gland deposits are the boundaries, landmarks and focal centres for all social life. In the absence of scent marks (e.g. in a new area), all ages and sexes become alert and begin to seek or make them. While the male is the principal marker and defender of an area, his movements are entirely subordinate to those of the female – in a real sense *he* marks *her* territory. Territories may vary in size from 0.3 to 35ha. Densities range from 5 to 20 per km². Territories generally contain a mosaic of dense and more open ground with 6–13 stations where several dung and urine latrines are visited regularly. Where these are on a boundary two families may contribute, each sticking to its own side of the dung-marked border. Females and young contribute but males always scratch and superimpose their own contribution.

While many disturbances evoke a crouching or a creeping departure, any sudden flight tends to elicit breathy whistles from both partners in a territory, sometimes in a duet. Reunions involve face-rubbing in which females may lick the males' preorbital glands (which flow in response to excitement). Flight is usually short but very swift (up to 42kph has been recorded).

ADAPTATIONS The flexible proboscis is lined with numerous blood vessels in the mucus membrane. These are cooled by increasing the normal breathing rate from one to nearly eight breaths per second. The cooled blood returns to the heart via a sinus where hot blood going to the brain is cooled in a form of 'radiator' or *rete mirabile*. Selective cooling allows general body temperature to rise without risking brain function.

*M. s. phillipsi*

Salt's Dikdik

SALT'S DIKDİK *Madoqua saltiana*

OTHER NAMES Fr. *Dik-dik de Salt*. Ger. *Eritrea-Dikdik*.

MEASUREMENTS HB 520–670mm. T 30–45mm. Sh. ht 330–405mm. W 2.5–4.0kg.

RECOGNITION A small antelope with a short, squared-off, furry nose. Short male horns are up to 90mm. The coat is agouti-freckled and the legs sandy or reddish. There are five regional forms: two are dull-coloured (Salt's and Swayne's), two are very brightly coloured (Phillips' and Lawrence's), and one (the Harar Dikdik) is dark and somewhat intermediate. This is possibly best viewed as a superspecies but awaits further definition.

GEOGRAPHIC VARIATION (some may be full species) *M. s. saltiana* (Eritrea): reddish-grey back, large. *M. s. swaynei* (Web–Juba valleys): brown-grey back. *M. s. hararensis* (Hareрге): gingery back, dark-red flanks. *M. s. phillipsi* (Gulf coast): grey back, orange flanks. *M. s. lawrencei* (Obbia coast): silver back, russet flanks.

HABITAT Evergreen and semi-deciduous bushlands and thickets in the Horn of Africa from Suakin and Hadendowa (SE Sudan) to the mouth of the R. Juba. Predominantly a nocturnal and crepuscular species, lying up in dense shade during the day. Predation must be the main factor suppressing bright colours in the western part of their range. Colours appear to correspond with colour-coding for aggressive and submissive gestures. Subordinates (of both sexes) lower their forequarters and expose their greyer backs. Dominant animals flare their red or yellow crests and strut in high-stepping, side-on displays of the red or yellow limbs and flanks.

FOOD Herbs, foliage and shoots, especially *Acacia*, browsed close to ground level.

STATUS Numbers have decreased in densely settled areas but are otherwise probably little changed. Not endangered overall.

SILVER DIKDİK *Madoqua piacentinii*

OTHER NAMES Piacentini's Dikdik. Fr. *Dik-dik argenté*. Ger. *Piacentini Dikdik*.

MEASUREMENTS HB 450–500mm. T (est.) 30–40mm. Sh. ht 300–330mm. W (est.) 2–3kg.

RECOGNITION The smallest dikdik, with very soft, fine fur and a distinctive black border to the ears. The back and sides are a uniform silvery grizzle, particularly fine on the neck and haunches. Limbs, ears and muzzle are sandy ochre, cheeks and crest are creamy yellow and the bridge of the nose is often a vivid russet.

HABITAT Shared with Lawrence's Dikdik (an eastern representative of the *M. saltiana* complex). This is possibly the most primitive and least arid-adapted of dikdiks. It inhabits very low, dense thickets growing along the Obbia coastal littoral on fertile,



Silver Dikdik

sandy soils under a powerful offshore wind. This specialised wind-shaped, sand-blasted community has year-long, low-level green growth, partly due to the sea's cooling and moisturising effect.

FOOD Shoots and foliage of shrubs and herbs in undergrowth of the Obbia littoral thicket.

STATUS The Silver Dikdik is hunted with nets and is without formal protection within its very restricted range. Its long-term survival (and that of many other endemics) must depend on conservation areas being established in this unique ecological zone.

KIRK'S DIKDİK *Madoqua (kirkii)* (4 species)

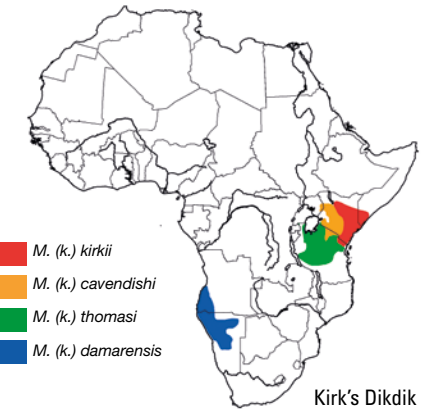
OTHER NAMES Fr. *Dik-dik de Kirk*. Ger. *Kirkdikdik*. Swah. *Suguya, Digidigi*.

MEASUREMENTS HB 550–720mm. T 40–60mm. Sh. ht 350–450mm. W 3.8–7.2kg.

RECOGNITION A group of very slender, small-snouted antelopes with grizzled or salt-and-pepper grey coats more or less suffused with warm red or yellow ochre tints. Face, coronal crest and legs are tawny while the eye is bordered with white; ear lining, chin and belly are also white. Sharp, corrugated male horns grow to 100mm. In spite



Silver Dikdik



Kirk's Dikdik

- *M. (k.) kirkii*
- *M. (k.) cavendishi*
- *M. (k.) thomasi*
- *M. (k.) damarensis*

Kirk's Dikdik *M. (k.) kirkii*Naivasha Dikdik *M. (k.) cavendishi*Damara Dikdik *M. (k.) damarensis*Ugogo Dikdik *M. (k.) thomasi*

of close external resemblances, each species has different numbers of chromosomes and cannot produce fertile offspring.

GEOGRAPHIC VARIATION There are four well-demarcated species:

Kirk's Dikdik, *M. (k.) kirkii* (Somali/Kenya coast and lowlands to foot of Pare/Usambara Mts): 47 chromosomes in males.

Naivasha Dikdik (Cavendish's Dikdik), *M. (k.) cavendishi* (uplands from E Uganda to Mbulu): 46 chromosomes.

Ugogo Dikdik (Thomas's Dikdik), *M. (k.) thomasi* (central Tanzania bushlands and thickets).

Damara Dikdik, *M. (k.) damarensis* (SW Africa): specialised hooves without pedal glands.

HABITAT A very wide range of habitats but with distinct geographic and ecological subtypes. Superficial resemblances were formerly interpreted as a sign of relatively recent dispersal. Contemporary molecular studies indicate an older and subtler adaptation of these dikdiks over their very wide and scattered range.

In Namibia they favour very dense thickets on hard, stony ground and limestone pavements. In Tanzania (Ugogo Dikdik) thickets dominated by *Grewia*, *Baphia* and *Pseudopropis* are typical habitat. In the E African highlands (Naivasha Dikdik) the commonest bush is an olive (*Olea*) while the main thicket shrubs are *Aspilaea*, *Tinnaea*, *Turraea* and *Psiadia*, with *Sansevieria* and aloes being favourite retreats. In the hot, flat lowlands, north-east of these cooler uplands (Kirk's Dikdik), the vegetation is again different, with many more acacias, *Indigofera*, *Duosperma* and *Boswellia*. Thus, these dikdiks inhabit regions that have few major physical barriers but which are very distinct in flora, soils, altitude, temperatures and rainfall pattern. In combination these may serve to keep adjacent populations genetically distinct (yet, in Samburu, *M. (k.) kirki* lives within sight of *M. (k.) cavendishi* with, apparently, no hybrids (a situation that begs further study).

These dikdiks are both diurnal and nocturnal (especially active during full moon) and have similar habits to other dikdiks, including a tendency to add their dung to any new, strong-smelling intrusion into their territory. A tendency to sprinkle elephant dung with their own minuscule pellets has an amusing bite in one local folk tale. This tells that the dikdik, on stumbling over an elephant bolus, keeps piling up his own pellets in the hope that one day he will trip up the elephant.

Males are also persistent whistlers. When whistling is initiated by the approach of a dog or Leopard its immediate effects are to cause females and young to hide. The whistles also serve to distract or 'mob' the predator and to broadcast an alarm. Another important, delayed effect is social cohesion. Once the danger has past female and male invariably join up, with much nuzzling and scent-marking. **FOOD** It browses evergreen shoots and foliage of the herbs, shrubs and succulents typical of each region.

STATUS Although exterminated in many localities (as a result of agriculture, hunting and dogs), all types remain widespread and common.

■ GÜNTHER'S DIKDIK *Madoqua guentheri*

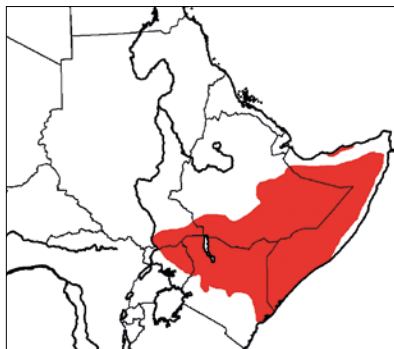
OTHER NAMES Fr. *Dik-dik de Günther*.

Ger. *Güntherdikdik*. Swah. *Digidigi ya pua murefu*.

MEASUREMENTS HB 550–650mm. T 30–50mm.

Sh. ht 340–380mm. W 3.2–5.5kg.

RECOGNITION A small, slender antelope, similar in colour to the Naivasha Dikdik, i.e. grizzled grey with brown or reddish flushes on sides and neck, reddish-fawn legs, nose and back of ears. Belly, chin, fur in the ear and around the eye are white. The nose is appreciably longer and more elastic than any other dikdik. In general the premaxilla and nasals are very reduced but even here intermediate skulls of both *kirkii* and *guentheri* sometimes make identification difficult. Hybrids have been bred in captivity (and might occur in the wild) but are known to be sterile. Intermediate forms make all documentation of Günther's and Kirk's Dikdiks provisional. Molecular studies have revealed that this species can have 48 or 50 diploid chromosomes and that crosses produce offspring with 49 chromosomes that are themselves fully fertile.



Günther's Dikdik

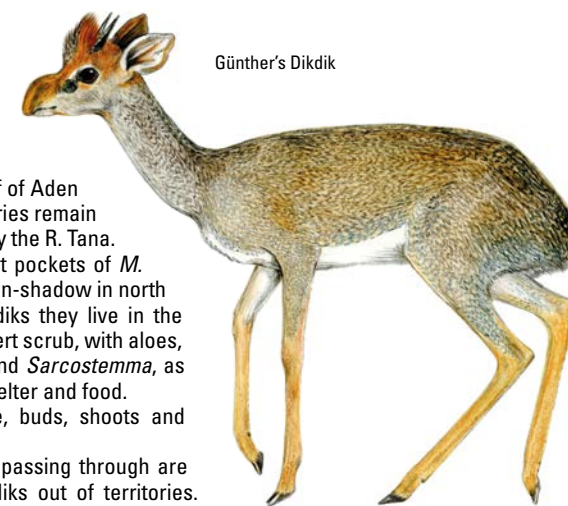
GEOGRAPHIC VARIATION

(*M. g. wroughtoni*, *hodsoni*, *smithi*.) Variation and confusion with *kirkii* types makes subdivision premature.

HABITAT Distribution centres on L. Turkana, reaching the Nile at Mongalla and possibly the Gulf of Aden at Maydh. South-eastern boundaries remain uncertain but possibly bounded by the R. Tana. However, it remains possible that pockets of *M. guentheri* occur along the arid rain-shadow in north and central Tanzania. Of all dikdiks they live in the driest, hottest desert and subdesert scrub, with aloes, *Euphorbia*, *Sansevieria*, *Cissus* and *Sarcostemma*, as well as *Acacia*, providing both shelter and food.

FOOD Green (and wilted) foliage, buds, shoots and bark of dwarf shrubs and herbs.

STATUS Large herds of livestock passing through are known to temporarily force dikdiks out of territories. These dikdiks survive well in dense, thorny thickets where livestock are less able to overbrowse. Very widespread and not endangered.



Günther's Dikdik

GAZELLINE ANTELOPES Antilopini

Gazelles

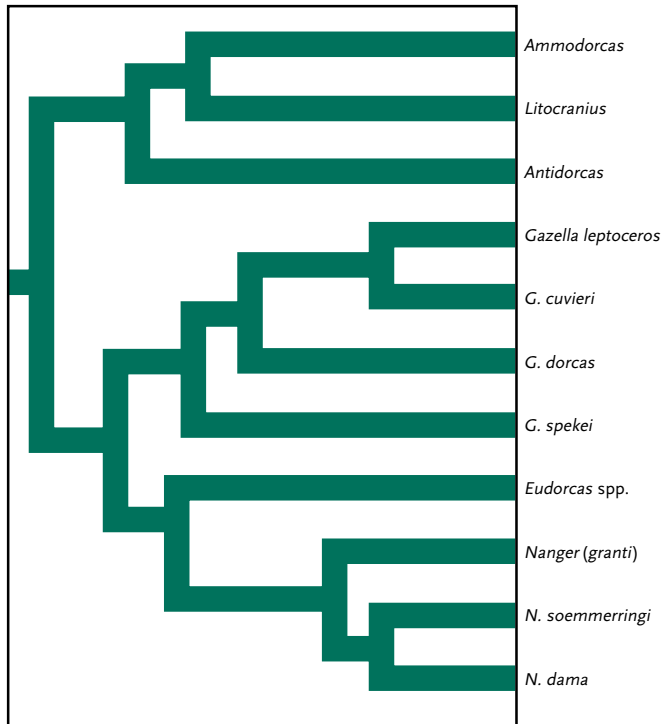
Slender gazelles	<i>Gazella</i> (4 species)
Ring-horned gazelles	<i>Eudorcas</i> (4 species)
Greater gazelles	<i>Nanger</i> (5 species)
Dibatag	<i>Ammodorcas clarkei</i>
Gerenuk	<i>Litocranius walleri</i>
Springbok	<i>Antidorcas marsupialis</i>

Long-legged, long-necked antelopes with light-coloured coats, large, sensitive eyes and ears, a small mouth and, in the smaller species, preorbital glands. In dentition and skull structure they greatly resemble enlarged dwarf antelopes.

Fossils attributable to this group date back to between 12 and 15 mya in both East and North Africa. In basic tooth structure they show surprisingly little change since that time. This is one of the few antelope groups that have been outstandingly successful outside Africa; they are spread across an arc from North and NE Africa through Arabia to arid Asia. A major factor influencing their success in this region must have been their tolerance of heat and ability to extract adequate moisture from their diet. All rely on high-quality, protein-rich diets (and this limits how large they can get in very impoverished habitats).

All are exceptionally alert to both sound and movement. In most species males are territorial while females and non-reproductive males are mobile, with individuals coming and going, assembling and dispersing without difficulty. In richer environments they remain tied to a resident home-range but for the most part they are nomadic over large areas.

The temperature regulation device typical of dry-country dwarfs (such as the dikdiks and Beira) has been taken still further in many gazellines. They too have increased the flexibility of their noses (to improve their performance as blood-cooling bellows) by freeing them from the constriction of a bony nasal tube. In *G. spekei* its nasal balloon serves as both sonic amplifier and visual flag. The antilopine trend of lengthening limbs and necks has been carried to extremes in the Giraffe-like Gerenuk, *Litocranius*, and Dibatag, *Ammodorcas*. What may have begun as an aid to greater mobility and speed in these species became a means of reaching more elevated sources of food.

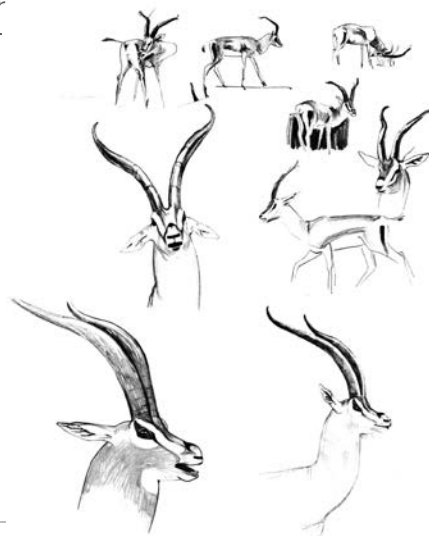


Tentative phylogenetic tree of Antilopini (modified after Hassanin *et al.* 2012).

In spite of all these innovations, the diets, teeth, stomach structures and brains of antilopines have remained very conservative.

GAZELLES *Gazella*, *Eudorcas* and *Nanger*

Slender gazelles	<i>Gazella</i>
Dorcas Gazelle	<i>G. dorcas</i>
Speke's Gazelle	<i>G. spekei</i>
Cuvier's Gazelle	<i>G. cuvieri</i>
Rhim Gazelle	<i>G. leptoceros</i>
Ring-horned gazelles	<i>Eudorcas</i>
Red-fronted Gazelle	<i>E. rufifrons</i>
Thomson's Gazelle	<i>E. thomsoni</i>
Eritrean Gazelle	<i>E. tilonura</i>
Mongalla Gazelle	<i>E. albonotata</i>
Greater gazelles	<i>Nanger</i>
Grant's Gazelle	<i>N. granti</i>
Tana Gazelle	<i>N. petersi</i>
Bright's Gazelle	<i>N. notata</i>
Soemmerring's Gazelle	<i>N. soemmerringi</i>
Dama Gazelle	<i>N. dama</i>



Field sketches of a gazelle (*Nanger (granti) granti*).

RECOGNITION Very slender, fawn or rufous antelopes; often with a dark flank-mark separating the body colour from the white underparts. A pale brow-streak runs from eye to nose, with a dark stripe below. Glands, sometimes vestigial, occur on the face, in the groin and between the toes. The tail is very short.

GENEALOGY Very ancient antelopes (at least 10 million years) that partly owe their diversity to emigration back and forth between Africa and Eurasia. The Palearctic branch, having adapted to much colder conditions in Asia, reinvaded Africa (probably during Ice Ages) to colonise some marginally cooler niches in North Africa.

GEOGRAPHY Restricted to North and NE Africa, Arabia and India, with the sand gazelles distributed as far as China.

ECOLOGY The four groups represent four adaptive trends. The *dorcas* group are small desert gazelles. The *rufifrons* group are small gleaners adapted to less arid but very open steppes around the margins of the Sahara proper. The Palearctic *leptoceros* group are cold-adapted species. The *Nanger* gazelles are large, desert gazelles (in East Africa they have maintained occupation of benign habitats that were formerly drier).

NATURAL HISTORY Horns and horn shapes are influenced by population density because frequent fighting selects for stronger weapons and more effective defence. Thus Grant's Gazelle (more consistently numerous and densely distributed) has the longest and heaviest horns (up to 800mm.) The Saharan Dama Gazelle normally lives at low densities and has horns half this length. Soemmerring's Gazelle, between the two extremes, has horn lengths of up to 580mm.

At an early stage in their evolution gazelles would have combined their ecological shift into more open habitats with a behavioural change towards visual rather than olfactory or vocal signals. As a result most species are highly conspicuous, with prominent signal patches (usually white) on head, rump, flanks and feet. All gazelles flag their head, posture, wag their tail, shudder their flanks, bounce, leap or race around. All are messages intended for other gazelles. Conspicuousness, in turn, has reinforced their dependence upon open country (where they normally have adequate warning of the approach of predators). Only as fawns do gazelles hide like the dwarf antelopes, with which they share a common ancestry.

ADAPTATIONS Heat tolerance in desert gazelles is achieved through a refinement of the nasal blood-cooling found in dikdiks. The less arid-adapted rufous gazelles are more wasteful of water, using conventional panting to cool down. Desert gazelles accumulate adequate moisture by feeding on dew-soaked vegetation late at night.

■ DORCAS GAZELLE *Gazella dorcas*

OTHER NAMES Fr. *Gazelle dorcas*. Ger. Dorkasgazelle.

MEASUREMENTS HB 900–1,100mm. T 150–200mm.

Sh. ht 550–650mm. W 15–20kg.

RECOGNITION The smallest gazelle but proportionally the longest limbed, with small, fine hooves. It is notable for its very long ears. Horns, on both sexes, are long (up to 380mm), with up to 25 annular rings, and lyre-shaped (out then in at the tips). Colour is light fawn with poorly differentiated flank stripes but light and dark streaks down the face.

GEOGRAPHIC VARIATION *G. d. dorcas* (E Sahara), *G. d. massaesyla* (W Sahara), *G. d. isabella* (east of the R. Nile), *G. d. beccarii* (Eritrean uplands), *G. d. pelzelni* (N Somali coast).

HABITAT North and NE Africa in driest subdeserts, mainly on stony or compacted soils with very sparse vegetation. Resident animals tend to disperse in small parties but converge on localised resources in larger numbers. When nomadic, they may aggregate in herds of up to 100. They are fecund, with a 6-month gestation. Sexually mature in 18 months, they live for more than 12 years.

FOOD Herbs (notably *Chrozophora*), succulents and, especially during the driest periods, shoots of shrubs such as *Acacia*, *Maerua* and *Leptadenia*. Dorcas Gazelles are mainly active at night and around dawn and dusk.



Dorcas Gazelle



Dorcas Gazelles

STATUS Endangered or exterminated in many localities but still widespread over much of its range. Not endangered overall.

■ SPEKE'S GAZELLE *Gazella spekei*

OTHER NAMES Fr. *Gazelle de Speke*.
Ger. *Spekegazelle*.

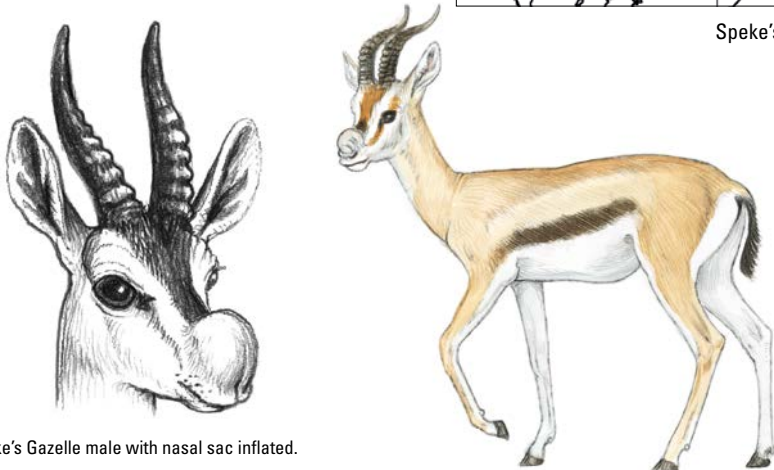
MEASUREMENTS HB 950–1,050mm. T 150–200mm.
Sh. ht 500–600mm. W 15–25kg.

RECOGNITION A rather small gazelle with an inflatable nasal region just behind the nostrils. It is fawn with a crisp black flank stripe (and paler band above it), white buttocks with dark margins, a pale face and undulating horns with broad annulations.

HABITAT The Indian Ocean littoral of Somalia in stony semi-desert dominated by stunted succulents,



Speke's Gazelle



Speke's Gazelle male with nasal sac inflated.

aloes, shrubs and sparse desert grasses (*Panicum* and *Eragrostis*). The centre of its range is the Nogal Valley where small groups, occasionally numbering up to 20, gather or disperse in response to the sparse vegetation. It is notable for a loud sneeze, said to be an alarm call (probably as much an advertisement of status), that is made by inflating and emptying the nasal sac, which is such a prominent feature of this species.

FOOD Grass, herbs, shrubs and succulents.

STATUS Still widespread, although intense competition from livestock may have reduced numbers in some areas. Not endangered.

■ CUVIER'S GAZELLE *Gazella cuvieri*

OTHER NAMES Atlas Gazelle, Edmi Gazelle. Fr. *Edmi*.
Ger. *Echtgazelle*.

MEASUREMENTS HB 950–1,050mm. T 150–200mm.
Sh. ht 600–690mm. W 15–20kg (♀); 20–35kg (♂).

RECOGNITION A tallish grey-brown gazelle with broad, lighter and darker bands across the flanks, a white belly and buttocks, and a black tail. The top of the nose has a prominent black spot. The face is well striped and the ears are pale, long and narrow. Horns are long (250–370mm) and well formed in both sexes; strongly annulated, they rise vertically before diverging out and back; the smooth tips curving in and forwards.

HABITAT From Morocco to Algeria (formerly to Tunisia) in maquis scrub mosaics, open parkland of pines (*Pinus halappensis*) evergreen oak thickets and patches of rushes (*Juncus*). It favours both stony and sandy ground on hills and plateaus. Here it lives in widely spaced territories where males attend one or more females and their young. It is rarely seen in groups of more than eight. Mating takes place in early winter with births in the spring (April–May).

FOOD Grass, herbs and shrubs; often visits cultivated fields.

STATUS Rare and now scattered in a decreasing number of localities, Cuvier's Gazelle is protected in a few reserves. Because it is heavily poached and suffers continuing habitat degradation, mainly from overgrazing by livestock, it is in danger of extinction.

■ RHIM GAZELLE *Gazella leptoceros*

OTHER NAMES Slender-horned Gazelle, Loder's Gazelle. Fr. *Rhim*. Ger. *Dünengazelle*.

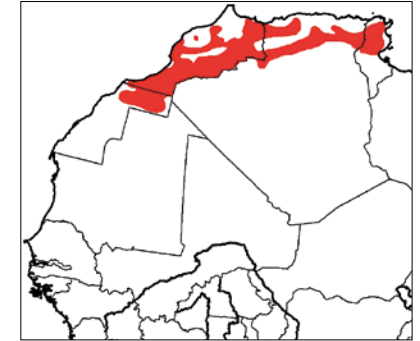
MEASUREMENTS HB 1.0–1.1m. T 150–200mm. Sh. ht 650–720mm. W (est.) 14–18kg.

RECOGNITION A medium-sized gazelle of very pale yellowish-grey colour, only faintly marked with face and flank stripes. The ears are long and narrow. Horns (appreciably thicker and longer in males) are long and nearly straight, with 20–25 well-defined annulated rings. Outer hooves are broader than the inner ones.

GEOGRAPHIC VARIATION Eastern Rhim *G. l. leptoceros*; Western Rhim *G. l. loderi* (validity uncertain).

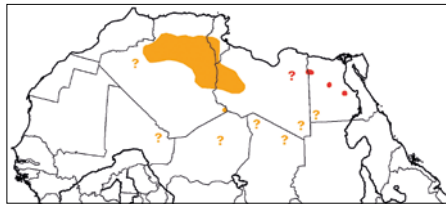
HABITAT Strictly confined to the great sand deserts, or ergs, of the E Sahara from Algeria to Egypt. Here it lives among the dunes in very small parties, usually a male with one or more females and their young.

FOOD Main grass reported to be a feather grass (*Aristida pungens*, or 'drinn'); also foliage of *Acacia raddiana*, fruit of *Colocynthis* and the halophytes *Nitraria* and *Anabasis*, as well as succulents,



Cuvier's Gazelle





G. i. leptoceros
Rhim Gazelle
G. i. loderi
(a very provisional subspecies)



Rhim Gazelle

herbs and foliage of scarce shrubs. The Rhim Gazelle feeds at night and in the early morning. Water requirements are drawn solely from moisture in its food.

STATUS In spite of its remoteness, the Rhim Gazelle has been a traditional quarry for mounted (and now motorised) hunters and its horns used to be sold as ornaments in N African markets and shops. Known to be rare, possibly endangered. Precise status not known.

RED-FRONTED GAZELLE

Eudorcas rufifrons

OTHER NAMES Fr. *Gazelle à front rouge*.
Ger. *Rotstirngazelle*.

MEASUREMENTS HB 800–1,200mm.
T 150–270mm. Sh. ht 550–820mm. W 15–25kg (♀); 20–35kg (♂).

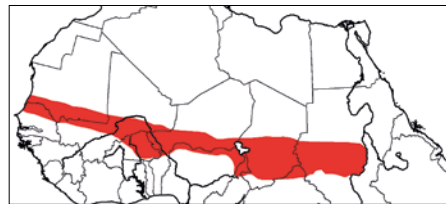
RECOGNITION An elegant gazelle with a warm reddish back and white underparts separated by a black flank band. The white buttocks contrast strongly with the deep russet colour on the back which extends to the root of the all-black tail. The face is white with red or brown stripes, the ears are narrow and pointed. The double-arched horns have numerous annulations.

GEOGRAPHIC VARIATION Red-fronted Gazelle: *G. r. rufifrons* (W Sahel), *G. r. laevipes* (E Sahel), *G. r. kanuri* (South of L. Chad). Red Gazelle – *G. r. rufina*? (Algeria – extinct).

HABITAT They prefer dry steppes and *Acacia/Combretum/Lanana* shrublands of the Sahel. Migratory animals, they form, fragment and reform easily. In Waza NP densities of 0.5–2.5 per km²

FOOD Growing green grass in rains; switches to herbs and foliage of *Acacia*, *Balanites* and *Boscia* in the dry season.

STATUS Once widespread throughout their range, Red-fronted Gazelles now occur in fragmented and declining patches. Not endangered overall.



Red-fronted Gazelle



THOMSON'S GAZELLE *Eudorcas thomsoni*, ERITREAN GAZELLE *Eudorcas tilonura* and MONGALLA GAZELLE *Eudorcas albonotata*

OTHER NAMES Fr. *Gazelle de Thomson*.

Ger. *Thomsongazelle*. Swah. *Swala tomi*.

MEASUREMENTS HB 800–1,200mm. T 150–270mm.
H 550–820mm. W 15–25kg (♀); 20–35kg (♂).

RECOGNITION A compact little gazelle with a warm sandy back and white underparts separated by a bold black flank band. The white buttocks have black marginal stripes and the colour on the back extends to the root of the all-black tail. The face is boldly striped (with much individual variation) and the ears are of moderate length. The mildly undulating horns have numerous sharp corrugations.

GEOGRAPHIC VARIATION The Thomson's Gazelle group now comprises three species:

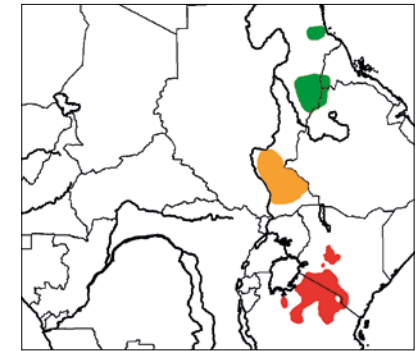
Thomson's Gazelle *E. thomsoni*
(L. Victoria/Eastern Rift Valley region);

Eritrean Gazelle (Heuglin's Gazelle)
E. tilonura (E Sudan and W Eritrea);

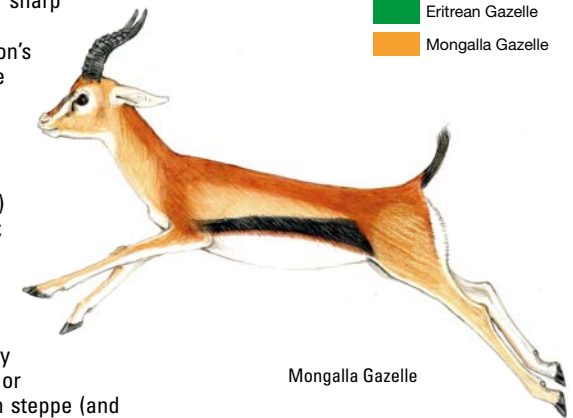
Mongalla Gazelle *E. albonotata*
(Sudd region of SE South Sudan, east of the Nile).

HABITAT The dry grasslands and shrubland habitats in E Africa. They prefer heavily grazed, trampled or burnt grasslands or naturally open steppe (and stay on pastures long deserted by larger herbivores as long as some miniature growth remains). Socially they are exceptionally flexible. They are migratory animals, without lasting ties between individuals, spread out in a loose mosaic of overlapping female herds. Each individual shares with many others a particular home-range within which activities such as going to water (treks of 15km are not unusual), resting and moving to fresh pasture are often coordinated. Such temporary associations among a large number (up to 100 or more) suggest that, in spite of their individual independence, each gazelle knows and remembers a large number of 'friends', 'clan' members or other relatives. Males are less flexible and mature individuals fight to hold and defend territories within the females' favourite pastures. When resources are exhausted only thirst or hunger drives them away. Solitary territorial males in an empty landscape are a common sight.

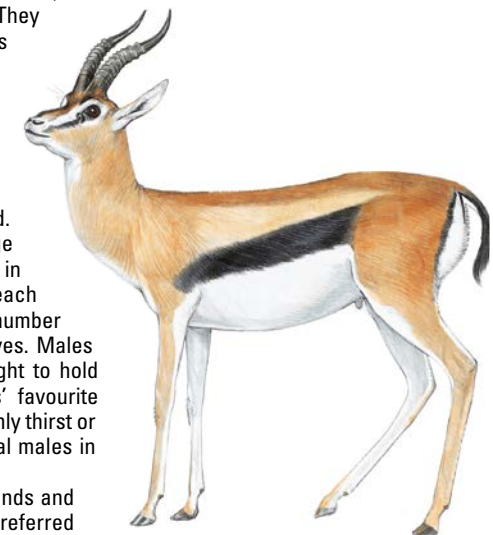
This species retains active preorbital glands and males mark grass stems and twigs at preferred spots (often hillocks or compacted bare patches).



