MAMMALIAN SPECIES No. 422, pp. 1–8, 3 figs.

Okapia johnstoni.

By Richard E. Bodmer and George B. Rabb

Published 10 December 1992 by The American Society of Mammalogists

Okapia Lankester, 1901*a*

Okapia Lankester, 1901*a*, 1901*b*:280. Type species *Okapia johnstoni* (Sclater, 1901), by monotypy.

CONTEXT AND CONTENT. Order Artiodactyla, Suborder Ruminantia, Infraorder Pecora, Family Giraffidae, Subfamily Palaeotraginae. There are only two living giraffids, the okapi (*Okapia johnstoni*) and the giraffe (*Giraffa camelopardalis*).

Okapia johnstoni (Sclater, 1901)

Okapi

Equus(?) *johnstoni* Sclater, 1901:50. Type locality "in sylvis fluvio Semliki adjacentibus" (= in the gallery forests along the Semliki River, Zaire; Johnston, 1900).

Okapia johnstoni: Lankester, 1901*a*:281. Type locality "forest on the borders of the Congo Free State" [Zaire] (Lankester, 1901*c*).

Helladotherium tigrinum Johnston, 1901:270. Type locality "forests bordering the Semliki River, in Central Africa" [Zaire].

Okapia liebrechtsi Major, 1902*a*:73. Type locality "Mundalah, on road from Mawambi to Beni (N.E. frontier of the Independent Congo State)" [Zaire].

Okapia erikssoni Lankester, 1902*a*:417. Type locality "Semliki forest" [Zaire] (Lankester, 1902*b*).

Ocuapia kibalensis Gatti, 1936:295. Type locality the Kibale-Ituri forest, as "delimited by the Epulu, Lenda, Lindi and Semliki rivers" [Zaire].

CONTEXT AND CONTENT. Context as in generic account above. *Okapia johnstoni* is a monotypic species (Allen, 1939; Ansell, 1971; Lydekker, 1914*a*).

DIAGNOSIS. The okapi (Fig. 1) is a medium-sized giraffid, with a pair of supraorbital, hair-covered frontal horns present only in males. The brachyodont cheek teeth and dolichocephalic skull are like those of other palaeotragines. However, unlike its fossil relatives of the Palaeotraginae, *O. johnstoni* has slightly smaller permanent incisors, slightly larger permanent cheek teeth (Churcher, 1970), and the second upper deciduous molar lacks an external cingulum (Bohlin, 1926). Large palatine sinuses are also distinctive of the okapi among giraffids (Colbert, 1938).

The okapi is readily distinguishable from its nearest extant relative, *Giraffa camelopardalis*. The body of the okapi is smaller than the giraffe, with the neck and leg proportions of the okapi more resembling those of bovid and cervid ruminants than those of giraffe (Dagg, 1960). Cervical vertebrae of the okapi are unelongated, unlike those of the giraffe (Lankester, 1908). There are usually five sacral vertebrae in the okapi in contrast to three or four in the giraffe (Haltenorth, 1963). Unlike giraffe only male okapi possess ossicones; however, small rudimentary horns may be present in females (Lankester, 1907). The individually variable tapered white or creamy white horizontal stripes extending anteriorly from the posterior face of the hindlimbs and rump of the okapi contrast with the coloration of the giraffe (Lydekker, 1914*b*; Pocock, 1946). The two species are allopatric; the okapi occurs in rain forests of central Africa and the giraffe inhabits sub-Saharan savanna and woodlands (Dagg, 1971).

GENERAL CHARACTERS. The okapi has a striking visual appearance: the generally dark velvety pelage of the body contrasting with tapered white or creamy white horizontal stripes on the rear haunches and upper front legs and with the anklets and stockings of white on the lower legs. The cheeks, throat, and the distal ventrum are whitish to grey or tan and provide additional contrast to the dark reddish brown to black colors of the back and sides (Gijzen, 1959; Grzimek, 1958; Pocock, 1946).

Body masses of adult okapis average 250 kg and range from 200 to 300 kg (Gijzen, 1959; Grzimek, 1958). Average total body length is 2.5 m and average height at the shoulders is 1.5 m (Gijzen, 1958; Landsheere, 1957). Females average 4.2 cm taller than males (Landsheere, 1957).

Only male okapis have hair-covered horns (Lankester, 1907; Rothschild and Neuville, 1909). The hair on the tips often is rubbed to the bone (Fraipont, 1908). Horns are variable in girth and length, but do not exceed 15 cm above the skull, are fused to the frontal bones supraorbitally and inclined posteriodorsally (Churcher, 1990; Colbert, 1938). Female okapis possess hair whorls where the horns of males are located (Lankester, 1903). There are no other cranial features of the okapi that have been found to be significantly dimorphic (Jaspers and De Vree, 1978).

