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Author: Leslie, David M.

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Boselaphus tragocamelus (Artiodactyla: Bovidae)

DAVID M. LESLIE, JR.

United States Geological Survey, Oklahoma Cooperative Fish and Wildlife Research Unit and Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK 74078-3051, USA; cleslie@usgs.gov

Abstract: *Boselaphus tragocamelus* (Pallas, 1766) is a bovid commonly called the nilgai or blue bull and is Asia's largest antelope. A sexually dimorphic ungulate of large stature and unique coloration, it is the only species in the genus *Boselaphus*. It is endemic to peninsular India and small parts of Pakistan and Nepal, has been extirpated from Bangladesh, and has been introduced in the United States (Texas), Mexico, South Africa, and Italy. It prefers open grassland and savannas and locally is a significant agricultural pest in India. It is not of special conservation concern and is well represented in zoos and private collections throughout the world. DOI: 10.1644/813.1.

Key words: antelope, Asia, blue bull, exotic species, India, nilgai, ruminant, Texas, ungulate

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Boselaphus de Blainville, 1816

Antelope Pallas, 1766:5. Part.

Cerophorus de Blainville, 1816:74. Part; said to be equivalent to contemporary Bovidae (Ellerman and Morrison-Scott 1966:379); no type species selected.

Boselaphus de Blainville, 1816:75. Type species *Antelope tragocamelus* Pallas, 1766, by subsequent designation (Sclater and Thomas 1900:91); originally used as a subgenus of *Cerophorus* de Blainville, 1816.

Cemas Oken, 1816:729. Part; unavailable name (International Commission on Zoological Nomenclature 1956:Opinion 417).

Damalis Hamilton-Smith, 1827a:343. Part.

Portax Hamilton-Smith, 1827b:366. Type species *Damalis risia* Hamilton-Smith, 1827a, by monotypy; used as a subgenus of *Damalis* Hamilton-Smith, 1827a.

Tragelaphus Ogilby, 1837:138. Type species *Tragelaphus hippelaphus* Ogilby, 1837, by original designation; preoccupied by *Tragelaphus* de Blainville, 1816.

Oreades Schinz, 1845:448. Part; used as a subgenus of *Antelope* Pallas, 1766; contained *Antelope picta*, *A. oreas*, and *A. canna*; no type species selected.

Buselaphus Reichenbach, 1845:142. Incorrect subsequent spelling of, but not *Boselaphus* de Blainville, 1816 (see "Nomenclatural Notes").

Bosephalus Horsfield, 1851:169. Incorrect subsequent spelling of, but not *Boselaphus* de Blainville, 1816 (see "Nomenclatural Notes").

Boselaphas Allen, 1939:586. Incorrect subsequent spelling of, but not *Boselaphus* de Blainville, 1816 (see "Nomenclatural Notes").

CONTEXT AND CONTENT. Order Artiodactyla, suborder Ruminantia, family Bovidae, subfamily Bovinae, tribe Boselaphini, genus *Boselaphus*. *Boselaphus* is monotypic.

Boselaphus tragocamelus (Pallas, 1766) Nilgai or Blue Bull

Antelope tragocamelus Pallas, 1766:5. Type locality unknown; name based on zoo specimen from "Bengal [= northeastern India] from a very remote Part of the Mogul's Dominions" (Parsons 1745:465).



Fig. 1.—Male *Boselaphus tragocamelus* in characteristic defecation posture (foreground), Koleado National Park, western India, December 2004; note beard below the white gular patch and short, pointed horns, both unique to males. Photograph courtesy of David Behrens (<http://www.pbases.com/dbehrens>).

- [*Antilope*] *albipes* Erxleben, 1777:280. Type locality “India;” name based on zoo specimen (Hunter 1771; Pennant 1771).
- Antilope leucopus* Zimmerman 1777:541. Type locality “India Orientali;” name based on zoo specimen (Pennant 1771).
- Ant[ilope]. picta* Pallas, 1777:14. Type locality “Indiae orientalis forte propria;” name based on zoo specimen (Pennant 1771).
- C[emas]. tragocamelus*: Oken, 1816:729. Name combination.
- C[emas]. picta*: Oken, 1816:729. Name combination.
- [*Cerophorus (Boselaphus)*] *picta*: de Blainville, 1816:74–75. Name combination.
- Boselaphus albipes*: Desmarest, 1816:199, plate A.33. Name combination.
- D[amalis]. risia* Hamilton-Smith, 1827a:363. Replacement name for *Antilope picta* Pallas, 1777.
- D[amalis (Portax)]. risia*: Hamilton-Smith, 1827b:366. Name combination.
- Damalis picta*: Brookes, 1828:64. Name combination.
- [*Damalis (Portax)*] *picta*: Lesson 1836:304. Name combination.
- T[ragelaphus]. hippelaphus* Ogilby, 1837:138. Replacement name for *Antilope picta* Pallas, 1777.
- A[ntilope (Oreades)]. picta*: Schinz, 1845:448. Name combination.
- P[ortax]. tragelaphus* Sundevall, 1846a:198. Incorrect subsequent spelling of *Antilope tragocamelus* Pallas, 1766; see Sundevall (1846b).
- P[ortax]. tragocamelus*: Sundevall, 1846b:323. Name combination.
- Antilope (Damalis) picta*: Schniz, 1848:44, plate xlv. Name combination.
- A[ntilope (Cephalophus)]. picta*: Giebel, 1855:323. Name combination.
- Ant[ilope (Bubalus)]. picta*: Laurillard, 1861:625. Name combination.
- Boselaphus tragocamelus*: Sclater, 1883:137. First use of the current name combination.

CONTEXT AND CONTENT. Context as for genus. *B. tragocamelus* is monotypic.