Thomson's Gazelle
Eritrean Gazelle
Mongalla Gazelle



Mongalla Gazelle

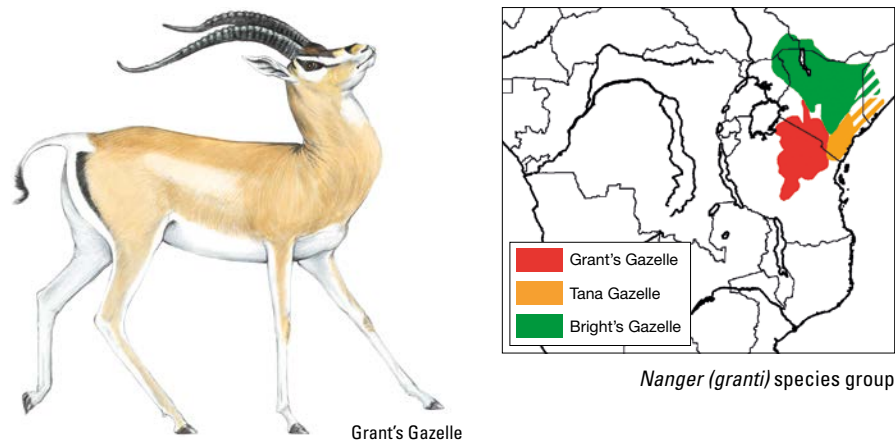


Thomson's Gazelle

They also drop dung at these places. Frequent fights and stand-offs help maintain boundaries between neighbours. Males attempt a mild, ineffectual 'herding' of females in order to delay their departure but their primary interest is in finding oestrous females to mate with.

FOOD Mainly growing grass in the wet season but switches to herbs, the foliage of shrubs and seeds of *Acacia*, *Balanites*, *Sida* and *Solanum* in the dry season. *Themeda*, *Cynodon* and *Harpachne* are preferred grasses in Kenya.

STATUS All populations are declining but are still locally common at reduced densities. In some areas their status is unchanged, but *E. tilonura* is now rare. Not endangered overall.



Nanger (granti) species group

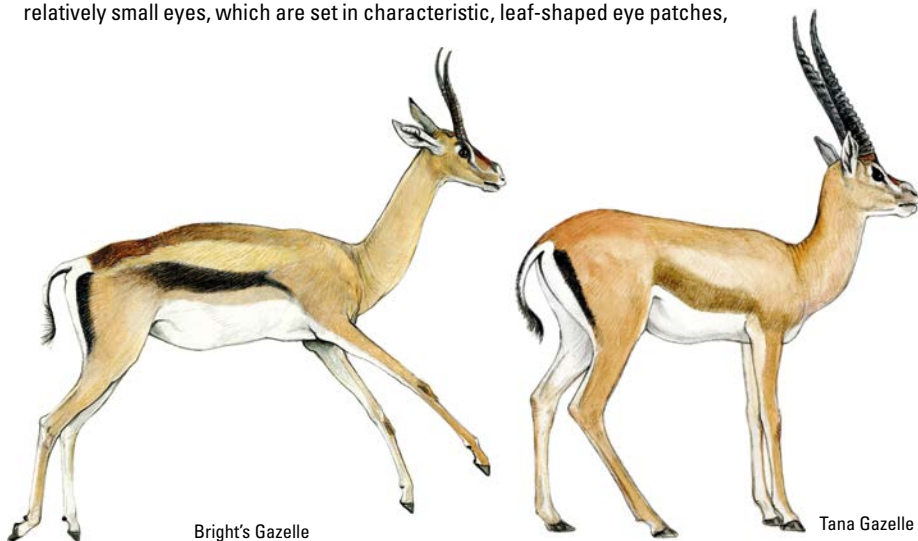
Grant's Gazelle

■ **GRANT'S GAZELLE** *Nanger (granti) granti*, **TANA GAZELLE** *Nanger (granti) petersi* and **BRIGHT'S GAZELLE** *Nanger (granti) notata*

OTHER NAMES Fr. *Gazelle de Grant*. Ger. *Grantgazelle*. Swah. *Swala granti*.

MEASUREMENTS HB 1.4–1.6m. T 200–280mm. Sh. ht 780–830mm (♀), 850–910mm (♂). W 38–67kg (♀), 60.0–81.5kg (♂).

RECOGNITION Large, pale gazelles with upright stems to the long horns above relatively small eyes, which are set in characteristic, leaf-shaped eye patches,



Bright's Gazelle

Tana Gazelle

or 'masks', of jet-black skin and hair incorporating vestigial preorbital glands. Above the nostrils there is a slightly inflatable nasal sac. The tail is markedly tapered and carries a wispy fringe. There are hoof and knee glands. The root of the tail is white, extending the buttock patch into a bold white configuration (the rectangularity of which is emphasised by a dark vertical stripe down each thigh). Colour varies individually, especially on the flanks, but with distinct regional trends. Thus, females often have dark flank stripes, but less often in the north-east, while the flanks of males are also dark only around L. Turkana. Horns also vary individually and regionally (500–800mm). Male horns west of L. Eyassi and L. Natron tend to splay at a sharp angle, with downward curls at the tip. North of Mt Kenya horns tend to be more parallel.

Some ten forms have been described; the most distinctive being the Tana, or Peters's, Gazelle, *N. petersi*, which has a back that is fawn-brown from neck to tail, with a white buttock patch reaching only to the anus. Overall proportions are smaller. Facial stripes are faded. The horns are almost straight.

GEOGRAPHIC VARIATION The Grant's Gazelle group now comprises three species:

Grant's gazelle, *N. (g.) granti* (S Kenya and N Tanzania, from Mt Kenya to Ruaha valley);

Tana Gazelle, *N. (g.) petersi* (lower Tana valley);

Bright's Gazelle, *N. (g.) notata* (NE Uganda, S Ethiopia, N Kenya [north of Mt Kenya] and S Somalia).

HABITAT This species group could be called 'Rift Valley gazelles' because their distribution spills over from the central axis or 'spine' of the East Rift. This upland distribution coincides with rain-shadows and with an arid corridor of unstable climate across the East African plateau that is known to have been very much more arid in the past. The Tana species lives in the lower Tana valley, Lorian swamp, Wajir and the Dheere-Madheeri depressions (west of the R. Juba in Somalia). Here the gazelles live on very flat plains that are briefly flooded during occasional and unpredictable rains (when they do flood it tends to be in April or December). Where their range becomes dense bush the gazelles are restricted to glades or open, scrubby valleys. However, in the 1950s elephants became so numerous in Tsavo that they cleared large areas of woody growth (a clearance extended recently by charcoal-burners) and the Tana Gazelles expanded west and south, meeting up with *N. (g.) granti* across a broad front south of the Galana valley. Where conditions suit them all year, both sexes are resident, the males on midden-marked territories of 8ha to 10km², the females circulating over still larger areas. Elsewhere, seasonal movements take them from higher, well-drained areas during the rains out onto flat, grassy valleys in the dry season. They do not tolerate soft soils but will live in bush and tall grass more readily than any other gazelle (but only seasonally). Fighting and territorial displays, characterised by flicking of the raised head on the bulging neck and slow, stiff circling, increase during biannual mating peaks (December and May north of the Equator). Births follow a 6-month gestation. Rainy-season births appear to take place in denser cover. The fawn remains hidden for several weeks. At this time mothers may actively attack small predators.

FOOD Herbs and shrub foliage are preferred during the later wet and dry seasons; grass is grazed only while it is young and green. The fruits of *Balanites* and *Solanum* have also been recorded. Intense grazing by other species removes grass, thereby favouring herbs and the gazelles that feed on them. Grant's Gazelle is typically found in herbivore concentration areas, such as the Serengeti plains, and are commonly seen in mixed groups. Herds of these gazelles may number up to 500 at such times.

STATUS Although eliminated in some agricultural regions and areas where poaching is uncontrolled, these gazelles are still widespread and common both within and outside national parks and reserves.

■ **SOEMMERRING'S GAZELLE** *Nanger soemmerringi*

OTHER NAMES Fr. *Gazelle de Soemmerring*. Ger. *Sömmerring-gazelle*.

MEASUREMENTS HB 1.25–1.5m. T 180–230mm. Sh. ht 810–900mm. W 38–46kg.

RECOGNITION A large, generally pale gazelle with extensive white on the rump, strongly marked facial blazes, a large head and heavy, short, backwardly swept horns that form a lyrate shape with in-pointed hooked tips. It is long in the leg, with big hooves and a relatively short neck. The tail, like that of other *Nanger* gazelles, is short and tapered, with a mainly white fringe of short hairs.

GEOGRAPHIC VARIATION *N. s. soemmerringi* (Sudan and Eritrea): brown face, shorter horns. *N. s. berberana* (Somalia and NE Ethiopia): black face, longer horns. *N. s. butteri* (S Ethiopia): dark flank, thigh stripes. An unnamed dwarf from Kebir I. in the Dahlak archipelago (Eritrea) has differently



Soemmerring's Gazelle



Soemmerring's Gazelle

curled horns and could be a distinct island species.

HABITAT Endemic to the Horn of Africa where they once inhabited most of Somalia and the last, lowest foothills of the Ethiopian massif on its northern and eastern faces. Here they once gathered in hundreds on open plains and made

substantial seasonal migrations (notably down from the upper Atbara valley to spend the wet season on the exposed plains below Kasala). They favour rough, hilly country with scattered evergreen thickets and *Acacia/Commiphora* steppe, as well as open, short-grass plains. Today they are seldom seen in herds larger than about 15. These are often groups of females and their young herded by a single male on his midden-marked territory. Like Grant's Gazelle, males flick their heads during confrontations. They yank their hooked horns sideways during fights in efforts to destabilise the opponent. When tending or herding females, males make a nasal croak. A mating peak has been recorded between September and November. Gestation lasts 198 days and the young lie up for a month. They are weaned by 6 months and reach sexual maturity by 18 months. Animals live for 14 years.

STATUS Exterminated over the greater part of their range, these gazelles now exist in numerous small pockets. Although hunting may have played a significant part in this decline, overgrazing and habitat degradation by domestic stock is probably the main cause. Listed by IUCN as threatened.

■ DAMA GAZELLE *Nanger dama*

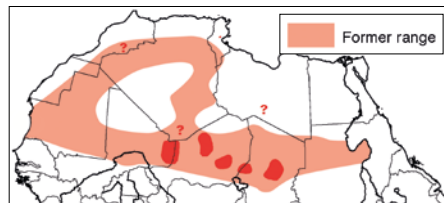
OTHER NAMES Addra Gazelle. Fr. *Gazelle dama*. Ger. *Damagazelle*.

MEASUREMENTS HB 1.40–1.65m. T 250–350mm. Sh. ht 0.9–1.2m. W 40–75kg.

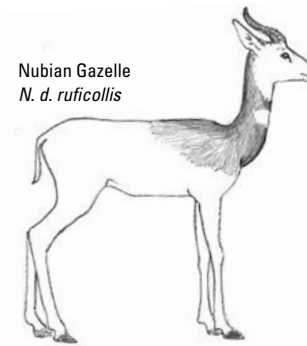
RECOGNITION The largest of all gazelles, with long legs and neck, a big head and short, compact, double-curved horns. The face and underparts are white in all forms; the most westerly resemble Soemmerring's Gazelle in pattern but are a vivid rufous rather than fawn. The most easterly populations are very variable but have many individuals where the rufous element is confined to the neck and upper shoulders but are otherwise white. The tail is short and white, with a sparse fringe.

GEOGRAPHIC VARIATION Dama Gazelle, *N. d. dama* (W Sahara); Nubian Gazelle, *N. d. ruficollis* (Sahara west of the Nile). There was formerly a wide zone of very variable integration between these two. Mhorrr Gazelle, *N. d. mhorrr* (North Africa to Mauritania).

HABITAT Until recently one of the most widespread and common of Sahara gazelles, making mass movements between its wet-season pastures deep in the Sahara and dry-season range



Dama Gazelle

Nubian Gazelle
N. d. ruficollisDama Gazelle
N. d. damaMhorrr Gazelle
N. d. mhorrr

Dama Gazelle

in the semi-deserts and open bushlands of the Sahel. Herds of many hundreds used to be seen on the move before dispersing into smaller groups numbering up to about 15. The principal mating peak in the Sahara was between March and June, the wettest months. Births would peak in about December, by which time the gazelles had moved well to the south so that the newborn could find shelter in the light scrub and grassland of the Sahel. Similar movements between moister and drier parts of their range took place in Morocco and Algeria. Here they travelled south into the Sahara, returning north where they preferred reg and hammada pastures. The last animals here were seen in the 1950s.

FOOD Mainly herbs, succulents and shrubs (notably *Acacia*, which the gazelles could browse above 2m by standing up on the hindlegs like a Gerenuk). These gazelles were also reported to eat coarse desert

grasses. Their seasonal movements were symptomatic of their need for moisture (albeit moisture contained in browse).

STATUS Dependence on movement into the Sahel was fatal for Dama Gazelles. Large, very conspicuous antelopes, they came into contact with ever-increasing numbers of livestock and people along almost the entire length of their range and declined very rapidly between the 1950s and 1970s. They are now extinct in Algeria, Mauritania, Senegal and Burkina Faso, nearly so in Mali, Niger and Sudan. The principal authority on wildlife in this region, J. E. Newby, wrote in 1990: 'the problems for these animals and for the people trying to conserve them have been exacerbated by a new wave of hunters invading the Sahelian countries in search of new hunting grounds'. Wealthy and irresponsible foreigners are purchasing a part in the extermination of Sahelian wildlife. Less accessible parts of this vast region may allow survival for a while but only in Chad do Dama Gazelles have a realistic hope of recovery once fighting ceases. Since 1990 the situation has worsened and the Sahara may soon be empty of all its larger endemic ungulates. Listed by IUCN as threatened with extinction.

■ DIBATAG *Ammodorcas clarkei*

OTHER NAMES Clarke's Gazelle. Fr. *Dibatag*.
Ger. *Lamagazelle*.

MEASUREMENTS HB 1.52–1.68m. T 300–360mm.
Sh. ht 800–880mm. W 22–29kg.

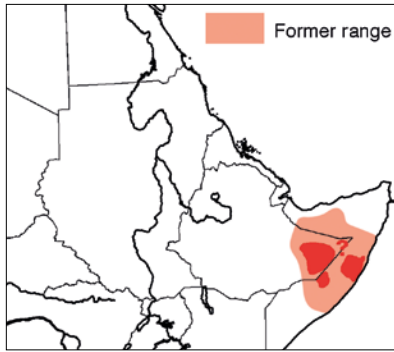
RECOGNITION A very tall, slender antelope with large eyes, long, black-tipped ears and a face with typical gazelline markings down an elongated but sharply tapered muzzle. The mouth, teeth and jaws are minuscule. The males have shortish horns with heavy, annulated bases and tips that are sharply angled forward. Its name means 'erect tail' in Somali and the heavily furred black tail, carried like a wagging baton, is indeed its most conspicuous feature. During flight the tail and head are carried erect which distinguishes this species from the Gerenuk, which adopts a more horizontal posture. The body colour is a uniform fawn-grey, with ochre-coloured legs and a red forehead. The undersides and brow stripe are white and the long buttock hair can be flared out into a brilliant white signal. There are preorbital glands and glandular 'brushes' below the knees.

DISTRIBUTION Restricted to a single vegetation type in central Somalia and the Ogaden (Ethiopia). Here it prefers areas of well-drained, sandy soils. It avoids dense thickets and very stony ground.

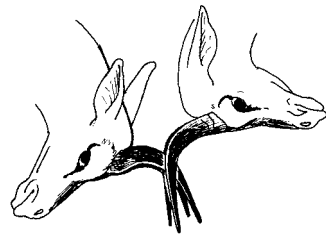
HABITAT A plant community called camel-brush or 'gedguwa'. This is an *Acacia/Commiphora* deciduous bushland and thicket in which important evergreens are *Boscia*, *Dobera*, *Salvadora*, *Grewia* and *Cadaba*. During and immediately after the rains it visits more open glades and in general prefers a mosaic of thickets and grassland with scattered trees.

FOOD Mainly the foliage of *Acacia* (at least six species noted), *Commiphora* and other evergreen trees and shrubs, but probably less dependent on woody growth than the Gerenuk. It has been reported to graze on herbs and new grass during the rains. Sodom apples (*Solanum*) have also been recorded in its diet. The small, mobile, very pointed but muscular lips assist the plucking of minute items, such as buds and shoots, from within dense barricades of thorns. The Dibatag can reach up into small trees and bushes by balancing on its hindlegs, keeping balance with lightly propped forelegs but this mode of feeding is thought to occur less frequently than in the Gerenuk.

BEHAVIOUR Males are territorial, visiting their latrines daily to renew the piles of small, dark, oblong pellets, but they are also reported to make periodic small-scale shifts in range. Up to five females and their young have been seen with single adult males but singles or twos are commoner. Captive males rub their facial glands on the female's rump and both sexes have been seen to nibble or lick one another's glands. Males douse their muzzles in female urine and lip-curl like all other bovids. There is a mating peak during the heavy rains in April and May.



Dibatag



Dibatag horn-wrestling

After 6 months' gestation a single fawn is born during the short rains (October–November) and lies up in thick bush. Young remain concealed for 2 weeks and reach sexual maturity at between 12 and 18 months. The Dibatag is thought to live for 10–12 years.

ADAPTATIONS The contrast between great height, substantial weight and extreme delicacy of mouth-parts poses special problems for fighting males. Not only must they avoid injury to the muzzle, they also risk toppling because tall, heavy animals are easily thrown off balance. Males squaring up for a fight therefore tuck their vulnerable noses between their forefeet. Their horns are sufficiently long to force them into a standing contest. Their thick, heavy napes and upper necks engage and the horns clash along their curved back surfaces. From this position, pushing hard and wrestling from the pivot of their broad napes, each animal seeks to hook his opponent off balance. This technique of fighting ensures that there is little risk to their fragile muzzles and it is the rumps of fleeing losers that are more likely to get stabbed by sharp horn tips.

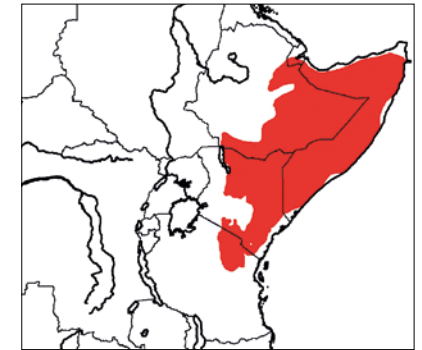
STATUS This species has lost at least half of its known recent range and probably occupies a much smaller fraction of its original area of distribution. There are two or three remaining pockets where it remains fairly common but poaching and displacement by domestic stock makes continued decline likely. Proposed conservation areas at Hobyo (Obbia), Haradere-Awale Rugno in Somalia and E Ogaden in Ethiopia must await more peaceful times to be implemented. Listed as vulnerable (IUCN).

■ GERENUK *Litocranius walleri*

OTHER NAMES Waller's Gazelle. Fr. *Gazelle de Waller*.
Ger. *Giraffengazelle*. Swah. *Swala twiga*, *Njonga*.

MEASUREMENTS HB 1.4–1.6m. T 220–350mm.
Sh. ht 0.8–1.05m. W 28–45kg (♀); 31–52kg (♂).

RECOGNITION A very tall, long-necked, long-eared antelope with a two-toned chestnut back, light fawn sides and white underparts. Like the Dibatag it has extremely small mouth-parts for a large antelope. The contrast is greatest in the very heavily horned male where the upper neck is thicker than its lower part and the dainty little muzzle protrudes from a heavily reinforced brain-case. The horns have thick, diverging shafts, rising in a bold arc and then curling forward in a tight hook towards the tip. It has preorbital face glands, scented brushes below the knees and glands between the hooves.



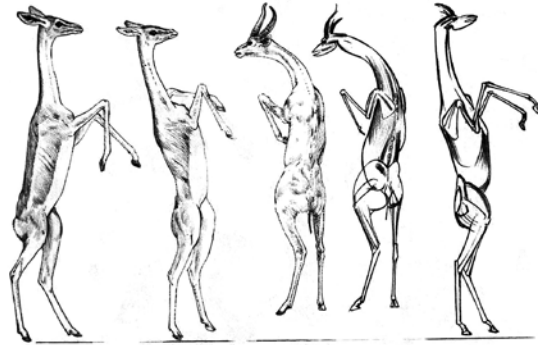
Gerenuk



female



male



Gerenuk female and male in bipedal posture.

GEOGRAPHIC VARIATION Two ill-defined subspecies are listed, which are sometimes regarded as full species. The southern nominate race, *L. w. walleri*, has smaller cranial measurements than *L. w. sclateri* in the northern part of its range.

DISTRIBUTION The Horn of Africa extending into NE Tanzania. Mainly semi-arid bushland below 1,200m. Known to have been more widely spread in the more distant past (up the Red Sea littoral).

HABITAT Dependent on an abundance of bushes and small trees, including evergreens. It avoids true, dense thickets and is commonest on flats where *Acacia*, *Commiphora* and other bushland species are well spaced or in small clumps. It has a wider tolerance of bushland types than the Dibatag.

FOOD Almost exclusively a tree-foliage browser (creepers and vines being the main exception). *Acacias*, with their very small, nutritious leaflets, are the major staple but seasonal and regional variations follow what plants are in leaf or in bud at the time. Skunk Bush, *Premna resinosa*, is a favourite in Kenya but 87 different trees and shrubs have been recorded in the diet. The Gerenuk habitually rises on its hindlegs to reach a zone over 2m high (where Giraffes are the only, partial, competitors). Its minute, pointed muzzle can extract leaves from very thorny tangles.

BEHAVIOUR The Gerenuk is normally very residential, living in well-spaced home ranges of 3–6km². Here single adult males exclude other adult males but regularly associate with females and their offspring. In some cases males share exactly the same range as one or more females, regularly visiting or following them. Shifts of range are known but are probably rarer with age. Males in particular become more strictly residential with age. Males mark out their territories by inserting twigs into their preorbital glands. Unlike the Dibatag, they do not make dung middens (which in other antelope species tend to abut the ranges of other males and are often contributed to by both neighbours). It is therefore interesting that Gerenuk facial gland deposits are distributed along the borders of very small domains that do not abut those of neighbours, suggesting that males live in such large home-ranges that they can only mark core areas. It is possible that some kind of no-man's-land lies between male gerenuk territories. Among females, overlaps in range and sporadic associations (sometimes larger aggregations) hint at the existence of local 'clans' of related animals that know one another. The contact call is a frog-like humming grunt.

Like Dibatag, Gerenuk males rub their face glands on females. Occasionally they threaten them, making a low rumble (apart from a buzz of alarm they are otherwise rather silent animals). Young are born after a 7-month gestation and most births occur during the rains. The newborn is well hidden and only emerges to join its mother after several weeks. A mother may be accompanied by more than one offspring (female young become independent at about 12 months, males parting later, at up to 18 months). Animals are thought to live for 10–12 years.

ADAPTATIONS In spite of many similarities, Gerenuk and Dibatag males differ most in the shape of their horns. The Gerenuk's fighting technique differs fundamentally, as its much heavier horns, which curve in the opposite direction, are clashed together with violent downward nods of the head. Backward extension of the very hard brain-case provides the immediate leverage for the hammer-like blows exchanged by fighting males.

STATUS Although eliminated from parts of its range in East Africa, the Gerenuk is still widespread both within and outside national parks and reserves. Not endangered overall.

■ SPRINGBOK (SPRINGBUCK)

Antidorcas marsupialis

OTHER NAMES Fr. *Antidorcas*. Ger. *Springbuck*.

MEASUREMENTS HB 1.2–1.5m. T 140–280mm.

Sh. ht 680–900mm. W 20–43kg (♀), 30–59kg (♂).

RECOGNITION In size and general proportions the Springbok is very gazelle-like, and they share striped faces and bands on thighs and flanks. They are generally assumed to be a sort of 'southern gazelle.' However, there are several differences that distinguish them. Their white underparts extend well up the sides, rump and dorsal midline. The head is also white but marked from crown to mouth with brown streaks (which conceal the very protuberant eyes). The white ears are exceptionally long and narrow. Upperparts are cinnamon fawn above an arc of black or brown on the flanks. The Springbok differs from gazelles in having a longer, broader and less flexible bridge to the nose, deeper, more muscular cheeks, and horns that sweep backwards and hook inwards from peculiarly swollen bases above the eyes. The white dorsal crest is normally hidden beneath two long folds of scent-secreting skin that run along the lower spine but it can be erected (as can the white hair on the buttocks) to create an eye-catching, and presumably odoriferous, signal.

GEOGRAPHIC VARIATION Smaller south-western populations grade into larger north-eastern ones. Individual variation has led to 11 subspecies being named (from a single population in a continuous range). None are now considered valid. Dark and pale morphs have been selected on some South African farms.

DISTRIBUTION SW Africa, the Namib, Kalahari and Karoo deserts. This species or its immediate antecedents was once sufficiently common in East Africa to become the most frequently fossilised of all antelopes (three species found over a period of more than 2 million years).

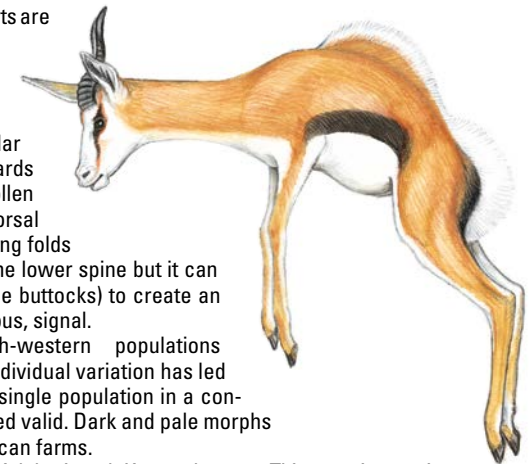
HABITAT Dry, open plains with a marked preference for flat drainage lines and the fringes of pans where soil conditions or overgrazing keep grasses and herbs low. It lives in dry *Acacia* savannas in the Kalahari, bushy shrubland in Namibia, dwarf and grassy shrublands in the Karoo. It is exceptionally mobile, moving long distances to find scarce pastures during droughts but instantly returning to traditional and well-known localities when the rains break. Vast herds of migrating Springboks formerly earned the Afrikaner name of *treckbokken*. It avoids tall grass, thick woodland and broken ground. Pliocene fossils from the Atlas Mts show that Springboks (of the living genus, *Antidorcas*) were already adapted to cool Eurasian-type habitats some 4 mya. Today's Springboks survive in SW Africa, the main region of the continent that has remained both dry and (periodically) cool. This region has been connected with N and NE Africa by arid corridors during every major Ice Age.

FOOD Broadly a summer grazer and winter browser, the Springbok can survive on the residual moisture in plants. In the absence of any surface water it seeks out succulents, cucurbits and even paws out shallow roots. It feeds most intensively around dawn and dusk. The staple in some areas consists of nine species of grasses and 11 species of shrubs but it has varied tastes. Some of the grasses favoured are coarse- or hard-stemmed species, such as bristle grass (*Aristida*), love grass (*Eragrostis*), stargrass (*Cynodon*), buffalo grass (*Panicum*) and rush grass (*Sporobolus*).

ADAPTATIONS Several adaptive traits distinguish this antelope and its numerous fossil antecedents. One of the most important is modification of the teeth for coping with coarse plants on dry winter pastures. Springbok teeth are more like those of a coarse-grass grazer than the narrower teeth of herb- and leaf-eating gazelles. A more abundant food supply permits bigger, denser herds to form and



Springbok



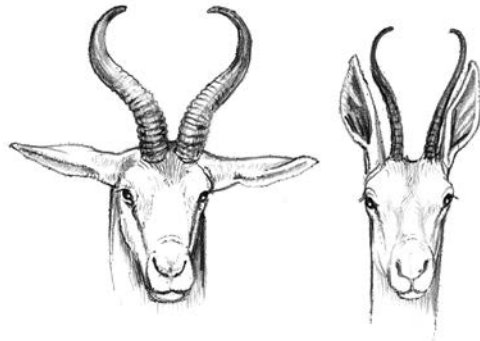
more competition among Springbok males during the rut. Another is accommodation to permanent, large herds (as opposed to scattered groups on territories) involving increased competition, expressed in more frequent and severe head-butting. Severe buffetings of the head favoured the development of hollow, backward-swept horns which are better able to absorb the force of heavy blows and so better insulate the brain.

BEHAVIOUR Females are highly mobile, moving quite independently of one another (but with current offspring). Because they form no close attachment to others or to territory, less is known of them than males, which comprise three main classes: immatures; unattached, non-breeding 'bachelors'; and territorial, breeding males. Breeding males normally ignore subordinate 'bachelors' but periodically enter a rut in which they become fiercely intolerant of all other males and seek to detain passing females within their 25–70ha territory. The rut can occur at any time and lasts 5–21 days; females that are not already pregnant may come into oestrus within a day or so of the male's rut. Large numbers of young are therefore born about 6 months later in a synchronised but unpredictable birth peak. However, births tend to peak in summer within the summer rainfall area of the Cape. Newborns lie up for a few days and run with their mother's group within 3 or 4 weeks. Females are sexually mature at 7 months but males are seldom sexually active until they have full-sized horns and have won a territory. They are known to live for at least 10 years (probably a lot more).

ADAPTATIONS The name 'Springbok' comes from the mainly juvenile and subadult habit of leaping up in a series of 'pronks', or hunch-backed bounces, that appear somewhat haphazard or playful at a superficial glance. In fact the pronking animal is extremely alert and watchful as it circles round or casts about from left to right. By slowing down the speed while maximising the height of its jump the young animal can take a series of bearings, not only on its physical surroundings but also on the position of predators and other Springboks. It was formerly assumed that pronking was a warning or, more recently, a 'flaunting of fitness' in the face of disturbance by humans or other predators. Both explanations could be incidental benefits but a primary function of pronking is learning orientation in inexperienced animals; adults seldom pronk, presumably because they already know their surroundings and neighbours.

There is also a social dimension to pronking. The white hairs that flare up into view with each jump are saturated with scent from the glands that line the spinal pouch or marsupium. As a result, jumps broadcast both visual and olfactory messages to other Springboks. A static version of the pronk suggests a meaning for the message and a possible precursor for the evolution of both pouch and pronk. Young animals appease threatening adults by lowering their heads and presenting their rear ends for an olfactory inspection. 'Presenting' during a soaring and eye-catching jump may represent a fast and efficient way of broadcasting an appeasing message. All ages and sexes tend to pronk more frequently immediately after rain, when evaporation and drying-out fills the air with strong soil and plant scents that superimpose upon those of the buck. The release of dorsal scent by all or most members of a group superimposes the Springbok's signature on its surroundings. The scent may be both generally attractive to all Springboks, as well as containing specific indications about the status of an individual. If this social ritual is combined with scanning and memorising the landscape and its signposts, pronking evidently contributes to survival in at least two important ways. Just how well the Springbok remembers geography is revealed by its phenomenal capacity to 'home' back to small territories after months of travelling. Its return journey can begin at a moment's notice when the rains return.

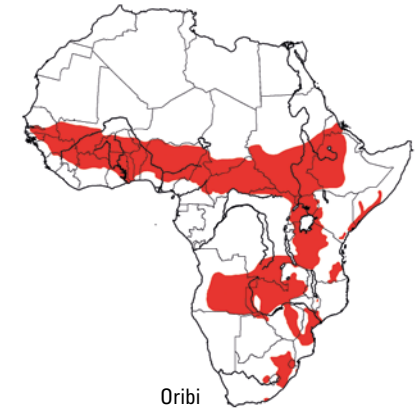
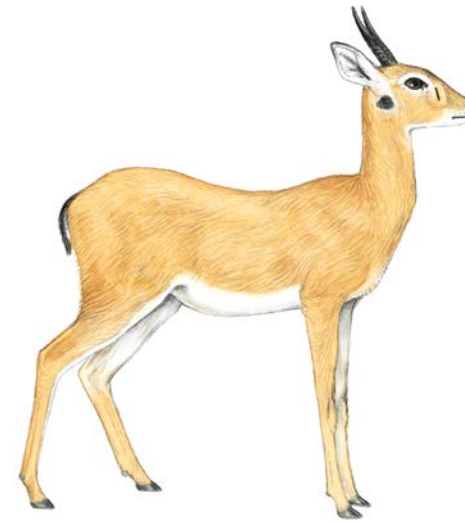
STATUS Most Springboks in South Africa are now effectively a form of livestock that lives on fenced farmland. In parts of Namibia and in the Kalahari nomadic movements continue but are increasingly constrained by steady expansion of the livestock industry.



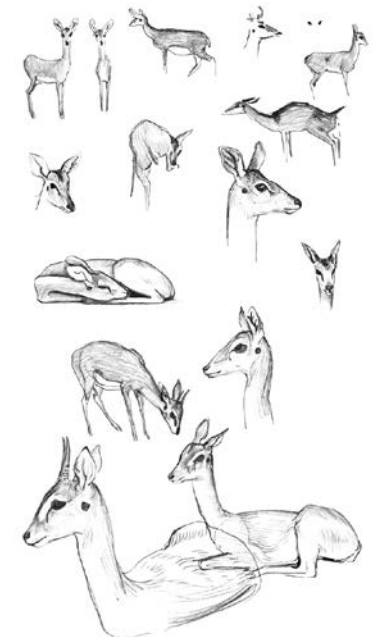
Springbok, male (left) and female (right)

ORIBI *Ourebini*

Formerly included in Neotragini, Oribi is a highly distinctive form of antelope with some distant and still to be studied relationships with the Reduncini.



Oribi



ORIBI *Ourebia ourebi*

OTHER NAMES Fr. *Ourébi*. Ger. *Bleichbockchen*. Swah. *Taya*.

MEASUREMENTS HB 920–1,400mm. T 60–150mm. Sh. ht 500–670mm. W 12–22kg (♀ ave. 2kg heavier).

RECOGNITION A tall, slender antelope of medium-small size and sandy body colour (yellowish or reddish tinted), with white undersides, upper throat, mouth and ear linings. The light-coloured muzzle deflects down sharply from the forehead (unlike the black-bridged retroussé nose of the Steenbok; nor are the eyes rimmed by intensely black lids as in the Steenbok). The ears are of moderate size. In addition to hoof (pedal) and groin (inguinal) glands, the Oribi has scent brushes below the knees and ankles and black gland patches below the ears. The face glands (preorbital) are also exceptionally well developed. Alert and shy, the Oribi's piercing whistle is frequently heard as it flees from the observer with a characteristic rocking-horse gait.