The skull (Fig. 2) shows primitive characteristics for the family, including a large parietal region, short diastema, and large auditory bullae (Bohlin, 1926; Colbert, 1938). Large auditory bullae are a common feature of many forest-dwelling ruminants and are related to an acute sense of hearing (Colbert, 1938). In accord, there are large external ear lobes, 25 cm in length from the crown, that are readily flexed (Gijzen, 1959). Both features may be correlated with infrasonic sound reception.

The dental formula is 0/3, 0/1, 3/3, 3/3, total 32, which is consistent with all giraffids. The deciduous and permanent canines are incisor-like and bilobate. The incisors form a semicircle at the end of the lower jaw. The relationships between length of the forelimbs and hind limbs are similar to those found in other artiodactyl genera. The okapi has a relatively longer neck than other ruminants, which is perhaps correlated with locomotor coordination of the giraffid pacing gait (Colbert, 1938). Unlike the giraffe, the okapi has interdigital glands on all four feet, with the glands being slightly larger on the front feet (Gosling, 1985; Pocock, 1936).

DISTRIBUTION. Okapis are endemic to tropical forests of northeastern Zaire (Lönnberg, 1905; Schouteden, 1946) and are generally limited to altitudes between 500 and 1,000 m (Ansell, 1971; Fig. 3). However, they have been reported at altitudes above 1,000 m in the eastern montane rainforests, with one sighting at 1,450 m on Mt. Hoyo in the upper Ituri (Curry-Lindahl, 1956). They do not occur lower than 500 m or in the swamp forests of western Zaire (Verschuren, 1978). In general, the geographical range is limited in the east by high montane forests, in the west by swamp forests, in the north by savanna of the Sahel/Soudan, and in the south by open woodland (Schouteden, 1946; Sidney, 1965). The specific distribution ranges through the Ubangui, Uele, Aruwimi, and Ituri rainforests; from Libangi on the Ubangui River in the west to near Lakes Kivu and Edward in the east, north to Faradje, and south to the Sankuru and Maniema districts (Haltenorth and Diller,

FIG. 1. Five-year-old male *Okapia johnstoni* at the Chicago Zoological Park, Brookfield, International Studbook no. 271. Photograph by M. Greer.

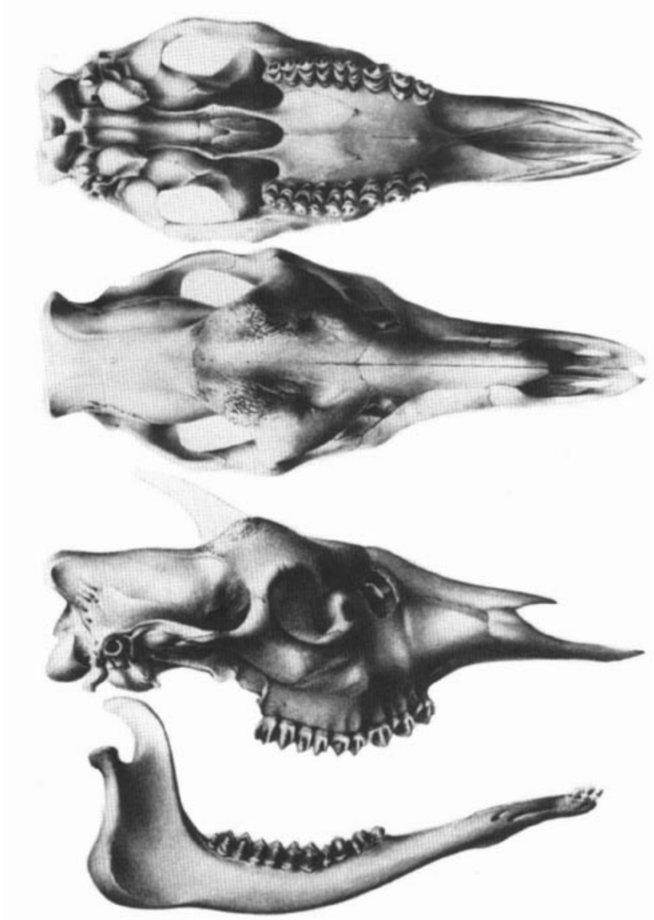

FIG. 2. Ventral, dorsal, and lateral views of cranium, and lateral view of mandible of *Okapia johnstoni* (from Lankester 1910), courtesy of the British Museum of Natural History. Greatest length of skull is 464 mm (BMNH G.12.27.1).