NOMENCLATURE NOTES. The expression “... of, but not *Boselaphus* de Blainville, 1816” for the last 3 entries in the generic synonymy is used to include apparent misspellings of *Boselaphus* that were applied to ≥ 1 species that did not include *Antilope picta* or any of its synonyms (A. L. Gardner, United States Geological Survey, Patuxent Wildlife Research Center, pers. comm.) but could result in potential confusion in the nomenclatural history of *Boselaphus*. In previously published generic synonymies of *Boselaphus* de Blainville, 1816 (e.g., Grubb 2005:693; Lydekker and Blaine 1914:224), the incorrect subsequent

spellings *Buselaphus* Reichenbach, 1845 and *Bosephalus* Horsfield, 1851 sometimes have been included. I did not find Allen’s (1939) *Boselaphus* presented in any previous generic synonymy, but his usage deserves mention.

Reichenbach’s (1845:141–142, table XLIII, plates 242–244) use of *Buselaphus* was inserted as a generic synonym after his description of *Antilope caama*, which was accompanied by 3 unambiguous illustrations of “der hartebeest” from Africa. Before 1845, the specific epithets *buselaphus* and *caama* were associated with the nomenclatural history of the red hartebeest (*Alcelaphus caama*) of southern Africa and the common hartebeest (*A. buselaphus*) of northern Africa (Grubb 2005:674). Therefore, this use of *Buselaphus* has little direct bearing on the nomenclatural history of *Boselaphus tragocamelus* (= nilgai) and probably references the species-level, not the generic-level, epithet for the hartebeest, *buselaphus* Pallas, 1766 (although Reichenbach misattributed the epithet to Hamilton-Smith, undated, for which I could find no reference).

Horsfield’s (1851:169) use of the epithet *Bosephalus* appeared in a museum catalog of the Honorable East-India Company. It listed specimen 239 as “*Bosephalus caama*” and gave its synonyms as *Antilope caama* and *Acronota caama*, its vernacular name as “La Caama,” and its occurrence as southern Africa. Horsfield’s use of *Bosephalus* may have been a lapsus for the generic epithet *Alcelaphus* de Blainville, 1816, perhaps from confusion with the specific epithet *buselaphus* Pallas, 1766, or Reichenbach’s (1845) use of *Buselaphus*. Critically, specimen 242 in Horsfield (1851:170) was identified as *Portax picta* (= *Boselaphus tragocamelus*) and labeled the “nylghau” (= nilgai) from the “Peninsula of India.” Therefore, Horsfield (1851) used the epithet *Bosephalus* only to describe a hartebeest and did not confuse it with the nilgai. As such, the epithet *Bosephalus* seems more appropriately regarded as an incorrect subsequent spelling of *Alcelaphus* de Blainville, 1816.

Allen (1939:470–472, 541–543, 586) presented the misspelling *Boselaphus* in his Index but used the correct spelling relative to the nilgai, *Boselaphus*, as various synonyms of *Alcelaphus* and *Taurotragus* (eland). Grubb (2005) did not list *Boselaphus* as synonyms for either genus. The misspelling stands only as a “header” for various specific epithets in the Index, and it would seem most appropriately included in generic synonymies of *Alcelaphus* and *Taurotragus* as “*Boselaphus* Allen, 1939:586. Incorrect subsequent spelling of *Boselaphus* de Blainville, 1816.” Regardless, Allen’s use of *Boselaphus* for hartebeest and eland has little direct relevance to the nomenclatural history of the nilgai.

In his review of artiodactylan taxonomy, Grubb (2005:693) designated the lectotype of *Antilope tragocamelus* Pallas, 1766, as “a male nilgai in London” (based on accounts by Cais, Gesner, and Ray [no dates] and the description by Parsons 1745). However, according to Article



Fig. 2.—Three tawny-colored female *Boselaphus tragocamelus* in a game park in Roseburg, Oregon, United States; note the characteristic white cheek spots and the 2 white rings above the fetlocks, which led to the early common name, white-footed antelope. Photograph courtesy of Faye Pekas (<http://www.pbase.com/fayeppek>).

74.7 of the *International Code of Zoological Nomenclature* (International Commission on Zoological Nomenclature 1999:83; K. Helgen, Smithsonian Institution, pers. comm.), such a designation cannot be made after 1999 without meeting 3 criteria, including “an express statement of the taxonomic purpose of the designation” (Article 74.7.3). I found no reference to such a purpose in Grubb (2005:693) and concluded that this designation is not valid under the current *Code*.

DIAGNOSIS

Boselaphus tragocamelus has no congeners; it is easily distinguished from the 4-horned antelope (*Tetracerus quadricornis*), the only other genus in the tribe Boselaphini, also monotypic, by its larger mass (9 times greater) and height (2.3 times greater) and lack of anterior horns. *B. tragocamelus* is distinguished from related tragelaphine antelopes of comparable stature (e.g., kudu [*Tragelaphus*] and eland [*Taurotragus derbianus*]) by short, straight, and sharp horns and pronounced frontal beard on the neck of males (Fig. 1) and distinctive coloration and patterning of both sexes (Fig. 2).

GENERAL CHARACTERS

Boselaphus tragocamelus is sexually dimorphic; coloration, male-only horns, and body mass are the most disparate characteristics (Figs. 1 and 2). Blanford’s (1888) early description has been amended through time: somewhat equine (Prater 1980), neck deep and compressed; tufted tail reaching hocks; hind limbs shorter than front legs with high

withers (Prater 1980); preorbital gland small with no lachrymal fossa; interdigital and unguicular glands present but no inguinal glands (Gosling 1985; Pocock 1910); adult males dark gray but varying from bluish to brownish gray except mane, terminal one-half of the ear outside and 2 spots inside, and tip of the tail are black; and a patch on the throat (gular patch), 2 spots on each cheek, lips, chin, inside of ears (except for the 2 black spots), lower surface of the tail, abdomen, and 2 rings above and below the fetlock are white. Females, calves, and young males are tawny brown with the same white markings as males (Schaller 1967). Males have a pronounced “pennant” or beard of coarse hair directly beneath the gular patch (Fig. 1); it is rudimentary in females (Fig. 2). Both sexes have a short and bristly mane that extends the length of the neck and terminates in tuft at the base of the neck (hog-mane—Sclater and Thomas 1900); the mane and hog-mane are darker and more prominent in adult males than females and other age classes (Blanford 1888; Schaller 1967; Sclater and Thomas 1900).

