Oryx callotis (Artiodactyla: Bovidae)

DANA N. LEE, RICHARD W. DOLMAN, AND DAVID M. LESLIE, JR.

Department of Zoology, Oklahoma State University, Stillwater, OK 74078, USA; dana.lee10@okstate.edu (DNL)
Oklahoma Cooperative Fish and Wildlife Research Unit, Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK 74078, USA; richard.dolman@okstate.edu (RWD)
United States Geological Survey, Oklahoma Cooperative Fish and Wildlife Research Unit, Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK 74078, USA; cleslie@usgs.gov (DML)

Abstract: *Oryx callotis* O. Thomas, 1982 (fringe-eared oryx) is a relatively large, long-bodied bovid, with an appropriate common name because of its distinguishing tufts of hair extending from the ends of the ears. It occupies arid lands in Kenya and Tanzania. *O. callotis* can go up to a month without drinking water if succulent vegetation is available. Some herds have been semidomesticated, and 60% of the presumed 17,000 wild individuals exist in wildlife reserves, currently receiving some protection from settlement and poaching. *O. callotis* is considered "Vulnerable" by the International Union for Conservation of Nature and Natural Resources but as a subspecies of *O. beisa*, which is listed as "Near Threatened."

Key words: East Africa, fringe-eared oryx, Galana Ranch, Kenya, oryx, savanna grasslands, Tanzania

Oryx de Blainville, 1816

Capra Linnaeus, 1758:69. Part (*Capra gazella* Linnaeus, 1758).
Antilope Pallas, 1766:16, 17. Part (*Antilope gazella* Pallas, 1766:17 [= *Capra gazella* Linnaeus, 1758] and *Antilope leucoryx* Pallas, 1766:17).
Cemas Oken, 1816:741. Unavailable name (International Commission on Zoological Nomenclature 1956: Opinion 417).
Cerophorus de Blainville, 1816:74. Part; a collective name for horned ruminants (Palmer 1904:172; Ellerman and Morrison-Scott 1966:379); no type species selected.
Oryx de Blainville, 1816:75. Type species *Antilope oryx* Pallas, 1766, by original designation; proposed as a subgenus of *Cerophorus* de Blainville, 1816.
Onyx Gray, 1821:307. Incorrect subsequent spelling of *Oryx* de Blainville, 1816.
Antilope: Cretzschmar, 1826:22. Not *Antilope* Pallas, 1766.
Antilope: Rüppell, 1835:14, plate 5. Not *Antilope* Pallas, 1766.
Aegoryx Pocock, 1918:221. Type species *Aegoryx algazel* Pocock, 1918, by monotypy.

CONTEXT AND CONTENT. Order Artiodactyla, suborder Ruminantia, infraorder Pecora, family Bovidae, subfamily Antilopinae, tribe Hippotragini. We followed the new ungulate taxonomy of Groves and Grubb (2011), who thoroughly and quantitatively updated the family Bovidae,
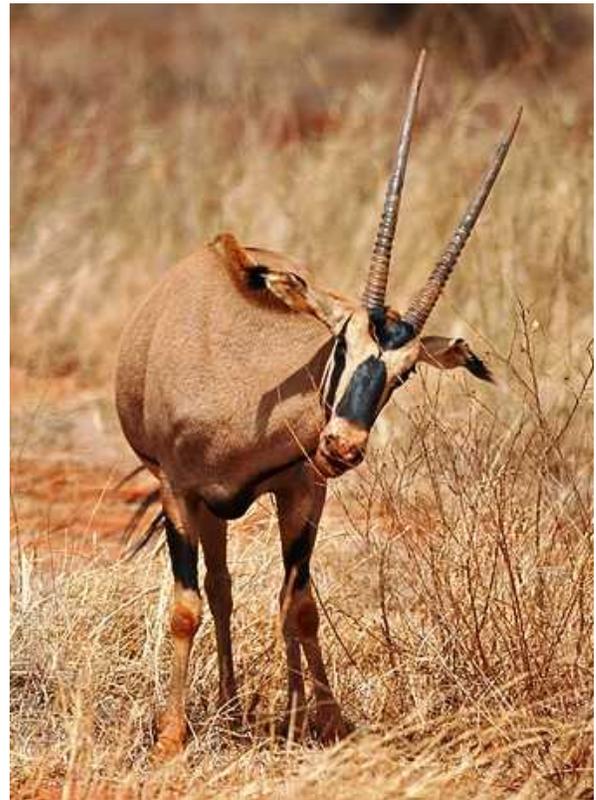

Fig. 1.—Mature male *Oryx callotis* south of Mount Kenya in central Kenya; note the diagnostic tufts of hair extending from the ends of the ears, pronounced horn rings, and the selective browsing. Photograph by Pål A. Olsvik used by permission.

among others, and reduced the traditional subfamily and tribal arrangement from Simpson's (1945) 5 subfamilies and 12 tribes to 2 subfamilies (Bovinae and Antilopinae) and 11 tribes. Groves and Leslie (2011) provided a narrative synthesis of those familial changes, followed by individual accounts and maps of each of the 279 species (Groves et al. 2011)—an increase from the 143 bovid species listed by Grubb (2005).

Forms of *Oryx* are found from the Arabian Peninsula westward into East Africa across the Sahara and southward into southwestern Africa, which represents a morphocline from primitive to derived species, related to horn length, skull breadth, and associated body size (Grubb 2000; Groves and Grubb 2011). Grubb (2005) recognized 4 species of *Oryx* (*O. beisa*, *O. gazella*, *O. dammah*, and *O. leucoryx*), whereas Groves and Grubb (2011) and Groves (2011) split *O. beisa* into 3 distinct species: *O. beisa*, *O. gallarum*, and *O. callotis*. The latter 2 were most recently considered subspecies of *O. beisa*, despite *O. callotis* being originally described as a separate species by O. Thomas (1892). This new taxonomy is rooted in the phylogenetic species concept and extensive morphological analyses. It is supported by expanding knowledge and interpretation of mitochondrial and nuclear DNA analyses across many species of ungulates (Groves and Grubb 2011) and, here, species of *Oryx* in particular (Iyengar et al. 2006; Masembe et al. 2006). The following key was prepared with specific characteristics, measurements, and statements provided by Groves and Grubb (2011) and Groves (2011).

1. Pelage very pale white, with washed-out, light reddish markings on face and neck, and a vague stripe along the lower flanks to the haunches; very long horns on both sexes, "scimitar" shaped, sweeping upward, backward, and downward, generally >34 horn rings; extinct in the wild but formerly throughout Saharan Africa . . . . *O. dammah*
   Pelage brown to ocher-gray to near white with various black, often distinct, black markings on face, flanks, and legs; horns on both sexes arise parallel to the plane of the face, with slight to no downward projections at their ends; generally <34 horn rings 2
2. Pelage white, with distinct black markings from the eye downward to jaw connecting with throat patch; uniformly chocolate-brown to black legs with white patches just above the hooves; formerly throughout the Arabian Peninsula and extinct in the wild, now several reintroduced, free-ranging populations there . . . . *O. leucoryx*
   Pelage varies from gray to ocher-gray to dull brown with various dark body markings; black facial markings below the eye not connecting to the throat patch; legs with various bands or patches of dark brown to black; occurs in southwestern or northeastern Africa 3
3. Pelage pale fawn-gray, with a 90- to 116-mm black dorsal stripe and a very wide and distinct 119- to 129-mm flank band; mean greatest lengths of skulls from various locations, 409–425 mm; occurs in southwestern Africa . . . . *O. gazella*
   Pelage ocher-gray (pinkish wash) to dull brown, less pronounced dorsal stripe and flank band; greatest lengths of skulls from various locations, 347–398 mm; occurs in northeastern Africa 4
4. Pelage dark, dull, and brown to fawn; generally no connection between nasal and median face bands; dorsal stripe very reduced; diagnostic ear tufts of 5.1- to 7.6-cm hairs; occurs south of the Tana River in central Kenya south to northeastern Tanzania . . . . *O. callotis*
   Pelage ocher-gray (pinkish wash) to pale-to-pure gray; dorsal stripe more pronounced; lacking ear tufts. 5
5. Pelage ocher-gray (pinkish wash) but not extending below the 20- to 44-mm flank band; dorsal stripe 30–43 mm but generally vague or lacking; occurs north of the Tana River in northern Kenya, presumably some distance into Somalia and southeastern Ethiopia . . . . *O. gallarum*
   Pelage pale-to-pure gray; flank band 39–58 mm; dorsal stripe up to 71 mm in males, sometimes extending to the withers and in some cases fully up the neck; occurs in northern and central Somalia, northern Ethiopia, and western Eritrea . . . . . *O. beisa*

Oryx callotis O. Thomas, 1892
Fringe-eared Oryx

Oryx callotis O. Thomas, 1892:195, plate XIV. Type locality "neighbourhood of Mount Kilimanjaro."