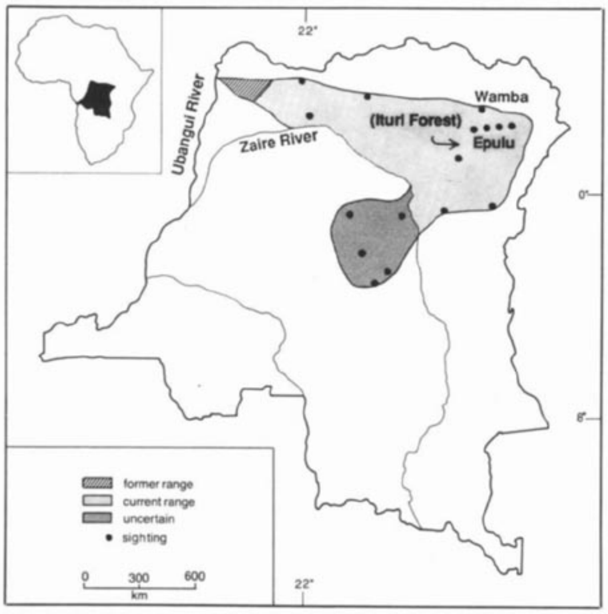

FIG. 3. Geographical distribution of *Okapia johnstoni* in Zaire. The northeast section shows the former range, and the section southeast of the Zaire River illustrates the possible range.

1980). They always have been most common in the Wamba and Epulu areas (Verschuren, 1978). Most okapis in zoos are descendants from animals captured near Epulu (Gijzen and Smet, 1974). The present distribution, as represented by blocks such as the Ituri forest, is considered to have been the largest late Pleistocene refuge in central Africa for primates and other forest animals (Chapman, 1983).

FOSSIL RECORD. A right ossicone (horn) from the Kaiso Village, Kaiso Formation, Late Pliocene, Uganda, has been assigned to *Okapia* and an isolated right lower third premolar from Nyaweiga, Kaiso I, may also be from *Okapia* (Cooke and Coryndon, 1970). A Pleistocene giraffid originally reported as *Okapia stillei* (Dietrich, 1941) was considered to be a misidentified specimen of *Giraffa* by Harris (1976).

FORM AND FUNCTION. The senses of okapis appear to be particularly tuned for tropical forests. The high proportion of rod cells in the retina can be considered an adaptation for low-light vision (Brückner, 1950). They also have surprisingly large bullae (Colbert, 1938) and a good olfactory system (Anthony and Coupin, 1925).

One of the most outstanding features of giraffids is the long-prehensile tongue, with that of the okapi being proportionately longer than that of the giraffe. The darkly-colored tongue of the okapi has a pointed extremity, smooth base, and a surface covered with many papillae. It can be extended for roughly 25 cm beyond the snout and commonly is used to wipe the eyes, clean the nostrils, and groom the body from anus forward. Tongue muscles are similar to those of the giraffe and accordingly differ from other ruminants (Burne, 1917). The shapes of the premaxillae and symphysial region of the mandible correlate with the shape of the tongue (Solunias et al., 1988).

Okapis have distinctively narrow frontal bones and comparatively primitive proportional relationships of the skull elements (Colbert, 1938). There are frontal sinuses, large palatine sinuses and a long nasal cortex (Anthony and Coupin, 1925; Colbert, 1938; Lankester, 1910). Brain mass is 500 g (Portmann and Wirz, 1950), with a ratio of brain mass to body mass larger in okapis than giraffes (Le Gros Clark, 1939; Portmann and Wirz, 1950). Convolutional patterns are similar to other giraffids (Black, 1915).

The larynx is simple in structure, with no recesses or pouches and only rudimentary vocal cords (Burne, 1917). The okapi accordingly has a limited vocal repertoire (Crandall, 1964; Dagg and Foster, 1976; Lang, 1957). The thyroid body is of usual ruminant type. This gland is bilobed, with each lobe an oval approximately 47 by 16 mm. The thymus is small and triangular, measuring about 64 by 55 mm. The tonsils are similar to those of bovid and cervid ruminants (Burne, 1917).

As in other ruminants, the left lung has two lobes and the right has four lobes, which includes an azygous lobe. The lower lobe of the left lung is prolonged, resulting in a finger-like projection (Burne, 1917). The right lung of an adult female weighed 1.5 kg and the left lung 1.9 kg, whereas the right lung of a 28-kg neonate weighed 280 g and the left 230 g (Pearson et al., 1978). The trachea, bronchial tubes, and pulmonary vessels are similar to those of sheep (Burne, 1917), and the pectoral muscles resemble those of other ruminants (Bourdelle, 1939).