Frontals and parietals of the skull (Fig. 3) are almost in a single plane, forming a right angle with the occipital (Blanford 1888). Cranial measurements (in mm) of a male *B. tragocamelus* were: length of temporal fossa, 96; breadth of braincase, 86; breadth of skull between orbits, 145; breadth of frontal at horn-cores, 165; breadth of skull at mastoid, 123; height of occipital, 91; distance between horn-cores, 70; distance between primary keels of horn-cores at base, 41; distance between external face of horn-core and inner keel, 43; distance between outer edge of occipital condyles, 69; breadth of foramen magnum, 26 (Pilgrim 1939:163).

DISTRIBUTION

Boselaphus tragocamelus is endemic to the Peninsular Indian and Indus divisions of the Indian Subregion in the Asian Indomalayan Region (Fig. 4A; Corbet and Hill 1992). Native range of *B. tragocamelus* in Asia includes the foothills of the Himalayas in Nepal (Dinerstein 1980), northeastern Pakistan (Mirza and Khan 1975), and almost all of India, except eastern Bengal, Assam, east of the Bay of Bengal, and the Malabar coast (Blanford 1888; Ellerman and Morrison-Scott 1966; Prater 1980).

Introduced *B. tragocamelus* also exist in southern North America (Fig. 4B), where latitude, climate, and habitat characteristics are comparable to those of India (Ables and Ramsey 1972; Sheffield et al. 1983). The species was introduced into fenced areas of about 5,000 ha in southern Texas, United States, between 1924 (1st translocation of 2 females and 1 male according to Sheffield et al. [1971], but 5 individuals according to Presnall [1958]) and 1949 (releases of 3–5 individuals probably from the San Diego Zoological Park, San Diego, California). By 1971, *B. tragocamelus* occurred in 9 counties in Texas and Nuevo Laredo, Mexico (Ables and Ramsey 1972; Schmidly 1994; Sheffield et al.



Fig. 3.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of adult male *Boselaphus tragocamelus* (National Museum of Natural History, specimen 269127). Greatest length of skull is 376 mm. Photograph courtesy of Don Hulbert.

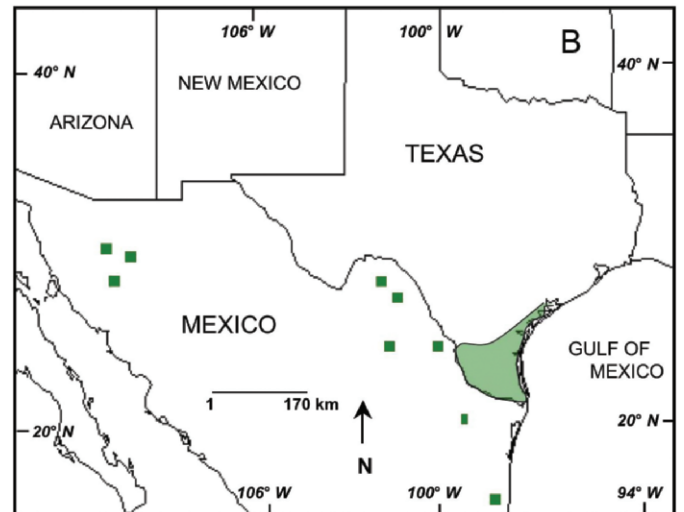
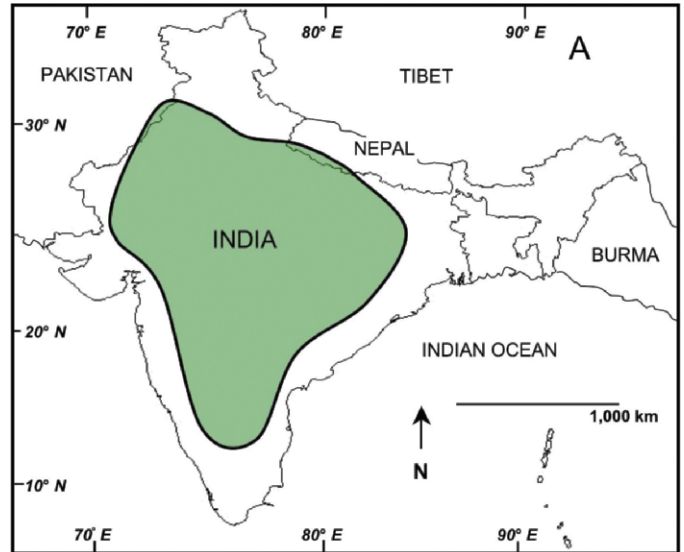


Fig. 4.—Distribution of *Boselaphus tragocamelus* in A) native India, Nepal, and Pakistan and B) southern North America (green squares = distinct areas of occurrence in Mexico), where exotic free-ranging populations occur.

1971, 1983); by 1992, the largest semiconfined population occurred in Kennedy and Willacy counties, Texas, with additional confined populations on 36 ranches in 25 counties (M. Traweek and R. Webb, in litt.). By 2005, 10 populations occurred in 5 Mexican states (Fig. 4B; Coahuila, 3; Nuevo Leon, 2; Sonora, 3; Tamaulipas, 1; Veracruz, 1—Álvarez-Romero and Medellín 2005). Several populations are confined to > 85,000-ha ranches in South Africa (Lever 1985), and introduced *B. tragocamelus* near Rome, Italy, disappeared during World War II (Long 2003). Fences have not provided complete confinement of *B. tragocamelus* in the United States, and in many areas of southern Texas, populations can now be considered free-ranging (B. R. Winton, in litt.).