Oryx beisa callotis: Lydekker, 1908:285. Name combination.

Oryx gazella subcallotis Rothschild, 1921:209, 210. Type locality "S. Brit. E. Africa" (=southern Kenya); perhaps a synonym of *Oryx gallarum* Neumann, 1902 (Groves and Grubb 2011:207).

O[ryx]. g[azella]. callotis: Rothschild, 1921:209. Name combination.

CONTEXT AND CONTENT. Context as for genus. No subspecies are recognized.

NOMENCLATURAL NOTES. The generic name *Oryx* can be variously traced in Greek to mean pickax referring to the sharp horns and in Latin to mean gazelle. The specific epithet *callotis* is from the Greek words *call* meaning beautiful and *ot* referring to the ear. "Beautiful ears" aptly describes the fringe-eared oryx (Fig. 1).

DIAGNOSIS

Oryx callotis is appropriately named for its most distinguishable feature, sharply pointed ears adorned with terminal black tufts of hair 5.1–7.6 cm long (Thomas 1892) that extend past the edges of the ears (Sclater and Thomas 1899) and often droop downward as they lengthen with age (Fig. 1). The other 5 species of *Oryx* (Groves 2011:plate 40; Groves and Grubb 2011) have generally rounded ears and all lack ear fringes (Thomas 1892). *O. callotis* has long, straight horns similar to those of *O. gazella* (gemsbok), *O. beisa* (beisa oryx), *O. gallarum* (galla oryx), and *O. leucoryx* (Arabian oryx), but they are not curved backward and downward like those of *O. dammah* (scimitar-horned oryx) or spirally twisted like those of *Addax nasomaculatus* (addax—Krausman and Casey 2007). Tips of the horns are 231–409 mm apart, which is wider than on *O. beisa* and *O. gallarum*; horns of *O. callotis* are relatively short and thick at the base and most comparable in thickness to those of *O. gallarum* (Groves 2011; Groves and Grubb 2011).

Pelage color of *O. callotis* most closely resembles that of *O. beisa*, and it is duller, darker, and browner than on *O. gallarum*. As on *O. beisa*, there is a black line passing through the eyes of *O. callotis*, but its black markings extend farther down to under the throat than on *O. beisa* (Thomas 1892). The flank band on *O. callotis* is 30–44 mm wide ($n = 2$), and the dorsal stripe is reduced (25–30 mm wide), faint, and confined to the rump (Groves and Grubb 2011). In contrast, the flank band on *O. beisa* is 39–58 mm wide; the dorsal stripe is 56–71 mm wide in males ($n = 2$) and 31–46 mm wide in females ($n = 2$), and it often extends "fully up the neck, or three-quarters of the neck, or just to the whithers" (Groves and Grubb 2011:207). *O. gazella* has the most pronounced flank band (119–229 mm wide) and dorsal stripe (adults, 90–116 mm wide; juveniles, 54–74 mm wide—Groves and Grubb 2011).

GENERAL CHARACTERS

All species of *Oryx* are compact and muscular, with relatively long bodies, short and slender legs, and broad necks (Kingdon 1997). There are no marked differences between male and female *Oryx callotis*. The body of both sexes is a rich fawn color with a distinctive, narrow (3–4.4 cm—Groves 2011), horizontal black band across the flank region and black tufts of hair above the hooves resembling false hooves (Kingdon 1997). The muzzle is white with striking black markings across the front and on the side of the face through the eyes and below the base of the ear down to the throat (Sclater and Thomas 1899; Thomas 1892; Groves 2011). The skin on the neck of *O. callotis* is extraordinarily thick (Sclater and Thomas 1899), and a short, stiff, chestnut-brown mane is present (Estes 1991;

Groves 2011). The long and slender tail ends with a flowing brush of long black hairs (Estes 1991).

Few measurements have been reported specifically for *O. callotis* (Groves 2011; Groves and Grubb 2011). Generally, mature individuals of the northeastern African oryx group weigh 116–188 kg (females) and 167–209 kg (males), shoulder heights are 110–120 cm, head-to-body lengths are 153–170 cm, and tail lengths are 45–50 cm (Kingdon 1997; Groves 2011; Groves and Grubb 2011). One sample of 16 *O. callotis* of unreported sex in southeastern Kenya had a mean body mass of 126.9 kg (coefficient of variation [CV] = 11.5%—Ssemakula 1983), suggesting that the sample was dominated by immature individuals. The only age-specific insight on mass is for two 3-year-old male *O. callotis* that had dry-season masses of about 176 kg, based on dressed carcass mass of 95 kg ± 5.0 *SD*, 54% of the total mass (Onyango et al. 1998).

Horns of both sexes are long, straight, and very slightly curved backward and downward (Estes 1991). They are heavily ringed from their bases up to about one-half of their lengths (Fig. 1), depending on wear from jousting and "brooming" on vegetation, and then smooth to their tips. Mean number of rings per horn tends to be lower for *O. callotis* (16.25 rings, range 13–23 rings, $n = 4$) than for *O. gallarum* (21.17 rings, range 17–24 rings, $n = 12$) and *O. beisa* (20 rings on a single sample—Groves and Grubb 2011:table 56). Horns of all *Oryx* taxa arise from the top of the skull, parallel to the plane of the face (i.e., premaxillae, nasal, and frontal bones; Fig. 1); this contrasts with many other bovids, including other Hippotragini (e.g., *Hippotragus*), horns of which arise upward from the top of the skull and are not parallel to the plane of the face.

Unlike many horned ungulates, female and male *O. callotis* (and other *Oryx* species) are very difficult to differentiate based on shape and length of their horns (Groves and Grubb 2011; C. P. Groves, pers. comm.). According to early reports, horns on female *O. callotis* are 76–81 cm long (Thomas 1892) and are typically longer, straighter, and thinner than those of males, which may serve females better as a defense against predators (Packer 1983). Horns of males are somewhat shorter but thicker at the base (circumference 12–14 cm—Groves 2011) than those of females, permitting twice as much force in intrasexual combat (Packer 1983). Female and male *O. callotis* are also difficult to distinguish in the field unless external genitalia or obvious sexual behaviors can be seen, or offspring are present with females.