GEOGRAPHIC VARIATION *O. o. ourebi* (S and SE Africa), *O. o. hastata* (SE Africa between R. Ruaha and R. Zambezi/R. Shire), *O. o. cottoni* (upland E Africa), *O. o. montana* (NE Africa east of the R. Nile), *O. o. haggardi* (coastal Kenya and Somalia), *O. o. goslingi* (northern savannas, R. Chari/R. Nile), *O. o. quadriscopa* (Senegal to Chari, savannas).

DISTRIBUTION Mainly Sudanic, E and SE Africa on fire-climax grasslands but under relatively reliable rainfall regimes.

HABITAT Grasslands maintained by fire or heavy grazing. They prefer flats or gentle slopes and are commonest on open lawns of grass kept short by compaction, termites, poor soils, fast drainage,

trampling or heavy grazing by large herbivores. Such herds not only improve the Oribis' range, but may also buffer them from predation; Oribis tend to decline wherever such herds have been severely reduced or exterminated. On extensive floodplains Oribis favour the less waterlogged areas where termitaries, herbs and woody growth provide cover and supplement the diet. In exceptional habitats densities of 45 per km² have been recorded.

FOOD Mainly fresh green grass typical of fire-climax communities, i.e. *Themeda*, *Hyparrhenia*, *Loudetia* and *Eulalia*. However, many other grasses are taken, as well as various grassland herbs and the foliage of several shrub and tree species. Oribis cluster on scarce, short lawns within the sea of rainy-season long grass. Movements out of territories are typically oriented towards favourite mineral licks, which are visited regularly.

BEHAVIOUR Females are larger than males and are independent in their movements but, by becoming the object of continuous attention from a single male, each adult female determines the area within which he is intolerant of other males. This area becomes a shared territory in which each partner repels others of the same sex (but females tolerate adult female offspring). Pairings last for many years. Such territories adjoin supplementary pastures, refuges or salt-licks where other families may gather. Each territory is traversed daily by the male, who exchanges scents with females and their young during elaborate, shared 'dung ceremonies'. Throughout the day he assiduously marks plants and soil with his own excreta and secretions.

Seasons, predators and reproduction all influence activity. Thus Oribis rest longer on hot afternoons and may lie up during heavy rain. In exposed areas they prefer to graze at night, notably during full moons during the dry season. Their whistle may serve as both alarm and also to advertise shifting positions and movement. More breathy, puffing whistles keep neighbours informed. They bleat if pursued or captured. There is a mating peak in southern Africa during April with births 7 months later. The precocious young is adept at concealment for 3–4 days. Thereafter it begins to follow the mother but still seeks shelter from time to time. Growth is very rapid and near adult height is reached, with weaning, by about 4 months. Females are fertile at 14 months. A preponderance of males develops in some areas and territories may be dominated by older, even aged males. Animals are known to live for up to 14 years.

ADAPTATIONS Female Oribis are thought to excrete attractants that provoke continuous interest in males. Male alertness to female excretory posture, urine and dung is relentless and stimulates him into non-stop glandular marking. On an adult male, there are 14 sites secreting odours and all likely to contribute to saturating the core of his territory with his individual scent signature. Techniques for marking out small male territories within dense thicket were evolved by ancestral dwarf antelopes. Their modification for use in much larger territories in open grassland has involved the specialisation of male Oribis into full-time factories and dispensers of odours. It is known that these odours are not only charged with information about their producers but have the potential of strongly influencing the behaviour of those smelling them. Because all inhabitants of a territory mix and exchange scents at daily 'dung ceremonies', dangerous, costly confrontations are avoided through repetitive habituation. More important, a female is so frequently assailed with reminders of her partner's particular signature that she becomes habituated to his particular scent signature as an essential attribute of her environment. The male gains an important reproductive advantage in that the female stays within an area that he can control without physical coercion.

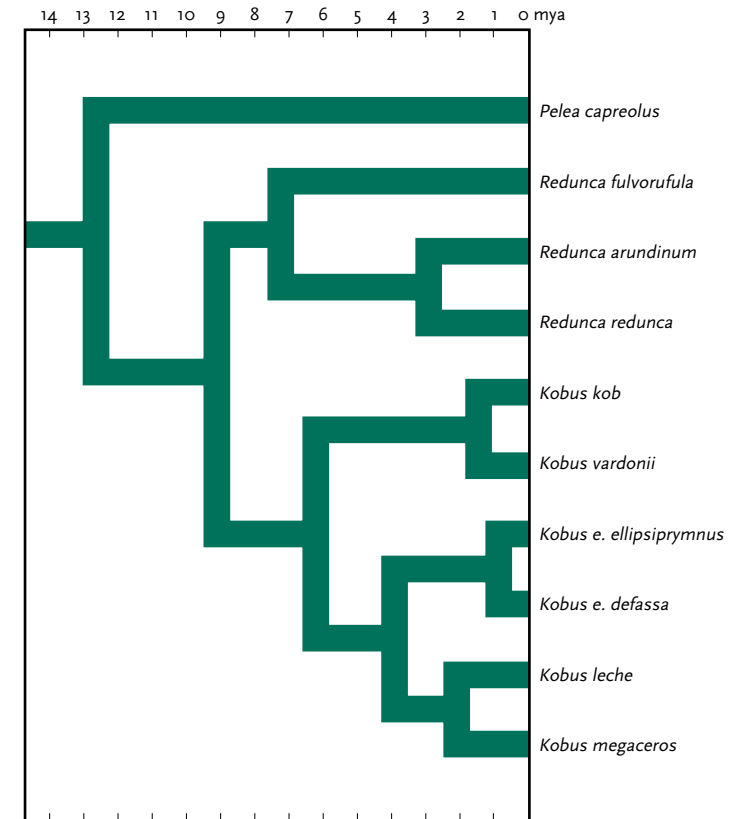
STATUS Residential habits may make Oribis poor colonists and this may influence the very patchy distribution of at least seven subspecies. Elimination from many localities has taken place this century. Nonetheless, the species is still widespread and not endangered overall.

REDUNCINES, KOBES Reduncini

Rhebok	<i>Pelea capreolus</i>
Reedbucks	<i>Redunca</i> (3 species)
Kobs	<i>Kobus</i> (5 species)

RECOGNITION Medium-sized to large antelopes with slender to stocky legs, a long, well-muscled body and a relatively thick neck (especially in males). The largest species are shaggy; smaller ones are sleek or slightly fleecy. Most are tawny or tan but males of the larger species can be dark brown or even black (usually with white or off-white markings). Horns, on males only, are

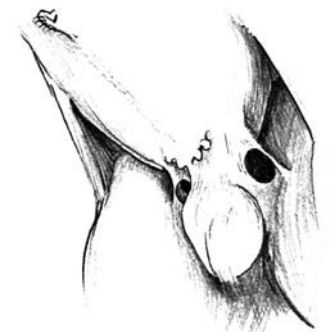
Tentative phylogenetic tree for Reduncini (modified from Hernández Fernández & Vrba 2005).



annulated and always curl forward at the tip (this corresponds with forward striking with the head, powered by muscles that help shape the bulging neck). Both preorbital and pedal glands are vestigial or absent but all have well-developed inguinal glands in the groin. All have a pungent overall odour that emanates from sebaceous glands and films the entire body. This provides a seal against water loss and possibly some insulation against temperature extremes but is also likely to carry socio-sexual signals (as must their musky urine). Reedbucks have black, glandular patches below the ears, which, among other messages, advertise the female's breeding condition. The smaller reduncine species make ritualised 'rocking-horse' displays that apparently signify subordination. These may be the long-grass equivalent of the 'stotting' or 'pronging' of antelopes in more open habitats.

The enigmatic Rhebok is a uniquely South African species. Its scientific name, *Pelea*, latinises its Tswana name, *phele*, while *capreolus* means 'goat-like' or 'sheep-like', a reference to its chunky, mountaineering hooves and short, crinkled wool.

GENEALOGY Reduncines probably began to evolve from neotragine grazers about 14 mya. The earliest fossils, about 11 million years old, come from East Africa but reduncines were present in India by 5 million years ago. Earlier names betrayed much uncertainty about the Rhebok's affinities. The archaic and obsolete *Cemas*



Reduncine inguinal glands (in male Reedbuck).

embraced such diverse antelopes as Klipspringers, Oribis, Springboks and reedbucks. *Redunca villosa* and *Eleotragus villosus* (both meaning 'hairy reedbuck') put it firmly in the kob tribe while *Antilope lanata*, 'woolly antelope', was suitably generalised and descriptive. Sustained adaptation to a unique herbivorous niche in the temperate mountains of southern Africa has resulted in some convergence with sheep and disguised hints of likely common origins with Oribis and the kob tribe.

GEOGRAPHY Now restricted to well-watered areas of Africa, the reduncines' dispersal to India and North Africa implies long periods of moist conditions along the Nile valley, other rivers and along coastal forest zones. This is because they are poor dispersers, keeping a close attachment to their natal area.

ECOLOGY Sumplands are rich in food but are unstable because they dry out or catch fire. Antelopes find it difficult to cope with their fluctuating water levels, sticky soils and rapid growth of impenetrable grasses. Only lechwes, with swamp-adapted hooves, can reside permanently in wetlands. For the rest, accommodation to radical seasonal changes inhibits extreme specialisation, making the kob tribe unusually homogeneous. The smaller Mountain Reedbucks are the most conservative but are secondarily adapted to coarse grazing and cool climates in upland pastures.

The instability of their enormously productive habitats encourages substantial fluctuations in numbers. This is exacerbated by a weak ability to disperse. Seasonal changes lead to short-distance movements that also cause crowding, sometimes of spectacular proportions (notably in Kob).

NATURAL HISTORY To accommodate both crowding and dispersal, reduncines have very flexible relationships between the sexes. Females are usually independent and, while in oestrus, are the object of intense competition between males. Big differences in the size, morphology and behaviour of the sexes correspond to separate male and female strategies. The females of reduncine species have more in common than the males (which look and behave very differently from species to species).

Study of their social systems, which are largely mediated by invisible scent cues, have scarcely begun. However, it appears that fundamentally different social systems correspond with the particular kind of refuge sought by each species. Because reduncines lack stamina an animal facing danger has three possible sources of refuge: (a) thick cover (reedbucks, Waterbuck); (b) water (most species, but especially lechwes); (c) dense herds (Kobs). All species appear to track each other like bloodhounds and clearly broadcast much information through glandular scents.

ADAPTATIONS Because they are the major bovid lineage adapted to valley grasslands, reduncines have considerable potential for rational exploitation, having the fastest growth rates of any bovid, insignificant disease problems and very acceptable meat and hides. Large populations of the more social species are unlikely to survive unless their potential for scientifically monitored sustained-yield cropping is realised because they occupy habitats with a high priority for agriculture or for inferior forms of livestock development.

■ RHEBOK *Pelea capreolus*

OTHER NAMES Grey Rhebok, Vaal Rhebok.

Fr. *Rhebuk*, *Péléa*. Ger. *Rehantilope*.

MEASUREMENTS HB 1.05–1.25m. T 100–200mm.

Sh. ht 700–800mm. W 18–30kg.

RECOGNITION A long-legged, long-necked antelope with a woolly, tawny-grey coat rounding the body contours. The long, narrow muzzle ends with a small mouth below a blunt, swollen nose. The ears are very long and pointed, the forehead swollen and the black-lidded eyes are very prominent in a white surround. The tail is bushy and white below. Undersides are pale. The males have very vertical spike horns that can be as long as 290mm. During ritualised postures, with erect neck and tucked-in chin, the unusually short back of the head becomes noticeable.



Rhebok

DISTRIBUTION Mainly in upland South Africa but actually descends onto sand dunes in the Cape. Most numerous in strongly seasonal pastures above 1,000m, staying on the heights during the rains but descending to lower slopes when dry.

HABITAT Highveld, 'sourveld' and secondary grasslands, mainly on plateaus and mountains.

While some of its pastures are maintained by fire, most are on dry, deeply drained slopes where very severe frosts deter tree growth. These are patchy but extensive, well-established and ancient pastures that are peculiar to southern Africa. The grasses tend not to grow very tall or rank so that the Rhebok has a clear view. Unlike reedbucks, it avoids very tall grass.

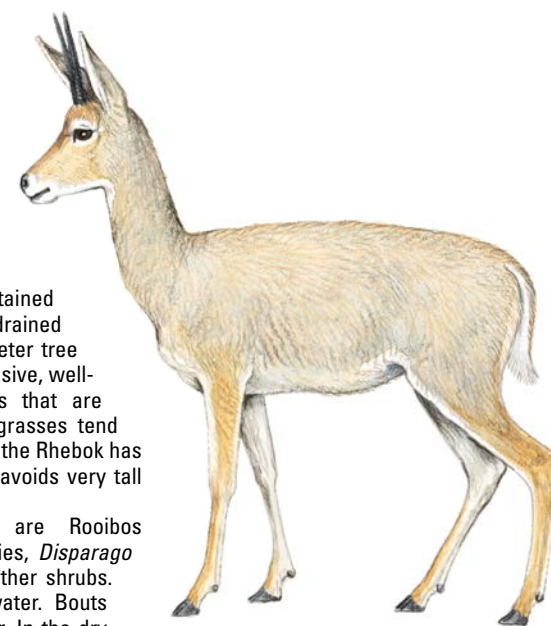
FOOD Preferred browse plants are Rooibos (*Aspalathus linearis*) and the daisies, *Disparago* and *Metalasia*, as well as many other shrubs.

The Rhebok is independent of water. Bouts of grazing and resting are irregular. In the dry season it tends to browse for longer (and at night) in valley bottoms. While the weather is hot it rests up during the heat of the day.

BEHAVIOUR Harems comprising a single male and up to five females and their offspring provide a basic social unit that can proliferate into a small herd (maximum 14). These live on stable home-ranges of 15–135 ha (smaller and higher in summer, larger and lower in winter). The harem male spends much time patrolling and marking out their home area with urine (loaded with extra scents and melanin pigment from a preputial gland that is unique to the Rhebok). He regularly surveys and postures from the top of mounds or ridges, or near rocks and trees where he also excretes (but not on a midden). If in sight of another male he stamps, makes a sharp, clacking call and prances with various bouncy, rocking-horse gaits. Rhebok are very vocal with a repertoire of whistling barks, bleats, hisses and snorts. Confrontations between males are frequent along boundaries but charges nearly always stop about 1m apart, with heads down and horns lunging and stabbing without actual contact. Territorial defence and 'air-cushion fighting' are commonest during the summer mating season (January–April). After a 7-month gestation one, occasionally two, young are born in a secluded place. The young remain concealed for 6 weeks before joining the mother and her group. Yearling males are evicted from harems. From about two years of age such males seek to take up territories of their own. Short visits from females still in their parental groups gradually get prolonged until they become permanent residents of the new territory. Male scent and male behaviour appear to be actively attractive to female Rheboks and there are few signs of them being coerced by males.

ADAPTATIONS Although it has been suggested that the Rhebok could share a common ancestry with sheep, their similarities are certainly convergent. Cold South African winters on dry, stony uplands are miniature copies of environments in the mountain chains of Eurasia where sheep evolved. Rhebok flee uphill, seeking exposed heights where they can monitor any disturbance below.

STATUS The Rhebok is well represented in numerous reserves, national parks and private farms where it is, for the most part, compatible with livestock. Although it has been exterminated over a large part of its former range, which is now very fragmented, it is common within these fragments. Not endangered but very susceptible to depredation by dogs.



Rhebok

REEDBUCKS *Redunca*

Mountain Reedbuck *Redunca fulvorufula*

Bohor Reedbuck *Redunca redunca*

Southern Reedbuck *Redunca arundinum*

■ MOUNTAIN REEDBUCK *Redunca fulvorufula*

OTHER NAMES Fr. *Redunca de montagne*.
Ger. *Bergriedbock*. Swah. *Tohe ya milima*.

MEASUREMENTS HB 1.10–1.36m. T 170–260mm.
Sh. ht 600–800mm. W 19–35kg (♀), 22–38kg (♂).

RECOGNITION A moderately-sized antelope with slender legs and a chunky body. The soft, fleecy fur is tawny grey, with white underparts and a bushy white underside to the tail. It is the smallest of the reedbucks and its eyes and their sockets are peculiarly prominent, as is the black gland-patch below the ear and, in males, the short, forward-curved black horns.

GEOGRAPHIC VARIATION *R. f. fulvorufula* (South Africa), *R. f. chanleri* (E and NE Africa), *R. f. adamuae* (N Cameroon).

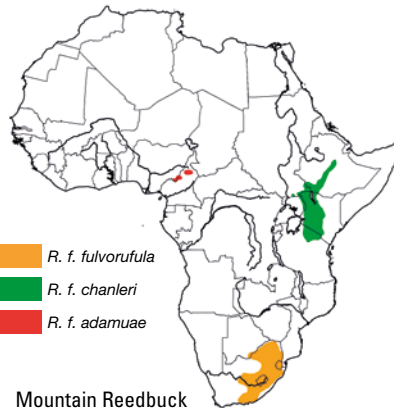
DISTRIBUTION Widely separated mountains in S and NE Africa, with an outlying relict population on Mt Adamua in the Cameroon uplands. They live in cool, rather dry, mountainous regions mostly above 1,500m and up to 5,000m. These may be the vestiges of its range during more favourable glacial periods.

HABITAT They prefer grassy ridges in broken rocky country, on small outcrops and volcanic lava flows and cinder cones. In Kenya, Mountain Reedbucks prefer the scrub-grass ecotone between slopes covered in camphor (*Tarchonanthus*) and open grassy valleys. They are often less nocturnal than other reedbucks.

FOOD Almost wholly grazers, with *Themeda*, *Hyparrhenia* and *Cymbopogon* recorded as favourite food plants. Mountain Reedbucks can live for a while without water but lose condition rapidly. Fluctuating food leads to fluctuating numbers.

BEHAVIOUR Females with young form parties of two to eight but temporary aggregations of up to 50 can form. Female home-ranges in southern Africa are 36–76ha but male territories average 28ha. Female ranges are unusual, therefore, in overlapping those of several males that do not control their movements. Ranges cover a sample of the available habitats and run from hilltop to valley. 'Bachelor' groups are temporary and tenuous in where they can live and high mortality among males tends to skew sex ratios. A single young is born after an 8-month gestation. It remains well hidden for up to 3 months before joining its mother's group. Prolonged hiding may reflect special risks from eagles, large cats, jackals and baboons in their habitat.

ADAPTATIONS Intimate knowledge of their home-ranges allows them to mitigate predation while the ubiquity of grass seldom makes them limited by food. However, strictly sedentary habits inhibit dispersal and render isolated populations vulnerable to extermination during prolonged droughts or after sustained over-hunting.



Mountain Reedbuck

■ BOHOR REEDBUCK *Redunca redunca*

OTHER NAMES Common Reedbuck. Fr. *Redunca*.
Ger. *Gemeiner Riedbock*. Swah. *Forhi, Tohe*.

MEASUREMENTS HB 1.00–1.35m. T 180–200mm.
Sh. ht 650–890mm. W 35–45kg (♀), 43–65kg (♂).

RECOGNITION A medium-sized, sandy-coloured antelope in which the slender proportions of females contrast markedly with the thick-necked, hook-horned males. It has deeply pocketed glands in the groin, black patches below the ears and is oily or greasy all over from sebaceous ducts at the roots of all hairs. Its loud whistles (mainly uttered at night) are the surest guide to its presence, especially in tall, wet-season grasslands, where it is seldom seen. The size of horns appears to correspond to some extent with densities, i.e. stubby horns in East Africa at dispersed, lower densities and longer, splayed horns in the Nile valley with seasonally concentrated, high densities.

GEOGRAPHIC VARIATION *R. r. redunca* (northern savannas), *R. r. cottoni* (Sudd region), *R. r. bohor* (Ethiopia), *R. r. wardi* (East Africa).

DISTRIBUTION From Senegal to Ethiopia, south to L. Tanganyika and the Rovuma valley. Particularly wide shallow floodplains associated with major lake and river systems, i.e. R. Niger, R. Nile, R. Rufiji, L. Chad and L. Victoria.

HABITAT Mostly large-scale sump grasslands that are highly unstable, with extensive annual flooding, drought and fires. They are peculiarly well adapted to cope with these extremes and to changes in height and quality of the food supply and shelter grass. While they are dispersed, densities of about five animals per linear kilometre of valley bottom are common. During periods of concentration, densities of more than 100 per km² have been observed and they are not uncommonly found at distances of 25km from water during droughts on open floodplains.

FOOD Exclusively grazers, with a recorded preference for typically dominant species, i.e. *Hyparrhenia*, *Sporobolus*, *Heteropogon* and *Themeda*. Feeding mainly after dark, Bohor Reedbucks may make nightly forays to graze up to 8km from their day-time refuge. As the quality of the grazing declines during the dry season, nocturnal feeding alone becomes insufficient. Eventually some animals may keep grazing both day and night.

BEHAVIOUR Females disperse into discrete home-ranges during the wet season (when most young are born). Males also appear to be very scattered at this time (in the absence of females they can be quite tolerant of each other). Fires and drought (beginning in about October in the northern savannas) drive the animals into larger groupings. By the early dry season males are intensely intolerant of each other and it is probably repeated fights and stand-offs with neighbours that define, perhaps temporarily, their 'territories'. In rare situations where home-ranges are stable, 'territories' may be an appropriate term but their typically unstable habitat favours a system in which females search out the best and safest remaining pastures while males fight for mating rights over each female or group of females.

The glandular ear patch is thought to play a part in advertising oestrus. In courtship males circle females making a bleat like a toy trumpet. After a gestation



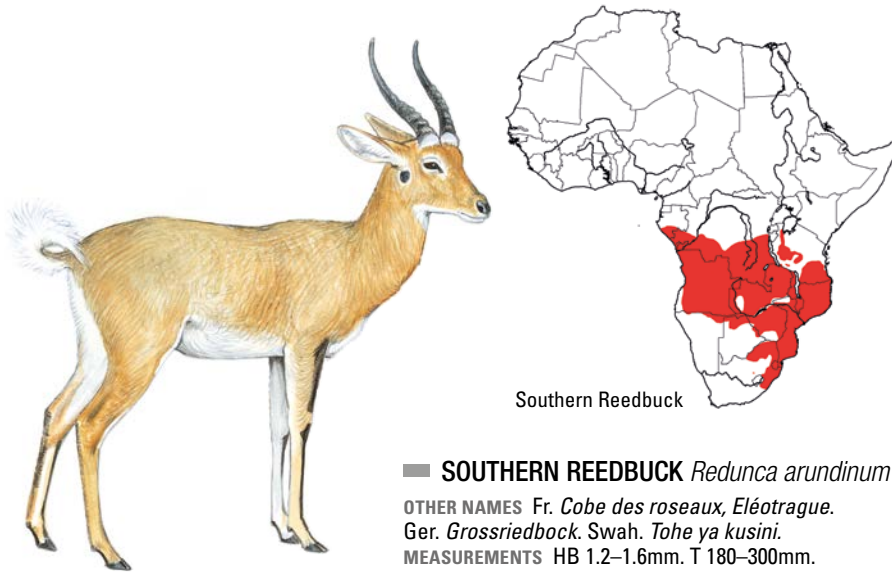
Bohor Reedbuck



of 7 months one young is born and it remains well hidden (but with daily changes of retreat) for at least 2 months. Young males sometimes form 'bachelor' groups before becoming fully mature at about 4 years. Females are fertile by 1 year. Animals live for at least 10 years.

ADAPTATIONS Whistling and ritualised bounding are two conspicuous features of Bohor Reedbuck behaviour. Both are effective forms of communication in their dense, obstructed habitat. Leaps differ in amplitude, length and style. Likewise, whistles vary in number of blasts and in pitch. In the dry season choruses of whistling can be heard whenever animals change their positions, especially at night as they emerge to graze.

STATUS Very common and widely distributed. This reedbuck continues to survive even in the face of agricultural expansion.



Southern Reedbuck

■ **SOUTHERN REEDBUCK** *Redunca arundinum*

OTHER NAMES Fr. *Cobe des roseaux*, *Eléotrague*.

Ger. *Grossriedbock*. Swah. *Tohe ya kusini*.

MEASUREMENTS HB 1.2–1.6m. T 180–300mm.

Sh. ht 0.65–1.05m. W 50–85kg (♀), 60–95kg (♂).

RECOGNITION The largest reedbuck, with a fine, almost woolly coat. Some are light buff, some dark brown, others are in between. The underside is paler, as is the chin and throat. Black-and-white markings on the front of the forelegs are prominent. The horns, only on males, grow up to 450mm long and resemble a diminished version of the Waterbuck's, with a pale base. The tail is large and bushy, with white on the underside.

GEOGRAPHIC VARIATION *R. a. arundinum* (south of the Zambezi), *R. a. occidentalis* (tropical Africa).

DISTRIBUTION SE and central Africa, with a substantial overlap in range with the Bohor Reedbuck in Tanzania (where it is rare).

HABITAT Widely distributed in the rank grass valleys and glades within miombo (*Brachystegia*) woodlands where the greater part of their range is contained. Best adapted to mosaics of scrub and grass. They decline if denser, taller thicket replaces more open country but flourish in tall grass patches on the margins of more waterlogged swamps.

FOOD Favourites are dominants in their habitat, i.e. *Hyparrhenia*, *Panicum* and *Leersia*, but Southern Reedbucks are not selective or specialised grazers. Much feeding is nocturnal and they are dependent on water.

BEHAVIOUR Converging on water sources in the dry season, they only disperse widely when it is wet and the grass grows tall again. Home-ranges get compressed to 5–35ha during the dry season but expand greatly during the rains. Births peak in the rains and both mothers and their young tend to remain well concealed in the long grass. As water gets scarcer and the fires begin female attachment to males becomes more obvious and frequent. Each male actively keeps other males away from one female (more if he is able). Contact is maintained by means of whistles and leaping displays but it is thought that scent trails through the grass provide the main clue to each animal's whereabouts.

One young is born after a 31-week gestation. Female young are unusual in being the first to leave their mother, as they become fertile at about 1 year. Males may remain with their mothers into their third year, by which time their horns are conspicuous and frequent appeasement of their mothers' 'consort' may be necessary.

ADAPTATIONS Both females and young males make 'rocking-horse' displays towards adult males. Running around at speed they throw up their rumps and white tails in long, floating bounds. A popping sound is often made with the leaps, just as the hindlegs jerk back and out at the peak of each leap. The noise appears to result from a release of scented air from the inguinal pockets situated in each groin. Whistles are also commonly uttered with these jumps and the whole sequence would seem designed to appease the adult males.

STATUS Although their total range is now very fragmented, Southern Reedbucks are well represented in reserves and parks. Not endangered.

KOBS *Kobus*

Kob	<i>Kobus kob</i>
Puku	<i>Kobus vardoni</i>
Southern Lechwe	<i>Kobus leche</i>
Nile Lechwe	<i>Kobus megaceros</i>
Waterbuck	<i>Kobus ellipsiprymnus</i>

■ **KOB** *Kobus kob*

OTHER NAMES Fr. *Cobe de Buffon*.

Ger. *Grasantilope*. Swah. *Mraye*.

MEASUREMENTS HB 1.6–1.8m. T 100–150mm.

Sh. ht 0.82–0.92m (♀) 0.9–1.0m (♂).

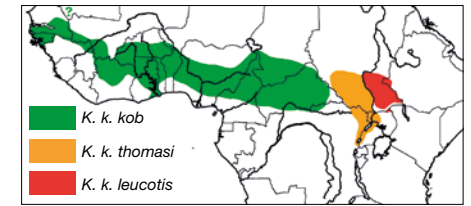
W 60–77kg (♀), 85–121kg (♂).

RECOGNITION A medium-sized antelope with a muscular, deep, rounded body and neck (especially in males) and robust limbs. The males have thick, lyrate horns. Females are various shades of reddish or yellowish ochre, with a white underside and markings on the face, ears and hocks. Male colouring varies from rich cinnamon rufous, or pale yellowish brown, to black and white in the Sudd floodplain. Piebald colouring corresponds with fewer predators. Dark markings or tints occur on Kobs from other large flood-plains and around the Sudd margins, blurring the boundaries between forms.

GEOGRAPHIC VARIATION Western Kob, *K. k. kob* (northern savannas); Uganda Kob, *K. k. thomasi* (East Africa and NE DR Congo); White-eared Kob, *K. k. leucotis* (Sudd floodplain).

DISTRIBUTION Senegal to W Ethiopia to L. Victoria littoral.

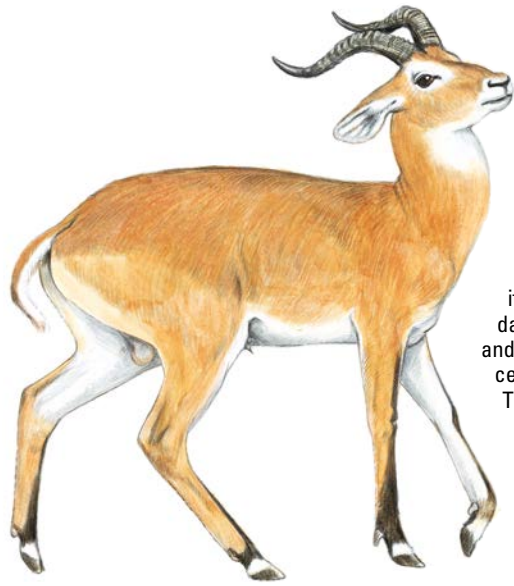
HABITAT Low-lying flats or gently rolling country close to permanent water, without seasonal extremes. They favour short swards, cropped and trampled by concentrations of large ungulates or fire-induced grasslands. Where numerous enough, they keep down limited areas of sward ('kob fields') through the sheer weight of their own numbers. Totally dependent on regular drinking, Kobs remain tied to areas within a short walk of water. They retain strong attachments to both grazing grounds and watering points, returning day after day and season after season.



Kob



White-eared Kob *K. k. leucotis*, male head

Uganda Kob *K. k. thomasi*

FOOD Grazers of the commonest grasses, notably *Hyparrhenia*, *Brachiaria*, *Setaria* and *Paspalum* species, among many others. Seasonal changes in diet (i.e. *Cenchrus* in the rains) emphasise the Kobs' preference for a short sward.

BEHAVIOUR Kob populations are prone to great fluctuations in numbers but these get compressed because attachment to locality and routine inhibits dispersal. Resident populations move daily between habitual grazing grounds and watering places. These grounds are parcelled out into male territories of up to 50ha. The female strategy of going to water en masse leads to female aggregations that increase the stimulus that they present to males. The males respond with more competition and fighting among themselves. Mating appears somewhat chaotic and would be more so without lengthy pauses at specific spots along the route from the grazing grounds to drinking places. Sexually active males scramble

for matings in these heavily contested 'assembly fields' where up to 40 males may cluster in an area of about 1ha. Triangular territories radiate out from one or more 'hubs' within such areas, each 'hub' being signposted by a steady accumulation of dung and urine-soaked soil. Recent research has shown that the primary attractant that draws sexually active adults of both sexes to these heavily scented 'hot-spots' is the oestrogen-charged urine of oestrous females. Under the influence of the pervasive musk wafting from such centres, receptive females allow themselves to be mounted by one or more of the associated territorial males. The considerable expenditure of energy required to defend their minuscule patches in the 'assembly fields' ensures that males are quickly exhausted. Tenancies may only last a few hours, so males are almost as transitory as females. By contrast, territories on the grazing grounds may last a year or more.

Stereotyped, small-scale movements of a few kilometres are typical of populations resident in enclosed valley systems. Where the sump area is larger, as in the Sudd, Kobs become migratory but their movement over many hundreds of kilometres is equally bound by tradition. Here too, mass movement induces the formation of territorial 'slices' of ground arranged around beacons of female urine. These radial slices of territory are fiercely contested by males.

In South Sudan virtually all females give birth along the south-eastern borders of the Sudd basin towards the end of the rains (September–December). After migrating 200km or more north, mating takes place along the eastern rim of the basin at a time when the plains are at their driest. After an 8-month gestation one young is born. Like reedbucks, their first 6 weeks are spent in hiding, after which they join their mothers and other Kobs on the grazing grounds. Females are fertile at one year, males become sexually active at 3 years.

ADAPTATIONS If Kobs evolved from a type of reedbuck their major innovation is the ability to congregate. Unlike some semi-social antelopes (such as Oribis) they do not scatter when chased or attacked but often move as a single mass. This inhibits smaller predators while their open habitat protects them from some larger ones (Lions are temporary, nomadic visitors to floodplains).

STATUS In spite of having been eliminated from many areas (notably from all the shores of L. Victoria), Kobs readily recover from near extermination. In terms of energetics, they assimilate poor-quality food, convert it to meat and grow faster than any other bovid. Kobs are potentially an exceptionally valuable resource. Fortunately they are still widely distributed and are not endangered, but a blinkered, primitive livestock industry still fails to appreciate the value of indigenous African ecosystems and species.

■ PUKU *Kobus vardoni*

OTHER NAMES Fr. *Puku*. Ger. *Puku*. Swah. *Puku*.

MEASUREMENTS HB 1.26–1.42m. T 280–320mm.

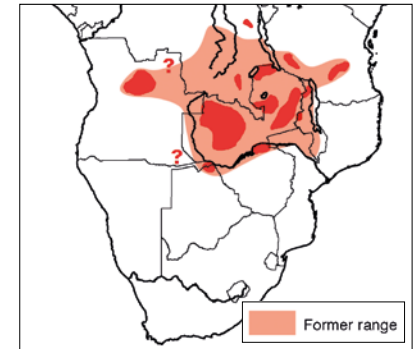
Sh. ht 770–830mm. W 48–78kg (♀), 67–91kg (♂).