Some of the most replete published ecological and behavioral insight on *B. tragocamelus* comes from introduced populations in North America. Detailed research was conducted in 2 adjacent fenced areas of 4,857 ha and 5,680 ha on what was considered a free-ranging population in southern Texas from the late 1960s to the early 1980s (e.g., Sheffield et al. 1983). Although the population was somewhat restricted by fences, basic ecological and behavioral characteristics likely were not greatly affected. Syntheses of that information are provided herein to permit comparison to native populations of *B. tragocamelus* and to fill gaps where information is missing.

FOSSIL RECORD

Fossils related to the tribe Boselaphini are well represented in Africa and Eurasia from the Miocene and represent the earliest bovids that arose 16–18 million years ago (e.g., *Eostragus*—Gentry 1978; Ginsburg and Heintz 1968; Solounias 1990). Extant *B. tragocamelus* and *T. quadricornis* are Miocene relicts and most related to early bovids (Pilgrim 1939; Pitra et al. 1997; Prothero and Schoch 2002), with horn morphology representing the primitive condition (straight and circular in cross section—Geist 1966; Janis 1982; Lundrigan 1996). Extant *Boselaphus* and *Tetracerus* and related fossil forms share the same primitive horn-core ontogeny (Solounias 1990).

The artiodactylan fossil fauna of India is rich and includes extinct genera and species closely related to extant *B. tragocamelus* (Colbert 1935; Pilgrim 1937, 1939). India may have been the “developmental centre,” or close to it, of Bovinae because from the lower Miocene “onward the number and variety of Bovine genera found in India is out of all proportion to what is the case in other parts of the world” (Pilgrim 1939:27). Bovid differentiation considerably during the middle Miocene; extinct *B. namadicus* and 6 boselaphine-like genera (*Duboisia*, *Perimia*, *Proboselaphus*, *Selenoportax*, *Sivaportax*, and *Tetracerus*) with similar “circular or equilaterally triangular cross-section[s]” of their horn cores are represented in the fossil record of India (Pilgrim 1939:191). *Sivaportax* may have represented the most primitive stage in the *Boselaphus* lineage (Pilgrim 1939). Today, *B. tragocamelus* can have traces of the anterior horns of extant *T. quadricornis*, suggesting close affinity between the 2 species (Pilgrim 1939).

Unlike extant *B. tragocamelus*, females of many related fossil boselaphines had horns with similar morphology and developmental processes as other bovids (e.g., Janis and Scott 1987; Kostopoulos 2005). Late Miocene boselaphine fossils from the eastern Mediterranean region are common (Kostopoulos 2005; Kostopoulos and Koufos 2006). Boselaphine and boselaphine-like fossils from the Pleistocene have been found eastward from India to Burma (Colbert 1943; Dassarma et al. 1982). Bones of *B.*

tragocamelus occur in caves of Pleistocene origin in southern India (Prasad 1996; Prasad and Yadagiri 1986), and use by Mesolithic humans is evident 5,000–8,000 years ago (Murty 1985).

FORM AND FUNCTION

Form.—Koppiker and Sabnis (1981) describe hairs from *B. tragocamelus* that are 23–27 cm in length (collection site on the body not specified), 140 μm in diameter at the proximal end, and fragile and easily broken; scales are imbricate with flattened edges; color is nearly white proximally and gradually changes to brown or black distally (color and length match those from the nape of the neck described by Sclater and Thomas [1900]). Abnormally light-colored (almost white but not albino) individuals were observed twice in Sariska National Park in Rajasthan, India (Ranjitsinh 1987); unusual coloration also was noted on a captive female that had large white spots on the neck and trunk, both sides of her body, and buttocks (Smielowski 1987).

Maximum reported masses of adult males are 270 kg in India (Brander 1923) and 288 kg (Sheffield et al. 1983) and 268.0 kg \pm 7.0 SE (6-year-old males—Lochmiller and Sheffield 1989) in southern Texas; mean mass of males in southern Texas is 241 kg. Maximum reported mass for adult females is 212 kg in southern Texas; mean mass was 169 kg (Sheffield et al. 1983). Other body measurements (in cm) are head-to-body length: 180–210 for males and 170 for females; girth at highest point of the shoulders: 160 for males and 130 for females; shoulder height: 120–140 for males and females; hip height: 110 for males and females; head length: 46 for males and 43 for females; tail length: 46–53 for males and 45 for females; and ear length, 15–18 for males and 15 for females (Blanford 1888; Sheffield et al. 1983).

Male-only horns characteristically arise close together just behind the orbits directed upward (Fig. 3) and are short, nearly straight with no catching arch, black, generally smooth, sharp, and 15–24 cm long at maturity (Blanford 1888; Schaller 1967; Sheffield et al. 1983). Horns are subconical above and triangular at the base (circumference about 20 cm) with a flat posterior side and a ridge in the front (Blanford 1888); they may develop ≥ 1 base rings annually after maturity (about 3–4 years old—Sheffield et al. 1983). Horn characteristics of adult male *B. tragocamelus* are: length, 14.0 cm; core surface, 70.8 cm²; sheath surface, 100.7 cm²; sheath thickness, 0.38 cm (Picard et al. 1996). Chitampalli (1983a) observed a male *B. tragocamelus* with downward-curved horns in Umarzari, India, and although rare, local Shikaris observed similar individuals frequently enough to call them “Mendha nilgai,” meaning “sheep nilgai.” Vision and hearing of *B. tragocamelus* are well-developed but sense of smell, less so (Brander 1923; Dharmakumarsinhji 1959; Fall 1972).

Dentition of adult *B. tragocamelus* is typical of bovids: i 0/3, c 0/1, p 3/3, m 3/3, total 32. Molars are very hypsodont with tall crowns and a large accessory column on upper molars (Blanford 1888; Lydekker and Blaine 1914). Age-specific eruption and wear patterns of teeth of male *B. tragocamelus* ($n = 15$, Natural History Museum of London—Kostopoulos 2005:767–768) are 1–2 year olds: M3 within alveoli, M2 just erupted, and milk dentition weakly to moderately worn; 3 year olds: premolars unworn, last milk tooth worn, and M3 just erupted; 4–5 year olds: full permanent dentition in 1st stages of wear; > 6 years old: full permanent dentition in advanced stages of wear. Exotic *B. tragocamelus* in southern Texas can be aged in annual classes ≤ 9 years old by examination of tooth wear on the mandible and counting annuli of p1, p2, and m1; precise aging ≥ 10 years is not possible (Brown 1976; Sheffield et al. 1983).