DISTRIBUTION

Oryx callotis currently is found in southeastern Kenya and northeastern Tanzania (Fig. 2), having expanded into the Serengeti Plain in Tanzania in the 1970s (Walther 1978; Estes 1991; Groves 2011). Populations of *O. callotis* and the *O. gallarum* are geographically separated by the Tana River
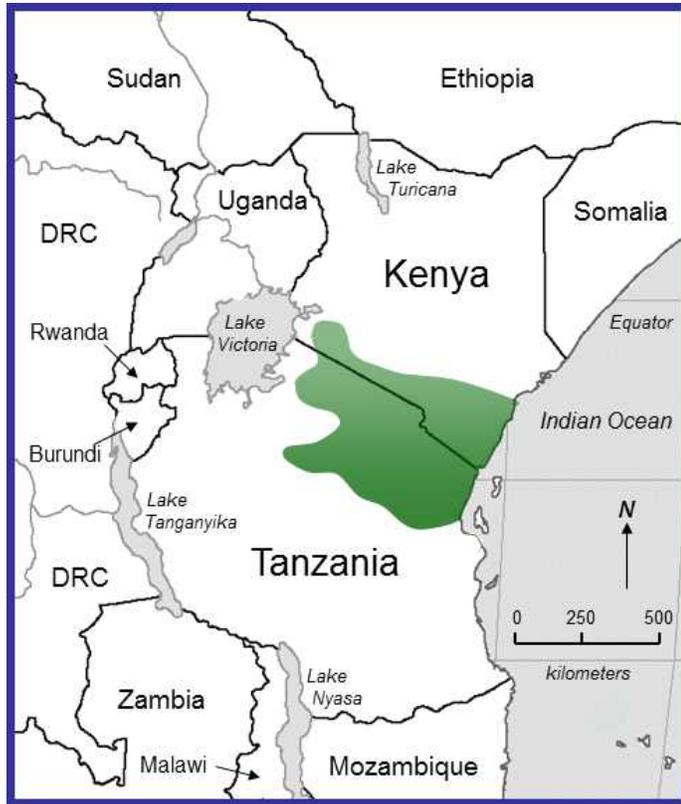
Fig. 2.—Distribution of *Oryx callotis* in Kenya and Tanzania, East Africa; the northern distributional boundary in Kenya is the Tana River (base map from Brigham Young University Geography Department, https://geography.byu.edu/pages/resources/outlineMaps.aspx).

and the Aberdare Mountains in southern Kenya (Stewart and Stewart 1963; Ansell 1972; Groves 2011). Groves and Grubb (2011:207) remarked on specimens of *O. callotis* "from S of Mt. Longido, and from 100 mi. S of Kilimanjaro."

Much of what is known about the ecology and physiology of *O. callotis* came from studies on the Galana Ranch (5,000 km^2) in southeastern Kenya during the 1970s. More than 150 individuals were reared in semidomestication as part of a mixed wild–domestic ranching effort (Stanley Price 1978). When Kenya banned commercial production and sale of wildlife in 1977 (Groves and Leslie 2011), the ranch suspended its work with *O. callotis* (see "Husbandry").

FOSSIL RECORD

Fossil evidence (Gentry 2000; Bibi et al. 2009) and phylogenetic analyses of behavior and various aspects of morphology and anatomy (Vrba and Schaller 2000) suggest that the tribes Hippotragini (oryxes and roan and sable antelopes), Alcelaphini (hartebeests and wildebeests), and Caprini (sheep, goats, and relatives) form a monophyletic clade of bovids, with a common ancestor dating to the middle Miocene, about 15 million years ago. Fossil genera such as *Protoryx*, *Pachytragus*, *Tethytragus*, and *Gentrytragus* may be early offshoots of the common ancestor of the Hippotragini–Alcelaphini–Caprini clade (Bibi et al. 2009).

The most recent common ancestor of all Hippotragini was found at Toros-Menalla, Chad; these fossils had "a mix of derived and primitive characters" (Bibi et al. 2009:5) and were dated from the late Miocene, about 7 million years ago (Bibi et al. 2009; Geraads et al. 2008; Harris et al. 1988). Younger fossils, specific to *Oryx*, were found scattered within 750 m of exposed strata on the northwestern shore of Lake Turkana in the extreme northwestern corner of Kenya, near the Ethiopian border (Harris et al. 1988)—an area now within the distribution of *Oryx gallarum* (Groves 2011); specimens were dated at 1.0–3.4 million years old. These fossils were used in cladistic analyses to estimate that the African oryx lineage originated during the late Pliocene–early Pleistocene, about 2.5 million years ago (Vrba 1995).

FORM AND FUNCTION

The skull of *Oryx callotis* is "comparatively broad" (Fig. 3) relative to other northeastern African oryxes (Groves and Grubb 2011:207). Few skull measurements of *O. callotis* have been published, but skull characteristics that have been measured include (mean $\pm$ SD in mm): skull length, 377.40 $\pm$ 9.156 ($n = 15$, not differentiated by sex); biorbital breadth, 157.36 $\pm$ 8.031 ($n = 18$); toothrow length, 105.94 $\pm$ 4.176 ($n = 18$); horn length, 743.42 $\pm$ 70.21 ($n = 19$); horn breadth, 127.50 $\pm$ 10.308 ($n = 5$); and horn tip-to-tip distance, 293.00 $\pm$ 81.273 ($n = 4$—Groves and Grubb 2011:table 56). Dental formula of *O. callotis* is i 0/3, c 0/1, p 3/3, m 3/3, total 32.

Oryx callotis is categorized as a roughage grazer and eats primarily coarse, fibrous plants (Hofmann and Stewart 1972). It has a ruminal, 4-chambered digestive system that slows passage of food and enhances breakdown of plant material, and there are no absorptive papillae in the rumen (Hofmann and Stewart 1972). Fecal particle sizes from digestive residue (Poppi et al. 1980) reflect dietary choice in ruminants, and those from *O. callotis* suggest it is primarily a grazer; percentage of fecal particles passing through various sieve sizes are: 4-mm sieve, 0.72%; 2-mm sieve, 5.10%; 1-mm sieve, 4.47%; 0.5-mm sieve, 8.69%; 0.25-mm sieve, 15.05%; 0.125-mm sieve, 24.07%; and <0.125-mm sieve, 41.90% (Clauss et al. 2002). In contrast, passages of fecal particles in an intermediate feeder such as the nilgai (*Boselaphus tragocamelus*—Leslie 2008) are: 4-mm sieve, 2.72%; 2-mm sieve, 1.23%; 1-mm sieve, 5.40%; 0.5-mm sieve, 9.32%; 0.25-mm sieve, 12.71%; 0.125-mm sieve, 14.05%; and <0.125-mm sieve, 54.57% (Clauss et al. 2002). In feeding trials with a free-ranging mixed herd of 5 *O. callotis* (tame and castrated males), 5 sheep, and 5 zebu cattle on the

Fig. 3.—Ventral, dorsal, and lateral views of skull and lateral view of mandible of *Oryx callotis* (United States National Museum of Natural History, specimen 18944, sex unknown), collected by W. L. Abbott (date unknown) near Taveta in southern Kenya and the northern border of Tanzania. Greatest length of skull is 374.4 mm, average basal circumference of horns is 15.2 cm, left horn length is 70 cm, and tip-to-tip distance is 22.8 cm. The basal circumference of horns may suggest a male specimen, but the high degree of similarity of horn and skull measurements of female and male *O. callotis* makes it impossible to know the sex of this specimen (C. P. Groves, pers. comm.).

Galana Ranch in southeastern Kenya, daily fecal output in grams per day and percent fecal nitrogen concentrations of *O. callotis* were 1,378 ± 91.2 *SE* and 1.22 ± 0.051 in the dry season (April–August) and 969 ± 67.5 and 1.57 ± 0.022 in the wet season (January–May—Stanley Price 1985). The relatively low levels of fecal nitrogen suggested diets of only 7.6–10.2% crude protein (Leslie et al. 2008) and reflected the low-quality grasses that *O. callotis* generally consumed, regardless of season (Stanley Price 1985).