RECOGNITION This southern relative of the Kob is sometimes treated as a mere subspecies. It has heavier proportions (particularly noticeable in the female), a coarser coat and shorter, less lyrate horns with less 'stem' than the Kob.

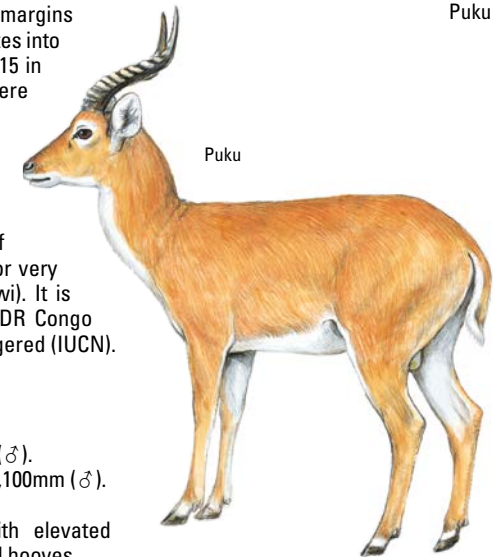
HABITAT Upper basins of the R. Zambezi, Congo R. and R. Rufigi. It inhabits the margins of lakes, swamps, rivers and floodplains and is more tolerant of narrow grasslands and park-like woodlands than the Kob. It lives on higher ground in the rainy season, descending in the dry season to graze the margins of lakes and rivers. It sometimes amalgamates into parties of 50 or more in the dry season (3–15 in the rains). Territories are spaced out and there is year-round breeding.

FOOD Preferred grasses are *Brachiaria* (especially January–March), *Eragrostis* (July–August) and *Vossia* shoots (December). The Puku will feed off lawns.

STATUS Exterminated from several parts of its range, the Puku is locally endangered or very rare (Tanzania, Botswana, Namibia, Malawi). It is still common and widespread in parts of DR Congo and Zambia, where it is listed as not endangered (IUCN).



Puku



■ SOUTHERN LECHWE *Kobus leche*

OTHER NAMES Fr. *Cobe lechwe*. Ger. *Litschi*.

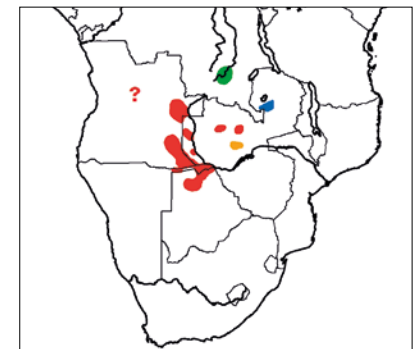
MEASUREMENTS HB 1.3–1.7m (♀), 1.6–1.8m (♂).

T 300–450mm. Sh. ht 850–950mm (♀), 850–1,100mm (♂).

W 60–95kg (♀), 85–130kg (♂).

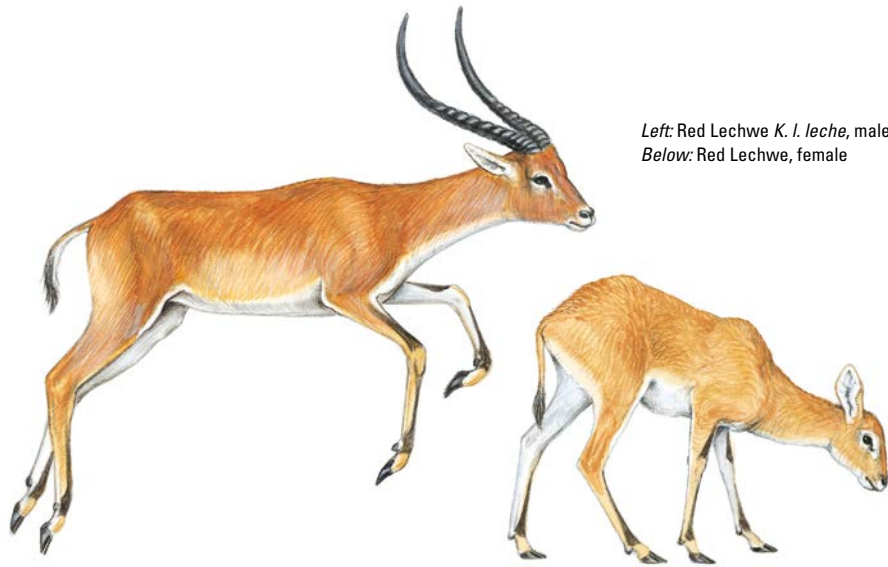
RECOGNITION A heavily built antelope with elevated haunches, notable for its splayed, elongated hooves (generally hidden from view in water, mud or grass). It has large, widely spaced eyes, a rather short muzzle and, in males, long, slender but heavily annulated horns that sweep back (500–920mm). Females are red to tawny, graduating to white on the underside and throat, with white borders around the eyes and muzzle. Male Red Lechwe have similar colouring but black fronts to the white legs extend up onto the body in other subspecies. Here they spread with age. In one population, the Black Lechwe, this spread continues until fully mature males are boldly black and white. Normally phlegmatic, they rush through the shallows when disturbed, with clumsy, galloping bounds which sometimes begin with what David Livingstone described as a 'waddling trot'.

GEOGRAPHIC VARIATION Red Lechwe, *K. l. leche* (NW Zambia, Angola, Botswana); Kafue Lechwe, *K. l. kafuensis* (Kafue flats); Katanga Lechwe *K. l. anselli* (DR Congo); Black Lechwe, *K. l. smithemani* (Bengweulu basin, R. Chambeshi).



Southern Lechwe





Left: Red Lechwe *K. l. leche*, male
Below: Red Lechwe, female

DISTRIBUTION Restricted to the flat, silted-up river basins of the central African plateau (mainly the headwaters of the R. Zambezi and southern Congo R. tributaries) where they occur only in permanently waterlogged areas, being totally dependent on water to drink and in which to find food and shelter.

HABITAT Along the unstable margins between swamps and shallow floodplains. The larger and flatter the basin, the larger are both the habitat and lechwe numbers. Females and their young tend to stay on the wetter end of this zone, adult males on the drier end. Keeping to the shallows/dry land margin involves continuous movement and distances of up to 80km may be travelled in very wet years (R. Chobe). Concentrations in favoured areas can reach temporary densities of 1,000 per km². In some areas herds may move inland to graze on short pastures following fires, moving mostly at night.

FOOD Favoured grasses are *Echinochloa*, *Panicum*, *Brachiaria*, *Paspalum*, *Acroceras* and *Oryza*; also the fresh shoots of trampled reeds (*Phragmites*). Most feeding takes place for a few hours before dawn and after dusk.

BEHAVIOUR Females seek out the best grazing, concentrating whenever it is localised, dispersing when it is widespread. They are unencumbered by any lasting bonds except with their young. The majority give birth during the late, hot dry season between July and October, but some breeding continues throughout the year. Males have a protracted rut during the early wet season (November–February) but sexual interest and the size of the testes decline throughout the late wet season and the dry season. All sexes tend to remain dispersed but sexually inactive males are forced into peripheral ‘bachelor’ herds that can become quite large (50 or more members). This pattern changes with the rising flood levels during the early rains.

Before the grasses have regrown, herds are at their densest and it is at this time that the rut begins. As females come into oestrous, and are presumably drawn by the scents of other sexually active animals of both sexes, they gather at ‘hot-spots’. Access to these is fiercely contested by males, who crowd around them. Those closest to the hot-spots occupy the smallest areas and achieve the highest number of copulations but are quickly exhausted. Further from the centres, pressure is less continuous and intense. The males here exclude each other from larger areas more effectively and hold much longer tenancies (but they presumably inseminate fewer females). One young is born after a 225-day gestation. After lying up for some weeks the young emerge to join the female herds. Females are fertile by 18 months, males take more than 2 years and are not fully mature until 5 years. Animals live for up to 15 years.

ADAPTATIONS Slow and clumsy on hard ground, lechwes are very strictly tied to swampy floodplains by their physiology and their soft hooves.

STATUS Southern Lechwes are known to have been exterminated in many peripheral areas, indeed one race (the Luena Lechwe, *K. l. robertsi*) has already become extinct this century. They are very poor colonisers and recolonisers. The separation and subsequent speciation of Southern and Nile Lechwes implies a much wider distribution in the past. Both the Kafue and Black Lechwes are well represented in national parks. Elsewhere they are being progressively displaced by cattle that are markedly less productive users of the habitat.

■ NILE LECHWE *Kobus megaceros*

OTHER NAMES Mrs Gray’s Lechwe. Fr. *Cobe de Mme. Gray*. Ger. *Weissnacken moorantilopen*. Dinka dialect *Abiok*.

MEASUREMENTS HB (est.) 1.3–1.7m (♀); (est.) 1.6–1.8m (♂). T 450–500mm. Sh. ht (est.) 0.80–0.85m (♀), (est.) 1.00–1.05m (♂). W (est.) 60–90kg (♀), (est.) 90–120kg (♂).

RECOGNITION A robust swamp antelope with longish hair, yellowish to russet in the hornless, smaller female. Like Southern Lechwe, it has a rather short face. The hooves are exceptionally elongated, the inner hoof much narrower than the outer. Males have double-curved, lyrate horns (500–870mm long) and their coats slowly darken over several years, changing from tawny russet to a pale reddish grey that darkens until it is a deep chocolate black. The underside, tail, back of the neck and upper shoulder are creamy white, as are the muzzle and surround of the eyes.

DISTRIBUTION The Sudd region of the White Nile close to the various tributaries that converge near Malakal. This is a single, spidery swamp system flowing over an alluvial plain with surface gradients as shallow as 70mm per km.

HABITAT Mainly confined to the river-flooded grasslands that lie between deep swamp (dominated by *Cyperus papyrus* and Sudd Grass, *Vossia cuspidata*) and the drier rain-flooded grasslands (dominated by thatch grass, *Hyparrhenia rufa*). This river-flooded zone, or toic, is dominated by Swamp Antelope Grass (*Echinochloa stagnina*), rice grass (*Leersia*) and wild rice (*Oryza*) and has numerous pools edged with bulrushes and water-lilies. Within the toic, Nile Lechwes follow the fluctuating margins between shallow floodwaters and drier ground. This involves continuous seasonal drifting up and down the flood tide lines. As floods deepen (about May) the animals move further from the river and/or upstream, travelling as far as 30–40km between their high- and low-flood seasonal pastures. Because movement is now severely constrained by dense settlement and livestock herds all round the swamps, Nile Lechwes tends to converge on levees and tertiary complexes within the toic until the floods begin to subside in about October. By the time fires are burning the floodplain (January–March), the animals are occupying the patchy margins of the permanent swamp, where they avoid Papyrus but are commonly found in Sudd Grass. At this time competition for grazing is keen and large herds of cattle tend to force the Nile Lechwes deeper into the swamps.



Nile Lechwe

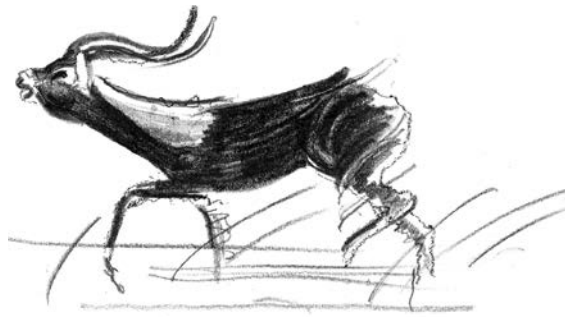


FOOD Grazes on growing *Oryza* during the early flood season but mainly *Leersia*, *Echinochloa* and *Vossia* as the floods recede.

BEHAVIOUR Females determine movements but spaced-out, fully adult, piebald males drive competing males away from female groups. In the early dry season (November–December) single males successfully exclude other piebalds from herds that can be in excess of 100. This is the period of peak births. By February calves have emerged from lying-up in the reeds and sometimes gather for playful chases, circling and jumping through the shallows. As females move, gathering and fragmenting into larger and smaller groups in response to the state of the pasture or disturbances, they attract the attentions of piebald males. By March these males are spaced out in a rather linear scatter along the swamp margins and there is much sexual activity that would seem to peak in about April. Piebald males often tolerate the presence of several other well-horned males in their vicinity but these can always be graded by colour and clearly represent hierarchically ordered age-classes. Dominant males squirt urine onto their own throats, which may then get rubbed onto females. Because actual horn-to-horn engagements often submerge heads, male fights in water tend to be brief tests of strength with very vigorous pushing and wheeling. Once the loser breaks away there is a token chase and the winner returns to the females (if present). Exhausted males seclude themselves in trampled arenas within the reedbeds. Males may utter squeaky grunts while fighting. Females are extremely vocal and there are choruses of toad-like croaking in herds that are actively on the move. Gestation has not been recorded but is probably about 8 months. Longevity is also not known but, given the slow, graduated maturation of males, probably resembles the Southern Lechwe's 15 or more years.

ADAPTATIONS The male's bold black-and-white colouring is probably made possible by a scarcity of predators on very extensive floodplains. Crocodiles and pythons are known to take them but these predators do not hunt by sight. It may be significant that the one Southern Lechwe population in which the males are black also lives on a very wide, flat floodplain with few resident predators. Colour-coding for age-ranks assists hierarchies while marked differences between males and females would appear to allow each sex to pursue an independent life cycle. Males head-flag at the boundaries between their very ephemeral territories. Flagging involves sudden sweeping tosses of the head (as if to chase a fly off the flanks). This violent movement momentarily exposes the white ears, neck and shoulder patch and flourishes the horns. This intimidation display helps define temporary boundaries through repetitive stand-offs.

STATUS About 16,000 Nile Lechwes lived on the east bank of the Nile in 1983. A similar number has been estimated for the west bank. Nearly 1,000 have been estimated for the Machar marshes. Although constrained by competition from cattle, and subject to some hunting, numbers are probably stable. Plans to resuscitate the Jonglei Canal, introduce irrigation or exploit oil could dramatically change this. Listed as threatened (IUCN).



Nile Lechwe adult male in pursuit. At a distance the white nape draws attention to the length of the horns.

■ WATERBUCK *Kobus ellipsiprymnus*

OTHER NAMES Fr. *Cobe defassa*. Ger. *Wasserbock*. Swah. *Kuru*.

MEASUREMENTS HB 1.77–2.35m. T 330–400mm. Sh. ht 1.20–1.36m. W 160–200kg (♀), 200–300kg (♂).

RECOGNITION A big, shaggy animal, rather variable in colour, with dark grey and rufous individuals sometimes occurring in mixed groups. Males tend to be darker and have long horns (500–990mm). Females are without horns and tend to be warmer in colour. The angle of the chin, muzzle, ears and eye-surrounds are white, with black margins and tips to the ears. The dark legs also have short white spats.

GEOGRAPHIC VARIATION Common Waterbuck *K. e. ellipsiprymnus* (SE Africa): white rump crescent. Defassa Waterbuck *K. e. defassa* (NE, central and W Africa): all white under tail.

DISTRIBUTION Well-watered valleys, mainly in tropical Africa and sandwiched between desert and forest. Absent from the dry north, north-eastern and south-western regions of Africa.

HABITAT Sedentary in savannas, woodlands and forest/non-forest mosaics where there is permanent water. They favour woods or thickets, where they inhabit the fringes of valley grasslands. They could be described as 'dry-land lechwes'.

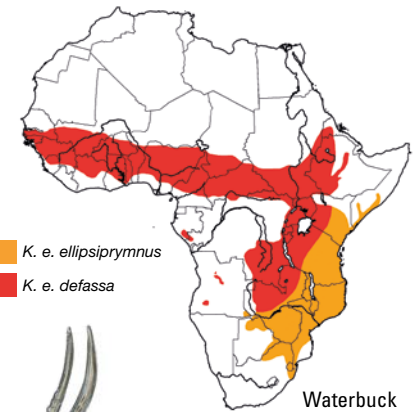
FOOD Many grass species, including reeds and rushes (*Phragmites* and *Typha*). Where green grass is scarce, Waterbucks may browse leaves or even fruits.

BEHAVIOUR Both males and females remain for long periods (up to 8 years) on the same home-range. Females travel over the larger areas (typically 200–600ha) but travel contracts with age. Males are most vigorous between 6 and 10 years of age, when they hold the largest territories (ranging from 4 to 146ha), with continual change and readjustment as the relative status of neighbours waxes and wanes. Familiar males that appease territory-holders are tolerated. Females travel at will over many territories, usually in ones and twos but sometimes assembling in temporary aggregations of up to 70. Young animals go through a stage of being chased and may emigrate to distances of up to 30km.

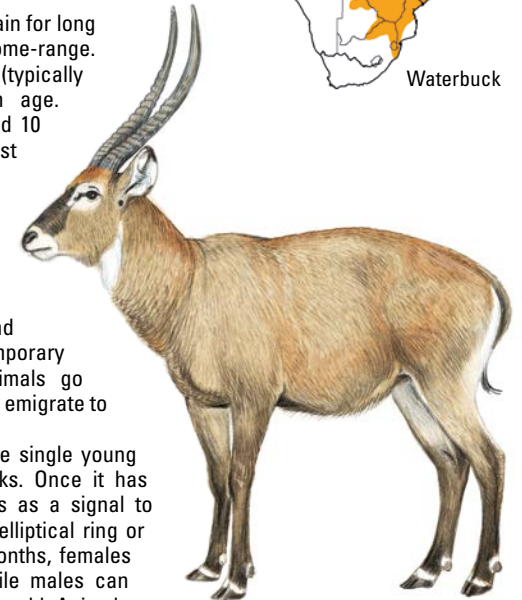
Gestation lasts over 8 months and the single young remains concealed for at least 2 weeks. Once it has joined its mother her raised tail serves as a signal to follow (the signal is emphasised by an elliptical ring or wholly white buttocks). Weaned at 6 months, females generally mature at about 3 years while males can scarcely compete before they are 5 years old. Animals are known to live for 18 years.

ADAPTATIONS Scent is clearly of paramount importance for Waterbucks and their own odour is so strong that it can sometimes be detected at a distance by the human nose. Partly or wholly uneaten kills by Lions have led to the suggestion that they are distasteful but this is contradicted by the fact that Lions, hyaenas and other large predators will kill Waterbucks more frequently than their abundance would merit. It would appear that this is the price they pay for being easy to find by other Waterbucks. The benefits of living both in herds and being able to come and go, assemble and dissolve, in response to an unstable environment appear to outweigh the extra risk from predators.

STATUS Although Waterbucks have been eliminated from many localities in their very extensive range they remain widespread and well represented in parks and reserves.



Waterbuck



Defassa Waterbuck *K. e. defassa*



Rear views of female *K. e. ellipsiprymnus* (above right) and male *K. e. defassa* (right).

KLIPSPRINGER *Oreotragini*

A unique type of basal antelope with a fossil of the extant species from 1.6 mya. Klipspringers are most likely to have evolved on the Ethiopian massif. Digital bones and hooves have been uniquely modified for traversing over rocky surfaces. Being a long-established and conservative lineage with widely separate populations, arguments have been made for multiple species. These are treated as subspecies here because observable differences between them are very minor, mostly featuring subtle gradations in the tinting of their pelage.

■ KLIPSPRINGER *Oreotragus oreotragus*

OTHER NAMES Fr. *Oréotrague*. Ger. *Klippspringer*. Swah. *Ngurunguru*, *Mbuzi mawe*.

MEASUREMENTS HB 750–1,150mm. T 65–105mm. Sh. ht 430–600mm. W 8–18kg (average weights vary regionally, 10–15kg).

RECOGNITION A small, compact antelope, unique for walking and jumping on the tips of its hooves and for its dense cloak of lightweight fur, which is brittle, coarse and rustles when shaken or touched. This fur gives the illusion of greater size, especially when erect (when the animal is hot or sick). Widely spaced eyes behind a contracted and narrow muzzle give the animal a short, wedge-shaped face and binocular vision. There are strong regional differences in colouring but also much individual variation. Animals from the arid north-east are a creamy yellow, graduating into grey on the legs, with pale sepia hocks. Ethiopian populations are less bleached but similar. Bold colour contrasts and patches of softer fur are most apparent in animals from humid uplands of central and SE Africa. In East Africa boundaries between yellowish north-easterners and russet-shouldered central African animals become blurred and both colourings co-exist. The Zambezi marks the northern margin of southern African forms. The Klipspringer only signals from 'the front end' and displays none of the tail-wagging so typical of other small antelopes. Instead, its black-edged ears have tracts of white fur that readily catch the eye when flicked. The males have short, upright horns and in some populations (Tanzania, Uganda,

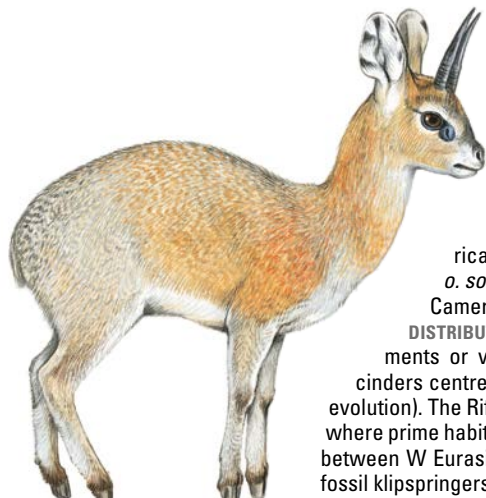


Klipspringer

Ethiopia) there is a high incidence of horned females. Their horns are generally no more than 90mm long but male horns of 160mm have been recorded.

GEOGRAPHIC VARIATION *O. o. oreotragus* (coastal regions of far south and Cape), *O. o. tranvaalensis* (upland South Africa and Drakensberg), *O. o. tyleri* (Namibian escarpments and uplands), *O. o. aceratos* (SE Africa between R. Rufiji and R. Zambezi), *O. o. centralis* (south-central Africa), *O. o. schillingsi* (East Africa), *O. o. saltatrixoides* (Ethiopian highlands), *O. o. somalicus* (N Somalia), *O. o. porteousi* (Nigeria/Cameroon, Central African Republic).

DISTRIBUTION Mostly steep, rocky hillsides, escarpments or valleys or open screes of loose pebbles or cinders centred on Ethiopia (the most likely centre for their evolution). The Rift Valleys link this region with southern Africa where prime habitats are also extensive. Numerous exchanges between W Eurasia and Ethiopia help explain the presence of fossil klipspringers outside Africa some 5 mya.



Animals can withstand day/night temperature fluctuations swinging from 42° C in the shade to freezing. This ability is clearly due to the insulating effect of their hollow-shafted fur. Klipspringers occur up to 4,000m on Mt Kilimanjaro and on the summit of Mt Meru (4,500m), where frost and snow are frequent.

HABITAT The very varied habitats and latitudes in which Klipspringers are found have two features in common: rocky, stony ground and abundant short vegetation. Food rather than cover is the crucial resource. Where drought or fire temporarily deprive them of food they tend to move down to escarpment or even valley bottoms. At such times Klipspringers also abandon their territorial behaviour. Over most of their range they are greatly outnumbered by hyraxes, which are presumably their main competitors for food resources.

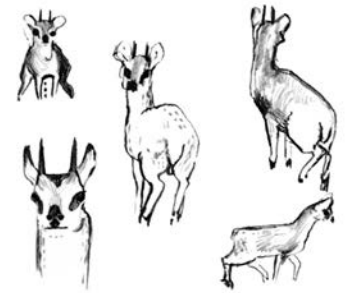
FOOD Herbs and low foliage are the main items throughout the range, with green grasses mainly a wet-season food. In Ethiopia grass forms about 17% of the annual diet while herbs account for more than half, and bushes, shrubs, and creepers the rest. In some areas, seeds, fruits, buds, twigs and bark are important seasonally; ephemerals such as *Vellozia* lilies can be temporary staples. Food distribution, temperature and disturbance all influence the duration and times of feeding. Klipspringers generally rest during the heat of the day and after midnight. Moonlight invites more activity than dark nights. Early morning sunning is important at high altitudes.

BEHAVIOUR It is rare for Klipspringers to remain solitary for very long. A female is generally attended or followed by a male and she commonly has a young one or an adult offspring with her or nearby. Males are much more vigilant than females. This may have benefits in spotting predators but appears to be primarily directed at keeping other males away. Pairs are permanently resident in territories that range from 7.5 to 49ha. Males remain almost continually aware of their female's whereabouts and 'duets' of whistling are a means of regaining contact after any disturbance. Mutual face-rubbing follows each reunion. Whistles also advertise territory and are an immediate response to predators. Conspicuous fluctuations in the size of facial glands have been observed to coincide with heightened sexual behaviour.

Mating peaks are recorded from several areas. After the lengthy gestation of several months a well-developed young is born and immediately hides. Only visited three or four times a day for suckling, the kid tends to remain a hider for up to 3 months. Over that period it gradually increases the time it spends with the mother. This prolonged hiding may be a response to heavy predation from the eagles that are very abundant in Klipspringer country (which is also hyrax country). Females are sexually mature at 1 year, males somewhat later, passing through a 'dispersal' phase during which they have no territory. Klipspringers are known to live for 15 years.

ADAPTATIONS Moisture and nutrients on eroding hillsides and cliffs support a rich vegetation that is not accessible to herbivores without special skills in negotiating rocks and screes. The time required to evolve appropriate capabilities handicaps latecomers and favours pioneers. Conservative traits in Klipspringer cranial anatomy suggest that their ancestors derived from the very earliest stock of African antelopes. Feet and hooves have gradually modified to the point at which no later bovids can compete. Even the Ibex, a late colonist from Eurasia, has not displaced the Klipspringer in Ethiopia.

STATUS An incapacity to escape local vicissitudes and very limited ability to disperse or recolonise lost ground suggests that the Cameroon model (steady shrinkage to vestigial proportions) will overtake other populations unless active reintroductions to suitable habitats are initiated. With careful management the survival of this species could not only be assured but improved. Listed as endangered (IUCN) in Cameroon, Nigeria and Uganda but not endangered in other parts of their range.



Klipspringer

IMPALA *Aepycerotini*

Virtually unchanged in 5 million years, and with a suggestive ancestral fossil at 14 mya, the Impala has a number of significant adaptations. Its special evolutionary significance is that this seems to be the sole survivor of an 'enlarged dwarf' lineage that eventually gave rise to several other large-bodied lineages, notably alcelaphines, hippotragines and caprines.

■ IMPALA *Aepyceros melampus*

OTHER NAMES Fr. *Impala*. Ger. *Schwarz Fersen Antilope*. Swah. *Swala pala*.

MEASUREMENTS HB 1.2–1.6m. T 300–450mm. Sh. ht 750–950mm. W 400–600mm (♀), 450–800mm (♂).

RECOGNITION A medium-sized gazelle-like antelope with a brown or yellowish-brown back that becomes lighter on haunches, shoulder, neck and head, and sharply lighter on the flanks. Underside, chin, mouth and ear linings are white. Ear tips, thigh stripes, midline of tail and back, and bushy fetlock glands are black (there are bold black eye-stripes and a black bridge to the nose in an isolated Namib population). Adult males have long, narrow horns, with shallow, well-spaced annulations, that arch up and out then back and up.

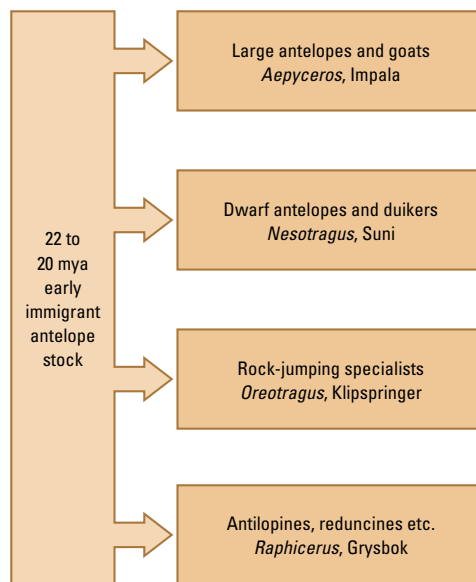
During rutting the necks of males thicken, their coats become darker from the grease of sebaceous secretions and they acquire a musky scent. There are no preorbital glands but the entire forehead is glandular and fossils reveal preorbital pits in ancestral forms.

GEOGRAPHIC VARIATION Common Impala, *A. m. melampus* (SE Africa). Black-faced Impala, *A. m. petersi* (SW Africa): a relict population with several conservative features – sometimes treated as a species.

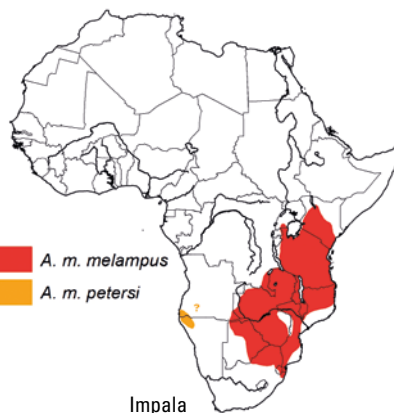
DISTRIBUTION A patchy scattering from Kenya south to the Transvaal, Botswana and E Angola. The Black-faced Impala is an isolated population in SW Angola and a small area of Namibia.

HABITAT 'Edges' between grassland and denser woodlands, notably *Acacia*, are preferred. They require high-quality fodder (whether grass or leaves), moisture, shade and cover. This unstable mosaic is characteristic of SE Africa, where Impalas are known to have been present for at least 4 million years. In favourable localities numbers can reach more than 200 per km². Grassland is occupied during the rains, woodland more in the dry season. Adult males have a greater tendency to remain in denser vegetation than females. In all areas Impalas are highly residential, seldom moving more than 10km and even then only temporarily.

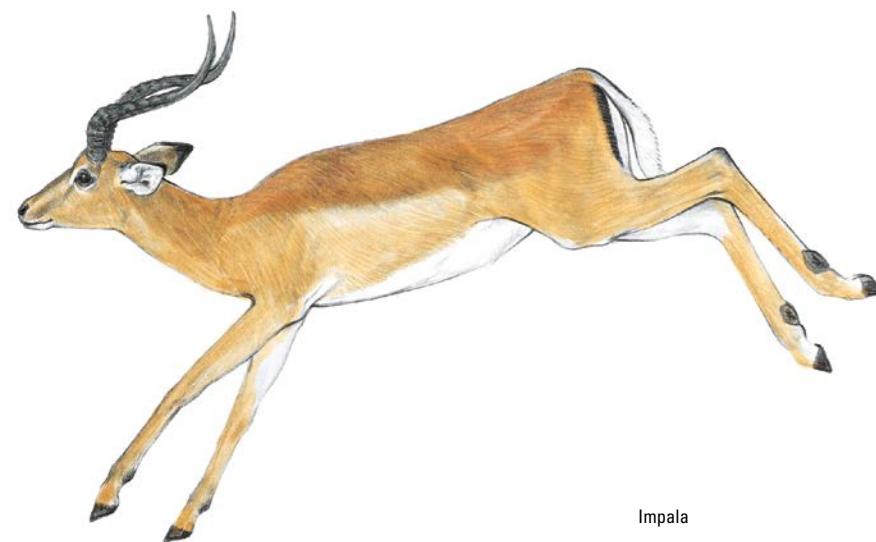
FOOD Almost wholly grazers during the rains. The amount of grass in the diet drops to about 30% in the dry season, when Impalas are mostly in the woodlands, browsing on shrubs, herbs, pods and seeds. *Acacia*, *Combretum* and *Grewia* are important in most areas. Feeding usually takes place



Four antelope radiations over the last 20 million years and the most conservative surviving genus in each.



Impala

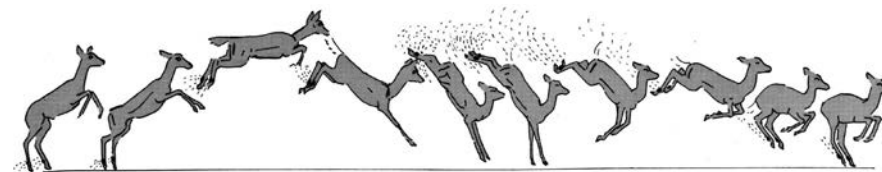


in two major bouts (around dawn and dusk) and two minor bouts (midnight and early afternoon), with shading and ruminating in between.

BEHAVIOUR Recent research has shown that females form 'clans' of 30–120 animals with home-ranges radiating out from fairly stable centres but extensively overlapping the ranges of neighbouring female clans. From such centres year-round movements may extend for about a kilometre but core ranges have been estimated at 80–180ha. Although gregarious, neither females nor males form any lasting associations (not even with their young).

Male offspring share their mother's home-range but begin to wander more widely as they mature (shifting their focus up to 4km away from the mother's range). Full horn and neck development is reached by males at about 4 years but the intolerance of other males restricts their movements and forces them to defend themselves within an area much smaller than their parental home-range. Their attachment to this area becomes more marked with age. The nature of their 'tenure' changes or cycles with their own hormonal condition and with that of other males that share part or all of their home-range. Most healthy adult males become intensely intolerant of other males when in the presence of oestrous females. This intolerance is expressed in direct challenges and fights during the rut. In southern Africa the rut lasts only a few weeks and, since males are almost continually inspecting, herding and copulating with females, confronting other males or rushing around roaring and chasing, they are soon exhausted and capitulate to fitter males. At the highest densities any single male's tenure of a 'territory' is ephemeral, lasting only 3–13 days.

If both the boundaries and the tenure of male territories appear unstable this is because being excluded or becoming an excluder depends on the presence and sexual condition of females. Mating peaks coincide with the rains in both southern and tropical Africa, but in the latter region two seasonal peaks are very much less sharply defined. One young is born in a secluded spot after a gestation of about 200 days. The mother remains nearby and visits only to suckle it. After some



Impala female leaping and making 'empty kicks'.

days the young begins to follow but seeks shelter at the least alarm. About half of all young are lost to predators within the first few weeks. Females are sexually mature in 18 months and animals live for up to 15 years.