Function.—Hemoglobin of *B. tragocamelus* contains 3 polypeptide chains with 1 beta and 2 alpha chains (John and Barnabas 1978). Mean ($\pm SD$) blood chemistry values are: aspartate aminotransferase, 31.1 ± 10.9 IU/l; alanine aminotransferase, 12.0 ± 3.5 IU/l; creatinine phosphokinase, 94.2 ± 84.6 IU/l; lactate dehydrogenase, 368 ± 213 IU/l; gamma glutamyl transpeptidase, 5.04 ± 1.31 IU/l; alkaline phosphatase, 183 ± 199 IU/l; glucose, 7.91 ± 2.08 mmol/l; urea, 7.76 ± 2.11 mmol/l; uric acid, 43.7 ± 10.7 mmol/l; creatinine, 209 ± 39 mmol/l; cholesterol, 1.89 ± 0.36 mmol/l; triglycerides, 0.21 ± 0.07 mmol/l; total bilirubin, 6.8 ± 2.7 μ mol/l; protein, 6.84 ± 1.45 g/dl; albumin, $59.5\% \pm 10.1\%$; albumin–globulin ratio, 1.6 ± 0.7 ($n = 7$ adults—Peinado et al. 1999). Carbohydrate-free pancreatic ribonucleases from *B. tragocamelus* are relatively unique among bovids and compare most closely with the “swamp-type” water buffalo (*Bubalus bubalis*—Beintema 1980).

Boselaphus tragocamelus is herbivorous with a ruminal digestive system. Dry weights of ruminal contents of 79 adult males, adult females, and subadults (< 2 years old) of either sex in southern Texas averaged 2.1, 1.8, and 1.0 kg, respectively; wet weight contents averaged 35, 27, and 15 kg, respectively (Sheffield et al. 1983). Assuming 3 feeding periods/day and a 10-h passage rate of digesta through the rumen, 75% of ruminal contents at any point in time is from a single feeding bout, and 4.7, 4.0, and 2.3 kg of dry weight are consumed daily by adult males, adult females, and subadults, respectively (Sheffield et al. 1983).

Percent in vitro dry matter, organic matter, and cell wall digestibilities, respectively, in *B. tragocamelus* (70.9%, 69.4%, and 34.6%) are comparable to those of domestic cattle (69.5%, 68.3%, and 33.6%) and goats (68.3%, 67.4%, and 33.8%) but higher than those of white-tailed deer (*Odocoileus virginianus*; 57.9%, 57.4%, and 20.2%—Priebe et al. 1987). Retention of digesta in the reticulorumen and overall mean retention time for *B. tragocamelus* on formulated diets are 14.9 h and 20.6 h, respectively (Priebe 1985). A positive relationship exists between in vivo digestible organic matter of *B. tragocamelus* and in vitro

digestible organic matter using cattle rumen inoculum, but in vivo digestible organic matter of *B. tragocamelus* was about 15% higher than in vitro digestible organic matter estimates (Strey 1987). Based on nitrogen-balance studies on subadult *B. tragocamelus*, levels of dietary crude protein of about 5% (dry-matter basis) maintain nitrogen equilibrium (Priebe 1985; Priebe and Brown 1987).

Unique fungal isolates from feces of *B. tragocamelus* enhance in vitro apparent digestibility, true digestibility, and neutral detergent fiber digestion of high-lignin–cellulose diets (Paul et al. 2004). Methane production from methanogenic bacteria in feces of *B. tragocamelus* averages 107 CH₄ nmol g⁻¹ h⁻¹ (maximum = 175 CH₄ nmol g⁻¹ h⁻¹), a level comparable to that of other ruminal and cecal digesters (Hackstein and van Alen 1996). The “modulus of fineness” (Poppi et al. 1980) of fecal particle size from digesta residue suggests that *B. trgaocamelus* (modulus of fineness = 2.72) is an intermediate feeder; percentage of fecal particles passing through various sieve sizes are: 4-mm sieve, 2.72%; 1-mm sieve, 5.40%; 0.25-mm sieve, 12.71%, and < 0.125-mm sieve, 54.57% (Clauss et al. 2002).

ONTOGENY AND REPRODUCTION

Sexual maturity of female *B. tragocamelus* in southern Texas typically occurs at 2 years of age with the 1st parturition after 3 years of age; ovaries of 2-year-old female *B. tragocamelus* can have corpora lutea (Mungall 2000; Mungall and Sheffield 1994; Sheffield et al. 1983), and accessory corpora lutea have been reported (Amoroso 1955). Four inguinal mammae are present. Twinning is common; 50% of births are twins in southern Texas, and triplets are occasionally noted (Sheffield et al. 1983). Gestation is 243–247 days (Brown 1936; Sheffield et al. 1983). Females can breed shortly after parturition. Interparturition intervals for 3 captive females were 319–664 days ($n = 8$ litters) and averaged 436 days; 1 captive female produced 7 litters in 7 years and 8 months (Acharjyo and Misra 1975). Captive female *B. tragocamelus* can breed at just over 2 years of age (Acharjyo and Misra 1971, 1973), and births in captivity occur in any month of the year when males and females are housed together (Acharjyo and Misra 1972).