The heart is similar to other ruminants (Burne, 1917; Candaele and Ghys, 1958), weighing 1.85 kg in an adult female, 200 g in a 28-kg neonate (Pearson et al., 1978), and 145 g in a 14-day-old animal (Candaele and Ghys, 1958). The jugular vein closely resembles that of giraffes; however, the axillary and brachial veins are less complex in the okapi (Amoroso et al., 1947).

The digestive system of okapis is generally similar to other browsing ruminants. However, the esophageal connection to the rumen is not as cranially positioned as in the giraffe (M. Mantino, in litt). The latter is considered a primitive condition for Artiodactyla (Janis and Scott, 1987), but the differences between the giraffids indicate this is not a straightforward proposition. The stomach has large and flat rumen papillae, resembling those of giraffes (Burne, 1939; Derscheid, 1924). The omasum has many folds and the abomasum is similar to bovid and cervid ruminants (Burne, 1939). Salivary glands are large and resemble those of the giraffe (Burne, 1917). The okapi also has a large cecum and colon that assist in microbial digestion of food (Derscheid and Neuville, 1924). As in the giraffe, a gall bladder is ordinarily not present (Burne, 1917).

Uterine caruncles, arranged in four rows in each uterine horn, number <50, but 100–150 in the giraffe. In both species, the cervical configuration is somewhat tortuous, with the cervical lumen directed laterally (Loskutoff et al., 1988). The placental morphology of the okapi and giraffe is cotelydenary and epitheliochorial (Hradecky, 1983; Hradecky et al., 1987). The chorioallantoic villi of the okapi placenta show minimal branching and surface corrugation, whereas these villi in the giraffe placenta are extensively branched and are corrugated at the surface (Loskutoff et al., 1988). Females have four inguinal mammae. Milk has a high concentration of protein, approximately one-third greater than cow's milk, and a low fat content (Faust, 1968; Gregory et al., 1965; Senft, 1978; Shaul, 1962).

Urine of captive adult individuals is alkaline (pH = 8.0–9.0), in accordance with their browsing diet (Glatston and Smit, 1980). The blood chemistry of the okapi is more like other ruminants than the giraffe—Ca: 9.5–13.4 mg %, P: 6.0–9.8 mg % (International Species Inventory System, 1987; Rabb, 1978).

The okapi is a browser (Gijzen, 1959). A fast rate of food passage for okapis and giraffes results in a lower cell wall digestion than for other ruminants (Prins and Domhof, 1984). Daily food intake (dry matter) of captive okapi ranges from 4.3 to 5.0 kg (Prins and Domhof, 1984).

ONTOGENY AND REPRODUCTION. Estrus cycles in captive okapis occur approximately every 15 days throughout the year (Nouvel, 1958). However, these cycles often are irregular (Loskutoff et al., 1982; Nouvel, 1958) and sometimes have long periods of quiescence (Nouvel, 1958). The follicular phase averages 8.3 days (Loskutoff et al., 1986). Levels of progesterone and estrogens have been studied from radioimmunoassay of urine samples. Progesterone levels measured by pregnanediol-3-glucuronide assays (Loskutoff et al., 1982) and hormone metabolite profiles are correlated with overt behavioral estrus (Loskutoff et al., 1983). Urinary estrogens increase sharply 1 day after complete luteal regression and peak on the 2nd day, whereas, pregnanediol-3-glucuronide levels rise around the 8th day after complete luteal regression (Loskutoff et al., 1982). Pregnant okapis show rises in estrogens begining 50 days postmating (Loskutoff et al., 1983) and lactating okapis have pregnanediol-3-glucuronide levels at baseline concentrations for at least 6 months postpartum (Loskutoff et al., 1986). The estrogen cycle is not precisely determinable from urinary metabolites because of their extremely low concentrations in the urine. Higher levels of estrogen metabolites are present in the feces, and reliable assays are now possible (Nancy Czekala, in litt.).

Gestation periods range from 414 to 493 days, with an average of 440 days (Gijzen and Smet, 1974; Nouvel et al., 1970; Rabb, 1978). Matings may occur during pregnancy (Gijzen, 1958; Nouvel et al., 1970). Successful matings can occur as early as 1 month postpartum (Gijzen and Smet, 1974). Embryos of okapis at 1 month old (Burckhardt, 1906), 3 months (Gijzen, 1958), and 6 months of age (Naaktgeboren, 1966) show development patterns similar to other ruminants. There is no evidence of seasonal periodicity in fertility of males; however, individuals have been aspermic for several months. Semen has been collected from males to insure propagation of captive populations (Rüedi et al., 1984).

Okapis breed readily in captivity, but rearing of calves has been problematic; until the 1950s, roughly 50% died during the 1st month (Gijzen and Smet, 1974; Senft, 1978). Okapis usually give birth to 1 offspring, with only one record of twinning (Pearson et al., 1978). Abortions occur in captives; maternal illness or stress often have been assumed to be the causes. However, in most cases the actual causes of abortions are unknown (Benirschke, 1978).