ADAPTATIONS Fetlock glands, unique to Impalas, assist the laying of trails, presumably by helping temporarily detached or 'lost' individuals to find company. This function relates not only to trails left while walking; high kicks (another Impala peculiarity) send out puffs of scent that may help dispersed animals to regroup after a scare. Roaring of males allows them to space themselves acoustically, to intimidate potential rivals and assess risks with respect to other males within a wooded environment.

STATUS Widely distributed, fecund and well represented in numerous national parks, Impalas are vulnerable or endangered only on the outer margins of their range, as in Uganda and Rwanda.

ALCELAPHINES, TOPI AND ALLIES *Alcelaphini*

Hirola	<i>Beatragus hunteri</i>
Bontebok/Blesbok and Topi	<i>Damaliscus</i> (2 species)
Hartebeest	<i>Alcelaphus buselaphus</i>
Gnus	<i>Connochaetes</i> (2 species)

RECOGNITION Alcelaphines have a long face and legs, double-curved, hollow horns, fast gaits and a part or wholly grass diet in common. The Hirola resembles many other antelopes (and even deer) in its dimensions. The larger Topi, Hartebeest and wildebeest (gnus) have diversified into more distinctive types. The Impala was previously judged to be a primitive alcelaphine but this has proved to be too restrictive of its larger significance and it now occupies a tribe of its own. Its resemblance to the Hirola serves as a reminder that the larger species have evolved relatively recently from smaller ancestors.

GENEALOGY Most of the alcelaphine peculiarities were already present, albeit in a less marked form, in both fossil ancestors and in their modern descendants. Alcelaphines emerged late (less than 8 mya) and their fossil remains demonstrate very rapid change. Their hollow horns and forehead permit remodelling of the skull so that closely related forms can easily acquire very different horn shapes. The hammer-shaped head of the Hartebeest is due to a bending of axes, the muzzle tipping downwards while the horns twisted round (as is revealed by a good fossil series) until their hooked tips were literally 'back to front'.

GEOGRAPHY Alcelaphines evolved in Africa and were very successful. Some early forms spread out to India but later became extinct there. Advanced, water-dependent grazers, they have always been most abundant and diverse on the eastern side of Africa. Nonetheless, their recent range included the North African littoral, the West African savannas and the Horn, where they lived in immense numbers on a variety of pastures. Most of these populations belonged to the Hartebeest group, *Alcelaphus*.

ECOLOGY Alcelaphines are grazers adapted to live at high density on a very abundant but unstable food supply. They tolerate substantial seasonal fluctuations but few do well in really arid habitats. Exposure on open plains has selected for great speed and stamina.

NATURAL HISTORY As high-density grazers living in close proximity, alcelaphines have evolved advanced, but somewhat unusual, social systems dependent on scent-marking of bodies rather than sites in the environment. All have retained very active pedal scent glands and most species kick, stamp or cavort to disperse scent during social displays. The combination of an intensely competitive social life and a capacity for great speed means that a number of displays are performed on the run, such as ritualised gaits, prances and postures.

ADAPTATIONS The usual effect on limbs of increasing body weight is for them to become proportionately shorter and thicker. However, the larger alcelaphine species have retained fast gaits, long legs and a heavy, muscular body, but without elongating the neck in proportion. This disproportion has therefore led to a long face that is able to reach the ground. The short, muscular neck is an essential adjunct to the frequent horn-fighting necessary in a high-density, competitive society.

HIROLA *Beatragus hunteri*

OTHER NAMES Fr. *Antilope hirola*. Ger. *Hirola*. Swah. *Hirola*.

MEASUREMENTS HB 1.20–2.0m. T 300–450mm. Sh. ht 1.00–1.25m. W (est.) 80–118kg.

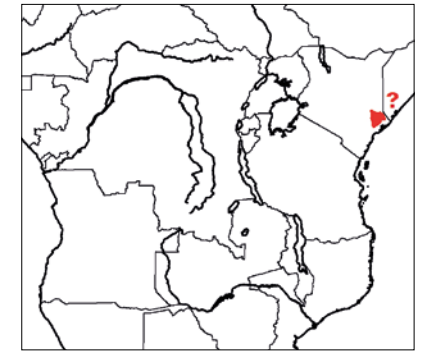
RECOGNITION An antelope with unusual proportions and colouring, of medium weight, with long legs and a long body but a relatively short neck and a long face. The lyrate horns are not unlike those of the Impala but have less flare and much heavier bases with pronounced annulations. The uniform sandy colouring gives way to a slaty grey in older males. The long tail and black-tipped ears are startlingly white, as are the 'spectacles' around the eyes (patterns that emphasise the eyes are typical of some kob types but most antelopes have a dark 'mask' that conceals the eyes). The structure of its large preorbital gland and muzzle differs from that of the Topi and Hartebeest. Pleistocene *Beatragus* was substantially larger.

DISTRIBUTION Since the mid-Pleistocene, less than 1 mya, the emergence of more advanced, high-density grazers, Hartebeest, probably contributed to the Hirola's steady decline. Whatever its history, it is now confined to a rapidly shrinking corner of SE Kenya (it no longer survives in Somalia).

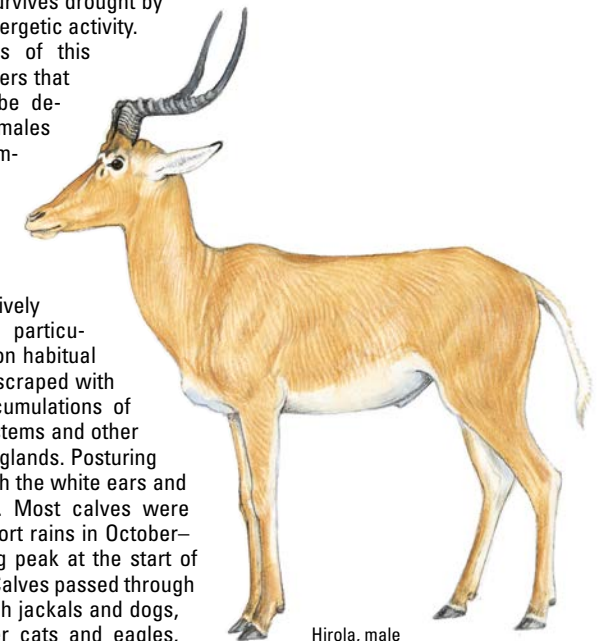
HABITAT A narrow strip of seasonally arid, grassy plains sandwiched between the waterless *Acacia* bush of the hinterland and forest-savanna mosaic on the coast (desert and thicket barriers might have served to exclude Hartebeest from this area). The northern margins of its range coincide with a type of very dry *Acacia* scrub where the grass cover becomes very much more sparse. Richer pastures used to be shared with moderate numbers of other grazers.

FOOD Strictly a grazer, feeding on the dominant grasses, notably species of *Chloris*, *Cenchrus* and *Digitaria*. The large molars are well suited to chewing such coarse grasses. It feeds most intensively in the early morning and evening. Able to go without drinking, it also survives drought by laying down fat and avoiding energetic activity.

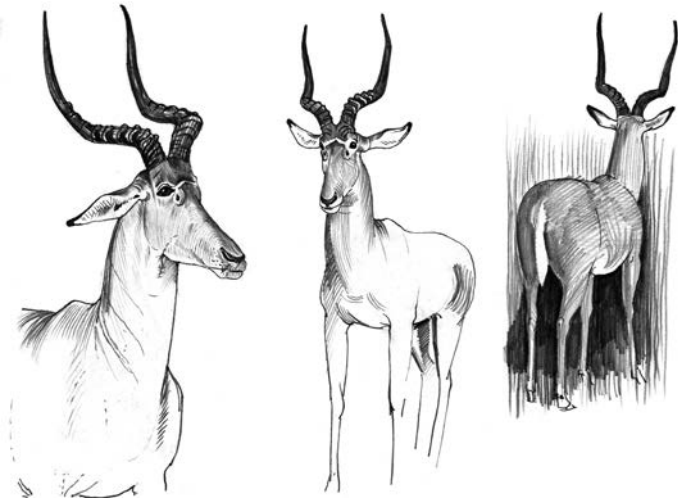
BEHAVIOUR The last individuals of this species exist in such low numbers that their natural behaviour must be described in the past tense. Females with young formed groups numbering between 5 and 40, often attended by a single territorial male. All-male groups were common, occasionally associated with Topi males. Herds were thought to be relatively sedentary and solitary males particularly so. Such males postured on habitual stamping grounds, which they scraped with the feet and marked with accumulations of dung. They also marked grass stems and other vegetation with their preorbital glands. Posturing included head-flagging, in which the white ears and spectacles were conspicuous. Most calves were born at the beginning of the short rains in October–November, suggesting a mating peak at the start of the main rains in March–April. Calves passed through a very vulnerable stage in which jackals and dogs, as well as hyaenas, the larger cats and eagles,



Hirola



Hirola, male



Hirola, adult male frontal and rear views

might all have been significant predators. The Hirola's lifespan is not known but capture experiments revealed that it was subject to muscular dystrophy. Delicacy during capture might have been due to a lowered metabolism in the dry season.

ADAPTATIONS A peculiarity of the males is the very thick skin of the nape (a necessary protection against the sharp horns of rivals during fights), which folds up behind the horns when the ears are pricked. Animals apparently fight on their knees when in earnest and in a standing position when sparring.

STATUS IUCN has classified this species as critically endangered. In its last (nominally protected) reserve there are now 232 sheep, goats, cattle and camels for every one Hirola. An intensive aerial survey in 2011 yielded a count of 245 individuals. It is extremely unlikely that this unique and beautiful animal can now survive. Yet, as recently as 1981, the population was estimated at 16,000 animals. Any chance of survival would have depended upon protection, and exclusion of the vast livestock holdings of the region from the 533km² Arawale Reserve which was specifically designated for Hirola. Medieval local livestock interests are fiercely aggressive and will never allow this to happen. Outside, in Tsavo NP, a small herd introduced in the 1960s and another in 1996 are only just managing to sustain their numbers in the face of regular Lion predation. Both situations illustrate the true process of extinction in our time, as at any other time.

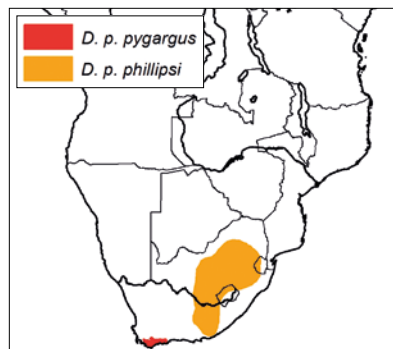
■ BONTEBOK/BLESBOK

Damaliscus pygargus

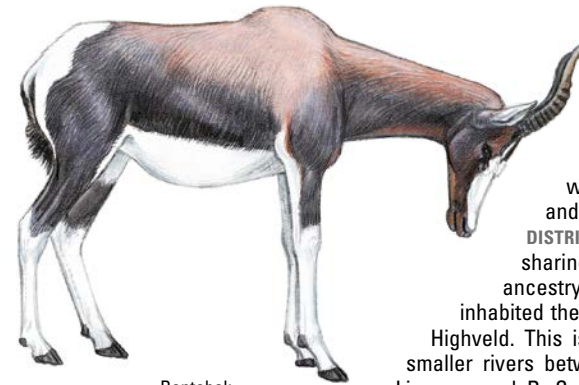
OTHER NAMES Fr. *Bontebok*, *Blesbok*.
Ger. *Buntbock*, *Blessbock*.

MEASUREMENTS HB 1.4–1.6m. T 300–450mm.
Sh. ht 0.85–1.0m. W 55–70kg (♀), 65–80kg (♂).
Bontebok an average 8kg lighter.

RECOGNITION Smaller southern cousins of the Topi, with very strong contrasts of colour in adults but fawn young with completely different, gazelle-like colouring. They have a compact body, short neck and a long nose with an expanded muzzle. Their horns resemble enlarged gazelle horns. The tail is short with a black, tufted tip. The differences between subspecies are given below.



Bontebok/Blesbok



Bontebok

GEOGRAPHIC VARIATION

Bontebok, *D. p. pygargus* (W Cape): glossy dark purplish-brown with white buttocks and 'stockings'; very dark horns. Blesbok, *D. p. phillipsi* (Highveld): dull reddish brown with ill-defined off-white buttocks and off-white lower legs; paler horns.

DISTRIBUTION South African isolates sharing a geologically recent common ancestry with Topi. The Blesbok formerly inhabited the plateau grasslands known as the Highveld. This is the watershed for innumerable smaller rivers between the larger valleys of the R. Limpopo and R. Sundays. 'Sweepstake' colonisation of the Cape (probably across the Nieuwveld range and within the last few thousands of years) led to physical and

genetic isolation of the Bontebok. Derived from a small number of founders, it was unlikely to have been widespread, even before the arrival of humans with livestock.

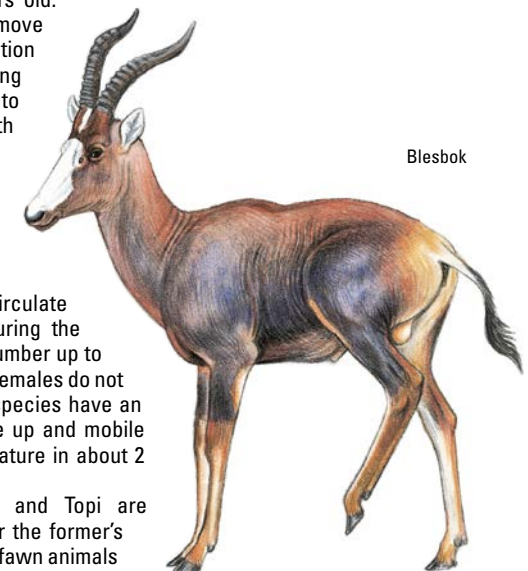
HABITAT The Blesbok originally ranged over the entire Highveld, grazing the fire-climax grassland dominated by Red Oat Grass, *Themeda*. The Bontebok inhabited a different Cape fynbos habitat where grassy areas were scarcer. In both parts of their range, animals had regular access to water.

FOOD Red Oat Grass, *Themeda triandra* (at various stages of growth), *Eragrostis* and *Chloromela* form the main part of the Blesbok's diet. A species of *Setaria* is taken only in winter and there are seasonal changes of pasture. The Bontebok also feeds on *Eragrostis* species but local dominants, *Bromus* and *Danthonia*, are the preferred grasses.

BEHAVIOUR The Blesbok formerly tended to migrate between seasonal pastures, forming huge mixed herds in the autumn and winter. Where the pastures in modern enclosures are sufficiently extensive to support them Blesboks still gather in semi-nomadic herds. Even in smaller groups within still smaller enclosures both subspecies retain the habit of circulating around their available range in loose herds. The membership and numbers of these mobile aggregations are unstable but include sexually inactive males and younger, but independent females less than 2 years old.

Adult females with offspring tend to move over much smaller areas, a restriction reinforced by the territorial males living there. These males have focal centres to their territories which are marked with dung and urine on middens. Although the spacing between males varies greatly, their inner core of 'markable' and 'defendable' territory is always less than 5ha. Female Bonteboks seldom gather in groups of more than 10 (including their young) and they circulate over two or three male territories during the February rut. Blesbok female groups number up to 25 and mating peaks in April. Pregnant females do not leave the herd to give birth. Both subspecies have an 8-month gestation and their young are up and mobile within an hour or two of birth. They mature in about 2 years and can live for up to 17 years.

ADAPTATIONS The young of Blesbok and Topi are apparently identical at birth except for the former's smaller size. Both begin as pale, sandy-fawn animals



Blesbok

with creamy undersides. First the bridge of the nose darkens, then dark leg and flank stripes (like those of Springboks or gazelles) begin to extend over the sides and limbs. This darkening proceeds until there are more or less separate black patches in tropical Topi. Pale undersides become ochre-coloured in Topi, white in Bontebok. The pale root to the tail is very similar in some Topi and Blesbok. As the Bontebok matures this cream-coloured area turns white and forms a sharply defined genital beacon. In both Blesbok and Bontebok the bridge of the nose becomes the badge of maturity. As their horns lengthen it turns white with crisp black borders against the sides of the face. Most Topi keep a black nose but rare individuals switch colours as they mature and have white blazes as conspicuous and of the same shape as those of the Bontebok. These transformations during the development of individuals and the variation evident even in today's impoverished herds illustrate the potential for rapid differentiation in isolated populations.

That Blesbok and Topi have diverged very recently is shown by a perfect intermediate form, a supposed common ancestor, being very common in both southern and eastern African fossil deposits that are less than 1 million years old. *Damaliscus agelaius* was similar in size to the Blesbok, suggesting that this lineage has become more than twice as heavy in the rich sumplands of the tropics while their southern counterparts on the leached Highveld have remained more conservative. One reason for their divergence may have been the emergence of a new competitor, the Hartebeest, taking over as dominant grazer in dry savanna grasslands.

STATUS The Blesbok is now commercially ranched livestock and very few occur in formal conservation areas. The Bontebok is also kept on farms (one having been made into a national park). Although both are now extinct as wild animals their survival is now more secure.

■ TOPI/TIANG/TSESSEBE

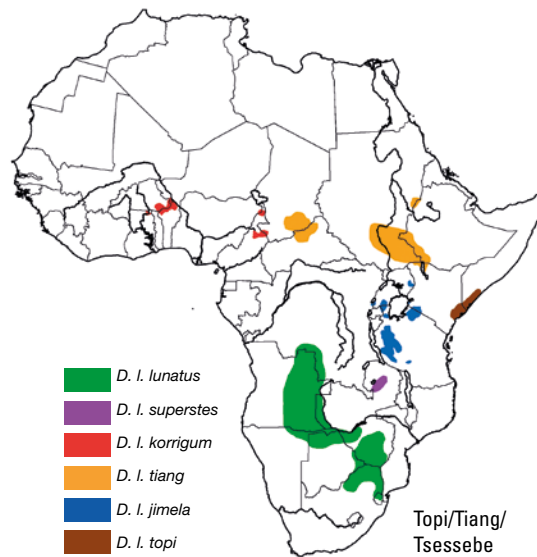
Damaliscus lunatus

OTHER NAMES Fr. *Damalisque*. Ger. *Leierantilope*. Swah. *Nyamera*, *Topi* (at least two of the local names are synonymous with 'mud', reflecting these animals' sumpland habitats).

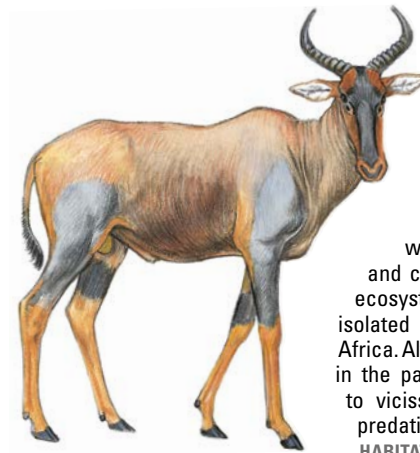
MEASUREMENTS HB 1.5–2.3m. T 360–420mm. W 75–150kg (♀), 120–160kg (♂).

RECOGNITION A large, compact antelope with a deep chest, prominently ridged shoulders, a rather short neck and a long face. The tail is narrow and fringed. Horns vary from one region to another in their splay and arching but all have backward-curving stems and forward- or inward-curving tips. The body colour varies from rather yellowish, bleached brown to red or even purplish brown. There are black patches on the hindquarters and forelegs above ochre-coloured 'stockings'. The bridge of the nose is black (very occasionally turning white with maturity). The coat of healthy animals is always tight and very glossy. The hooves are narrow and splay out on soft ground.

GEOGRAPHIC VARIATION *D. lunatus* is recently evolved but climatic vicissitudes within each separate sump result in periodic boom/bust population crashes followed by genetic founder-effects in the survivors. This probably helps explain rapid differentiation within each separate sumpland region. This ecological history has failed to influence the Phylogenetic Species Concept doctrine that regards any perceptibly different population as a species. Proponents of PSC taxonomy have proposed that each of 10 sumpland populations is a full species. That course is not followed here, but six subspecies are recognised as follows:



- *D. l. lunatus*
- *D. l. superstes*
- *D. l. korrigum*
- *D. l. tiang*
- *D. l. jimela*
- *D. l. topi*



Tsessebe

Tsessebe, *D. l. lunatus* (southern Africa);
Bangweulu Tsessebe, *D. l. superstes* (NE Zambia);
Korrigum, *D. l. korrigum* (Senegal to W Nigeria);
Tiang, *D. l. tiang* (NE Nigeria to W Ethiopia);
Nyamera, *D. l. jimela* (Great Lakes region);
Topi, *D. l. topi* (E African coast).

DISTRIBUTION Sumplands and floodplains in otherwise relatively dry regions south of the Sahara, East and central Africa. All populations centre on large-scale ecosystems and they are absent from the many small, isolated floodplains that are scattered throughout tropical Africa. Although there must have been continuous connections in the past, small isolated groups appear to be vulnerable to vicissitudes of climate (and possibly competition and predation).

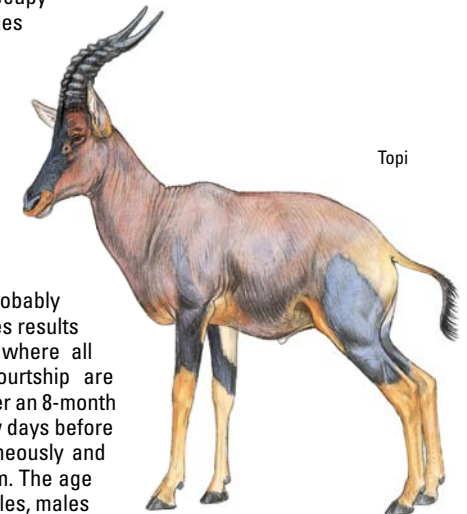
HABITAT These antelopes live in seasonally flooded grasslands where they follow receding waters in the dry season and retreat onto slightly higher ground in the rains or flood

season. Failed rains or floods can lead to very extensive die-offs.

They favour naturally short or medium-height pastures (such as alkaline pans), regrowth after burns or else concentrate in large herds in tall grass (commonly on wet-season higher ground retreats). Here heavy trampling soon opens up large glades and stimulates continuous regrowth. These annual cycles of movement can involve huge herds of tens of thousands in round journeys of nearly 1,000km, small circuits within closed valleys, or sustained residence on 'permanent' pockets of suitable grassland. The instability and unpredictability of floodplain pastures renders the last group peculiarly vulnerable. The advantages of living in very large, mobile herds include reduced predation and optimum grazing, partly due to their own trampling. Younger animals benefit from older animals' knowledge of the region's pastures.

FOOD Most valley grasses are taken. Longer rather than very short leaves are stripped from the stems with a nodding action that finely balances raking wrenches with clipping bites.

BEHAVIOUR Although many Topi live in large migratory herds, they may be neighbours to (or co-exist with) small clusters of residential animals. The residential animals are probably offshoots of the larger aggregations but display different behaviour in that they occupy territories defended by males (and sometimes also by females). Scattered residents tend to be less seasonal in their breeding. Large groups instead tend to have very intense periods of rutting while herds are at their most concentrated. In some areas mating may take place 'on the hoof' but in most instances it tends to focus on territorial clusters. Close proximity may stimulate hormones in both sexes and the build-up of scent in particular 'hot-spots'. Males fight for access to oestrous females, who are probably drawn in by the scent. Competition among males results in ever smaller territories (down to 0.05ha) where all the elaborate preliminaries of prolonged courtship are abbreviated and intensified. Young are born after an 8-month gestation. The sandy-fawn calf lies up for a few days before joining its mother. Young often gather spontaneously and females may form a defensive ring around them. The age of sexual maturity varies (12–28 months in females, males



Topi

up to 42 months). Loss of teeth after about 15 years results in death. Females are fertile to the end and bear young even as the last roots of their teeth fall from their jaws.

ADAPTATIONS Adaptation to living on floodplains appears to be relatively recent in Topi as their feet are only slightly modified for walking in soft soils. It is possible that ancestral Topi ceded the greater part of a formerly more extensive grass-eating niche to the larger Hartebeest which is a more recently evolved, more advanced grazer. Greater speed, stamina, mobility and versatility enable the Topi to compete with the kobs, lechwes and Waterbuck. **STATUS** Topi have been eliminated from the greater part of their range but can still reach very high densities in their remaining refuges. Currently well represented in reserves and national parks of eastern and southern Africa.

■ HARTEBEEST *Alcelaphus buselaphus* (incl. *lichtensteinii*)

OTHER NAMES Fr. *Bubale*. Ger. *Kuhantilope*. Swah. *Kongoni*.

MEASUREMENTS HB 1.60–2.15m. T 300–700mm. Sh. ht 1.07–1.50m. W 116–185kg (♀), 125–218kg (♂). **RECOGNITION** A large, high-shouldered, deep-chested antelope with long legs, a short neck and a very long, narrow face. The horns are carried on hollow bases, or 'pedicels', and show considerable variation (450–830mm) from individual to individual and from region to region. Coloration also shows considerable regional variation (red and black in the Kalahari, tan in East Africa, golden-brown in West Africa) and also individual variation, especially in the Korkay from Ethiopia (*A. b. swaynei*) in which the overall body colour ranges from silvery purplish to red or dark brown, and the blotches of black on shoulders and knees vary in shape and extent. The Hartebeest has preorbital and pedal (hoof) glands.

GEOGRAPHIC VARIATION **Bubal**, *A. b. buselaphus*

(N Africa), extinct 1925; **Kanki** (Western

Hartebeest), *A. b. major* (W Africa); **Lel-**

wel, *A. b. lelwel* (L. Chad to L. Turkana);

Korkay (Swayne's Hartebeest), *A. b.*

swaynei (Ethiopia); **Tora**, *A. b. tora*

(E Sudan and N Ethiopia); **Kongoni**

(Coke's Hartebeest), *A. b. cokii* (S

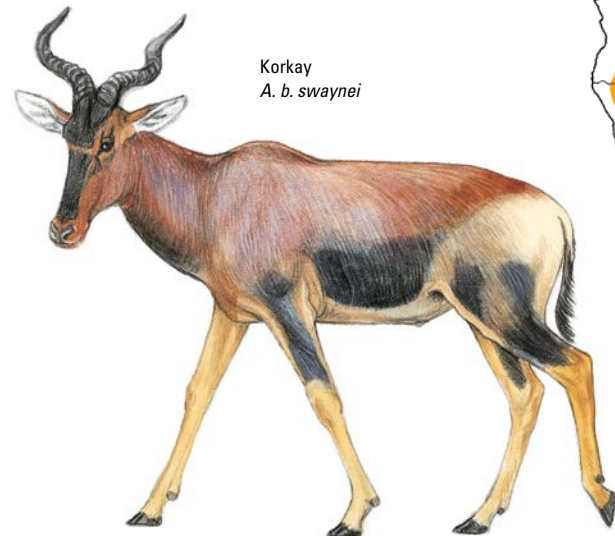
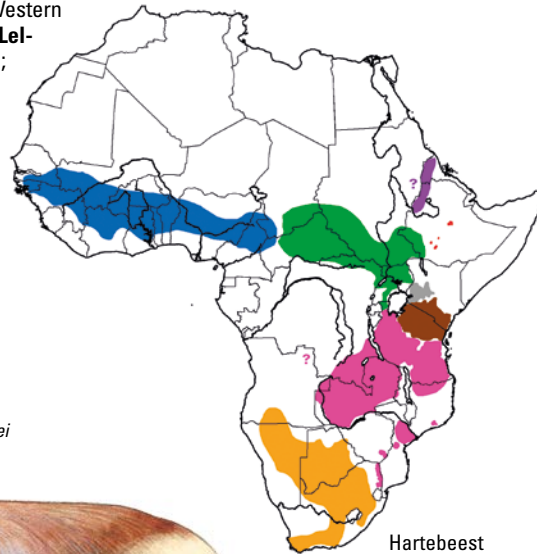
Kenya and N Tanzania); **Nkonzi**

(Lichtenstein's Hartebeest), *A. b.*

lichtensteinii (central and SE Af-

rica); **Khama** (Red Hartebeest), *A.*

b. caama (Cape, Kalahari).

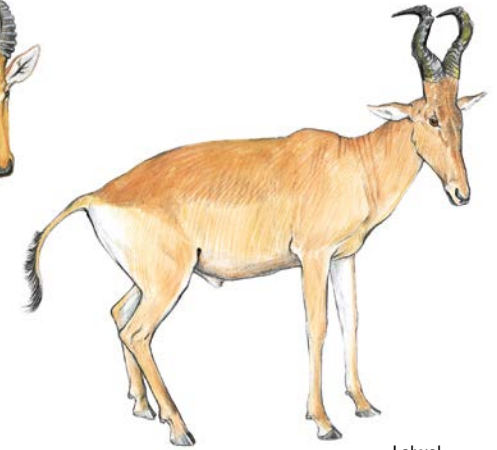


Korkay
A. b. swaynei

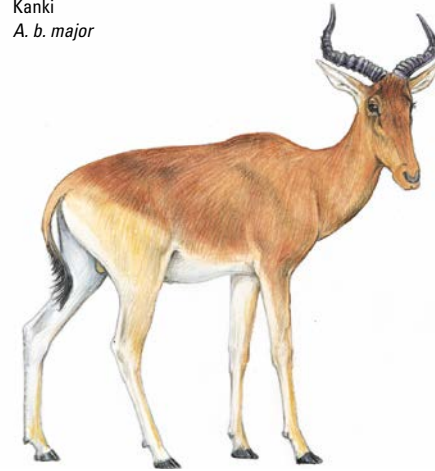
- *A. b. major*
- *A. b. lelwel*
- *A. b. swaynei*
- *A. b. tora*
- *A. b. cokii*
- *A. b. lichtensteinii*
- *A. b. caama*
- *A. b. cokii* × *A. b. lelwel*



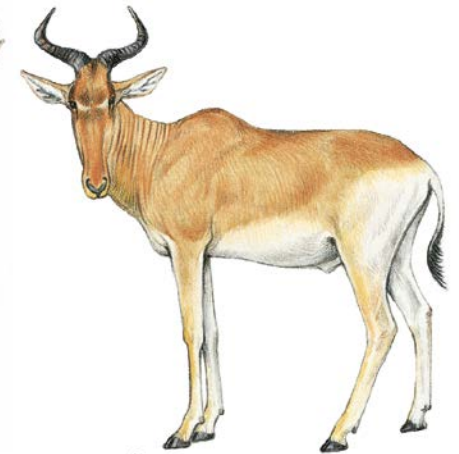
Kanki
A. b. major



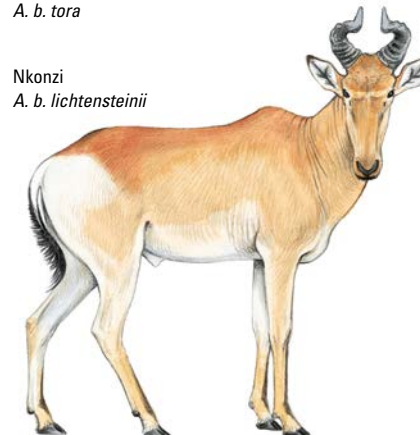
Lelwel
A. b. lelwel



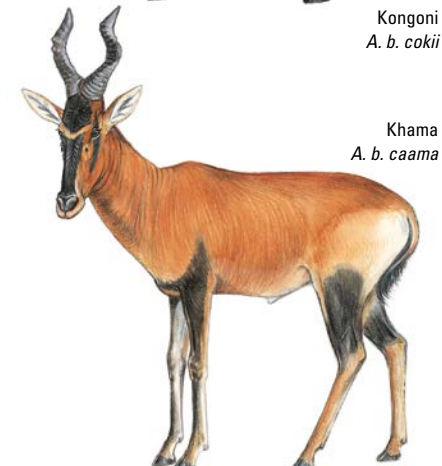
Tora
A. b. tora



Kongoni
A. b. cokii



Nkonzi
A. b. lichtensteinii



Khama
A. b. caama

The eight subspecies listed above have been generally recognised since 1894. Among some 50 named forms are many collected from interzones between the ranges of these eight subspecies. Most of these appear to be unstable hybrids rather than graduated intermediate forms, suggesting that former isolation has broken down as three forms, the Lelwel, Khama and Nkonzi, expanded their ranges.

DISTRIBUTION Formerly all African grasslands and savannas (except for a very narrow strip between the R. Juba and R. Tana and the South African Highveld). The short-pedicelled, more conservative subspecies (Tora, Korkay, Kongoni) live in NE Africa. The Khama in the Kalahari and Kanki in W Africa have high pedicels and are more advanced. The Lelwel, with the highest pedicels, appears to have intruded into the former ranges of all its neighbours, in each case creating hybrid zones. The Nkonzi, possibly derived from the same stock as the Kanki, has also colonised a vast territory wedged between the ranges of the Kongoni and Khama, apparently hybridising with both (how extensively remains to be determined).

HABITAT Although regional differences are substantial, Hartebeest are consistent everywhere in being grazers that live on boundaries between open grassy plains or glades and parkland, woodland or scrub (often on shallow slopes). They go to water regularly (but territorial males go without for quite long periods). They move down drainage lines for grass and water in the dry season and up onto better drained, thinly grassed woodlands during the rains.

FOOD Grazers, selective of neither species nor component parts of the grass. However, certain species are avoided, notably *Cynodon*, a grass that is readily grazed by other herbivores. All studies have shown that broad-leaf foliage accounts for less than 5% of the diet.

BEHAVIOUR Female Hartebeest are gregarious and to variable degrees move up and down shallow grassy valleys in pursuit of the best grass. Males become dispersed along the margins of each drainage line and establish dung-marked territories that embrace all the vegetation types from top to bottom of the slope. Where there is pressure from neighbours, territories may get narrowed but nearly always from the sides and not from above or below. Males waylay female groups as they pass through their territories. In some areas breeding is compressed into a short period during the rains (May in Uganda) and most males only become territorial at this time. In other areas some breeding continues throughout the year and territories are held more or less continuously. Males mark their territories with dung and posture with the head held upright and the legs placed well back. This is a gesture that suggests ritualised defecation and may serve to deter neighbouring males and attract passing females. Males fight most intensely in the presence of oestrous females and are especially aggressive towards attendant male offspring. At high densities males are sometimes killed in fights. Females defend their young vigorously and also form temporary all-female hierarchies in which threatening gestures with horns are noticeable. A single young is born after an 8-month gestation and growth rates are strongly influenced by nutrition. Sexual maturity is reached in 1 year in some populations and not until the fourth year in others. Animals live for up to 19 years.