Oryx callotis is physiologically adapted to survive in arid environments characteristic of Kenya and Tanzania by minimizing both water loss and heat gain (Taylor 1970a, 1970b; King et al. 1975; King 1979). Panting and evaporative cooling help keep the body temperature lower than ambient temperatures, but this increases the volume of water lost from an individual to the environment. To conserve water, *O. callotis* can reabsorb water during digestion, concentrate its urine, and extract most of the water from its feces (Estes 1991). Its body temperature can rise from its normal 35.7°C to 45°C before an individual begins cooling behaviors, such as nasal panting and sweating; cooling the blood as it passes through the nasal passages minimizes damage to the brain (Estes 1991). Other water-saving adaptations include seeking shade and reducing activities to slow heat gain (Estes 1991; King et al. 1975) and minimizing rumination during the hottest periods of the day (Lewis 1977; Stanley Price 1985).

In a comparative study of effects of trampling of vegetation and compaction of soil by wild and domestic bovids relative to subsequent erosion on the Galana Ranch, mean total hoof area and mean hoof pressure of 16 *O. callotis* (sex not reported) were 148.72 cm² ($CV = 10.1$%) and 0.86 kg/cm ($CV = 10.5$%), respectively (Ssemakula 1983). Both metrics place *O. callotis* between domestic sheep and goats on the low end (55.15–63.36 cm² and 0.69–0.73 kg/cm) and domestic cattle and common elands (*Taurotragus oryx*) on the high end (234.90–314.22 cm² and 0.98–1.09 kg/cm). Stocking densities and other management practices of mixed wild–domestic operations were potentially more responsible for trampling damage than "inherent differences in [species-specific] ecological impact" (Ssemakula 1983:327).

ONTOGENY AND REPRODUCTION

Oryx callotis is sexually mature by 18–24 months (Kingdon 1997), and gestation is 8.5–9 months (Wacher 1988). Neonates weigh 9–11 kg (Benirschke 2002) and are born with small horn-buds covered with hair (Estes 1991). Benirschke (2002) examined 3 captive pregnant females that died at the San Diego Wild Animal Park, California (United States), in different stages of gestation from early (neonatal mass = 51.6 g or just 0.5% of an average full-term mass of 10 kg, crown-to-rump length = 10 cm) to midterm (4.625 kg or 46%, 48 cm). All 3 pregnancies were in the right uterine horn, and there were no subplacentas. As in most mammals, very thick and abundant mucus occurred in the endocervical canal (Benirschke 2002). In the midterm pregnancy, 100 moderately convex cotyledons, 4–9 cm in diameter, were detected, and the epitheliochorial placenta weighed 1,200 g. The umbilical cords were 3–19 cm by 2.5 cm, depending on the length of pregnancy and fetal development; 2 were straight and the other was slightly spiraled to the right (Benirschke 2002).

Female *O. callotis* breed and give birth, usually to a single offspring, throughout the year, but young are often more numerous early in the dry season from June to August (Leuthold and Leuthold 1975). When it is time to give birth, the female moves away from the herd (Wacher 1988). The newborn stays hidden for the first 2–3 weeks, and both mother and offspring rejoin the herd 3–4 weeks after birth (Wacher 1988). Within a few weeks of rejoining the herd,

females can mate again (Wacher 1988; Estes 1991) and can produce an offspring every 10.5–11 months under good environmental conditions (Stanley Price 1978).

Cryopreserved sperm from a captive male *O. callotis* was considered to be of good quality because of its high survivability, motility, capacitation, and acrosome reaction and therefore suitable for in vitro fertilization (Kouba et al. 2001). Effective in vitro fertilization protocols could be implemented to increase genetic diversity and reduce the risk of inbreeding depression in captive *O. callotis*.

ECOLOGY

Space use.—*Oryx callotis* thrives in arid grasslands and bushlands, but its highest densities are found in grasslands and woodlands that receive annual rainfall of 400–800 mm (Kingdon 1997). *O. callotis* is typically found in grasslands of *Digitaria macroblephara* and *Panicum coloratum*, woodlands of *Acacia tortilis* and *Commiphora schimperi*, bushlands of *Acacia stuhlmannii*, and bushy grasslands of *Pennisetum mezianum* and *A. stuhlmanii* (Kahurananga 1981). Physiognomy of these varied habitats directly affects food availability and levels of nutrition, which in turn affect densities that populations of *O. callotis* and other East African herbivores can attain. For example, patterns of aboveground primary production (= food availability) vary considerably under canopies (705 g/m^2) and in root zones (430 g/m^2) of *Acacia*, and beyond into open grasslands (361 g/m^2), in Tsavo National Park, Kenya (Belsky et al. 1989).

Oryx callotis is nomadic, with home ranges typically <400 km^2 (Wacher 1988). Kingdon (1997) summarized home-range size for *O. beisa* in general as 200–300 km^2 for females and 150–200 km^2 for males. Location of rainfall and availability of green vegetation determine movements of groups (Wacher 1988). One herd traveled 17 km in the same direction in a single day, and a male walked as much as 4 km in an hour (Estes 1991). Densities of *O. beisa* appear to be low at 0.5–0.2 individuals/km^2 (East 1999; Graham et al. 1996; Thouless 1995). Comparable estimates are not available for wild populations of *O. callotis*, but the highest reported density of semiconfined *O. callotis* on Galana Ranch in southeastern Kenya was 1.4 individuals/km^2, with an estimated 6,000–8,000 individuals, in the late 1970s (Stanley Price 1978).

Diet.—Like other oryx species, *Oryx callotis* is herbivorous, eating >80% grasses, as seasonal changes in availabilities and nutrient content permit. In southern Kenya, grasses eaten by *O. callotis* include *Bothriochloa*, *Brachiaria*, *Chloris roxburghiana*, *Cymbopogon pospischilii*, and *Enneapogon cenchroides* (Field 1975). In addition to grasses, *O. callotis* eats large amounts of herbaceous *Commelina* and *Indigofera schimperi* in the wet season and tubers and swollen stems of *Pyrenacantha* in the dry season (Field 1975). The short face and dental morphology (wide incisor row and high-crowned molars) of *O. callotis* are adapted for selecting nutrient-rich parts of coarse grasses (Field 1975; King and Heath 1975; Estes 1991). Annual diets of *O. callotis* at Galana Ranch averaged 83.3% grass (± 16.2% SD), 8.5% forbs (± 13.5%), and 7.9% browse (± 7.9%) in 1970–1972 (Field 1975). Monthly diets varied considerably within and between wet (November–May) and dry (June–October) seasons: wet season = 47.9–98.7% grass, 0–38.6% forbs, and 0–13.5% browse and dry season = 43.6–99.1% grass, 0–51.9% forbs, and 0–27.8% browse (Field 1975).

To supplement drinking water, *O. callotis* eats succulent plant species and digs up roots, bulbs, and tubers (Ayeni 1975; Estes 1991; Kingdon 1997). Individuals have been observed repeatedly uncovering tubers of *Pyrenacantha malvifolia* by digging with one forefoot; after a tuber is exposed, they scrap off chunks with their incisors (King et al. 1975), staining their muzzles red with dirt in the process (Root 1972). Other selective feeding strategies probably extend the time *O. callotis* can go between drinking, such as feeding on the dwarf shrub *Disperma* predominately at night when the leaves can contain 40% preformed and metabolic water, if relative humidity is high, instead of only 1% water during the daytime (King 1979; Taylor 1968). Congeneric *O. gallorum* and Grant's gazelles (*Nanger granti*) could theoretically be independent of free water if they concentrated their feeding on leaves of *Disperma* at night when its percent water content can rise, at a relative humidity of 85%, from near zero to about 40% in 6 h after sunset (Taylor 1968).