Generally, males 4–5 years of age are the most active breeders (Brown 1976; Sheffield et al. 1983). Testes of most male *B. tragocamelus* in southern Texas ($n = 26$; 10 months–7 years old) are histologically active by 3 years old (Lochmiller and Sheffield 1989). By 4 years old, male *B. tragocamelus* have large seminiferous tubules (202–283 μ m) with large numbers of spermatogonia, spermatocytes, spermatids, and spermatozoa (Lochmiller and Sheffield 1989). Changes in percent seminiferous tubules and mean number of spermatozoa per seminiferous tubule are lower in summer (nonbreeding) than during all other months when no clear changes in testicular morphology or spermatogenic

activity are noted (Lochmiller and Sheffield 1989). Serum level of testosterone peaked at 11 ng/ml in a captive 8-year-old male after injection of 2,000 IU of human chorionic gonadotropin—considered normal (Bryant et al. 2004). A captive adult male *B. tragocamelus* displayed persistent penile frenulum from a combined congenital and acquired condition, rendering him incapable of breeding (Bryant et al. 2004); similar cases have not been reported in the wild.

In Keoladeo Ghana Sanctuary, India, an extended breeding season occurs in October–February with offspring born in June–October (Schaller 1967). Extended breeding (August–December) and birthing (April–August) seasons also occur in southern Texas, but neonates can be observed throughout the year (Sheffield et al. 1983). When *B. tragocamelus* was transported from tropical India to the United Kingdom, no change in the traditional time of rut (March–May) or parturition occurred (Duke of Bedford and Marshall 1942; Heape 1900).

ECOLOGY

Population characteristics.—Densities of *B. tragocamelus* in India vary widely depending on habitat conditions, competition with domestic livestock, predation, and degree of protection: 0.23–0.34 individuals/km², Indravati National Park (Pandey 1988); 0.39–1.47 individuals/km², Gir Lion Sanctuary (Berwick 1974; Berwick and Jordon 1971; Khan 1997; Khan et al. 1996); 0.40 individuals/km², Pench Tiger Reserve (Biswas and Sankar 2002); 0.44–7.81 individuals/km², Panna National Park (Awasthi et al. 1994; Mathai 1999); 6.60–11.36 individuals/km², Ranthambhore National Park (Bagchi et al. 2004); and 7.0 individuals/km², Keoladeo National Park (Bagchi et al. 2004). In Royal Karnali-Bardia Wildlife Reserve, Nepal, densities were 3.2 individuals/km² during the hot-dry season and 5.0 individuals/km² in April (Dinerstein 1980). In southern Texas, densities of a population in about 10,000 ha of fenced private property were 3.05–4.04 individuals/km² and 3.74–4.76 individuals/km² from helicopter and ground surveys, respectively (Brown 1976:56).

Maximum life span is 12–13 years in the wild (Berwick 1974; Mungall 2000; Mungall and Sheffield 1994) and 20–21 years in captivity (Grzimek 1990; Jones 1982); 1 female born at the National Zoo, Washington, D.C., lived 21 years and 8 months (Weigl 2005). Survival patterns among male and female *B. tragocamelus* are similar to those of other ungulates (Brown 1976) but vary depending on population density and status of particular populations, either on native or introduced range (cf. Berwick 1974; Sheffield et al. 1983). High rates of mortality are common for males in particular, but also females, before age 3 (Berwick 1974; Brown 1976). In Gir Forest, India, 34% of calves die each year, and there is a general linear decline of 52% of 2–10-year-olds of both sexes (Berwick 1974). In southern Texas, mortality of both



Fig. 5.—Male *Boselaphus tragocamelus* reaching for leaves of woody vegetation in Ranthambore National Park, Rajasthan, India, December 2004; browse is seasonally important in the diet in India and southern North America; note the characteristic “hogmane” at base of the neck. Photograph courtesy of David Behrens (<http://www.pbase.com/dbehrens>).

males and females is high from birth to 3 years of age and relatively low from 6 to 8 years of age (Sheffield et al. 1983). As a tropically adapted species, *B. tragocamelus* cannot endure low temperatures and maintains meager winter fat reserves; where introduced in southern Texas, 1,000 individuals died in a single winter due to exposure and presumed protein malnutrition (Brown 1976; Schmidly 1994; Sheffield et al. 1983).

Space use.—In India, *B. tragocamelus* is a habitat generalist (Mathai 1999) but tends to occur in “thin bush with scattered low trees or alterations of scrub and open grassy plains” with “either level or undulating” topography, rarely in thick forest but often on cultivated areas (Blanford 1888:518; Prater 1980). In agricultural areas, *B. tragocamelus* will feed throughout the night in open fields and retreat to the cover of forests during the day (Bohra et al. 1992; Mathai 1999; Pandey 1988; Prajapati and Singh 1994;

Sharma 1981; Shukla and Khare 1998). In southern Texas where confinement to large tracts of fenced land does not limit habitat availability, *B. tragocamelus* avoids dense woodlands and frequents improved pasture, sparse forests of live oak (*Quercus virginiana*) and scrub, and coastal prairies (Ables and Ramsey 1972; Schmidly 1994; Sheffield et al. 1971, 1983).

Boselaphus tragocamelus is nonmigratory, although individuals and groups are capable of considerable movement if ambient conditions (e.g., drought) dictate (Berwick 1974; Dharmakumarsinhji 1959; Sheffield et al. 1983). Home ranges of *B. tragocamelus* in a 5,680-ha fenced area in southern Texas averaged 4.3 km² (0.6–8.1 km²); males were transient, often traversing their entire home range daily, and were not completely impeded by fences (Sheffield et al. 1983).

Diet.—Premaxillary shape of *B. tragocamelus* suggests a mixed feeder (Solounias and Moelleken 1993). Dietary selection varies seasonally and includes grasses (*Cenchrus*, *Cynodon dactylon*, *Desmostachya bipinnata*, *Scripus tuberosus*, and *Vetiveria zizanioides*), woody vegetation (*Acacia nilotica*, *A. senegal*, *A. leucophloea*, *Clerodendrum phlomidis*, *Crotalaria burhia*, *Indigofera oblogifolia*, *Morus alba*, and *Zizyphus nummularia*), and herbaceous species (*Cocculus hirsutus*, *Euphorbia hirta*, and *Sida rhombifolia*—Khan 1994; Mirza and Khan 1975; Prajapati and Singh 1994; Sankar and Vijayan 1992; Sharma 1981; Shukla and Khare 1998; Solanki and Naik 1998). Woody vegetation dominates diets of *B. tragocamelus* in dry tropical forests of India (Khan 1994; Fig. 5).