ADAPTATIONS With the exception of the Nkonzi, *A. b. lichtensteinii* (which could be regarded as an incipient species), all subspecies have been recorded in very large dense herds at various times (the same was true of the Bubal in the 1830s and 1840s in Souf, Algeria).

Populations crash to very low levels during droughts, disease epidemics or under sustained competitive pressure from cattle. However, they recover quite rapidly when conditions improve. This capacity to build up their numbers is fuelled by subsistence on a normally super-abundant resource. They are also socially versatile, with females finding the best pastures at all density levels and the males adjusting the size and distribution of their territories accordingly.

STATUS Extinction of the Bubal should serve as a warning about the vulnerability of this species. At present the Tora, Korkay and Kanki are all at very low levels. The Korkay is now extinct in Somalia, where it was once present in vast herds. Apart from being easy to hunt and possessing very tasty meat, this antelope declines wherever there is competition from intensive cattle-keeping. The Tora is listed as endangered (IUCN) and the Korkay as threatened. Other subspecies are not endangered at present but the pastures of all remaining populations are coveted by livestock interests.

BRINDLED GNU *Connochaetes taurinus*

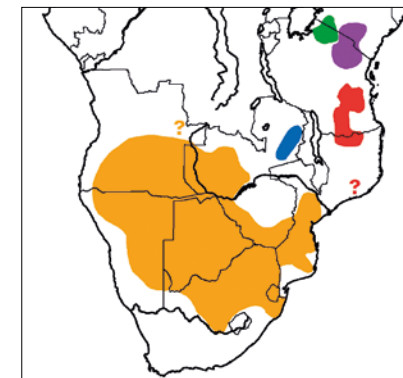
OTHER NAMES Common Wildebeest. Fr. *Gnou bleu*. Ger. *Streifengnu*. Swah. *Nyumbu*.

MEASUREMENTS HB 1.7–2.4m. T 600–1,000m. Sh. ht 1.15–1.45m. W 140–260kg (♀), 165–290kg (♂).

RECOGNITION A dumpy, thick-necked, long-faced antelope with horns that flare out sideways and then upwards (rather like a cow's). The flat, rather square nasal plate (with hair-lined, flap-edged nostrils) is bounded by an even broader, grass-nibbling mouth. Dense tufts of hair on the long, convex muzzle conceal very active preorbital glands and help to diffuse scent from them. The muzzle is black in all subspecies, as is the shaggy mane and tail. The body colours of the four or five different subspecies varies from dark grey-brown to slate blue to pale greyish fawn, with variable degrees of brindling. This strongly textured streaking of the neck, shoulders and flanks mimics the visual effect of a long, lank mane very closely. The neck and chin are bearded in long, black, brown, cream or white hair. The short legs are brown or ochre, with pedal glands between the large true hooves (there are prominent false lateral hooves).

GEOGRAPHIC VARIATION Brindled Gnu or Blue Wildebeest, *C. t. taurinus* (south of the R. Zambezi, Kalahari); Cookson's Wildebeest/Gnu, *C. t. cooksoni* (Luangwa valley); Johnston's or White-banded Wildebeest, or Nyassa Gnu, *C. t. johnstoni* (SE Africa); Eastern White-bearded Wildebeest/Gnu, *C. t. albojubatus* (S Kenya, NE Tanzania, east of the Rift Valley); Western White-bearded Wildebeest/Gnu, *C. t. mearnsi* (N Tanzania and S Kenya, west of L. Natron and L. Manyara).

DISTRIBUTION Open bushland and grassy plains in relatively dry areas of E, SE and south-central Africa. These animals, dependence on water limits their extension into drier regions but they persisted on the North African littoral into prehistoric and possibly historic times.



- *C. t. taurinus*
- *C. t. cooksoni*
- *C. t. johnstoni*
- *C. t. albojubatus*
- *C. t. mearnsi*

Brindled Gnu



Brindled Gnu *C. t. taurinus*, male



Eastern White-bearded Wildebeest *C. t. albojubatus*

HABITAT Short grasslands (maintained by fire, shade, rainfall, water table, drainage, soil chemistry, herbivore grazing and trampling), always within about 20km of permanent water. Migration permits them to rotate pastures where these requirements are seasonal.

FOOD A wide variety of nutritious grasses that form short swards. At times Brindled Gnu may be forced to strip leaves from tall stems but this is a temporary and inefficient expedient. They are unable to graze persistent rank growth, which helps to explain their absence from many areas of equatorial Africa and their inability to survive (as reintroductions) into long-grass areas.

BEHAVIOUR They are social grazers that congregate in response to the local distribution of short grass pastures and water. Where these are adequate throughout the year, females and their young can remain permanently on home-ranges of a few hectares. Other similar female groups may share some of their range without friction but external intruders can be severely harassed. Where their food and water dry out, resident gnus tend to move on to more extensive seasonal pastures. Here they join other gnus, soon losing their local identities in the amalgam of herds. These seasonal aggregations are sometimes quite temporary.

Permanent large herds are more continuously nomadic, with females joining up to lead mass movement from one major pasture to another. The celebrated Serengeti migration is just such a circuit, in which the dry season is spent on the grasslands of the L. Victoria littoral and the rainy season on ashy volcanic plains closer to the Rift Valley. During this annual cycle females initiate movement off the open plains as surface water and herbage begins to dry out. Both sexes are in peak condition after several months on the fertile volcanic pastures.

As with Kob, Topi and many other mammals, enforced collectivisation triggers the hormonal changes in both sexes that are known as 'the rut'. Rutting males attempt to exclude each other from access to oestrous females. Because movement along the route is jerky (the mega-herd moving on after exhausting each pasture), males tend to win 'territories' that are simply marked out by their own behaviour. They 'broadcast' sound, scent and eye-catching visual displays in the form of belching grunts and snorts, flurries of scent (transferred from the face to everywhere they can reach) and frantic leaping, cavorting and head-shaking. Such territories can be no more than a fraction of a hectare. Depending on the pace of movement the male can remain in one place for many days or a few hours as herds continue their relentless movement. A scatter of males remains in the wake of the herds, exhausting their energies in fruitless posturings and stand-offs with a fast-diminishing audience of other left-over territorial males.

One calf is born to each female in the following wet season, 8 months later. While some large carnivores can keep up with or waylay the herds, one of the benefits of nomadism is outmarching the predators. Synchronised calving also helps to reduce the toll from predators. Births take place on exposed pastures, almost all in the space of a few weeks, and calves born outside this period seldom survive.

The newborn begins walking within minutes. It is tan at first but acquires the distinctive gnu colouring by stages, beginning within 1 or 2 months of birth. Rates of maturity vary, with females becoming fertile by about 16 months. Males do not normally take up territories until they are 4 or 5 years old. Brindled Gnu are known to live for up to 20 years.

ADAPTATIONS Isolated individuals and scattered small groups are seldom found very far from the annual range of a much larger regional population. Attrition is generally quite swift in such vulnerable outliers. Although they have stamina and a fast turn of speed, adults can be outrun and killed by at least six major carnivore species. Their calves are vulnerable to many more. Gnus are therefore adapted to living in large, dense herds. As grass ruminants, a large part of their body mass is given over to the digestive tract. Since their security depends more in belonging to a herd than in outrunning predators (as Hartebeest can do), gnus do not need such long legs, heads and necks. This is a special advantage for males because they can specialise in becoming efficient fighters and horn-wrestlers with their heavy necks, heads and horns. Females must also be sufficiently robust in order to defend their offspring from the males.

STATUS Land settlement, livestock and their diseases, fences and easy poaching with modern weapons all represent threats. More than most species, the Brindled Gnu is dependent on deliberate conservation policies for its survival because its year-round requirements of water and pasture must be met and each local population must remain sufficiently numerous to be viable. Each subspecies is well represented in conservation areas and national parks but both protection and land areas are often inadequate. They continue to decline and are unlikely to survive outside such areas. Overall, the Brindled Gnu is rated as not endangered (IUCN) but that status will be tested in future years.

■ WHITE-TAILED GNU *Connochaetes gnou*

OTHER NAMES Black Wildebeest. Fr. *Gnou à queue blanche*. Ger. *Weisschwanz Gnu*.

MEASUREMENTS HB 1.7–2.2m. T 0.8–1.0m.

Sh. ht 0.9–1.21m. W 110–160kg (♀), 140–180kg (♂).

RECOGNITION A stocky, thick-coated antelope with heavily bossed horns that swing down, forward and upwards in tight angular hooks. The long muzzle is very broad, flat-fronted and covered in dense black fur. The flapped nostrils are set above a wide rectangular mouth. The body colour is dark brown, with a black beard and chest tassels. The upright mane hairs are off-white with intensely black tips. The long, flowing tail is wholly white.

The pelvis is peculiarly prominent. The large hooves of the forelegs have interdigital glands. Preorbital glands are also very active, especially in adult males (scenting not only the face but, by transfer, also the body and tail).

GEOGRAPHIC VARIATION None (there are four obsolete subspecies names).

DISTRIBUTION Originally migratory over a large part of the Karoo and Highveld. Overall range from the valley of the R. Vaal in the north to the R. Salt in the south, and from the Orange R. valley in the west to the Drakensberg Mts in the east. Now extinct as a wild animal.

HABITAT Temperate grasslands and Karoo shrublands where it migrated between summer pastures in the Karoo and eastwards to grasslands of the Highveld during the winter. These large-scale movements ceased when European settlement moved into the interior where, by the mid-19th century, this species had been brought close to extinction.

FOOD Grazes but supplements grasses with succulents and shrubs (such as *Pentzia*, *Salsola*, *Nenax* and *Osteospermum*), which permits grazing of the arid Karoo without regular water. It is more continuously active in cool weather but lies up for the heat of the day in summer.

BEHAVIOUR Unknown as a wild animal but some reconstruction has been possible on the basis of studies of small groups on fenced farms or reserves. Females wander in groups of up to 60 over home-ranges of about 100ha. As they pass through male territories they are inspected and the male attempts to deter them from passing on into the territory of his neighbours. This herding is most intense during the period of female oestrus. Because most females mate only at the end of the hot wet summer (March–April) it would appear that mating used to coincide with a massed eastward shift towards the Highveld winter pastures. Births more than 8 months later (250 days' gestation) would have been on their summer range in the Karoo. In confinement females form hierarchies and fight females not already known to them. By contrast, male bachelor groups generally show



White-tailed Gnu



White-tailed Gnu

few signs of aggression and some animals in the group have been observed to come to the rescue of bullied, bawling subordinates. This species has evolved particularly dangerous horns and, with them, elaborate appeasement gestures (including prostration). Yearling offspring are generally driven off by their mothers after the birth of a new calf. For the 6–9 months before weaning, mother and young remain very closely bonded. Young males do not normally take up territories until they are 4 years old, at which time they posture, fight challengers and mark the centre of their ranges with dung and urine in which the male paws and rolls. The thick coat is well suited to hold this scent (and that from the preorbital glands) and rutting males have a pervasive rank odour. They are also very vocal with a metallic snort, a two part 'ge-nu' (hence the Khoi name) and a very resonant, single 'hick' which is uttered with a violent spasm of the head and neck.

ADAPTATIONS The front-facing horns are extremely dangerous when hooked forwards and upwards from below. The animal's kneeling position while fighting greatly mitigates this danger while hefty bosses on the top of the head serve both as shields and battering rams during ritualised fights between rivals. However, in any normal frontal encounters with their environment (including other gnus) close contact is debarred not by spikes but by the rounded midshafts of the sharply angled horns. This barrier protects the muzzle and especially the preorbital glands from all such direct contacts. As a consequence White-tailed Gnus are unusual in hardly ever rubbing one another face to face, nor do they normally rub their face glands on the ground or vegetation. Instead, liquid secretion flows along hair tracts down into the beard and up into the bizarre tuft of long hair on the muzzle (found in both sexes). Beard and tuft therefore act as scent-dispensers as well as 'enlargers', extending, together with the mane and haired chest, the silhouette of the forequarters. In the intensely competitive context of migrating, mating herds, such characteristics would appear to have magnified the impression of physical power (further enhanced by dark colour which emphasises mass). Their cavorting, head-tossing and kicking would appear to exaggerate the energetics of movement while their amplified voices and behaviour such as rolling and pawing augment the social signals transmitted by strong scent. Their arched crests and long white tails served to make their large repertoire of displays highly conspicuous.

STATUS Private initiatives in the face of reluctant, indifferent or hostile policies have saved many species from extinction in South Africa, of which the White-tailed Gnu is one. Even now, many small farms are replacing livestock with indigenous herbivores. Vested interests in pastoral agriculture will probably not allow White-tailed Gnus sufficient space to begin behaving as wild animals again. Nevertheless, from a nadir estimated as low as 300–600 animals, present populations have risen to about 10,000 (however, inbreeding presents some problems). Currently rated as rare, but not endangered.

HORSE-LIKE ANTELOPES Hippotragini

Roan and Sable Antelopes	<i>Hippotragus</i> (2 species)
Oryxes	<i>Oryx</i> (3 species)
Addax	<i>Addax nasomaculatus</i>

RECOGNITION Large, barrel-bodied antelopes with long, slender and well-annulated horns, long ears and broad, heavy hooves (with well-developed pedal glands). False hooves are particularly well developed in the oryxes and Addax. The coat is sleek, in various shades of tan, white and black, and the face is striped rather like a goat or gazelle. The thick, tapering necks and mane earned these antelopes their Latin name, Hippotragini, which means 'horse-goat'. Sexes are similar but males are heavier and have thicker horns. Some species have vestigial preorbital glands.

GENEALOGY Horse-like antelopes share a common ancestry with caprines. Like them, they are arid-adapted and represent an early, grass-eating 'giant' branch. Two 7 million-year-old fossils from the south-eastern Sahara are thought to represent basal hippotragines. By 4 or 5 mya oryxes (in more or less modern form) were already abundant in North Africa. The fact that no other bovid has been able to challenge them for the larger-scale desert niche implies that they have had a long head-start in adapting to heat, drought and unpredictable desert pastures. The Roan Antelope and Sable Antelope occupy isolated positions in the spectrum of tropical antelopes and the teeth of fossils confirm their common origins with oryxes, suggesting that they moved south from drier, more northern habitats.

GEOGRAPHY Although now exclusively African, there are fossils from India and Europe which suggest that the ancestral lineage of these antelopes was once more widespread.

ECOLOGY All species are grazers, with molar teeth well suited to grinding hard grasses (Roan Antelopes possess particularly broad teeth). They have specialised in exploiting zones with an impoverished fauna and flora. Much of their range corresponds with the 'Precambrian Shield' – extensive areas of low fertility and leguminous vegetation. Their narrowed choice (even within the tropics) is due to their attachment to particular localities in which they build up intimate knowledge of large home-ranges (that may include systematic avoidance of areas with numerous predators and competitors).

NATURAL HISTORY Anatomy, ecological dispersal patterns, modes of communication and social structures have probably been influenced by an ancestral 'desert ordeal.' Young animals are exceptionally social and active. They spend much time playing or rushing around, with stylised gaits, horning objects or mock-fighting.

ADAPTATIONS Horse-like antelopes are unusual in that the females have horns as long as those of the males. Female social units tend to have closed membership. Horns provide them with the means of excluding outsiders from scarce resources and resisting any attempt by males to limit their movement or threaten their offspring.

■ ROAN ANTELOPE *Hippotragus equinus*

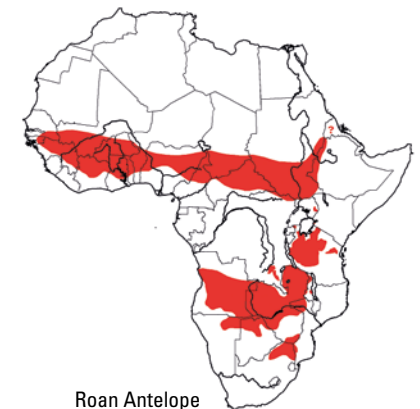
OTHER NAMES Fr. *Rouanne*, *Hippotrague*.

Ger. *Pferdeantilope*. Swah. *Korongo*.

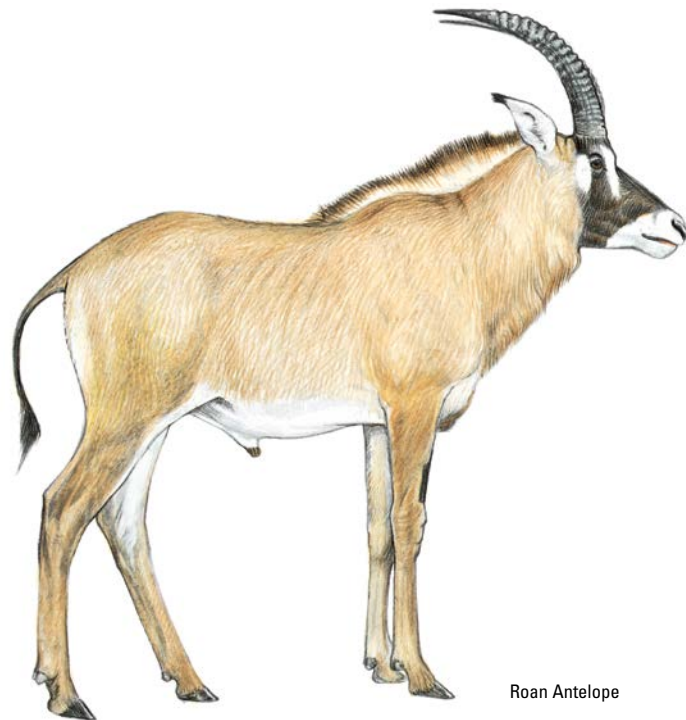
MEASUREMENTS HB 1.9–2.4m. T 370–480mm.

Sh. ht 1.26–1.45m. W 223–280kg (♀), 242–300kg (♂).

RECOGNITION A tall, powerful antelope with a thick neck, robust muzzle, long, droop-tipped ears, and massive, arched horns (500–1,000mm in males). The hooves are large (with pungent interdigital glands) and the false hooves are prominent. The coat is very coarse, becoming shaggy on the throat; hairs on the upright mane are dark-tipped. The face pattern varies individually but also regionally (the dark markings are more extensive in the north, the light ones in the south). Body colour is also subject to both individual and regional variation (from greyish in the south, more tawny in the north, to reddish in



Roan Antelope



Roan Antelope

the moister parts of its range). Tail lashes, earflaps and the penis of the male are all made more conspicuous by dark tips.

GEOGRAPHIC VARIATION Two main populations, provisional subdivision as follows. Northern savannas: *H. equinus koba* (Senegal to Nigeria), *H. equinus bakeri* (Chad to Ethiopia): reddish in south, i.e. *charicus* type. Southern savannas: *H. equinus equinus* (southern Africa), *H. equinus langheldi* (East Africa), *H. equinus cottoni* (central Africa).

DISTRIBUTION Formerly very widespread in northern savannas and woodlands and in the more westerly parts of the southern savannas. Largely absent from the eastern seaboard and its hinterland. They once ranged from Sahelian steppe (but only within reach of water) and flat floodplains through various woodland and savanna types to montane and plateau grasslands up to 2,400m.

HABITAT Roan Antelope habitats are definable less by the exact composition of plants than by the scarcity of other herbivores. Even within very diverse communities of herbivores, Roans prefer localities in which there are few competitors and carnivores. In many areas they have distinct wet- and dry-season ranges, dispersing in the former and concentrating in the latter. Areas of a few square kilometres are grazed intensively for weeks or even months but overall ranges in South Africa have been estimated at 60–120km². In Tanzania a herd of 14 animals was seen to inhabit an area of 12km² over a period of 17 years. Roans prefer grasslands with few trees, park-like savannas and mosaics where there are clumps of trees or woodland margins in which shade and quiet resting places can easily be found. Although predators might be an ultimate factor deterring Roan Antelopes from certain areas, they are not entirely passive and have been seen to face-off and threaten approaching Lions and African Wild Dogs on a number of occasions.

FOOD Grazers of medium to short grasses belonging to dominant species, such as Red Oat Grass (*Themeda triandra*), thatch grass (*Hyparrhenia*) and couch grass (*Digitaria*). Roans occasionally browse shrubs or herbs and pick up *Acacia* pods in the dry season. They drink regularly.

BEHAVIOUR Herds totalling 5–35 animals (average about 10) are made up of females and their young attended by a single adult male who excludes other males. Such groups circulate through

a well-known and mainly exclusive home-range but may converge temporarily on a pasture that is shared with other Roans while grazing. Such aggregations are rare and both individuals within herds and separate herds maintain a distance between one another. When adult males meet they strut in 'proud' lateral circuits before bounding forward, dropping on their knees as they clash their horns violently together. Submission is signalled by lowered head, concealed tail and mute, open mouth. Extreme submission may lead to crouching flat on the ground. Young animals within a herd associate very closely (and are sometimes left on their own).

Breeding takes place throughout the year but births are rare in the dry season. The gestation period is about 280 days. Births take place in seclusion and the mother returns to the herd within a week. Once the young can keep up it also emerges from hiding and joins the herd. Young Roan are a focus of attention and attraction not only from the mother but also from all other immature animals. Suckling lasts 4–6 months. Sexual maturity is reached by 2 years in females while males are expelled from their maternal group at about 3 years, spending the next 3 years in a peripheral 'bachelor' group (of up to ten young males) before winning an apparently permanent or semi-permanent association with a female herd. Roans are known to live for up to 17 years.

ADAPTATIONS The Roan Antelope derives from a giant species that is widespread in East and southern African fossil deposits. Although latterly both existed contemporaneously, the giant form has a longer history (going back at least 2 million years). The Roan's behaviour and ecological niche (e.g. a slow gait of less than 60kph, water dependence and occupation of extensive home-ranges) may be conservative characteristics appropriate to very large antelopes.

STATUS In spite of their extensive distribution, Roan Antelopes have seen a substantial contraction in range and numbers during the past century. The main threat has come from ever expanding livestock usurping their water and pasture. Their close attachment to localities and routines is linked with a very poor ability to colonise or recolonise. Their absence down the eastern littoral could be due to past depredations of disease and/or large human populations (before historic records). Although Roans are close to extinction in Mauritania, Niger, Uganda, Rwanda and Kenya, their overall status is not yet endangered (IUCN).

■ SABLE ANTELOPE *Hippotragus niger*

OTHER NAMES Fr. *Hippotrague noir*.

Ger. *Rappervantilope*. Swah. *Mbarapi, Palahala*.

MEASUREMENTS HB 1.90–2.55m. T 400–750m.

Sh. ht 1.17–1.43m. W 190–230kg (♀), 200–270kg (♂).

RECOGNITION A large, strongly built antelope with a thick neck, long, narrow muzzle, pointed ears, vestigial face glands, large, compact hooves and a longish, tufted tail. The Sable Antelope is celebrated for its magnificent, arched horns, which commonly exceed 1m in length and reach over 1.6m in the Angolan Giant Sable. The upright mane reaches to behind the shoulders. The coat is short and glossy in the tropics but grows longer in the south (and during the winter in captivity). Infants are dun-coloured and almost without markings. Older juveniles and young adults are rich russet, with white-striped muzzle and ears, belly and inner surfaces of the hindlegs. As males mature black tints on the face, flanks and shoulders begin to suffuse the red until, by 5 years (but for the white face pattern and underparts), they are black. Females of the southernmost population also turn black. In other populations females blacken more slowly and less completely.

GEOGRAPHIC VARIATION Southern or Black Sable, *H. n. niger* (south of the R. Zambezi); Miombo or Common Sable, *H. n. kirkii* (R. Zambezi to W Tanzania); Zanj Sable, *H. n. roosevelti* (East African littoral, north of R. Zambezi); Giant Sable, *H. n. variiani* (Angolan).

DISTRIBUTION Scattered through the central and eastern parts of the miombo (*Brachystegia*) woodlands, with an isolated population in Angola.

HABITAT Miombo (*Brachystegia*) woodland. In fact they are not wholly confined to the woods, living there from about October–May and shifting out as these well-drained and seasonally burnt



Sable Antelope



woodlands begin to dry out. They gather closer to permanent water, in valley-bottom grasslands, or mbugas, for the dry season. Here they have firm ground under foot and can exploit seasonal grassy mosaics (many created by local fires) but still remain close to the woodland–grassland edges. Such shifts may involve a few kilometres in richer more dissected landscapes or a wholesale seasonal shift in more impoverished ones. Estimates of the extent of home-ranges exceed 300km² in the latter situation and only 10–25km² in the former.

FOOD New grass growth or grasses of medium height belonging to locally dominant types are preferred. Well before the rains begin Sable Antelopes leave the valley bottoms (like horses they avoid deep mud if they can) and greatly increase the normally small proportion of woody foliage in their diet. Arrival of the rains and regrowth of the thin woodland grasses follow the temporary flush of leaves. This is a time of maximum dispersal in which small groups constantly rotate their pastures.

BEHAVIOUR Females form regional ‘clans’ of fewer than 100 animals that readily divide up into subgroups of unstable membership. The fission of these subgroups (about 10–30 animals) may range from a few hours up to a month or more. Longer periods apart eventually lead to the formation of separate clans. In spite of overlaps in their home-ranges, females from different clans are hostile to one another when they meet. Adult males sometimes follow these herds during their movements (a pattern typical of Roan Antelopes and oryxes) but the majority disperse themselves over the available pastures and control territories with boundaries that tend to coincide with rivers, forest margins, banks (or even roads). Here the males makes very vigorous attempts to detain any herd that passes through, persistently and very fiercely driving them back towards the centre of each territory. During the period they are kept there all adult females are inspected and oestrous females are mounted. Copulation is achieved in a matter of seconds, with a sudden bipedal lunge after long-

drawn-out preliminaries, including much chasing, testing, nudging and kicking. Breeding peaks occur but seem to have more to do with poorly understood social dynamics than with seasons. Gestation lasts 240–280 days. The sandy-coloured calf stays concealed for some 3 weeks and then joins the other youngsters in the mother’s group. It only seeks out its mother for milk but will call her with a high, piping call when lost. Males are driven out into ‘bachelor’ groups at about 3 years, joining 2–20 other young males. Females usually have their first calf after they reach 3 years old. Sables are known to live for 17 years.

ADAPTATIONS Sable Antelopes are secondarily territorial. One indication of their nomadic, open-country origins is the male’s reliance on visual self-advertisement. Unlike other woodland and forest antelopes scent-marks are subordinate to the male Sable’s posturings and direct herding of the females. Black colouring is both the mark of super-seniority in the colour-coded hierarchy of the female herd and also the central beacon of a defended territory. Battered bushes, dung piles and foot-scraps in the centre of a 3 or 4km² territory may help deter other males but it is the imposition of male physical presence that dominates both hierarchy and territory.

STATUS The Giant Sable is rated as vulnerable. The Shimba population is rated as endangered and in South Africa it is rated as rare (IUCN). Elsewhere expansion of the livestock industry is forcing Sables into steep decline but they are not endangered (yet).

■ SCIMITAR-HORNED ORYX

Oryx dammah

OTHER NAMES Scimitar Oryx. Fr. *Oryx algazelle*. Ger. *Sabelantilope*.

MEASUREMENTS HB 1.90–2.20m. T 450–60mm. Sh. ht 1.10–1.25m. W 135–140kg.

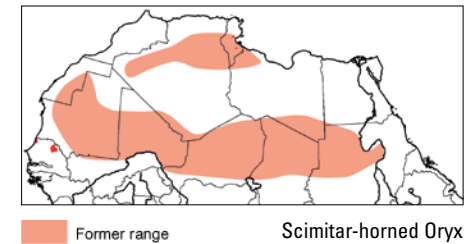
RECOGNITION A large, rotund antelope with a deep chest and relatively short, sturdy legs with broad hooves and prominent false hooves. The face is long with medium-sized ears and, unlike other oryxes, it has vestigial preorbital glands. Its horns are very long, slender and arched (1.00–1.15m), with many fine annulations. The tail is long and bushy. The vestiges of a structured pattern show up as pale apricot-brown tints on a predominantly white animal. Faint facial stripes run down the nose, cheeks and ‘through’ the eyes. The flanks and rump are also faintly striped or tinted while neck and shoulders look as though they are deeply stained with rust.

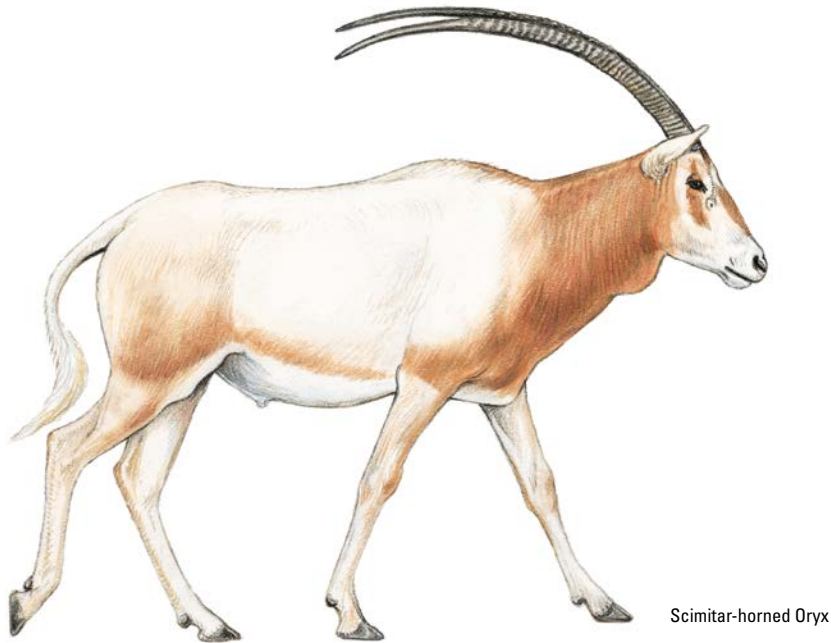
DISTRIBUTION Formerly from Morocco to Egypt and from Mauritania to Sudan along the interface between true desert and less arid Sahelian or Mediterranean habitats under an annual rainfall of between 75 and 150mm. Having originally ranged over more than 4 million km² it is now extinct in the wild.

HABITAT Semi-desert grasslands of the Sahel and their N Saharan equivalent. *Acacia*, *Commiphora* and Heglig (*Balanites*) growing in moisture-retaining troughs between dunes and outcroppings provided some woody cover and thin shade but it was flushes of grass that drew the nomadic oryxes back and forth across unknown distances. How far they travelled in order to take advantage of desert flushes was indicated by a single aggregation of 10,000 animals seen in Chad in 1936. An authoritative estimate of typical density suggests one oryx for every 40km² of desert habitat. At such a density the reservoir for this gathering was 400,000km², with the most distant animals coming in from about 300km away. This suggests that the potential range of an oryx group under every extremity might be in the order of 100,000km². The implications for their ability to orient as well as their stamina in a waterless desert are obvious.

FOOD Mostly grasses but herbs, shrubs, pods and fruits have been reported.

BEHAVIOUR The Scimitar-horned Oryx was nearly always seen in herds of 10 or more and it was capable of aggregating and dispersing in response to its very ephemeral pastures. Its reluctance to remain solitary was evident in the observed attachment of old males to parties of Dama Gazelles. While known to be opportunistic breeders, the oryxes were reported to have extended birth peaks around March and October. With a gestation of 242–256 days matings would have peaked at the end of winter and during the first rains. Birthing mothers sought a brief seclusion but both mother and baby rejoined the group within hours (some indication of the imperative to keep mobile at all times). Captive animals have lived for 17 years.





Scimitar-horned Oryx

ADAPTATIONS The almost white colouring of the Scimitar-horned Oryx is highly visible from a great distance. If its behaviour resembles that of the even whiter Arabian Oryx, then this colouring can be assumed to have helped 'lost' individuals to regain contact with the group. By standing on the top of a dune an individual would be able to see and be seen by other oryxes from a long way off.

STATUS One aspect in the decline of this species is the fact that it presents an easy standing target. However, given that the N Saharan populations became extinct hundreds of years ago, it seems likely that its decline may also have ecological causes. The most obvious is disruption and competition from expanding populations of domestic stock. It is now extinct in all Saharan nations but has been reintroduced to fenced parks in Tunisia, Senegal and Morocco. Conservation remains a low priority for all Saharan nations. This species was rated as critically endangered (IUCN) but is now extinct in the wild.

■ BEISA ORYX *Oryx beisa*

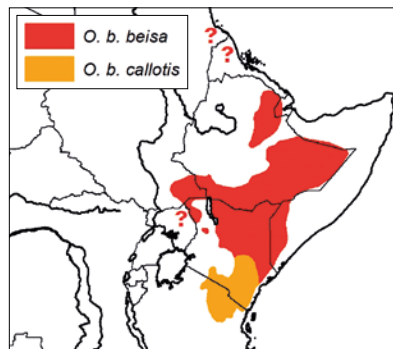
OTHER NAMES Fringe-eared Oryx. Fr. *Oryx beisa*.

Ger. *Beisa spießbock*. Swah. *Choroa*, *Bara bara*.

MEASUREMENTS HB 1.53–1.70m. T 450–500mm.

Sh. ht 1.1–1.2m. W 116–188kg (♀), 167–209kg (♂).

RECOGNITION A large, compact, muscular antelope with a thick neck, long face, long straight horns and distinctively shaped and patterned ears. The longish tail terminates in a black brush. Strong but slender legs terminate in large, very black hooves (and false hooves that are given extra visual emphasis by emerging from black tufts of hair). The brownish-grey coat is demarcated from black-and-white facial, flank and foreleg patterns. The line of the back-swept straight horns (600–1,100mm) continues right across the face in the form of a black stripe. Superficially there is very little difference between males and females.