If succulent grasses are available, *O. callotis* can survive up to a month without drinking standing water (Stanley Price 1978). One domesticated group refused water for 25 days (King and Heath 1975), but *O. callotis* will often drink if water is regularly available (Stanley Price 1985; Kingdon 1997). *O. callotis* has been observed visiting artificial water holes in Tsavo National Park, Kenya, but very infrequently (Ayeni 1975). In a controlled study on the Galana Ranch, Kenya, a group of *O. callotis* was provided water every other day, and each individual drank 34 ml kg W$^{-0.85}$ day^{-1} ± 6.6 SE (equivalent of 2.2 l/day) in the wet season and 56 ± 3.3 ml kg W$^{-0.85}$ day^{-1} (3.6 l/day) in the dry season, which was considerably less than domestic sheep and zebu cattle (Stanley Price 1985). *O. callotis* requires only 15–25% of the daily water that domestic cattle require (King and Heath 1975; Stanley Price 1978). Water turnover rates of *O. callotis* (30–124 ml kg^{-1} day^{-1}) are generally lower than those of dromedary camels (*Camelus dromedarius*—38–76 ml kg^{-1} day^{-1}), common elands (66–177 ml kg^{-1} day^{-1}), and domestic livestock (63–178 ml kg^{-1} day^{-1}—King et al. 1975; King 1979).

Diseases and parasites.—Chemical dipping for ectoparasites, as is often done for domestic livestock, is not required in captive populations of *Oryx callotis* because they rarely have ticks (King and Heath 1975; Stanley Price 1978).

Additionally, no trypanosomiasis antibodies have been recovered from captive individuals; thus, they are either not a reservoir for the parasite or are resistant to the disease (Stanley Price 1978). Viral malignant catarrhal fever is typical in cattle and wildebeest (*Connochaetes*) in East Africa. Antibodies to this necrotizing virus were isolated in herds of *O. callotis* at Galana Ranch, but viral particles were never recovered (Mushi and Karstad 1981).

Diarrhea from bacterial infections was identified to be the most frequent cause of death of neonates in captive zoo populations of *O. callotis*. Specifically, in San Diego Wild Animal Park from 1980 to 1981, the bacteria *Cryptosporidium* and *Salmonella typhimurium* were cultured from epithelial cells of the small intestine of 2 neonatal *O. callotis* (<21 days old) with diarrhea (Van Winkle 1985). Although these infections can be serious, mortality is usually low when young *O. callotis* are treated with supportive therapy (Van Winkle 1985). Twenty *O. callotis* from the Kilifi area in southeastern Kenya tested negative for caprine pleuropneumonia (*Mycoplasma* strain F38) in the late 1970s; this bacterial infection, which can cause acute and fatal pleuropneumonia, was documented in other ungulates capable of transmitting it to *O. callotis* (e.g., Cape buffalo [*Syncerus caffer*] and common impala [*Aepyceros melampus*]—Paling et al. 1978).

Interspecific interactions.—In Kenya and Tanzania, *Oryx callotis* can occur in the same area as Cape buffalo, common eland, Maasai giraffe (*Giraffa tippelskirchi*), southern gerenuk (*Litocranius walleri*), southern lesser kudu (*Ammelaphus australis*), ellipsen waterbuck (*Kobus ellipsiprymnus*), defassa waterbuck (*K. defassa*), common impala, Grant's gazelle, perhaps Peters's gazelle (*Nanger petersii*), and ostrich (*Struthio camelus*—Stanley Price 1978). *O. callotis* often was seen with herds of eastern Thomson's gazelle (*Eudorcas thomsonii*), Serengeti Thomson's gazelle (*E. nasalis*), kongoni (*Alcelaphus cokii*), plains zebra (*Equus quagga*), eastern white-bearded wildebeest (*Connochaetes albojubatus*), and Serengeti white-bearded wildebeest (*C. mearnsi*), although *O. callotis* did not interact or move with herds of other species in Serengeti National Park, Tanzania (Walther 1978).

Oryx callotis uses water holes during daylight hours in association with other "prey species" to enhance predator detection (Ayeni 1975). Individuals might give alarm snorts and watch intently if lions (*Panthera leo*—Haas et al. 2005) or cheetahs (*Acinonyx jubatus*—Krausman and Morales 2005) are nearby, but they usually pay no attention to golden jackals (*Canis aureus*) or spotted hyenas (*Crocuta crocuta*—Walther 1978). If individuals of another prey species are alarmed or flee, *O. callotis* will follow (Walther 1978). On Galana Ranch, Kenya, a few individuals of *O. callotis* were killed by lions and leopards (*Panthera pardus*) annually (King and Heath 1975).

HUSBANDRY

Efforts to domesticate *Oryx callotis* were initiated on Galana Ranch in southeastern Kenya in the early 1970s. More than 150 wild individuals were captured and transferred to a large holding pen. New individuals usually charged around the pen for the 1st few days, but then joined the captive herd within 6 weeks. During the day, they were herded out to graze and brought back to a corral at night (Stanley Price 1978). In the 1st year, only 10% of the newly captive *O. callotis* could not be successfully habituated to the captive conditions. After 3 years of capture and handling, techniques improved and mortality of *O. callotis* was reduced to 7% during the first 6 weeks and 4% thereafter (King and Heath 1975).

Oryx callotis is ideal for domestication because it breeds well in captivity, producing an offspring every 10.5–11 months (King and Heath 1975; Stanley Price 1978). In captivity, they require no routine veterinary care except for deworming, have low water demands, and survive well on a 10% protein diet because they digest protein and fiber better than cattle. Husbandry of *O. callotis* requires more herders than with other livestock operations because they need to be penned up at night (Stanley Price 1978). In a captive population at the San Diego Wild Animal Park, it is sometimes necessary to hold males in all-male groups, which increases aggression. Adding melengestrol acetate, a synthetic progestogen, to food significantly reduces aggressive contacts and pursuit among captive male *O. callotis* (Patton et al. 2001). Individual *O. callotis* have survived 20–22 years in captivity (Jones 1993; Kingdon 1997). A male *O. callotis* born at the Brookfield Zoo, Chicago, Illinois (United States), in 1960 lived 21 years and 1 month, and a female born at the San Diego Wild Animal Park in 1964 lived 20 years (Weigl 2005).

Some individuals in the domesticated herd at Galana Ranch were harvested for meat in the 1970s (King and Heath 1975), but changes in wildlife laws in Kenya in 1977 effectively stopped further domestication of *O. callotis*. In the 1970s, African market prices for oryx meat were comparable to those for beef, but profits were 20% lower because herding costs were higher (King and Heath 1975). Meat from the loin and leg of *O. callotis* has a pH of 5.6 and contains 75.9–76.6% water, 20.2–20.3% crude protein, 0.2–0.3% crude fat (of which about 68% is saturated fat and about 48% of that is C18:0 fatty acids), and 1.0–1.1% ash (Onyango et al. 1998). In contrast to meat from domestic cattle, plains zebra, and kongoni, meat from *O. callotis* had the highest lightness and chromaticity, with a tendency to accumulate myoglobins at the surface, giving it a bright appearance (Onyango et al. 1998). Meat of *O. callotis* is extra lean, which contributes to a cold-dressed carcass mass of 57% compared to 52% in cattle (King and Heath 1975).

Fig. 4.—*Oryx callotis* galloping across an open grassland habitat in southern Kenya; such a gait is typical during circular tournament displays in which linear hierarchies are learned, tested, and reinforced (Kingdon 1997). Photograph by Glen Tepke (www.pbase.com/gtepke) used by permission.

BEHAVIOR

Grouping behavior.—Typically, *Oryx callotis* lives in mixed herds of 30–40 individuals, but herds as large as several hundred individuals have been observed during the wet season when grasses are abundant. The majority of individuals (70–90%) in such herds are females and their offspring, and strictly bachelor herds are not common (Wacher 1988). Females may join a new herd more easily than males; incoming males have horn-to-horn fights with the alpha male and even subordinate males in the herd (Walther 1978).