Prepartum signs in females are swelling of the udder, viscous discharges from the vagina, and swelling of the vulva (Gijzen and Mortelmans, 1962; Rabb, 1978). The swelling of the udder may occur 2 months before the birth. Parturition, from first appearance of the forelegs to birth, takes 3–4 h. Females usually stand throughout birthing labor, but may recline for brief periods (Bullier, 1959; Davis, 1959; Gijzen, 1961; Lang, 1961; Van den bergh, 1959). The mother typically ingests the fetal membranes and placenta; the placenta ordinarily is discharged within 2 h of birth. Extensive maternal grooming and a high frequency of contact between mother and infant are characteristic of the period immediately following parturition (Gijzen and Mortelmans, 1962; Rabb, 1978). However, primiparous mothers may respond aggressively to the newborn, striking with head or hooves and sometimes killing the infant (Rabb, 1978). Similar response may occur if a mother is alarmed by the baby's bleats or certain other sounds.

Newborns are precocial, as are most ruminant species. In captivity, infants normally stand within 30 min and may initiate first nursing as soon as 21 min postpartum, with an average of 72 min (Rabb, 1978). Infants are typical hiding ungulates (Bodmer and Rabb, 1985; Rabb, 1978). After 1–2 days of following the mother and actively exploring the environment, the infant settles in one place. Nesting behavior of infants thereafter shows distinct behavioral stages distinguished by the time spent on the hiding site and changes in various infantile and maternal behaviors. Infants spend about 80% of their time at the nest during the first 2 months. The lack of activity during this first intensive hiding stage may serve to ensure rapid growth. Unusual sounds or activity may cause young animals to dash wildly, if off the nest, or to freeze, if on it. Females will aggressively defend the young by striking the aggressor with their forelegs (Bodmer and Rabb, 1985).

Okapis, like other hiding ruminants, nurse relatively infrequently. However, these nursing bouts usually are several minutes long and often include infantile bunts directed at the mother's udder (Bodmer and Rabb, 1985; Horwich et al., 1983; Rabb, 1978). In the Ituri Forest, Zaire, a lactating female increased her time foraging, apparently to compensate for energy expended in milk production (J. Hart and T. Hart, 1989). Similarly, lactating okapis in captivity noticeably lose weight for the first 2–3 months of suckling (G. Rabb, pers. obs.). Maternal grooming of the infant's hindquarters during suckling is as in other ungulates (Bodmer and Rabb, 1985).

Infants begin to take solid food by the 3rd week, and rumination may be seen by the 6th week. In captivity, infants ordinarily first defecate 1–2 months after birth (Bodmer and Rabb, 1985; Pearson and Wright, 1968). Regular daily defecations appear in the 3rd month. In natural conditions, this lack of defecation may reduce chances of predator detection while infants are hiding (Bodmer and Rabb, 1985). Bacterial composition of the fecal material shifts from a gram-positive flora in suckling infants (*Coprococcus* predominant) to gram-negative in adults (*Treponema* and *Butyrivibrio* predominant—Mansfield, 1986).

Infants weigh from 14–30 kg at birth, double their mass by the end of the 1st month, and triple it by the end of the 2nd month. Shoulder height of the newborn is 72–83 cm and by the end of the 2nd month infants have grown approximately 15 cm in height. Thereafter, the rate of gain slows as the young okapi becomes more dependent on solid food (Bodmer and Rabb, 1985). Weaning takes place at roughly 6 months, although young will sometimes continue to suckle for >1 year. Females in captivity will accept suckling by infants other than their own (Grzimek, 1958; Lang, 1956*a*, 1956*b*).

The pelage and color of infants are basically similar to those of adults, with several notable exceptions. Newborns have pseudo-eyelash markings around the eyes, which fade by 2 weeks after birth. The hairs of the white stripes are longer than the adjacent dark hairs. Young also have a stiff black dorsal mane that extends from the occiput to the rump, with hairs about 4 cm long. The mane gradually thins out and disappears when the young are 12–14 months old. Horn development in males begins at around 1 year (G. Rabb, pers. obs.).

Nearly erupted milk dentition was observed in a 7-week-old (Jaspers and De Vree, 1978). Pattern of tooth eruption is divisible into five categories: first juvenile stage (complete milk dentition), second juvenile stage (M1 erupted, M2 incompletely erupted), subadult (M1 and M2 erupted, M3 incompletely erupted, and permanent premolars in eruption), adult (permanent molars, premolars, and incisors erupted), and senile (all teeth heavily worn). These age groups also can be distinguished by the sequence of closure of the cranial sutures. Most of the sutures of the cerebral skull close during juvenile or subadult life, whereas the sutures of the facial skull close much later in adult life. Several cranial sutures, such as the frontonasal, do not close until the senile stage. With growth, the skull lengthens disproportionately in the facial region while the braincase becomes relatively narrower (Jaspers and De Vree, 1978).