Beisa Oryx

GEOGRAPHIC VARIATION Beisa Oryx, *O. b. beisa* (north of the R. Tana); Fringe-eared Oryx, *O. b. callotis* (south of R. Tana).

DISTRIBUTION The Horn of Africa from the Red Sea littoral (Haddendowa) to Somalia and south to arid central Tanzania. Their most westerly limit is Jebel Lafon in South Sudan and Karamoja in NE Uganda. Some parts of their range have up to 250mm annual rainfall, more humid than for any other oryx. The Southern Oryx, or Gemsbok, of the Kalahari is a close relative, often classed as the same species.

HABITAT These oryxes inhabit arid grasslands and bushland but avoid tall grass in the rains (and thick bush in the dry season). Both grazing and the condition of the ground underfoot influence seasonal movements. They move out of waterlogged or soft-soiled depressions during the rains up onto higher ground but may return in regular cycles of movement. In the driest parts of their range movement is less regular and large numbers gather or disperse unpredictably. Densities vary greatly, with up to 1.4 per km² in the choicest localities. Home ranges of 200–300km² have been recorded for females and 150–200km² for adult males.

FOOD Grasses, but will browse *Acacia* and other shrubs in the absence of grass, especially during the dry season. During droughts they dig out tubers and roots with their hooves for moisture. Where water is available they drink regularly but can do without, having a lower rate of water turnover than a camel.

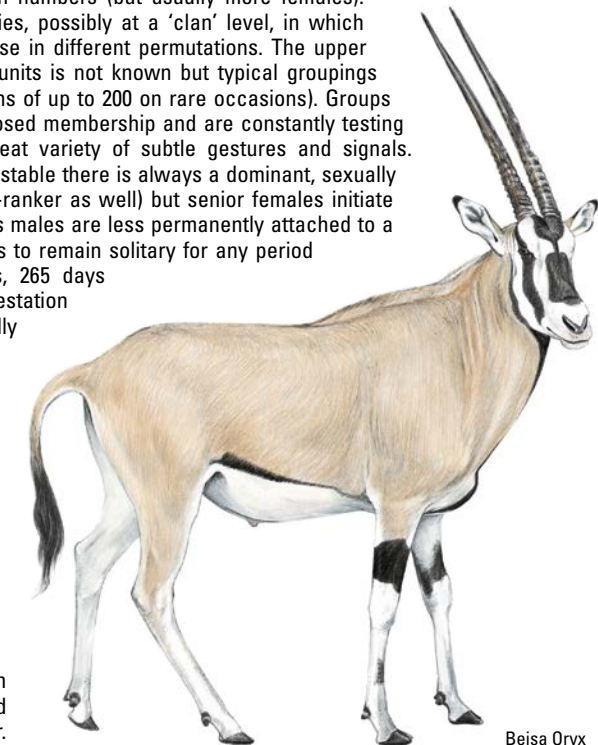
BEHAVIOUR Mixed herds are formed in which the sexes are sometimes equally balanced in numbers (but usually more females).

Both sexes establish hierarchies, possibly at a 'clan' level, in which subunits can join up or disperse in different permutations. The upper limit of such local population units is not known but typical groupings can reach 60 (with aggregations of up to 200 on rare occasions). Groups probably have more or less closed membership and are constantly testing or asserting status with a great variety of subtle gestures and signals. Where herds remain relatively stable there is always a dominant, sexually active male (usually a second-ranker as well) but senior females initiate and lead movement. As a class males are less permanently attached to a group and are the only animals to remain solitary for any period of time. Of several estimates, 265 days appears the most likely gestation period. Breeding is not normally seasonal but occasional crops of synchronised births have been reported. Calves lie up for very variable periods (between 2 and 6 weeks). They join other young to form peer groups and may stay together up to a year. They become fertile by 18–24 months and have survived for 22 years in captivity.

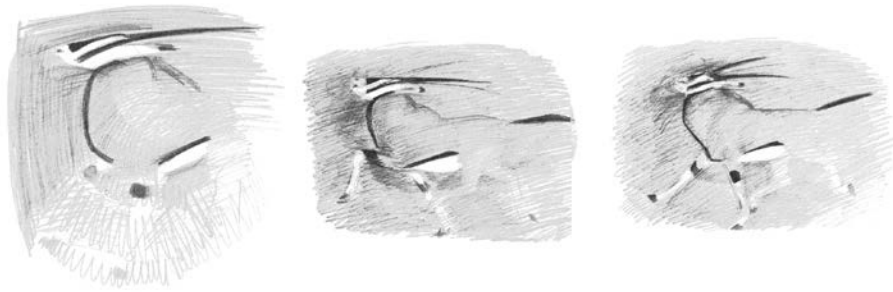
ADAPTATIONS Beisa Oryxes indulge in ritualised 'tournaments' the function of which appears to be the testing and reinforcement of rank order.



Beisa Oryx in subordinate head-low posture.



Beisa Oryx



Black-and-white signals of Beisa Oryx flagged during a tournament display.

Commonly seen at dawn or during a shower these start with one or more animals running in broad circles. A galloping spurt builds up the momentum to permit a long, high-stepping, 'floating' pace in which the neck is bunched, chin raised and the head swung from side to side in rhythm with the pace. The black-and-white head flashes in time with the high-stepping knees and flying hooves. Because the most frequent and active participants are juvenile or young animals, this performance may be a primary way of learning and exploring social position. It is also possible that there is a spatial dimension and that the runner is learning to 'take a fix' that reinforces its memory of the home-range.

STATUS This species is known to have declined, especially in its marginal ranges in Sudan, Uganda, Tanzania and most especially in Somalia and Uganda, where its formerly extensive range is reduced to fragments and it is in imminent danger of extinction. Its range is being progressively usurped by livestock. Elsewhere it is in decline but not yet endangered.

■ SOUTHERN ORYX *Oryx gazella*

OTHER NAMES Gemsbok. Fr. *Gemsbok*.

Ger. *Südafrikanischer Spießbock*.

MEASUREMENTS HB 1.80–1.95m. T 400–470mm.

Sh. ht 1.17–1.38m. W 180–225kg (♀), 180–240kg (♂).

RECOGNITION A large, very thick-necked antelope with long, straight horns (600–1,200mm) aligned with the muzzle, large, rounded ears and a long, bushy black tail. White muzzle, face-stripes, belly and 'stockings' contrast in every instance with bold black markings on the face, flanks, upper legs, midline and rump. Like other oryxes, the neck and shoulders are enveloped in exceptionally thick, inelastic and dense skin. This gives adult bulls a rather 'jacketed' appearance.

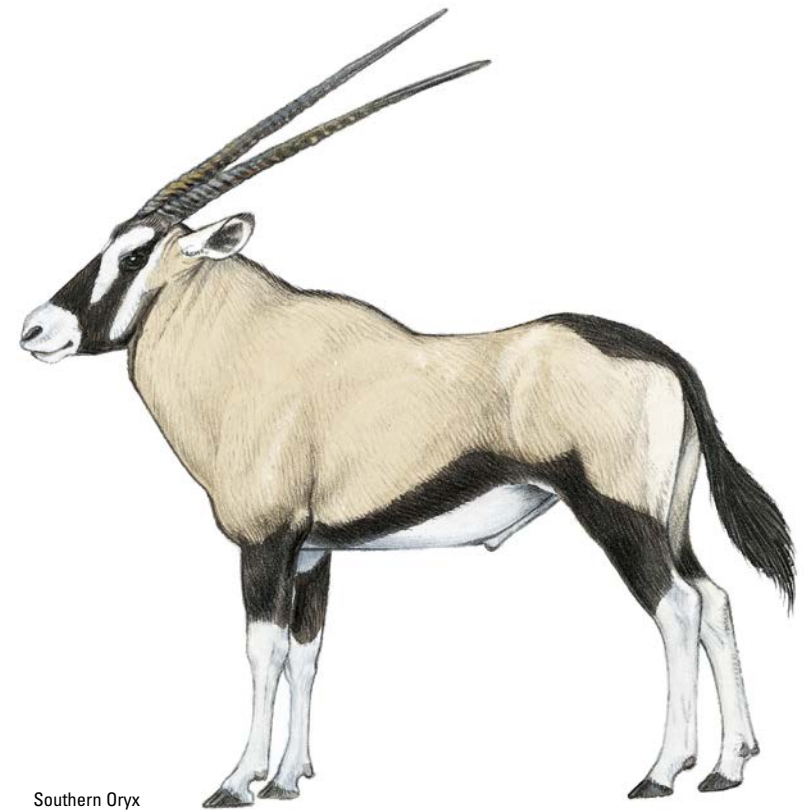
GEOGRAPHIC VARIATION Nine subspecies, none valid, but Angolan animals have narrower black markings.

DISTRIBUTION A Kalahari desert species that formerly ranged from the Karoo to near Benguela and from the Atlantic littoral to the upper Zambezi valley and W Transvaal. Exterminated from most of its South African range. It lives under an annual rainfall of 50–250mm.

HABITAT Wooded grasslands and *Acacia* bush of the central Kalahari and Karoo shrublands, entering wetter grasslands and bush along the margins of its main range. Its extensive distribution includes areas of very variable fertility and rainfall, with pastures permanent in some places, ephemeral in others. As a result, home-ranges vary from about 4km² to 400km². Female ranges, shared with other travelling companions, are always much larger than those of single males, which may centre on a particular locality for a long period. Animals are known to follow regular circuits between favourite localities where they may spend many weeks on small pastures. Their presence in such places may be marked by regularly used 'scoops' (for resting or ruminating in), pathways and neat little piles of excreta carefully placed by squatting males on bare pans or prominences.



Southern Oryx



Southern Oryx

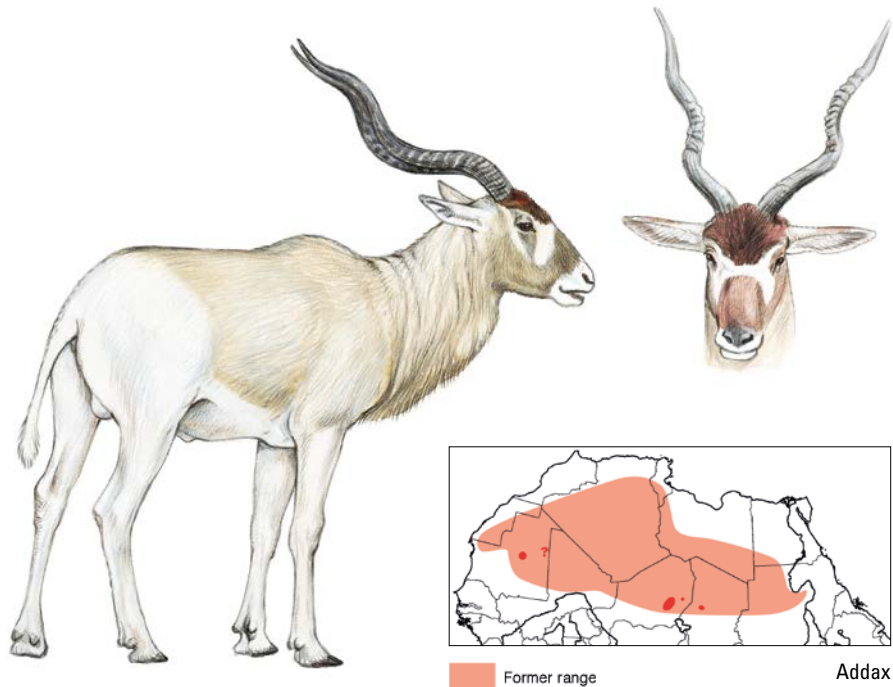
Seasonal and regional differences in the quality of their range are reflected in thick fat deposits under the skin and visible changes in their physical condition.

FOOD A grazer that will turn to browse or herbs in the absence of grass. It digs up tubers and roots for moisture and, in spite of being able to go without water, will go on long treks in order to find it and will dig deeply in dry riverbeds. Males will fight for access to water as well as to females. It regularly visits salt-licks.

BEHAVIOUR Although most female groups are nomadic and many males remain attached or in attendance, other, mostly old, males become much more sedentary. In Etosha NP, where year-round grass-growth can support them, a scatter of resident males may be less than 1km apart (behaving rather like Sable Antelopes in taking an interest in passing females). Female groups number up to 50 but occasionally aggregations of 400 or so have been seen. Breeding is not seasonal and one young is born after a 264-day gestation. Hiding places change frequently but newborn young remain concealed for 3–6 weeks. Animals mature at about 2 years and young males may remain in their mother's group for at least a year. They live for about 20 years.

ADAPTATIONS An observer with experience of all oryx species has noted that low-level aggressive behaviour is more sustained and continuous in this species than in other oryx populations. Such interactions involve threat displays, horn gestures, butting, circling and parallel-walking as well as outright fighting. Corresponding appeasement gestures are equally common; head-bowing, chin-lifting, head-throwing and bent-leg creeping are all directed at dominant individuals. Its very strong markings may enhance the semaphore of the Southern Oryx's intense social life.

STATUS In spite of great contraction of range, the Southern Oryx is well represented in major national parks as well as being tolerated in some of the large enclosures that now subdivide its former range. It is not endangered.



■ ADDAX *Addax nasomaculatus*

OTHER NAMES Fr. *Addax*. Ger. *Mendesantilope*.

MEASUREMENTS HB 1.20–1.75m. T 270–350mm. Sh. ht 0.95–1.15m. W 60–90kg (♀), 100–135kg (♂).

RECOGNITION A stocky, almost white antelope with long, annulated horns following loose spirals. The blunt, narrow head has a chocolate-brown tuft on the forehead, a paler-brown muzzle and eye-patches, a white face-mask, narrow ears and a short brownish fringe of hair down the throat. The broad, spatulate hooves have protruding false hooves and interdigital glands. Sexes differ very little in size and morphology.

DISTRIBUTION Formerly from the Atlantic to the Nile in the central Saharan desert; now extinct except for vestigial pockets in Niger, Chad and Mauritania, and possibly in Mali. Migrations in pursuit of seasonal flushes once brought Addaxes together in herds in excess of 1,000 animals.

HABITAT Sand-dune deserts (erg) and, formerly, clay-gravel plains (reg) and stony plateaus (hammada). The Addax is principally active at night and at dawn and dusk, resting up during the heat of the day.

FOOD Coarse desert grasses, but with distinct seasonal preferences. *Stipagrostis vulnerans*, *Panicum*, *Tribulus* and Drinn (*Aristida pungens*) were known staples. When grasses were absent the Addax browsed *Acacia* foliage and leguminous herbs, such as *Indigofera*. It was able to extract moisture from its food plants so effectively that one of the incentives for Saharan nomads to kill the Addax was to extract the copious water in its rumen.

BEHAVIOUR Formerly the Addax tended to travel in groups of 2–20 animals, sometimes aggregating in larger groups, very occasionally in hordes of many hundreds. Its movements within the Sahara tended to be longitudinal (oryxes reputedly made more latitudinal shifts). Groups were usually mixed but males would leave small piles of pellets (like oryxes) while females scattered their dung. Two birth peaks (autumn and late winter) were reported, suggesting that mating took place 8 months earlier during the coldest and hottest months of the year (but in each case at a time when there might have been movement and aggregations). Females mature at 18 months, males before they are 3 years old. Captive animals have lived for 19 years.

STATUS It is some measure of human penetration of the Sahara that this animal has been exterminated from a range of some 8 million km². At about the turn of the 20th century, in Ouargla

(the main Algerian city beside the great Eastern Sand Desert), fresh Addax meat was sold every week in the market. In less than a century, mounted or motorised hunters with modern firearms, together with expanding pastoral agriculture, have wiped out a species that has survived the vicissitudes of a desert environment for several million years. Critically endangered in Mauritania, Niger and Chad; extinct elsewhere.

SHEEP AND GOATS Caprini

Barbary Sheep	<i>Ammotragus lervia</i>
Nubian Ibex	<i>Capra ibex</i>
Walia Ibex	<i>Capra walie</i>

Mostly medium-sized, thick-legged, compact antelopes with limbs and hooves modified for climbing and leaping over rough or stony ground. Both sexes are horned but males have enormous arched or spiral horns. Scent glands are well developed and vary in site from species to species. All three African species have them between their hooves and on the underside of the tail.

As a distinctive Eurasian offshoot of the mainly African antelopes, the caprines may have diverged some 18 mya (while still resembling gazelles). In dentition and diet they have mostly remained adaptable and generalised but they have a modified physiology, limbs and social behaviour in order to cope with extreme climates and difficult terrain. Sheep and goats are thought to have split about 6 mya (the Barbary Sheep's closest affinity is with the Arabian Tahr, *Arabitragus jayakari*). A 1.5 million-year-old Ethiopian fossil, *Bouria anngettyae*, resembles an intermediate form, and late Pleistocene fossils of Barbary Sheep are numerous across northern Africa. By contrast, the ibex is an advanced type of goat and a more recent coloniser of Africa.

Evolving in Eurasia, caprines were restricted by the prior occupation of most richer habitats by deer. Their own exclusion of deer from extreme habitats in mountains may have derived from an early superiority under extremes of temperature and from their agility on broken ground. The N African mountains are a minor extension of the great mountain chains of Eurasia in which goat-antelopes evolved. Here they exploit unstable, seasonally variable pastures in relatively inaccessible terrain.

Within their restricted fastnesses, caprines are the most successful herbivores. Reaching high densities (especially in Asia), intense competition for mates among males has led to the evolution of very large horns in all the more advanced forms. Less specialised, small-horned species live in tropical Asian forests. Domestic species derive from non-African populations.

■ BARBARY SHEEP

Ammotragus lervia

OTHER NAMES Aoudad. Arui.

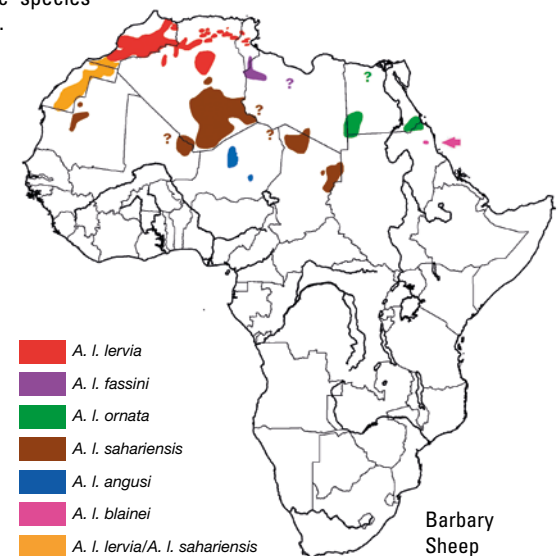
Fr. *Mouflon à manchettes*.

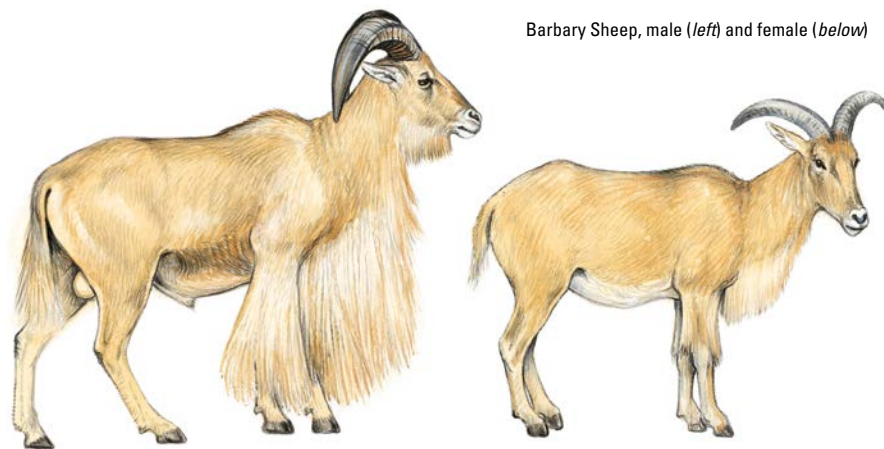
Ger. *Mähnenschaf*.

MEASUREMENTS HB 1.30–1.65m.

T 150–250mm. Sh. ht 750–900mm (♀); 0.90–1.0m (♂). W 40–55kg (♀), 100–140kg (♂).

RECOGNITION A heavily built, thick, short-legged animal that is intermediate between a sheep and a goat. It has outward-arching horns which are slender and rounded in females, thick, ridged and much longer in males (which have twice the body weight of females). The face is long and tapered, ears small and the white mouth-parts contrast





Barbary Sheep, male (left) and female (below)

with the pale tawny-brown coat colour. The fleece is woolly in winter, with a harsh texture, but moults to a sleek summer coat. Both sexes have tufts of hair on the upper foreleg and a hanging fringe down the throat but those of the males are denser and longer (almost reaching the ground). The short tail, naked below, like a goat's, has scent glands that are especially well developed in the male.

GEOGRAPHIC VARIATION *A. lervia* (Morocco to Tunisia), *A. l. fasini* (Hamra plateau, NW Libya), *A. l. ornata* (Egypt east of the Nile, and formerly in the Western Desert), *A. l. sahariensis* (Mauritania, Mali, C and S Algeria, and N Chad), *A. l. angusi* (Air Massif and Termit Massif, Niger), *A. l. blainei* (E Sudan).

DISTRIBUTION Sahara massifs and plateaus, originally from central Mauritania to the Hamra plateau in Libya and from the Algeria/Niger border area to Darfur in W Sudan. An isolated population occupied the Red Sea hills in Egypt and was reputed to have once ranged through Sinai.

HABITAT Desert hills and mountains, stony plateaus (hammada) and the slopes of valleys (wadis) well away from mountains. They avoid the sand deserts (ergs), which seem to have acted as barriers between regional populations. They prefer habitats with a choice of shady day-time retreats, either caves, rock overhangs or under trees, but at night will graze plains that are at some distance from any cover.

FOOD Grass and herbs; also browse shrubs and trees and will even get up onto their hindlegs in order to reach foliage. Barbary Sheep prefer to feed at dusk, dawn and during the night. They will drink water but can go without, extracting it from plants that become temporarily moister or are dewed at night.

BEHAVIOUR Barbary Sheep form small family parties in which a single adult male attends several females and their offspring. These tend to remain scattered but have been reported to gather into larger parties (i.e. 30 members) late in the dry season (July). A rut is thought to take place after the autumn rains (October) and births follow a gestation of 150–165 days. One or two young are born in a secluded site where mother and young lie up for a few days before rejoining their group. Females mature in about 18 months and captive specimens have been known to live for 24 years.

ADAPTATIONS Magnificent tassels on the forequarters of males are part of their intimidatory displays when competing for access to females.

STATUS It has taken centuries of expanding settlement and uncontrolled hunting to eliminate Barbary Sheep from most of their North African range. Competition and disturbance from livestock are probably the major causes of decline but hunting (with dogs and rifles) may have tipped the balance in some areas. Their meat has been reported to be a routine commodity on market stalls in Algerian and Moroccan towns and villages for nearly 100 years. In recent times military and oil-field personnel have used helicopters to reach their more remote haunts. The Barbary Sheep is now doing well on many ranches and reserves in the southern USA. In Africa it is vulnerable over all parts of its range.

■ NUBIAN IBEX *Capra nubiana*

OTHER NAMES Fr. *Bouquetin de Nubie*.

Ger. *Nubischer Steinbock*.

MEASUREMENTS HB 92–160cm. T 6.5–17cm.

Sh. ht 65–110cm (♀), 0.75–1.1m (♂). W 50–125kg.

Note: Nubian Ibexes average 80mm shorter and about 22kg lighter than *Walia Ibexes*.

RECOGNITION Close relatives of the domestic goat, ibexes have gone furthest in developing short, muscular limbs and chunky, rubbery hooves. Of all goats, male ibexes have developed the longest and most heavily reinforced horns (1.0–1.19m). They have short ears, a beard on the chin and a mane from nape to tail. The tail is short and secretes scent from glands on its lower surface. There are vestigial stripes on the face, flanks and thighs. The underside and inner limbs are white or cream, with white hock and knee patches. The Nubian Ibex is various shades of slaty brown.

GEOGRAPHIC VARIATION Ibexes comprise a mainly Eurasian superspecies with various forms in Europe and the Middle East. Nubian Ibex and *Walia Ibex* are now considered to be separate monotypic species but were previously united in *C. ibex*.

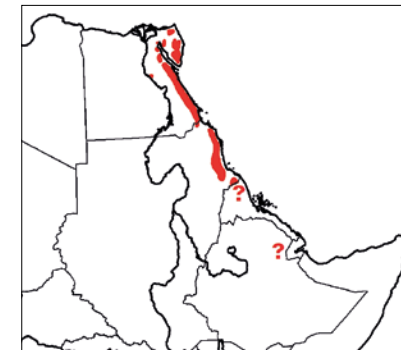
DISTRIBUTION The Nubian Ibex formerly ranged throughout the more hilly parts of Arabia, the Middle East and NE Africa, but today, in Africa, exists mainly as isolated populations in the Red Sea littoral hills of Egypt and Sudan, from Suez to Massawa. There are no recent records from Eritrea.

HABITAT Rocky mountains, gorges, outcrops and loose stony scree in areas with a sparse cover of trees, scrub and grass.

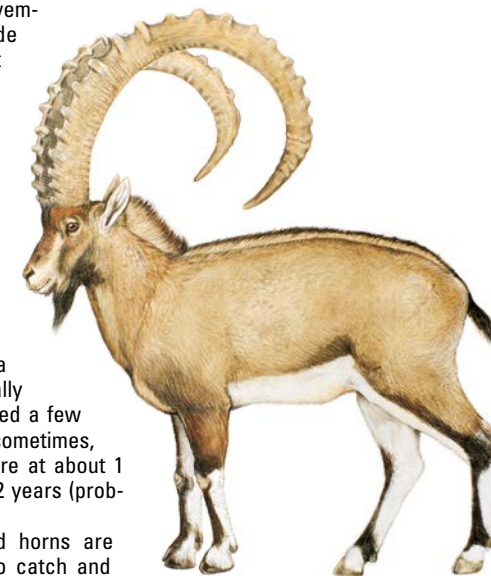
FOOD Grass is grazed but main food plants are herbs, shrubs and trees. Leaves, buds, fruits and, in some cases, bark and flowers are eaten from a wide range of desert and montane plants. A special liking for the foliage of *Cadaba* and *Pluchea* has been noted.

BEHAVIOUR Nubian Ibex live in confined ranges of a few km², or less. Females may be briefly on their own to give birth but normally have a loose association with other well-known females sharing the home-range. Females defend their young and fight strange male ibexes. Males lead an independent existence until the rut (between September and November) when dominant males seek to exclude all other males from oestrous females. At this time they eat little, fight and chase much, and suffer a marked deterioration in condition. Courtship involves a crouching approach, tongue-flicking, much wagging of the scented tail, urine-squirting onto chest and chin (the main function of the beard being scent-dispensing). The male also hisses, grunts and kicks; the combined impact of a barrage of sounds, scents and touches may both speed up oestrus and improve the female's receptivity. After a gestation of 150–165 days one, occasionally two, kids are born. They remain concealed a few days before joining their mother (also, sometimes, siblings of up to 3 years). Sexually mature at about 1 year; they are thought to live for about 12 years (probably more).

ADAPTATIONS The huge, knobbly, arched horns are designed to batter rivals in fights and to catch and



Nubian Ibex



absorb the blows of opponents. Contestants vie for more elevated points from which to leap up and accelerate down onto the defender. These contests begin from standing positions no more than a couple of metres apart but they generate enormous forces and must give each fighter an accurate, if sometimes stunning, measure of his opponent's strength.

STATUS The species as a whole is rated by IUCN as vulnerable, but populations in Egypt and Sudan should be considered as endangered. Competition with livestock and hunting are the major threats.

■ WALIA IBEX *Capra waliae*

OTHER NAMES Fr. *Bouquetin d'Ethiopie (Le Wali)*; Ger. *Aethiopischer Steinbock (Walia-Steinbock)*.

MEASUREMENTS HB 150–170cm. T 20–25cm. Sh. ht 90–110cm. W 80–125kg.

RECOGNITION The Walia Ibex has variable tints of russet on the upper limbs and trunk, with dark grey or black on face, neck, dorsal midline, tail and on lower flanks, shoulder and hindquarters. Black and cream patterning of the legs is inconspicuous. Striping on the face is muted by overall darkening. Horns resemble those of the Nubian Ibex but tend to have fewer knobs on their forward surfaces.

GEOGRAPHIC VARIATION None.

DISTRIBUTION The Simien Mts of northern Gondar, NW Ethiopia.

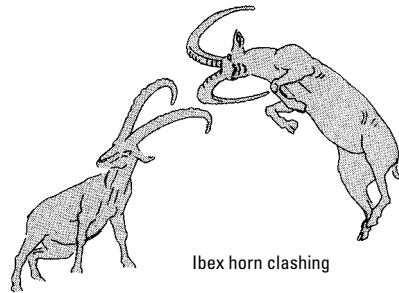
HABITAT Mostly above the timberline in the afroalpine and ericaceous zones, between 3000 and 4500m.

FOOD Similar to other goats, feeds on a variety of shrubs and herbs including *Lobelia* and *Erica* species.

BEHAVIOUR Similar to Nubian Ibex, but lived in a richer habitat before being displaced by livestock. Non-territorial. Groups tend to segregate by sex, but sexes mix during pronounced rutting peak between March and May.

ADAPTATIONS Able to traverse and inhabit very steep, arid, rocky terrain. Also withstands extreme cold.

STATUS Total surviving numbers of Walia Ibex have fluctuated between 150 and 750 individuals. Agricultural colonists of Simien National Park, together with their cattle, sheep and goats, have re-invaded the park in recent years, once again threatening the existence of one of Ethiopia's many emblematic endemics. It is urgent that the authorities reverse the irresponsible practices of recent Ethiopian governments and revive good conservation policies in this unique region of Africa.



Ibex horn clashing



Walia Ibex



Respect Africa

Africa is different. We now know, with absolute certainty, that the ecological matrix that is Africa provided that extraordinary cascade of opportunities that culminated in human beings. Africa is our mother-continent.

That makes conservation in Africa fundamentally different from conservation on any other continent. It is to Africa, to its animals, its plants, its landscapes and its succession of existential events, that we must turn to learn about humanity's natural history in all its subtlety, beauty and intelligence.

Respect for subtlety, beauty and intelligence was never a part of Africa's many oppressors and exploiters, past and present. Naked greed for commodities and a total lack of respect for the living fabric of life in Africa, plus deep ignorance, continues to drive events in Africa. Africa has suffered centuries of abuse by pre-colonial, colonial, post-colonial and home-grown despots, bribers, and bribees. The horrors of slavery were linked with plantation agriculture, and the ivory trade has fuelled the slaughter of millions of elephants. It has been said that the darkest thing about the dark continent has always been ignorance of it – ignorance, both cruel and proud, the ignorance of the powerful over the weak, the brutal over the talented, ignorance from within and from without. When it comes to the history and prehistory of humans in Africa the story of continuing ignorance looks more like a perverse conspiracy to silence curiosity itself.

From a conservation perspective, the deepest ignorance concerns the complex ecological interdependencies that have nurtured more than 1,000 mammal species, some 2,500 species of birds, and in South Africa alone, some 45,000 species of plants, around 16,000 of which are endemic to the Cape (for comparison, all of Europe has 12,500 plant species, 28% of which are endemic). Take almost any group of organisms: their diversity in Africa is exceptional. Historically the many natural wonders of the African continent, including its people and all their talents and knowledge, have had scant respect from slavers, colonisers and less obviously culpable powers.

New values emerging

In spite of a tragic history, there are brighter prospects too. To discover a new confidence, pride and respect for Africa and its nature, enter Africa's national parks, its universities and environmental organisations. Here, in the context of new educational institutions, reserves and intensive scientific research, we find the birth of a new and creative culture of environmental involvement. Africa's Naturalists have joined a world-wide web of like-minded people who share an emergent set of values that promise to become truly human, humane and potentially universal. It is also a culture founded upon respect for and action based upon probing analysis of the processes that underlie phenomena. Conservation is not simply about saving mammals or caring for forests. Nor do arguments from science, history, ethics, aesthetics and ecology provide the only rationales in support of it. The tourist industry in Africa is heavily dependent on large mammals as a major educational attraction. Tourism has generated many ancillary industries, including schools, and there is still great scope for investments in conservation and education on both a large and small scale.

Conservation societies and national institutions continue to grow in importance among the more progressive countries of Africa but visionary individuals are still crucial. Those who founded the great national parks and reserves fought real battles with bureaucracies and vested interests. In every case these protagonists were individuals whom we can name. Among Africa's most deserving heroes today are the conservators, wardens, scouts, teachers and researchers who often work under difficult conditions and sometimes live lonely lives. In the parks they care for, the increasing numbers of overseas visitors are actually but a tiny fraction of those who would come if only they had an idea of how much they were missing! Faced with the thrill of seeing Olduvai Gorge or the great fossil sites and living landscapes of South Africa and Ethiopia, scholars, citizens and tourists alike are beginning to travel way beyond glimpses of 'wildlife'. Witnessing such places challenges them to ask why and how our ancestors could have emerged as but one among so many African mammals. Within that quest for self-knowledge a new cultural value is emerging. It is a dawning realisation that the mysteries of human existence are rooted here, in Africa. To know yourself you must get to know Africa.

All modern societies are confronted by questions of values. Personal, communal, national, scientific, religious and material values all jostle for the political stage. Today the most compulsive value is the money you are offered for your work, talents, land, possessions or your captures. This is the value put upon a netted fish or a snared antelope in a market. A zoo-dealer, advertising the same animal in a catalogue, puts a price on every specimen – these are the values of the bazaar – but there are others.