In mixed herds, both sexes, predominately juveniles, participate in a "tournament" of interactions to learn, explore, test, and reinforce the established, typically linear hierarchy (Kingdon 1997). As described by Kingdon (1997:440) for *O. beisa* in general, and likely no different for *O. callotis*, tournaments typically occur at dawn or during a rain shower and begin with 1 or more individuals galloping in broad circles in a "high-stepping, 'floating' pace [with] the neck bunched, chin raised and the head swung from side to side in rhythm with the [fast] pace," and the "black and white head flashes in time with the high-stepping

knees and flying hooves" (Fig. 4). Male *O. callotis* have fights of low-to-medium intensity by clashing their horns frontally, parallel, or at an acute angle, but they do not attempt to gore each other. Fighting techniques include simple head butting, horn pressing, clash fighting, push fighting, and forehead pressing, with fencing and whirling as the most common tactics (Walther 1978; Estes 1991). If a powerful thrust is used, an attacker is capable of displacing his opponent 10–30 m. The alpha male sometimes defecates during a dispute, and both participants may take breaks to graze during the fight, but this only happens if the subordinate male initiates feeding (Walther 1978).

Male *O. callotis* control the herd's grouping and moving behavior (Walther 1978, 1991). The alpha male sometimes blocks the path if an individual is going in the wrong direction or straggling behind (Walther 1991). Females also coordinate herd movements by leading marches with a "pulling effect" (Walther 1978). During single-file marching, the alpha male brings up the rear. From this position, he may speed up or slow down individuals (Walther 1978, 1991). A herd also has coordinated movements for other activities such as lying, standing, grazing, or grooming. After a member changes activity, nearby members follow, and soon the whole herd has changed activity (Walther 1978). Herds of *O. callotis* may stay together for up to 1 year (Kingdon 1997).

Reproductive behavior.—Sexually receptive females are present in the herd throughout the year but not in a predictable location. Some males form territories of 5–8 km^2, but they typically cannot control all females, which leaves nonterritorial males opportunity to breed (Wacher 1988). Courtship begins with the female's ears back and head low. The male circles her while sniffing her backside and testing her urine for indication of estrus. If the female is receptive, the male lifts his forelegs and mounts her with his back legs bent, and his tail is typically held out. The male may nudge the female gently with his muzzle and occasionally rests his chin on her backside. The mating pair may copulate multiple times to ensure fertilization (Estes 1991).

Miscellaneous behavior.—Daily activity patterns of *Oryx callotis* consist of alternating sessions of feeding and resting and ruminating throughout the day and night (Walther 1978). A herd typically grazes from about one-half hour after daybreak until 1000 h, rests and ruminates from 1000 h until 1400–1500 h, and then grazes again until sunset when it returns to a night resting place to bed down at about 2000 h. Throughout the night, individuals intermittently rest and graze until daybreak (Walther 1978), and the majority of daily rumination occurs at night (>95% according to Stanley Price [1985]). In free-ranging feeding trials in southern Kenya, activity patterns of *O. callotis* over a 48-h period varied depending on season: 4.6 h walking, 15.6 h feeding, 6.1 h standing, 21.6 h lying, and 0.05 h running

during the dry season and 3.3 h walking, 10.4 h feeding, 12.5 h standing, 21.7 h lying, and 0.06 h running during the wet season (Stanley Price 1985). When ambient temperatures and solar radiation are high, *O. callotis* seeks shade for an average of 1.7 h, usually from 1100 h to 1500 h (Lewis 1978) to slow the rate of its rising body temperature (Estes 1991).

Throughout the day, individuals swat biting flies with their long tails (Mooring et al. 2007). Individual *O. callotis* rarely have ticks, probably because they groom themselves and each other with their teeth or by licking (Mooring et al. 2002). Comparisons of other bovids (e.g., Thomson's gazelle and kongoni) that are often syntopic with *O. callotis* show that the degree of grooming is correlated with body size and tick infestations; those species that groom often have fewer ticks (and a smaller body size with greater risk from blood loss because of their larger surface-to-body ratio) than those that do not (e.g., the large wildebeest—Olubayo et al. 1993). Male *O. callotis* spend less time grooming than females so they can remain more vigilant for predators, rival males, and estrous females; juveniles groom more than females because they accrue a large cost from weight loss with heavy infestations of ectoparasites and do not need to be as aware of danger as adults, who assume that role for them (Mooring et al. 2002).

GENETICS

Species of *Oryx* differ in their diploid number (*O. gazella*, 2n = 56; *O. dammah*, 2n = 56–58; and *O. leucoryx*, 2n = 57–58); however, *Oryx callotis*, *O. beisa*, and *O. gallarum* have indistinguishable karyotypes (2n = 58), as does the addax (Claro et al. 1996). All species of *Oryx* have 58 autosomal arms with a 1;25 centric fusion, and the X- and Y-chromosomes are conserved among the taxa. Specifically, *O. callotis* is distinguished by 2 metacentric autosomes and 54 acrocentric autosomes (Kumamoto et al. 1999). Mitochondrial cytochrome-*b* and control region DNA sequences show that *O. callotis* diverges significantly from *O. beisa* and *O. gallarum*, despite all 3 having the same karyotypes (Masembe et al. 2006). *O. callotis* is known to hybridize with *O. beisa* in captivity (Gray 1972).

CONSERVATION

During aerial surveys in the 1990s, East (1999) counted 8,050 *Oryx callotis* in Kenya and Tanzania, of which 5,240 (65%) were in protected areas; he extrapolated those numbers into a rangewide estimate of 17,000 individuals. The Species Survival Commission Antelope Specialist Group (2008) concluded that 10,000 breeding adult *O. callotis* remain in the wild, based on East's (1999) estimates, which have not been updated since the 1990s. Even though the majority (60%) of extant populations reside in protected

areas, a 10% population decline is projected over the next 3 generations (21–24 years—Species Survival Commission Antelope Specialist Group 2008). Eventually, all *O. callotis* in southeastern Kenya probably will be confined to areas in the Kajiado and Kilifi districts and in and around Tsavo National Park that are protected from settlement and poaching. In Tanzania, *O. callotis* probably will be restricted to Tarangire National Park and Mkomazi Game Reserve (East 1999; Species Survival Commission Antelope Specialist Group 2008).

Distributions of many populations of wild bovid species, particularly in Africa and Asia, are no longer continuous and have been fragmented due to a combination of habitat loss to agriculture, competition with livestock (possibly disease transmission), and unrestrained hunting and poaching (Sausman 1993; Groves and Leslie 2011). Sizes of many populations of bovids have declined substantially, and the status of most, particularly given the new taxonomy of Groves and Grubb (2011), is largely or totally unknown (Groves and Leslie 2011). *O. callotis* is considered "Vulnerable" by the International Union for Conservation of Nature and Natural Resources but as a subspecies of *O. beisa*, which it lists as "Near Threatened" (Species Survival Commission Antelope Specialist Group 2008). Conservation needs could be clarified by updating the current status of all 3 species of northeastern African oryxes, formerly grouped together under *O. beisa*.

ACKNOWLEDGMENTS

LITERATURE CITED

ANSELL, W. F. H. 1972. Order Artiodactyla. Pp. 1–84 in The mammals of Africa: an identification manual (J. Meester and H. W. Setzer, eds.). Smithsonian Institution Press, Washington, D.C.

AYENI, J. S. O. 1975. Utilization of waterholes in Tsavo National Park (East). East African Wildlife Journal 13:305–323.

BELSKY, A. J., R. G. AMINDSON, J. M. DUXBURY, S. J. RIHA, A. R. ALI, AND S. M. MWONGA. 1989. The effects of trees on their physical,

chemical, and biological environments in a semi-arid savanna in Kenya. Journal of Applied Ecology 26:1005–1024.

BENIRSCHKE, K. 2002. Fringe-eared oryx (*Oryx gazella callotis*). Comparative Placentation Project, University of California–San Diego, San Diego. http://placentation.ucsd.edu/cpa/sdeer.html, accessed 14 July 2012.