Okapis reach adult size at about 3 years. The youngest female to breed in captivity was 1 year 7 months at conception and the youngest male to breed was 2 years 2 months. Longevity of captives that survive past the 1st year is usually 15–20 years (Gijzen and Smet, 1974). One okapi was estimated to be 33 years old at death (Kruyfhooft, 1977) and a female successfully reproduced at 26 years of age (Gijzen and Smet, 1974).

ECOLOGY. The general relationships between the behavior and ecology of African ruminants described by Jarman (1974) and Estes (1974) can be extended to include the okapi (Leuthold, 1977). Okapis, relative to giraffes, are of small body size, inhabit forest or dense brush, forage selectively on browse, are solitary or in pairs (rarely over three individuals together), utilize concealment as an anti-predator strategy, and have small home ranges. Such comparisons suggest that many features of okapi behavior may be influenced or determined by habitat and food constraints (Hart and Hart, 1989).

Okapis have non-exclusive home ranges of several km^2 (Hart and Hart, 1989). Adult males have the larger home ranges, up to 10.5 km^2, and may move up to 4 km in a day. Females and subadults of both sexes appear to have smaller home ranges and move shorter distances daily (J. Hart and T. Hart, 1988). The density of okapis in the Ituri Forest near Epulu has been estimated at 0.6 animals/km^2 (Hart and Hart, 1989).

Okapis are limited in their distribution by ecological and physiographical conditions, such as large swampy areas or open savanna, rather than by specific species of plants (Lang, 1918). Forests inhabited are restricted to northeastern Zaire and can be classified into two major types of upland forest (Hart and Hart, 1989; Hart et al., 1986; Hart and Hart, 1986; Hart et al., 1989) and lowland swamp forest (J. Hart and T. Hart, 1988). One upland type, the mbau forest, is dominated by one tree species, *Gilbertiodendron dewevrei* (Leonard, 1952). The other upland forest type is characterized by a mixture of dominant trees, including *Brachystegia laurentii* and *Cynometra alexandri* (Hoyle, 1952; Leonard, 1952). The swamp forest is dominated by *Mitragyna stipulosa* (J. Hart and T. Hart, 1988).

The variation in forest types and seasonality in plant phenology are less important to the feeding habits of the okapi than the occurrence of preferred food species (Hart and Hart, 1989). Areas where trees have fallen account for about 5% of the forest areas inhabited, but provide a large share of the food of this highly-selective browser, which favors fast growing heliophilic species (J. Hart and T. Hart, 1988). The leaves of >100 species of plants are browsed in the wild. The most common understory species and the seedlings of the dominant canopy species are avoided. Monocots also are generally not eaten. Some 43 species of plants were eaten by okapis kept at the Epulu station (Gutzwiller, 1956; Ionides, 1955; Landsheere, 1957) and include species from the families Apocynaceae, Bignoniaceae, Caesalpiniaceae, Euphorbiaceae, Flacourtiaceae, Mimosaceae, Moraceae, Myristicaceae, Rubiaceae, Rutaceae, Sterculiaceae, Ulmaceae, and Violaceae. Among species preferred by okapi are *Aidia micrantha, Macaranga monandra, M. spinosa, Rinorea oblongifolia,* and *Tremma guineensis* (J. Hart, pers. obs.).

Okapis occur along stream beds, areas of secondary growth, and garden areas as well as in the primary forests. Okapis pull leaves off small branches with their long prehensile tongues, sometimes bending and breaking small trees to consume the foliage on the upper parts (Lang, 1918). They also consume smaller understory vegetation by clipping off the leafy upper portions. Okapis occasionally consume clay and burnt charcoal (Grzimek, 1972) and are reported to lick bat guano deposits in hollow trees (J. Hart and T. Hart, 1988).

Okapis may follow regular pathways through the forest (Bodmer and Gubista, 1988). Pitfall traps take advantage of this trait and are the principal means of capture of these elusive animals (Graham, 1956; Landsheere, 1957). Hunter-gatherer tribes of pygmies are indigenous to the forests inhabited by okapi, but depend largely on forest duikers (*Cephalophus* spp.) and other sources for their protein food rather than on the okapi (Hart and Hart, 1986). The leopard (*Panthera pardus*) is a significant cause of natural mortality for adults (J. Hart and T. Hart, 1988).