Frugivory occurs seasonally in India (Sankar and Vijayan 1992). Seeds of 34 plant species germinated in feces of *B. tragocamelus* from Keoladeo National Park, India. Seeds of *Paspalum distichum* occurred in feces year-round, seeds of *A. nilotica* and *Prosopis juliflora* (both with fleshy fruits, but the latter an invasive exotic species in India) occurred in feces during the hot-dry season, and seeds of *Enchinochloa crusgalli* occurred in feces during the monsoon (Middleton and Mason 1992). Easily collected, nutrient-rich, seed-laden feces of *B. tragocamelus* can be used in reforestation efforts in India; seeds of *A. nilotica* from feces germinated at about a 30% higher rate than seeds collected directly (Prajapati and Singh 1994). Albeit atypical, an adult male *B. tragocamelus* stepped on the back of a terrapin near Lake Nawegaon, India, and then pulled out the terrapin's head, neck, and some viscera and ate it; villagers confirmed seeing similar incidents (Chitampalli 1983b).

Boselaphus tragocamelus in southern Texas is more restricted regionally than it is in India, but its diet is equally cosmopolitan. It consumes at least 167 species (66 grasses, 89 herbaceous species, and 12 woody plants); average annual diet is 66% grass, 25% herbaceous species, and 15% browse (Sheffield 1983; Sheffield et al. 1983). Generally, adult males eat more grass throughout the year than adult females, and subadults eat more herbaceous vegetation than adults of

either sex; seeds, mainly from mesquite (*Prosopis glandulosa*), are seasonally important (Sheffield et al. 1983). Preferred genera in southern Texas are *Paspalum*, *Setaria*, and *Cenchrus* (grasses); *Lycium*, *Prosopis*, and *Celtis* (woody vegetation); and *Cassia*, *Rhynchosia*, and *Sida* (herbaceous vegetation). Dietary quality in southern Texas is: crude protein, 15.6% in spring to 7.5% in late spring and winter (annual average, 10%); calcium, 1.04% in April and November to 0.36% in October; phosphorus, 0.25% in autumn and as low as 0.10%; calcium–phosphorus ratios, 1.4:1–8.0:1; aside from low levels of phosphorus, those levels are comparable to standards for other wild ruminants and livestock (Sheffield 1983; Sheffield et al. 1983).

In India and Nepal, *B. tragocamelus* is limited by availability of free water (Bagchi et al. 2004; Berwick 1974; Dinerstein 1979, 1980). Wild adult males and calves in India will drink continuously for 2 min and 10 s and 1 min and 10 s, respectively (Bohra et al. 1992). Local distribution of *B. tragocamelus* in southern Texas also is constrained by need for free water, which is generally available within home ranges; all sexes and age classes visit water sources and are not adverse to entering water to drink (Fall 1972; Sheffield et al. 1983). During a drought in 1971, a radiocollared adult male established a new home range 1.6 km away in an area with standing water (Sheffield et al. 1983). Captive *B. tragocamelus* readily drink water (1 adult male consumed 14 l/24 h when ambient temperatures reached 40°C—Sheffield et al. 1983); captive neonates drink water at 3 weeks of age (Goldman and Stevens 1980).

Diseases and parasites.—*Boselaphus tragocamelus* harbors a variety of disease agents, but no particular pathogen or disease singularly affects the species or population levels (Sheffield et al. 1983). Many diseases, or disease-related conditions, are reported in captive individuals, including lesions associated with lymphoproliferative disease and malignant catarrhal fever (Blake et al. 1990), subclinical viral peste des petits ruminants (Furley et al. 1987), intestinal diverticulitis (Rajan et al. 1994), sarcocystotic cysts with associated pathology of a bluetongue-like disease (Acharjyo and Rao 1988), and mesothelioma and reticulum cell sarcoma and hepatoma (Rao and Acharjyo 1984). Domestic livestock likely transmit diseases to free-ranging populations of *B. tragocamelus* in India (Chhangani 2001), including foot-and-mouth disease (type “A” virus—Mukhopadhyay et al. 1975), suspected rinderpest (Mathur et al. 1975), and bovine tubercle bacilli (Datta 1954).

Parasites of free-ranging *B. tragocamelus* in India include nematodes *Ashworthius martinagliai*, *A. perrilli*, *Oesophagostomum venulosum*, *Stephanofilaria*, and *Trichuris globulosus* (Agrawal and Shah 1984; Chauhan et al. 1972; Hiregoudar 1974, 1976; Ortlepp 1935); trematodes *Cotylphoron cotylphoron* and *Gastrothylax crumenifer* (Ortlepp 1935); deer louse fly (*Lipoptena indica*—Hiregoudar 1976); eye worm *Thelazia rhodesii* (Chauhan and Pande 1973); and ticks *Hyalomma brevipunctata* (Hiregoudar 1976).

and *Haemaphysalis bispinosa* (Singh et al. 1978). In Uttaranchal in northwestern India, 41.6% of 161 fecal samples from *B. tragocamelus* were positive for single or mixed infections of *Amphistomes*, *Strongyles*, *Trichuris*, *Fasciola*, and coccidians (Banerjee et al. 2005). In southern Texas, 7 species of trichostrongylid nematodes occur in the gastrointestinal tract, including *Haemonchus*, *Ostertagia ostertagi*, and *Trichostrongylus axei* (Sheffield et al. 1983). External parasites in southern Texas include ticks *Boophilus* (Davey 1993), *B. microplus* (George 1990), and *Amblyomma cajennense* and likely *Dermacentor*, *Ixodes*, and *Halmaphysalis* (Sheffield et al. 1983). Additional internal parasites of captive *B. tragocamelus* include the spiruroid nematode *Gongylonema pulchrum* (Chakraborty 1994) and the protozoan *Toxoplasma gondii* (Ippen et al. 1981; Sedláč et al. 2004).