BIBI, F., M. BUKHSIANIDZE, A. W. GENTRY, D. GERAADS, D. S. KOSTOPOULOS, AND E. VRBA. 2009. The fossil record and evolution of Bovidae: state of the field. Palaeontologia Electronica 12(3):1–11.

CLARO, F., H. HAYES, AND E. P. CRIBIU. 1996. The karyotype of the addax and its comparison with karyotypes of other species of Hippotraginae antelopes. Hereditas 124:223–227.

CLAUSS, M., M. LECHNER-DOLL, AND W. J. STREICH. 2002. Faecal particle size distribution in captive wild ruminants: an approach to the browser/grazer dichotomy from the other end. Oecologia 131:343–349.

CRETZSCHMAR, P. J. 1826. Säugethiere. Pp. 1–78 in Atlas zu der Reise im Nördlichen Afrika. Zoologie. (E. Rüppell, ed.) Gedruckt und in Commission bei Heinr. Ludwig Brönner, Frankfurt, Germany.

DE BLAINVILLE, H. M. D. 1816. Sur plusieurs espèces d'animaux mammifères, de l'ordre des ruminans. Bulletin des Sciences par la Société Philomatique de Paris 1816:73–82.

EAST, R. 1999. African antelope database 1998: beisa & fringe-eared oryx. Occasional Papers of the International Union for the Conservation of Nature Species Survival Commission 21:230–232.

ELLERMAN, J. R., AND T. C. S. MORRISON-SCOTT. 1966. Checklist of Palaearctic and Indian mammals 1758 to 1956. Trustees of the British Museum (Natural History), London, United Kingdom.

ESTES, R. D. 1991. The behavior guide to African mammals including hoofed mammals, carnivores, and primates. University of California Press, Berkeley.

FIELD, C. R. 1975. Climate and the food habits of ungulates on Galana Ranch. East African Wildlife Journal 13:203–220.

GENTRY, A. W. 2000. Caprinae and Hippotragini (Bovidae, Mammalia) in the Upper Miocene. Pp. 65–83 in Antelope, deer, and relatives (E. S. Vrba and G. B. Schaller, eds.). Yale University Press, New Haven, Connecticut.

GERAADS, D., C. BLONDEL, A. LIKIUS, H. T. MACKAYE, P. VIGNAUD, AND M. BRUNET. 2008. New Hippotragini (Bovidae, Mammalia) from the late Miocene of Toros-Menalla (Chad). Journal of Vertebrate Paleontology 28:231–242.

GRAHAM, A., B. NETSERAB, AND C. ENAWGAW. 1996. Trends in large herbivore numbers of Omo and Mago National Parks. National Parks Rehabilitation in Southern Ethiopia Project, Technical Report 2.

GRAY, A. P. 1972. Mammalian hybrids: a check-list with bibliography. 2nd ed. Commonwealth Agricultural Bureaux Farnham Royal, Slough, United Kingdom.

GRAY, J. E. 1821. On the natural arrangement of vertebrose animals. London Medical Repository 15:296–310.

GROVES, C. P. 2011. Genus *Oryx*. Pp. 688–692 in Handbook of the mammals of the world. Vol. 2. Hoofed mammals (D. E. Wilson and R. A. Mittermeier, eds.). Lynx Edicions, Barcelona, Spain.

GROVES, C. P., AND P. GRUBB. 2011. Ungulate taxonomy. Johns Hopkins University Press, Baltimore, Maryland.

GROVES, C. P., AND D. M. LESLIE, JR. 2011. Family Bovidae (hollow-horned ruminants). Pp. 444–571 in Handbook of the mammals of the world. Vol. 2. Hoofed mammals (D. E. Wilson and R. A. Mittermeier, eds.). Lynx Edicions, Barcelona, Spain.

GROVES, C. P., ET AL. 2011. Species accounts for Bovidae. Pp. 572–779 in Handbook of the mammals of the world. Vol. 2. Hoofed mammals (D. E. Wilson and R. A. Mittermeier, eds.). Lynx Edicions, Barcelona, Spain.

GRUBB, P. 2000. Morphoclinal evolution in ungulates. Pp. 156–170 in Antelope, deer, and relatives (E. S. Vrba and G. B. Schaller, eds.). Yale University Press, New Haven, Connecticut.

GRUBB, P. 2005. Order Artiodactyla. Pp. 637–722 in Mammal species of the world: a taxonomic and geographic reference (D. E. Wilson and D. M. Reeder, eds.). 3rd ed. Johns Hopkins University Press, Baltimore, Maryland.

HAAS, S. K., V. HAYSSEN, AND P. R. KRAUSMAN. 2005. *Panthera leo*. Mammalian Species 762:1–11.

HARRIS, J. M., F. H. BROWN, AND M. G. LEAKEY. 1988. Stratigraphy and paleontology of Pliocene and Pleistocene localities west of Lake Turkana, Kenya. Contributions in Science, Natural History Museum of Los Angeles County 399:1–128.

HOFMANN, R. R., AND D. R. M. STEWART. 1972. Grazer or browser: a classification based on the stomach-structure and feeding habits of east African ruminants. Mammalia 36:226–240.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 1956. Opinion 417. Rejection for nomenclatural purposes of volume 3 (Zoologie) of the work of Lorenz Oken entitled Okens Lehrbuch de Naturgeschichte published 1815–1816. Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature, London, United Kingdom 14:1–42.

IYENGAR, A., F. M. DINIZ, T. GILBERT, T. WOODFINE, J. KNOWLES, AND N. MACLEAN. 2006. Structure and evolution of the mitochondrial control region in oryx. Molecular Phylogenetics and Evolution 40:305–314.

JONES, M. L. 1993. Longevity of ungulates in captivity. International Zoo Yearbook 32:159–169.

KAHURANANGA, J. 1981. Population estimates, densities and biomass of large herbivores in Simanjiro Plains, northern Tanzania. African Journal of Ecology 19:225–238.

KING, J. M. 1979. Game domestication for animal production in Kenya: field studies of the body-water turnover of game and livestock. Journal of Agricultural Science 93:71–79.

KING, J. M., AND B. R. HEATH. 1975. Game domestication for animal production in Africa: experiences at the Galana Ranch. World Animal Review 16:23–30.

KING, J. M., G. P. KINGABY, J. G. COLVIN, AND B. R. HEATH. 1975. Seasonal variation in water turnover by oryx and eland on the Galana Game Ranch Research Project. East African Wildlife Journal 13:287–296.

KINGDON, J. 1997. The Kingdon field guide to African mammals. Academic Press Limited, London, United Kingdom.

KOUBA, A. J., M. W. ATKINSON, A. R. GANDOLF, AND T. L. ROTH. 2001. Species-specific sperm–egg interaction affects the utility of a heterologous bovine in vitro fertilization system for evaluating antelope sperm. Biology of Reproduction 65:1246–1251.

KRAUSMAN, P. R., AND A. L. CASEY. 2007. *Addax nasomaculatus*. Mammalian Species 807:1–4.

KRAUSMAN, P. R., AND S. M. MORALES. 2005. *Acinonyx jubatus*. Mammalian Species 771:1–6.

KUMAMOTO, A. T., S. J. CHARTER, S. C. KINGSWOOD, O. A. RYDER, AND D. S. GALLAGHER, JR. 1999. Centric fusion differences among *Oryx dammah*, *O. gazella*, and *O. leucoryx* (Artiodactyla, Bovidae). Cytogenetic and Genome Research 86:74–80.

LESLIE, D. M., JR. 2008. *Boselaphus tragocamelus* (Artiodactyla: Bovidae). Mammalian Species 813:1–16.