Causes of mortality in captives are parasitism, aging, bacterial infections, fungal diseases, viral diseases, and accidental trauma (Benirschke, 1978; Hediger, 1950). Nematodes, trematodes and helminth parasites are common in wild and recently captured individuals (Appelman, 1962; Baer, 1950; Bruhin, 1950; De Bois and Van Elsacker, 1988; Gourden, 1953; Kreis, 1950; Sarwar, 1955; Smits and Jacobi, 1965; Teuscher, 1955; Vuylsteke, 1935; Wetzel and Fortmeyer, 1964). The parasite causing the greatest mortality is the nematode *Monodontella giraffae*, which affects the bile ducts and liver (Frank et al., 1963).

Aging in okapis results in arthritis, overgrown hooves, and worn teeth. Okapis are susceptible to common bacterial infections, with pneumonia and septicemia occurring relatively frequently (Benirschke, 1978). Fungal diseases of the lung may occur in neonates; in one case, aspergillosis and mucor were traced to hay bedding (Pearson and Wright, 1968; Peters, 1975). Pox infections have caused severe illnesses in captives, but usually do not result in deaths (Peters, 1975; Zwart et al., 1971). Wheel-shaped viral particles, typical of a rotavirus, induce diarrhea in captive okapis, particularly in neonates, by causing malabsorption of electrolytes and nutrients. Rotaviral infections are usually transitory unless the animal is simultaneously infected with a virulent enteric bacterium or another enteric virus (Raphael et al., 1986).

BEHAVIOR. Okapis are in general solitary animals (J. Hart and T. Hart, 1988, 1989; Lang, 1918; Lydekker, 1908). However, two adults, one juvenile, and one young simultaneously used the same sections of forest with the juvenile being the most solitary individual. On a separate occasion and in a different section of forest one adult, one juvenile, and one yearling okapi were observed feeding together (Bodmer and Gubista, 1988).

Anecdotal reports on the activity pattern of free-ranging okapis state that they are either nocturnal (Lang, 1918; Lydekker, 1908) or diurnal (Ionides, 1955). On the basis of 3 years of field studies of radio-collared animals, J. Hart and T. Hart (1988) described the okapi as diurnal, but with some additional activity during the first hours of darkness.

Most information on the social behavior of okapis comes from captive animals. Males mark small objects, such as bushes, with urine, while crossing their forelegs in a dancelike movement (Lang, 1956*a*, 1956*b*). Marking with urine is a specialized behavior that occurs most frequently during periods of courtship (Lang, 1956*a*; 1956*b*; Walther, 1984). Females sometimes use common defecation sites that might represent a form of marking behavior (G. Rabb, pers. obs.). Okapis rub their necks on trees, depositing the tarry dermal exudate that all okapis have.

Prior to mating, the male approaches the female with exploratory sniffing concentrated primarily around the analgenital region. Females nearing an estrus peak are restless and may walk rapidly for many hours. When a courting pair meets they may stand head to tail in a reverse parallel position, often accompanied by circling and by mutual sniffing of the inguinal areas (Gijzen, 1958; Walther, 1960). The female often licks the penial sheath of the male. During these activities, females occasionally urinate and males test the urine by flehmen. Females also flehmen while inspecting male urine markings. Males then go into a series of behaviors that include head and neck stretches, head forward and upward positions, erect postures, nose lifting, and leg kicking. The receptive female responds by a head-low posture (Walther, 1960), often with the tail shunted aside (Gijzen, 1958; Lang, 1956*a*).

Immediately prior to copulation, a male moves his chest against the female's genital region, sometimes licking the female's back. The slender, tapered penis may be erect at this time. The male then mounts the female with his neck and head raised high (Gijzen, 1958; Walther, 1960). The momentary copulation is terminated by the stepping forward of the female. If the female is not receptive, she often kicks backwards at the male. Males may strike non-receptive females with their horns (Walther, 1960).

Okapis usually are tranquil and non-aggressive. However, they have several aggressive behaviors, including kicking and head throwing (Walther, 1960). Animals may give solid slaps using the side or top of the head, usually as a blow to the flank or rump. Aggressive kicking is often symbolic, with no contact being achieved, and may be performed with either the rear or front legs. Dominant animals have a more erect head and neck posture than subordinates (Walther, 1984). Submissive behaviors by males or females during a first meeting may include a completely prostrate posture with head and neck on the ground (Walther, 1960).

Social grooming is common in captives and usually is focussed at the earlobes and neck, possibly because these are the only areas not reachable during self-grooming. Okapis sometimes invite allogrooming with weak head-throws towards the partner's chest or side. (G. Rabb, pers. obs.).