Africa is rich – it is the rest of the World that is poor

The species listed in this guide have no price on them, but continents, countries or parks with the richest variety and greatest numbers are, in a real sense, 'biological millionaires'. On this count, Africa is the richest entity on this globe and North America one of its poorest. A quick flick through the maps in this guide will reveal that some countries are particularly rich while others, such as Algeria, Egypt and Sudan, have already squandered much of their biological inheritance; other countries under irresponsible leadership now look set to follow. Their large mammal populations have gone, are very small or have become totally extinct. Worse still, their people now have so little contact with nature and so little access to scientific education, especially biological knowledge, that the population at large becomes ever more intellectually, scientifically and environmentally impoverished. By contrast, countries like Kenya, Tanzania and Botswana are nurturing an attitude where knowledge and concern for the local environment, local geology, ecology and natural history are coming to be seen as integral to a relevant education and responsible citizenship. Conservation is providing dignified and prestigious livelihoods for sizeable and influential proportions of our citizenry. Income from conservation confers a practical dimension on science and science education in these countries as well as prestige, a situation that is much envied by scientists from less enlightened societies in Africa and elsewhere.

The texts and maps in this guide are a bit like balance sheets, in that we can see *which* species have been lost, stolen or mislaid (sometimes even by *whom*). Maps can show us *where* species have become locally extinct; maps can help alert local people and their governments to just how localised some species are and how uniquely rich some tiny localities are. There are unique centres of endemism, such as around Mongiro springs in Bwamba, Uganda (the only locality in the world to boast 16 species of primates within a 10km radius!), Mounts Oku and Kupe in Cameroon, Udzungwa in Tanzania, Aberdare in Kenya (it is a list that could go on and on).

The worst aspect of Africa's degradation is that it is being promoted by impoverished thinking emanating from continents with impoverished faunas. A typical African landscape easily supports 100 or more mammal species, 400 or 500 bird species and countless other organisms, often adding up to the highest biomasses known on planet Earth. That represents a huge potential for diverse harvests for future human benefit, which seems to have little relevance for the agribusinesses, advisers, 'aid' experts and politicians who are driving the wholesale degradation of Africa. Globally, 75 percent of all agricultural land is used by a handful of domesticated species: cattle, sheep and goats. At the present time that represents 30 percent of Earth's land surface. With ox-eating spreading to ever more ox-eating humans, much of Africa's surface is projected to be converted into giant beef-lots. Yet 'bushmeat' still commands premium prices because indigenous foods are sensed as superior. Of the massive investment that has gone into animal husbandry, effectively none has been spent on the potential for Africa to feed its own on its own resources. This is because the beef is mainly for export, while the 'experts' are mostly non-African imports.

Alerting people to what they are losing is not only a task for this guide, this essay and for the conservation community; there is a real potential for indigenous, rather than foreign, resources being developed within and for Africa. We can reflect on the cultures that have saved or lost their natural resources, especially when savers and losers are immediate neighbours – in general, Kenya has a history of trying to conserve while Somalia destroys. Those who see today's resources as something we borrow from our descendants must condemn the destroyers of once-flourishing mammal populations as thieves or pirates. If we imagine today's disappearing habitats as the subject of future criminal court cases with their destroyers on trial, those in the dock will be out-of-control militias, agribusinesses, the livestock industry, irresponsible or corrupt politicians, logging companies, their accomplices, commercial bushmeat traders and, of course, actual pirates. However, the ultimate blame lies with world appetites for commodities that evade responsibility for environmental costs so long as such goods remain cheap. Curbing the purveyors of such goods

and getting them to support, rather than subvert conservation are among the many dimensions of contemporary conservation in a continent that is unlike any other.

Some of yesterday's 'biological millionaires' are today's destitutes. So, are today's 'biological millionaires' in danger of becoming tomorrow's paupers? Take Tanzania, for example. It has Kilimanjaro, with its unique alpine environments, as well as an extraordinary spectrum of habitats, ranging from forests and swamps to semi-desert. The country's status as one of the most important conservation regions of the world depends upon formal protection for viable and representative samples of every one of these habitats (this a primary target for all national conservation programmes). One of these unique areas is its only 'Somali-arid' sample, a small reserve called Mkomazi. Livestock interests continue trying to wrest this area away from the nation's conservation estate, so far without success. Here a small cabal of cattle-men, with huge herds that they hope to enlarge, threaten a vital asset – the range and depth of Tanzania's biological wealth. They seek to invade a viable ecosystem and impoverish one of the world's most fortunate nations. This is a struggle being played out all over Africa with ever-increasing severity. It is a struggle that began early in the 20th century with formal gazetted reserves and parks for large mammals. Even then there were people who appreciated the exceptionalism of African fauna and the fact that disappearing mammal populations were clear indicators of wider ecological collapse. Even then conservation had influential opponents.

Learning in the light of nature's own rules

Since then conservation initiatives have greatly diversified and passed through many stages. Today there is more respect for and understanding of the ecological and evolutionary processes that govern all life on earth. Environmental bodies seek to maintain biological diversity, monitor quality and study natural processes. Indeed, comprehending how the planet's ecosystems work is not just a technical challenge; caring for nature in the light of its own rules has become an urgent new moral imperative, imposed on us by our own power over global environments.

In Africa there is the fundamental difference that these were the ecological communities that nurtured the entire course of human evolution. The need to learn, and learn and go on learning about our own history and pre-prehistory, adds practical self-interest and the need for numerous future research projects to the many other justifications for conservation in Africa.

Our self-interest derives from entirely new insights coming from contemporary science. The language of genes, DNA within our eggs and sperm, reveals an unbroken thread of ancestry going back to the beginnings of life on earth. Of that immensely long lineage the mammalian part is relatively small but much of it was spent in Africa. The human part was smaller still but it was shaped in communities of African mammals such as we see today.

Science is not only retrieving our history from fossils and flints, it is re-examining our physiology, our anatomy, our susceptibility to diseases and our behaviour in order to project our past into the future. A picture of the most interesting and complex of all mammals is emerging and there is ever more evidence that the human animal is almost wholly African. Before any of our direct ancestors left Africa we were essentially modern humans. Long before there was agriculture, livestock or industrialisation we possessed qualities we still admire – technical and athletic skills, artistic and musical talents, eloquence, charisma, vivacity and physical beauty.

We became human in a very specific setting – within rich communities of African animals and plants. To destroy those communities is to detach ourselves, irrevocably, from our biological, even our intellectual past. To drift, senseless of our origins, is to impoverish science and medicine, to mythologise and trivialise our culture and to diminish us as descendants of countless generations of intelligent African mammals.

Ecological vandals identified

There is no other continent where the large mammal communities known to our ancestors can still be seen and studied. Eurasia, the Americas and Australia have been emptied of their large mammals and our collective history of vandalising the Earth can only be redeemed by conserving the full spectrum of surviving habitats in our mother continent. Twenty years ago I could still hope that the vision and political will might be found to teach invading cattle-men, loggers and land-grabbers to respect Africa. Instead, the situation has become much worse.

Parts of North Africa that are desert today were once bread-baskets for the Mediterranean. Later, the farming of wheat, corn and cattle spread to the steppes of central Asia, then the prairies of North America, then the pampas of South America: all now support mechanised monocultures on a gigantic scale. The corporate infrastructure behind a now global food (and energy) industry, 'Food Inc.', includes irresponsible banks as well as the manufacturers of machines, chemicals and seeds. Farmers have become its seed-dependent and chemical-dependent serfs. During the last 20 years, in the name of world food-security, agribusinesses have turned to Africa for new land to plough.

It could be argued that the prairies, the pampas and the Asian steppes were already semi-monocultures with impoverished flora and fauna and that ends justified means. That can never be said of Africa. Here, complex, biodiverse ecological communities are deliberately and mindlessly destroyed in their entirety to make way for monoculture crops. But for the technicians and businesspeople that drive 'Food Inc.' one continent is as good as another, given the right breeds, the right seeds, the right chemicals and the right machines. All can be imported if need be – Africa is no different to their own home prairie.

In facing adversaries as insensitive and powerful as 'Food Inc.' and their local political servants, African environmentalists must continue to insist that every major land holder sets aside and maintains between 10 and 20 percent of every holding in reserve for indigenous nature. Furthermore, where such reserves are situated must be determined by informed ecologists, especially wherever springs, headwaters and rivers are involved.

An anticipation of Africa's conversion into farmland has been provided by the logging industry. For centuries Africa's wharves have groaned as cadaverous tree-trunks and the teeth of elephants were levered into the holds of small ships owned by colonial agents. Today the scale of neo-colonial opportunism has vastly enlarged as processions of logging trucks run day and night into the docks of Monrovia, Grand Bassam, Takoradi, Douala, Libreville, Matadi and Luanda, all feeding fleets of giant vessels exporting timber and other raw materials to a greedy world. What does Africa get in return? Cranes, like mechanised Marabou Storks, unload shipment after shipment of bulldozers and trucks, chemicals, chain-saws, automatic assault weapons, short-lived electronic mass-products and luxuries for the elite. Some logging interests pretend that forest communities are renewable after intensive logging. High, climax rainforests are not renewable on any human time-perspective. When the high forests of West Africa are gone, they will, like the elephants of the Ivory Coast, be gone forever.

In general, the scattered and declining status of all natural resources in West, Central, North and north-east Africa reflects official apathy and, sometimes, an incomprehension that sometimes merges into hostility or contempt towards conservation. This attitude has been noted and repeatedly deplored by many concerned and distinguished citizens of those countries, so far with limited effect. Future generations will ask, how could today's governments have permitted extermination of the richest fauna on earth? Dismantling indigenous ecosystems to serve appetites on other continents looks like greedy stupidity today. Tomorrow it may look more like treachery.

The sorcerer's apprentices

A less well-known, but potentially more ominous aspect of the revolution in science and technology has been the application of genetics to the modification of domestic plants and animals. In theory, and increasingly in fact, livestock and crops can be engineered to grow anywhere on earth. For example, buffalo and their immediate ancestors have adapted to the vicissitudes of Africa and its environmental history over several million years. Buffalo genes (or those of any other indigenous organisms that are superior to non-African exotics) can now be patented and inserted into fully controllable and standardised food-producers (like cows or soy beans). Technology-based corporations that seek to standardise and universalise food-production have been quick to initiate, fund, patent and exploit these new applications of genetics.

Conversion of land to agriculture has been greatly speeded up by new chemicals, new techniques, machinery and by the collapse of all sensible restraints on banks and agribusinesses. Thus the most obvious change in Africa over the past 20 years has been hugely accelerated destruction of natural habitats and indigenous biota. In some areas this can be partly explained by great increases in human population but much of the worst destruction is taking place in areas of relatively low population but of great ecological significance. In such cases a lack of any curbs on such destruction has been due to rampant corruption both within and outside Africa. So vast blocks of land have been or are being purchased without any regard for local conservation or the rights of still unpoliticised peoples.

The international press has reported how, in the far north of Mozambique, 2,000 air km from its capital, Maputo, a Japanese/Brazilian conglomerate plans to convert 140,000km² into export plantations. This block of land is larger than the whole of England and is home to one of the most independent, original, talented and philosophically minded cultures in all of Africa, that of the Makonde people. The land for this planned plantation also represents one of the largest areas of natural habitats left in all of Africa. Another large-scale and recent land-grab should have taught lessons to its own and to other like-minded perpetrators. In Mali's far north, Libyan agribusiness leased 1,000km² of communally owned land from an equally distant government, thereby helping to precipitate a civil war. In Makeni, Sierra Leone, 400km² have been leased to a Swiss agribusiness to grow biofuels for export, providing less local earnings and less employment than would a national park (a mere 50 local people employed and profits going to shareholders overseas). These are merely three samples of the 'Second Scramble for Africa'. In spite of coercive tactics exerted by the sponsors and vassals of these vast land-grabs, the associated environmental degradation and loss of control should be a wake-up call to any analytical African thinker or responsible national politician. We *must* put a higher value on our heritage and impose necessary qualifications and restrictions on neocolonial entities bent on creating export-oriented, monoculture plantations. We *must* learn to value the time-tested viability of what is already here and support scientific research into the underlying biological processes that generated the African continent's incomparable biota.

Respect the land and communities that gave us life

Anyone seriously interested in conservation in Africa should become an active member of a conservation society (e.g. the Uganda wildlife clubs, the Ethiopian Natural History Society, or support an international body such as the widely respected WCS and FFI). Ideally every supporter of conservation should become a committed educator combating the deep ignorance of our commercial culture. It is vital that regional pressure groups have support from both within and outside their countries. There are also international conservation societies, each with its own special interests and emphasis. More voices are always required to help put across the case for conserving Africa's animals and their habitats. Above all, new ideas are required on how to achieve conservation aims. Among many encouraging initiatives have been community efforts to save the last natural habitats in the Cape, the creation of island sanctuaries in Lake Victoria (and elsewhere) and reintroductions of 'lost' species to vandalised habitats.

The short history of industrial urbanisation in Africa means that national parks have made a late start on cashing in on the recreational needs of city-dwellers. The world's first national park was described as a 'pleasuring ground' by its founders, who saw it as a sort of zoo-park. For the majority of the citizens of the first industrial societies, city parks, circuses, zoos and playgrounds served as the main places of recreation and escape from the constraints of city life. This is still true but there is more to our environment than a place in which to play.

The users of an early field guide could read without surprise that the mammals of Africa inhabited a 'unique, giant zoo'. When they are not reduced to trophies, meat and leather, African mammals are still often regarded as zoo specimens, now to be gathered up and their genes stored ahead of ecological collapse. Parks are increasingly manipulated by professional managers and there is a risk of mammals and ecological communities becoming domesticated in human minds. That is, perhaps, a greater risk than their actual domestication in man-made enclosures. Given a choice between total extinction and domestication, the latter is surely preferable. In practice, several species of large mammals are candidates for some form of domestication or semi-domesticated ranching: namely Kob and many antelope species, Giant Forest Hogs, rhinoceroses, hippopotamuses, perhaps even elephants.

We do need samples of nature in all its diversity and, yes, we should conserve future gene banks. We can portray mammals as characters on screens or in books, and certainly national parks should be managed for the delight and distraction of the work-weary as well as for research and learning, but there is a still larger issue. If we are not prepared to preserve viable natural habitats for their own sakes, to leave animals and plants spaces of their own, then, in a real sense, we will have lost sight of our place in this world. Parks in Africa will have failed if they do not encourage people to wonder at the natural order of life on Earth and to reflect upon the world beyond civilisation and its physical and mental boundaries, a world beyond grasping human hands where eyes, minds and memories alone can be touched by its eternal mystery and grace.

Information on mammals is mostly published in scientific papers. Our sister publication, *Mammals of Africa*, has extensive bibliographies of such papers, as well as comprehensive references for all species.

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There are many important monographs on individual species, families and orders. Books on evolution that are relevant to an understanding of the importance of mammals (especially African mammals) to humanity and the future of humanity include Charles Darwin's *Origin of Species*; Richard Dawkins's *The Ancestors' Tale*, *The Blind Watchmaker* and *The Magic of Reality*; Matt Cartmill & Fred Smith's *The Human Lineage*; Steven Jones's *The Language of the Genes*; Jonathan Kingdon's *Lowly Origin* and *Self-Made Man*; Richard Leakey & Roger Lewin's *Origins Reconsidered*; Christopher Stringer's *African Exodus*; and Edward Wilson's *The Diversity of Life*.

Adult	A physically and reproductively mature individual.
Afrotheria	A newly recognised taxon (supercohort) of mammals that originated in Africa.
Agouti	Grizzled appearance of the coat resulting from alternating light and dark banding of individual hairs.
Allopatry	Condition in which populations of different species are geographically separated (reverse of sympatry).
Amphibious	Able to live on both land and water.
Anal gland or sac	A gland opening either just inside the anus or on either side of it.
Apocrine glands	Cutaneous scent glands that produce complex and chemically variable secretions.
Aquatic	Applied to animals that live in fresh water. All aquatic mammals move readily on land.
Arboreal	Referring to animals that live in trees.
Arthropod	The largest phylum in the animal kingdom, including insects, spiders, crabs etc.
Bai	Large forest glade, often around a swamp or mere.
Biome	A major type of ecological community, such as savanna or desert.
Biotic community	A naturally occurring group of plants and animals in the same environment.
Bipedal	Two-footed stance or locomotion of four-footed animals.
Bovid	A member of the cow-like Bovidae family of the Cetartiodactyla.
Brachydont	Low-crowned characteristic of the molars of grazing mammals (opposite of hypsodont).
Brindled	Having dark streaks or flecks on a grey or tawny background.
Browser	A herbivore that feeds on shoots and leaves of trees, shrubs and forbs.
Bullae (auditory)	Globular, bony capsules housing the middle and inner ear structures. Built on to the underside of the skull.
Callosities	Patches of thickened skin and tissue (as on the hindquarters of monkeys or knees of some ungulates).
Canine teeth	The usually long pointed teeth, one in each quarter of the jaws, that are used by animal-eating mammals for killing their prey.
Catena	Series of related events, a biosequence or toposequence.
Carnassial teeth	In carnivores, the fourth upper premolar and first lower molar, specialised for shearing meat and sinew.
Carnivore	Any meat-eating organism but also a member of the mammal order Carnivora.
Caudal gland	An enlarged skin gland associated with the root of the tail. (Subcaudal: below the root; supracaudal: above the root.)
Caecum	A blind sac situated at the junction of the small and large intestine, in which digestion of cellulose by bacteria occurs.
Cellulose	Main constituent of the cell walls of plants. Very tough and fibrous, and can be digested only by the intestinal flora in mammalian guts.
Cervid	A member of the deer family Cervidae, of the Cetartiodactyla.
Cetartiodactyl	A member of the order Cetartiodactyla, the even-toed ungulates.
Chablis	Tree-fall opening in the forest.
Cheek-pouches	A pair of deep pouches extending from the cheeks into the neck skin, present in non-colobine monkeys and some rodents and used for the temporary storage of food.
Cheek-teeth	The row of premolars and molars used for chewing food.
Class	A taxonomic category. The mammals, Mammalia, are a class.
Colonial	Living together in colonies. Notably bats and rodents.
Competitive exclusion	Exclusion of one species by another when competing for a common resource.
Concentrate selector	A herbivore that feeds on plant parts that are rich in nutrients, such as shoots and fruits.
Conspecific	A member of the same species.

Convergence	The evolution of similarities between unrelated species occupying similar ecological niches.
Crepuscular	Active in twilight.
Crustaceans	Members of a class within the phylum Arthropoda, typified by crayfish, crabs and shrimps.
Cryptic	Concealing, inconspicuous. Usually referring to coloration and markings.
Cud	Partially digested vegetation that a ruminant regurgitates, chews, insalivates and swallows again.
Cursorial	Being adapted for running.
Cusp	A prominence on a cheek-tooth (premolars or molars).
Dahomey Gap	Region or corridor where drier habitats interrupt the forests of West Africa in Togo and Benin.
Dental formula	A convention for summarising the dental arrangement whereby the numbers of each type of tooth in each half of the upper and lower jaw are given. The numbers are always presented in the order; incisor (I), canine (C), premolar(P), molar(M). The final figure is the total number of teeth to be found in the skull. A typical example for Carnivora would be 3-1-4-3:3-1-4-3 = 44.
Dentition	The arrangement of teeth characteristic of particular species.
Dicot	Short for dicotyledon.
Dicotyledon	A plant with two seed leaves; the subclass of angiosperms containing most higher plants.
Digit	A finger or toe.
Digitigrade	Animals that walk on their digits rather than the whole foot.
Dimorphism	Two forms, typically the morphological differences between males and females (sexual dimorphism).
Dispersal	The movements of animals, often as they reach maturity, away from their previous home-range (equivalent to emigration).
Display	Any relatively conspicuous pattern of behaviour that conveys specific information to others, usually to members of the same species: can involve visual and or vocal elements, as in threat, courtship or 'greeting' displays. A behaviour pattern that has been modified (ritualised) by evolution to transmit information by a sender to a receiver.
Diurnal	Referring to species that are primarily day-active.
Dorsal	The back or upper surface(opposite of ventral).
Dung midden	Pile of droppings that accumulate through regular deposits, typically in connection with scent-marking (see also Latrine).
Ecological niche	The particular combination of adaptations that fits each species to a place different from that filled by any other species within a community of organisms.
Ecology	The scientific study of the interaction of organisms with their environment, including both the physical environment and the other organisms that share it.
Ecosystem	A community of organisms together with the physical environment in which they live.
Emigration	Departure of animal(s) usually at or about the time of reaching adulthood, from the group or place of birth. Also of biogeographic exchange between continents or regions.
Endemic	Native plants and animals.
Eocene	Geological epoch 55.8–33.9 mya.
Epidermis	The outer layer of the skin or surface tissue of a plant.
Equatorial	Geographical region bordering the Equator.
Erg	Windswept sandy desert with shifting sand dunes.
False hooves	Vestigial nails (digits 2 and 5) that persist in many ruminants as paired hooves or bumps on the fetlock.
Family	A taxonomic division subordinate to an order and superior to a genus.

Feral	Living in the wild (of domesticated animals, e.g. cat, dog).
Fetlock	Joint above the hooves.
Folivore	An animal whose diet consists mostly of leaves and other foliage.
Forbs	Herbs other than grass that are abundant in grassland, especially during the rains.
Fossorial	Adapted for digging.
Frugivore	An animal that feeds mainly on fruit.
Fynbo	Shrubland of southern Africa with numerous endemic species.
Gallery forest	Trees and other vegetation lining watercourses, thereby extending forested habitat into more open zones.
Generalist	An animal that is not highly specialised. For example, feeding on a variety of foods that require various foraging techniques.
Genotype	The genetic constitution of an organism, determining all aspects of its appearance, structure and function.
Genus (pl. Genera)	A taxonomic division superior to species and subordinate to family.
Gestation	The period of development between conception and birth.
Glands	Specialised glandular areas of the skin.
Gondwanaland	A former land mass that fragmented into Africa and the southern continents in the Mesozoic.
Grazer	A herbivore that feeds upon grasses.
Guard hairs	The outer coat that overlies the shorter, softer hairs of the underfur (underfur is sparse or absent in many tropical mammals, e.g. most ungulates and primates).
Gumivorous	Feeding on gums (plant exudates).
Hammada	Stony desert plain.
Hard pan	Zone of compacted soil restricting root-growth and drainage.
Harem group	A social group consisting of a single adult male, at least two adult females and immature animals.
Herbivore	An animal whose diet consists of plant food.
Herd	A social group; generally applied to gregarious ungulates.
Hierarchy	As applied to social groups, a usually linear rank order in which members dominate all those of lower rank and are dominated by all individuals of higher rank.
Hindgut fermentation	Process by which breakdown of cellulose occurs in the caecum and large intestine.
Home-range	The area occupied by an individual or group (usually determined by points where the individual(s) is seen over a period of time and plotting the perimeter).
Hypsodont	High-crowned characteristic of the molars of grazing mammals (opposite to brachydont).
Hybrid	The offspring of parents of different species.
Inguinal	Pertaining to the groin.
Insectivore	An animal eating mainly arthropods (insects, spiders).
Interdigital	Between the digits; e.g. the interdigital (hoof) glands of many antelopes.
Intestinal flora	Simple plants(e.g. bacteria) that live in the intestines of mammals. They produce enzymes that break down the cellulose in the leaves and stems of green plants and convert it to digestible sugars.
Invertebrate	Animal that lacks a backbone(e.g. insects, spiders, crustaceans).
Juvenile	Stage between infant and adult.
Karoo	Arid part of the interior plateau in temperate southern Africa. Dominated by dwarf shrubs and adjoined by Highveld grassland.
Keratin	Tough fibrous substance of which horns, claws, hooves and nails are composed.
Lactation	The secretion of milk from mammary glands.
Larynx	Dilated region of upper part of windpipe, containing vocal chords. Vibration of chords produces vocal sounds.

Latrine	A place where animals regularly deposit their excrement (see also Midden).	Paleocene	Geological epoch 65.5–55.8 mya.
Liana (liane)	A vine climbing woody plants; major constituents of rain forest.	Parturition	The process of giving birth.
Maghreb	Loosely defined region of NW Africa.	Perineal glands	Glandular tissue occurring between the anus and genitalia.
Mandible	The lower jaw.	Perissodactyl	A member of the order Perissodactyla, the odd-toed ungulates.
Maquis	Dense secondary scrub dominated by heathers and strawberry trees (Mediterranean).	Pheromone	Secretions whose odours act as chemical messengers in animal communication.
Masseter	A powerful muscle, subdivided into parts, joining the lower and upper jaws, used to bring jaws together when chewing.	Phylogenetic	(Of classification or relationship) based on the closeness of evolutionary descent.
Mbuga	Valley flat land of clay (black cotton soil), seasonally flooded.	Phylogeny	A classification or relationship based on the closeness of evolutionary descent. Often portrayed graphically by a branching tree.
Melanism	Darkness of colour due to presence of the black pigment melanin.	Phylum	A taxonomic division comprising a number of classes.
Mesozoic	Geological era 245–65.5 mya.	Physiology	Study of the processes that go on within living organisms.
Metabolism	The chemical processes occurring within an organism, including the production of protein from amino acids, the exchange of gases in respiration and liberation of energy.	Pinna	The projecting cartilaginous portion of the external ear (especially in bats).
Microhabitat	The particular parts of the habitat that are encountered by an individual in the course of its activities.	Placenta	Structure that connects the foetus and the mother's womb to ensure a supply of nutrients to the foetus and removal of its waste products.
Midden	A dung hill or latrine for the regular deposition of faeces by mammals.	Pleistocene	Geological epoch 1.6–0.01 mya.
Migration	Movement, usually seasonal, from one region or climate to another for purposes of feeding or breeding.	Pliocene	Geological epoch 5.3–1.6 mya.
Miocene	A geographical epoch 23–5.3 mya.	Polymorphism	Occurrence of more than one morphological form of individual in a population.
Miombo	Woodlands mostly growing on impoverished Precambrian landscapes, with trees dominated by leguminous <i>Brachystegia</i> species.	Population	Members of the same species that are within an area at the same time.
Montane	Referring to African mountain habitats, including forest, grassland, bamboo zone, moorland etc.	Post-partum oestrus	Renewed ovulation and mating within days or weeks after giving birth.
Morphology	Referring to an animal's form and structure.	Predation	The killing and eating of living animal prey.
Mucosa	Mucous membrane; a membrane rich in mucous glands such as the lining of the mouth and nasal passage ways.	Predator	Any animal that subsists mainly by eating live animals, usually vertebrates.
Mutation	A structural change in a gene that can give rise to a new heritable characteristic.	Preorbital	In front of the eye (where a gland occurs in many ungulates).
Natural selection	Process whereby the fittest genotypes in a population survive to reproduce; a determinant principle in evolution.	Presenting	The act of directing the hindquarters toward another individual, either in a sexual context or as a gesture of appeasement derived from sexual presenting.
mya (abbrev.)	Million years ago.	Pronking (also 'stotting')	A ritualised bouncy gait in which the animal (usually a bovid) is exceptionally alert.
Niche	The role of a species within the community, defined in terms of all aspects of its life history from food, competitors and predators to all its resource requirements.	Protein	A complex organic compound made of amino acids. Many different kinds of proteins are present in the muscles and tissues of all mammals.
Nocturnal	Active at night-time.	Proximal	Near to the point of attachment or origin.
Nomadic	The wandering habit. Among mammals, species that have no clearly defined residence most of the time; distinct from migratory species, which may be resident except when migrating.	Quadrupedal	Walking on all fours.
Nose-leaf	Characteristically shaped flaps of skin surrounding the nasal passages of leaf-nosed bats. Ultrasonic cries are uttered through the nostrils, with the nose-leaves serving to direct the echo-locating pulses forward.	Race	A subspecies.
Occipital	Pertaining to the occiput at back of head.	Radiation	Speciation by a group of related organisms in the process of adapting to different ecological roles.
Oestrogen	Hormone produced by ovaries and responsible for expression of many female characteristics.	Rainforest	Tropical and subtropical forest with abundant and year-round rainfall. Typically species-rich and diverse.
Oestrus	Behaviour associated with ovulation, being in most mammals the only time when females are sexually receptive ('in heat').	Range	(Geographical) area over which an organism is distributed.
Olfaction, olfactory	The olfactory sense is the sense of smell, depending on receptors located in the epithelium, or membrane lining the nasal cavity.	Rank order	A hierarchical arrangement of the individuals in a group.
Oligocene	A geological epoch 33.9–23 mya.	Realm	A biogeographic unit encompassing multiple zones and determinant factors.
Omnivorous	A mixed diet including both animal and vegetable food.	Relict	A persistent remnant population.
Opportunistic	Referring to animals that capitalise on opportunities to gain food with the least expenditure of energy.	Resident	Living within a definite, limited home-range, as opposed to being migratory or nomadic.
Order	A taxonomic division subordinate to class and superior to family.	Reticulum	Second chamber of the ruminant cetartiodactyl stomach.
Ovulation	The process of shedding mature ova (eggs) from the ovaries where they are produced.	Rinderpest	A lethal cetartiodactyl disease.
		Ritualisation	Evolutionary modification of a behaviour pattern into a display or other signal, through selection for improved communication.
		Ritualised	Referring to behaviour that has been transformed through the process of ritualisation.
		Rodent	A member of the order Rodentia, the largest mammalian order, which includes rats and mice, squirrels, anomalures and porcupines.
		Rumen	First chamber of the ruminant cetartiodactyl stomach. In the rumen the food is liquefied, kneaded by muscular walls and subjected to fermentation by bacteria.

Ruminant	A mammal with a specialised digestive system typified by the behaviour of chewing the cud. Its stomach is modified so that vegetation is stored, regurgitated for further maceration, then broken down by symbiotic bacteria. The process of rumination is an adaptation to digesting the cellulose walls of plant cells.	Terrestrial	Living on land.
Rut	Period of concentrated sexual activity, the mating season.	Territoriality	A system of spacing wherein home-ranges do not overlap randomly – that is, the location of one individual's or group's home-range influences those of others.
Sagittal	Mid-line over the cranium.	Territory	An area defended from intruders by an individual or group.
Savanna	Vegetation characteristic of tropical regions with extended wet and dry seasons. Dominated by grasses and scattered (predominantly leguminous) trees. The trees vary in type and density from broad-leaved, deciduous woodland in the wetter savanna to grassland with scattered thorn trees and <i>Acacia</i> bush grading into subdesert.	Testosterone	A male hormone normally synthesised in the testes and responsible for the expression of many male characteristics.
Scent gland	Area of skin packed with specialised cells that secrete complex chemical compounds that communicate.	Thermoregulation	The regulation and maintenance of a constant internal body temperature in mammals.
Sebaceous glands	The commonest type of cutaneous scent glands, consisting of localised concentrations of flask-shaped follicles that produce volatile fatty acids manufactured by symbiotic bacteria.	Thoracic	Pertaining to the thorax or chest.
Sedentary	Pertaining to mammals that occupy relatively small home-ranges.	Tooth-comb	A dental modification in which the incisor teeth form a comb-like structure.
Selection	Any feature of the environment that results in natural selection, through differential survival and reproductive success of individuals of differing genetic types.	Torpor	A dormant state.
Sexual dimorphism	A condition in which males and females of a species differ consistently in form, size and shape.	Tribe	A taxonomic category between family and genus.
Sexual selection	Selection of genotypes through competition between members of the same sex (usually males) and mating preferences by members of the opposite sex (usually female).	Tropical	The climate, flora and fauna of the geographic region between 231/232° N and S of the Equator. The latitudes reached by the sun at its maximum declination, known respectively as the Tropics of Cancer and Capricorn.
Sinus	A cavity in bone or tissue.	Tsetse fly	Two-winged blood-sucking flies, that transmit 'sleeping sickness' (trypanosomiasis) to man and domestic livestock. The flies' presence in the woodlands of Africa south of the Sahara slowed the pace of settlements and thereby preserved habitats for wild animals, which have a natural immunity to tsetse-borne diseases.
Solitary	Unsocial, referring to animals that do not live in social groups.	Undercoat	The soft insulating underfur beneath the longer, coarser guard hairs of the outer coat.
Speciation	The process by which new species arise in evolution. Typically occurs when a single species population is divided by some geographical barrier.	Ungulate	A member of one of the orders Cetartiodactyla (even-toed ungulates), Perissodactyla (odd-toed ungulates), Proboscidea (elephants), Hyracoidea (hyraxes) and Tubulidentata (Aardvark), all of which have their feet modified as hooves of various types.
Species	Population(s) of closely related and similar organisms that are capable of interbreeding freely with one another, and cannot or normally do not interbreed with members of other species.	Veld	Open uncultivated grassland in southern Africa.
Species-specific	Characters that serve to distinguish a species, such as its shape, markings or habits.	Ventral	The underside, lower surface of an animal, opposite to dorsal.
Spoor	Footprints.	Vertebrate	An animal with a spinal column and skeleton of bone, including amphibians, reptiles, birds and mammals.
Subadult	No longer an infant or juvenile but not yet fully adult physically and/or socially.	Vestigial	A characteristic with little or no contemporary use, but derived from one that was useful and well developed in an ancestral form or period.
Subdesert	Regions that receive less rainfall than arid zones, but more than true desert.	Vibrissae	Stiff, coarse hairs richly supplied with nerves, found especially around the snout and with a sensory (tactile) function.
Subspecies	Population(s) that has been isolated from other populations of the same species long enough to develop genetic differences sufficiently distinctive to be considered a separate race.	Vocalisation	Calls or sounds produced by the vocal chords of a mammal, and uttered through the mouth. Vocalisations differ with the age and sex of mammals but are usually similar within a species.
Superspecies (or species group)	A grouping of closely related species.	Watershed	Elevated land between drainage basins.
Swidden	Rotational agriculture within rainforest.	Yearling	A young animal between one and two years of age (referring to species that take at least two years to mature).
Symbiotic	A mutually dependent relationship between unrelated organisms that are intimately associated, e.g. the symbiosis between a ruminant and the microorganisms that live in its rumen.		
Sympatry	Condition of overlapping geographic distribution; applies to related species that coexist without interbreeding (reverse of allopatry).		
Systematics	The classification of organisms in an ordered system based on their supposed or known natural relationships.		
Tarsal	Pertaining to the tarsus bones in the ankle, articulating between the tibia and fibia of the leg and the metatarsals of the foot (pes).		
Termitary	Termite-hill.		