LESLIE, D. M., JR., R. T. BOWYER, AND J. A. JENKS. 2008. Facts from feces: nitrogen still measures up as a nutritional index for mammalian herbivores. Journal of Wildlife Management 72:1420–1433.

LEUTHOLD, W., AND B. M. LEUTHOLD. 1975. Temporal patterns of reproduction in ungulates of Tsavo National Park, Kenya. East African Wildlife Journal 13:159–169.

LEWIS, J. G. 1977. Game domestication for animal production in Kenya: activity patterns of eland, oryx, buffalo and zebu cattle. Journal of Agricultural Science 89:551–563.

LEWIS, J. G. 1978. Game domestication for animal production in Kenya: shade behaviour and factors affecting the herding of eland, oryx, buffalo and zebu cattle. Journal of Agricultural Science 90:587–595.

LINNAEUS, C. 1758. Systema naturae per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Holmiae, Impensis Direct. Laurentii Salvii, Stockholm, Sweden.

LYDEKKER, R. 1908. The game animals of Africa. Rowland Ward, Limited, London, United Kingdom.

MASEMBE, C., V. B. MUWANIKA, S. NYAKAANA, P. ARCTANDER, AND H. R. SIEGISMUND. 2006. Three genetically divergent lineages of the oryx in eastern Africa: evidence for an ancient introgressive hybridization. Conservation Genetics 7:551–562.

Mooring, M. S., D. T. Blumstein, D. D. Reisig, E. R. Osborne, and J. M. Niemeyer. 2007. Insect-repelling behavior in bovids: role of mass, tail length, and group size. Biological Journal of the Linnean Society 91:383–392.

Mooring, M. S., D. D. Reisig, J. M. Niemeyer, and E. R. Osborne. 2002. Sexually and developmentally dimorphic grooming: a comparative survey of the Ungulata. Ethology 108:911–934.

Mushi, E. Z., and L. Karstad. 1981. Prevalence of virus neutralizing antibodies to malignant catarrhal fever virus in oryx. Journal of Wildlife Diseases 17:467–470.

Neumann, O. 1902. Neue nordost- und ostaafrikanische Säugethiere. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 1902:93–101.

Oken, L. 1816. Okens Lehrbuch der Naturgeschichte. Vol. 3. Zoologie. August Schmid und Comp., Jena, Germany.

Olubayo, R. O., J. Jong, G. Orinda, J. G. Groothenhuis, and B. L. Hart. 1993. Comparative differences in densities of adult ticks as a function of body size on some East African antelopes. African Journal of Ecology 31:26–34.

Onyango, C. A., M. Izumimoto, and P. M. Kutima. 1998. Comparison of some physical and chemical properties of selected game meats. Meat Science 49:117–125.

Packer, C. 1983. The horns of African antelopes. Science 221:1191–1193.

Paling, R. W., K. J. Macowan, and L. Karstad. 1978. The prevalence of antibody to contagious caprine pleuropneumonia (*Mycoplasma* strain F38) in some wild herbivores and camels in Kenya. Journal of Wildlife Disease 14:305–308.

Pallas, P. S. 1766. Miscellanea zoological quibus novae imprimis atque obscurae animalium species describuntur et observationibus iconibusque illustrantur. Hague comitun. Petrum van Cleef, The Hague, Netherlands.

Palmer, T. S. 1904. Index generum mammalium: a list of the genera and families of mammals. North American Fauna 23:1–984.

Patton, M. L., et al. 2001. Aggression control in a bachelor herd of fringe-eared oryx (*Oryx gazella callotis*), with melengestrol acetate: behavioral and endocrine observations. Zoo Biology 20:375–388.

Pocock, R. I. 1918. On some external characters of ruminant Artiodactyla. Part III. The Bubalinae and Oryginae. Annals and Magazine of Natural History, Series 9, 2:214–225.

Poppi, D. P., B. W. Norton, D. J. Minson, and R. E. Hendricksen. 1980. The validity of the critical size theory for particles leaving the rumen. Journal of Agricultural Science 94:275–280.

Root, A. 1972. Fringe-eared oryx digging for tubers in the Tsavo National Park (East). East African Wildlife Journal 10:155–157.

Rothschild, W. 1921. On two new races of *Oryx*. Annals and Magazine of Natural History, Series 9, 8:209–210.

Rüppell, E. 1835. Neue Wirbelthiere zu der Fauna von Abyssinien gehörig, entdeckt und beschrieben. Säugethiere. Commission bei Seigmun Schmerber, Frankfurt, Germany.

Sausman, K. A. 1993. Conservation assessment and management plan for antelope. International Zoo Yearbook 32:117–124.

Sclater, P. L., and O. Thomas. 1899. Book of antelopes. Vol. IV. R. H. Porter, London, United Kingdom.

Simpson, G. G. 1945. The principles of classification and a classification of mammals. Bulletin of the American Museum of Natural History 85:1–350.

Species Survival Commission Antelope Specialist Group. 2008. *Oryx beisa* ssp. *callotis*. International Union for Conservation of Nature and Natural Resources Red list of threatened species. http://www.iucnredlist.org, accessed 14 July 2012.

Ssemakula, J. 1983. A comparative study of hoof pressures of wild and domestic ungulates. African Journal of Ecology 21:325–328.

Stanley Price, M. R. S. 1978. Fringe-eared oryx on a Kenya Ranch. Oryx 14:370–373.

Stanley Price, M. R. S. 1985. Game domestication for animal production in Kenya: the nutritional ecology of oryx, zebu cattle and sheep under free-range conditions. Journal of Agricultural Science 104:375–382.

Stewart, D., and J. Stewart. 1963. The distribution of some large mammals in Kenya. Journal of East African Natural History 24:1–52.

Taylor, C. R. 1968. Hygroscopic food: a source of water for desert antelopes. Nature 219:181–182.

Taylor, C. R. 1970a. Strategies of temperature regulation: effect on evaporation in East African ungulates. American Journal of Physiology 219:1131–1135.

Taylor, C. R. 1970b. Dehydration and heat: effects on temperature regulation of East African ungulates. American Journal of Physiology 219:1136–1139.

Thomas, O. 1892. Exhibition of, and remarks upon, a mounted head of an apparently new East-African antelope (*Oryx callotis*). Proceedings of the Zoological Society of London 1892:195–196, plate 14.

Thouless, C. R. 1995. Aerial survey for wildlife in Omo Valley, Chew Bahir and Borana areas of southern Ethiopia. Report to EWCO. Ecosystems Consultants, London, United Kingdom.

Van Winkle, T. J. 1985. Cryptosporidiosis in young artiodactyls. Journal of the American Veterinary Medical Association 187:1170–1172.

Vrba, E. S. 1995. The fossil records of African antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. Pp. 385–424 in Paleoclimate and evolution, with emphasis on human origins (E. S. Vrba, G. H. Denton, T. C. Patridge, and L. H. Burckle, eds.). Yale University Press, New Haven, Connecticut.

Vrba, E. S., and G. B. Schaller. 2000. Phylogeny of Bovidae based on behavior, glands, skulls, and postcrania. Pp. 203–222 in Antelope, deer, and relatives (E. S. Vrba and G. B. Schaller, eds.). Yale University Press, New Haven, Connecticut.

Wacher, T. J. 1988. Social organization and ranging behaviour in the Hippotraginae. Pp. 102–113 in Conservation and biology of desert antelopes (A. Dixon and D. Jones, eds.). Christopher Helm, London, United Kingdom.

Walther, F. R. 1978. Behavioral observations on oryx antelope (*Oryx beisa*) invading Serengeti National Park, Tanzania. Journal of Mammalogy 59:243–260.

Walther, F. R. 1991. On herding behavior. Applied Animal Behaviour Science 29:5–13.

Weigl, R. 2005. Longevity of mammals in captivity; from the living collections of the world. Kleine Senckenberg-Reihe 48:1–214.