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Okapia johnstoni. By Richard E. Bodmer and George B. Rabb

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**Okapia Lankester, 1901**

**Okapia Lankester, 1901a**

Okapia Lankester, 1901a, 1901b:280. Type species Okapia johnstoni (Slater, 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 (Slater, 1901)**

Okapi

Eguas[?] johnstoni Slater, 1901:50. Type locality “in sybis fluvio Semilki adjacentibus” (= in the gallery forests along the Semiliki River, Zaire; Johnston, 1900).

Okapia johnstoni: Lankester, 1901a:281. Type locality “forest on the borders of the Congo Free State” (Zaire) (Lankester, 1901c).

Hellaodotherium tigrinum Johnston, 1901:270. Type locality “forests bordering the Semilki River, in Central Africa” (Zaire).

Okapia liebreschi Major, 1902a:73. Type locality “Mundalha, on road from Mawambi to Beni (N.E. frontier of the Independent Congo State)” (Zaire).

Okapia erikssonii Lankester, 1902a:417. Type locality “Semiliki forest” (Zaire) (Lankester, 1902b).

Ocapia kibalea Gatti, 1936:295. Type locality the Kibale-Ituri forest, as “delimitated by the Epulu, Lenja, Lindi and Semiliki rivers” (Zaire).

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

**DIAGNOSIS.** The okapi (Fig. 1) is a medium-sized giraffe, 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 palaeantragines. However, unlike its fossil relatives of the Palaeotraginae, O. johnstonii 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, 1914a; 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 velvet pelage of the body contrasting with tapered white or creamy white horizontal stripes on the rear haunches and upper front legs and with the ankles 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 Neuvile, 1909). The hair on the tips is often rubbed to the bone (Fraiport, 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 postero-dorsally (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 300 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 Ubangu, Uele, Aruwimi, and Ituri rainforests; from Libangi on the Ubangi River in the west to near Lakes Kivu and Edward in the east, north to Faradja, and south to the Sankuru and Maniena 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.
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 mouth 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 symphysis region of the mandible correlate with the shape of the tongue (Sukinias 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 Wira, 1950), with a ratio of brain mass to body mass larger in okapis than giraffes (Le Gros Clark, 1939; Portmann and Wira, 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 (Bourdeille, 1959).

The heart is similar to other ruminants (Burne, 1917; Candaele and Ghs, 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 Ghs, 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 Neuvillé, 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 cotyledonary and epitheliochorial (Hra-
decky, 1983; Hradecky et al., 1987). The choioallantoic villi of the okapi placenta show minimal branching and surface corrugation, whereas those 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 (Glattstein and Smit, 1980). The blood chemistry of the okapi is more like other ruminants than the giraffe. The blood urea nitrogen level is 13.4 mg %, P concentration is 11.4 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 Dombrov, 1984). Daily food intake (dry matter) of captive okapi ranges from 4.3 to 5.0 kg (Prins and Dombrov, 1984).

**Ontogeny and Reproduction.** Estrus cycles in captive okapis occur approximately every 15 days throughout the year (Novel, 1958). However, these cycles often are irregular (Loskutoff et al., 1982; Novel, 1958) and sometimes have long periods of quiescence (Novel, 1958). The follicular phase averages 8.3 days (Loskutoff et al., 1986). Levels of progesterone and estradiol are reduced from radiosteriod assay of urine of okapis (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, progesterone levels rise around the 8th day after complete luteal regression (Loskutoff et al., 1982). Pregnant okapis show rises in estrogens beginning 50 days postmatting (Loskutoff et al., 1983) and lactating okapis have progesterone and 3-glucuronide levels at baseline concentrations for at least 6 months postpartum (Loskutoff et al., 1986). The estrus 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 Czarka, in litt.).

 Gestation periods range from 414 to 493 days, with an average of 440 days (Gijzen and Smet, 1974; Novel et al., 1970; Rabb, 1978). Matings may occur during pregnancy (Gijzen, 1958; Novel 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. No evidence of mating 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 twins (Pearson et al., 1978). Abortions occur in captive okapis; maternal illness or stress often have been assumed to be the causes. However, in most cases the actual causes of abortions are unknown (Bennichschke, 1978).