Play behavior includes gambols and capers, the pooky, and lie and rise play (Bodmer and Rabb, 1985; Walther, 1962). Gambols and capers of okapis take the usual ruminant form (Fagen, 1981). The pooky is a specialized behavior that is characterized by a head-low and forward posture with a rapid tail wag. This play behavior may be performed while the okapi stands, walks, runs in a circle, or spins (Bodmer and Rabb, 1985). The posture involved is suggestive of flehmen behavior. Lie and rise play always is performed in a social context and is characterized by animals lying on the ground, sometimes even rolling on their sides, and then rising again to their feet (Walther, 1962). These forms of okapi play have been observed in both sexes and all age classes (Bodmer and Rabb, 1985). Mock aggression or dominance behavior may also be displayed in play (Walther, 1962). Infants play far more frequently than adults, with the duration of play behavior oscillating greatly among days (Bodmer and Rabb, 1985).

Vocal communication is more frequent than in giraffes. The three best documented sounds emitted are the chuff, moan, and bleat (Bodmer and Rabb, 1985; Lang, 1957). Chuffs are contact calls commonly used by both sexes and all ages, with the response often being a reciprocal chuff accompanied by the animals meeting. Infants sometimes produce a bleat vocalization that results in an immediate response by the mother. Bleats are evoked by young animals in stressful situations and are only emitted by animals under several months old. As the animal ages, the high-pitched bleat takes on a tinny quality (Bodmer and Rabb, 1985). A soft moaning sound is sometimes made by males during courtship. Other sounds observed include a whistle and a bellow in acute distress (G. Rabb, pers. obs.). The chuff and other vocalizations have infrasonic frequency components (to 9 Hertz), as documented by Elizabeth von Muggenthaler and David Gonzalez (in litt.).

GENETICS. The chromosomes of okapis have been of considerable interest because of the likelihood of a Robertsonian fusion (Benirschke et al., 1983). The first analysis of the chromosomes revealed $2n = 46$ (Ulbrich and Schmitt, 1969). However, Hösli and Lang (1969) later found two animals that had $2n = 45$. Since that time, many okapis have been examined; in U.S. zoo collections in 1991, 21 had a $2n = 45$ and 12 had a $2n = 46$. The inheritance pattern indicates that either diploid number may be found in the offspring of parents of only one number (Benirschke et al., 1983). An okapi born in 1991 at Cincinnati Zoo was trisomic and died at the age of 26 days of conditions related to this anomaly (M. Cambell, J. Dubach, A. Kumamoto, in litt.). The chromosomes involved were not those of the Robertsonian fusion phenomenon.

REMARKS. Major (1902*b*) suggested that the okapi was a member of the Palaeotraginae. However, the okapi has been placed in its own subfamily, Okapiinae, largely because it lacks the cingulum on the second upper deciduous molar that is characteristic of the palaeotragines (Arambourg and Piveteau, 1929; Bohlin, 1926; Thenius, 1972). Hamilton (1978) considered *Okapia* a sister-group of the advanced giraffids, and Matthew (1929) and Colbert (1938) recognized the outstanding similarities between extinct palaeotragines and the extant okapi and placed them in the same subfamily. Churcher (1978) suggested that *Okapia* represented a later stage of giraffid evolution, since data on its evolutionary history are sparse and it seems not to be a mainline palaeotragine. Using cladistic analysis, Geraads (1986) concluded with uncertainty that *Okapia, Palaeotragus*, and *Giraffa* were all members of the tribe Giraffini, Subfamily Giraffinae.

An international studbook is kept on okapi, and genetic and demographic analyses have been made for the long-term maintenance of captive populations (De Bois, 1988; Foose, 1978). The okapi is a protected species in Zaire. Although sparsely distributed, it is not rare in parts of its range and, accordingly, is not listed as a threatened species by other countries or by international agreement. Nevertheless, illegal hunting and deforestation are reducing the natural range of the species (Lang, 1918; J. Hart and T. Hart, 1988). The okapi occurs in Maiko National Park and possibly still in Virunga National Park. A 1,372,625 hectare section of the Ituri forest was declared a national faunal reserve for okapi in 1992.

We thank M. Rabb for literature searches, P. Bares for the typescript, and L. Fitzgerald for the photographs in Fig. 2.

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Editors for this account were TROY L. BEST, GUY N. CAMERON, and KARL F. KOOPMAN. Managing editor was CRAIG S. HOOD.

R. E. BODMER AND G. B. RABB, CHICAGO ZOOLOGICAL SOCIETY, BROOKFIELD, ILLINOIS 60513. PRESENT ADDRESS (REB): DEPARTAMENTO DE ZOOLOGIA, MUSEU PARAENSE EMILIO GOELDI, CAIXA POSTAL 399, 66.040, BELÉM, PARÁ, BRAZIL.