Prepartum signs in females are swelling of the udder, viscous discharges from the vagina, and swelling of the vulva (Gijzen and Mortelmann, 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 through birth labor, but may recline for brief periods (Bullier, 1959; Davia, 1956; 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 Mortelmann, 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 'cries'-precocious, 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 actively, the infant begins to explore the environment, moving about in one place. Nesting behavior of infants thereafter shows distinct behavioral stages distinguished by the time spent on the hind 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 the 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 herbivorous ruminants, nurse relatively infrequently, however, these nursing bouts usually are several minutes long and often include infantile hunch directed at the mother's udder (Bodmer and Rabb, 1985; Horwich et al., 1983; Rabb, 1978). In the Iriu Forest, Zaire, a lactating female increased her time foraging, apparently to compensate for energy expended in milk production. Male age groups (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 3 months of age and may be seen walking on all fours by 6 weeks of age. Mature age groups may be seen by the 6th week. In captivity, infants ordinarily first defeate 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 the chances of predator detection while the infant is hiding (Bodmer and Rabb, 1985). Bacterial composition of the fecal material shifts from a gram-positive flora in suckling infants (Coprooccus predominant) to gram-negative in adults (Treponema and Butyrivibrio predominant—Mansfeld, 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 independent on solid food (Bodmer and Rabb, 1978). Infants reach full adult size 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 (Grimeek, 1958; Lang, 1956a, 1956b).

The pelage and color of infants are basically similar to those of adults, with several notable exceptions. Newborns have pseudoeasty 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 down the back toward the base of the neck, 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). Because of the differences in time of tooth eruption, it is divided 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). Tail 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. By the 3rd year the skull lengthens disproportionately in the facial region while the braincase becomes relatively narrow (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 old. There are no captive individuals 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 (Kruytbooth, 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 changes (1974) can be extended to include the okapi (L. Bodmer, 1971). 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 compar-
ions suggest that many features of okapi behavior may be influenced or determined by habitat and food constraints (Hart and Hart, 1989).

Okapis have a restricted home range of several km² (Hart and Hart, 1989). Adult males have the largest home ranges, up to 10.5 km², 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 Ekulu 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 by okapis 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 mba forest, is dominated by one tree species, Gilbertiodendron dewevrei (Leandri, 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 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 helophytic species (J. Hart and T. Hart, 1989). Okapis may eat leaves of 2-100 species of plants—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 in the Ekulu station (Cuttewiller, 1956; Jonides, 1955; Landsheere, 1957) and include species from the families Apocynaceae, Bignoniaceae, Caesalpinaceae, Euphorbiaceae, Flacourtiaceae, Mimosaceae, Moraceae, Myristicaceae, Rubiaceae, Rutaceae, Sterculiaceae, Ulmaceae, and Violaceae. Among species preferred by okapis are Meram, Nuxia, Mucuna, and Rinoea oehlensis, and Tremena 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 leaves of the upper layers. Okapis occasionally consume clay and burnt charcoal (Grzimek, 1972) and are reported to lick but guano deposits in hollow trees (J. Hart and T. Hart, 1989).

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 dwellers (Cephalophus sp.), 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 captive okapis include 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; Baur, 1950; Bruhin, 1950; De Bois and Van Elseghem, 1958; Gourdon, 1953; Kreis, 1950; Sarwar, 1955; Smith and Jacob, 1965; Truuscher, 1955; Vuylatéte, 1935; Wetzel and Fortemeyer, 1964). The parasite causing the greatest mortality is the nematode Monodentella 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 septicaemia 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, 1968b; Petersen, 1966). Infections caused severe illnesses in captive okapis, 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 (Jonides, 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 dance-like movement (Lang, 1956a, 1956b). Marking with urine is a specialized behavior that occurs most frequently during periods of courtship (Lang, 1956a; 1956b; 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 exudate that all okapis have.

Prior to mating, the male approaches the female with exploratory sniffing concentrated primarily around the anal region. Females nearing an estrus are restless and may urinate frequently 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 penis 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, and postures lifting and keeping the head on the hind legs. The receptive female responds by a head-lowering posture (Walther, 1960), often with the tail shrunk aside (Gijzen, 1958; Lang, 1956b).

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 associated with the 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 allo-grooming with weak head-throws towards the partner's chest or side. (G. Rabb, pers. obs.).

Play behavior includes gambols and capers, the pooky, and the rise and 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, some with their forelegs spread, 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 (Boodner and Rabb, 1985).
Vocal communication is more frequent than in giraffes. The three best documented sounds emitted are the chuff, moan, and bleat (Boodner and Rabb, 1985; Lang, 1957). Chuffs are contact calls commonly used by both sexes and all ages, with the response often being a reciprocating chuff accompanied by the animals meeting. Infants sometimes produce a brief 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 (Boodner 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 okapi 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, Hilde 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) suggested that the okapi was a member of the Palaeanotraginae. 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 palaeanotragines (Arambourg and Pivetaud, 1929; Bohl, 1926; Thien, 1972). Hamilton (1978) considered Okapia a sister-group of the advanced giraffids, and Mathew (1929) and Colbert (1938) recognized the outstanding similarities between extinct palaeanotragines 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 palaeanotragine. Using cladistic analysis, Geraads (1986) concluded with uncertainty that Okapia, Palaeanotragus, 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; Feosee, 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.

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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.