Interspecific interactions.—In India, *B. tragocamelus* is sympatric with axis deer or chital (*Axis axis*), blackbuck (*Antelope cervicapra*), chinkara (*Gazella bennettii*), chowsingha or 4-horned antelope (*T. quadricornis*), and sambar deer (*Rusa unicolor*) and less commonly with gaur (*Bos frontalis*) and water buffalo (Berwick 1974). Typically, some degree of habitat (Bagchi et al. 2003a, 2003b; Berwick 1974; Dinerstein 1979; Pandey 1988) and dietary (Berwick 1974; Khan 1994; Shukla and Khare 1998; Sheffield 1983) differentiation occurs. In Ranthambhore National Park, *B. tragocamelus* and chinkara form a “bovid guild” and select *Acacia*–*Butea* habitats during summer and winter, in contrast to sympatric axis and sambar deer that prefer *Anogeissus*–*Grewia* forests; in contrast to cervids, *B. tragocamelus* was tolerant of livestock grazing and associated degradation of grass cover (Bagchi et al. 2003a, 2003b). In southern Texas, differences in size and feeding preferences appear to minimize competition among native and domestic ungulates; however, when forage supplies are low, *B. tragocamelus* competes with cattle for grasses and white-tailed deer for herbaceous vegetation (Sheffield 1983; Sheffield et al. 1983).

In India, the endangered Indian tiger (*Panthera tigris tigris*) preys on *B. tragocamelus*, although it constitutes only 5–7% of prey items in Ranthambhore National Park (Bagchi et al. 2003c), 2.7% in Sariska Tiger Reserve (Sankar and Johnsingh 2002), and 3.6% in Nagarjunasagar Srisaillam Tiger Reserve (Reedy et al. 2004). In Pench National Park, India, tigers do not prey on *B. tragocamelus* (Biswas and Sankar 2002). In Nepal, 1.8% of tiger’s prey in the Royal Bardia National Park is *B. tragocamelus* (Støen and Wegge 1996). The rarity of Indian tigers suggests they do not limit any populations of *B. tragocamelus*.

Scats of the endangered Asiatic lion (*Panthera leo persica*) in Gir Forest, India—the only population in the wild—contain < 3% *B. tragocamelus* (Joslin 1984), paralleling predictions of Hayward and Kerley (2005) that *B. tragocamelus* is not a preferred prey item of lions in general. *B. tragocamelus* comprises 15.4% of the prey biomass of the leopard (*Panthera pardus*) in Sariska Tiger Reserve (Sankar

and Johnsingh 2002) but is not preyed on Kalakad-Mundanthurai Tiger Reserve (Ramakrishnan et al. 1999), reflecting leopard preference for smaller prey (Hayward et al. 2006).

Boselaphus tragocamelus comprises a small proportion (frequency of occurrence: winter, 5.2%; summer, 4.9%; monsoon, 7.5%) of the diet of the endangered Indian wolf (*Canis lupus pallipes*) in western India (Jethva and Jhala 2004), but wolves may prey on calves to a greater degree (Sharma 1981). Fourteen percent of 26 scats from striped hyenas (*Hyaena hyaena*) in the Sariska Tiger Reserve contained *B. tragocamelus* (Sankar and Jethva 2002). Cohen (1978) did not find published evidence that dhole (*Cuon alpinus*) prey on *B. tragocamelus*, but Sharma (1981) stated that they prey on calves.

BEHAVIOR

Grouping behavior.—*Boselaphus tragocamelus* is not as gregarious as other herding ungulates and occurs in relative small groups throughout the year. Adult males segregate from females and subadults during nonbreeding seasons. Annual group sizes in India are 1.9–2.9 individuals (Bagchi et al. 2004; Berwick 1974; Khan et al. 1996); male prevalence in groups during breeding in Nepal is 1 male, 37%; 2 males, 28%; 3 males, 20%; and > 4 males, 15% (Dinerstein 1980). Outside of the breeding season in India, herd composition changes constantly with small groups of 1 or 2 adult females and their offspring; mixed herds of 3–6 adult females, yearling females, and an occasional calf; and male groups of 2–18 individuals (Schaller 1967; Sharma 1981).

Reproductive behavior.—*Boselaphus tragocamelus* is polygynous, and mature adult males breed most often. Early accounts of free-ranging *B. tragocamelus* describe a territorial system with adult males forming breeding groups of 2–10 females (Schaller 1967). In captivity, male territoriality and female social hierarchy, perhaps a condition of confinement, have been suspected (Oguya and Eltringham 1991). However, most researchers find little evidence for territorial breeding or harem formation (Dharmakumar-sinhji 1959; Fall 1972; Sheffield et al. 1983). Solitary breeding males are not “spatially fixed” but maintain an “area of dominance” around themselves as they move among different groups of females; the system results in “mutual avoidance” (Fall 1972; Sheffield et al. 1983:43–44) and temporary dominance (Owen-Smith 1977) among breeding males.

As rut approaches, adult male *B. tragocamelus* interact aggressively, and vigorous fights occur to establish dominance. Dominance interactions between males include lateral displays with various head and neck displays that maximize appearance of the chest, white gular patch, and beard (arched-necked display and straight-necked display) and frontal head-erect displays (similar to alert posture)



Fig. 6.—Premounting behavior of *Boselaphus tragocamelus* in Koleado National Park, western India, December 2004. Photograph courtesy of David Behrens (<http://www.pbbase.com/dbehrens>).

often at distances of > 75 m between conspecifics (Fall 1972; Sheffield et al. 1983). Threats are more serious than dominance displays and include a straight-necked threat displayed frontally and usually ≤ 10 m from a conspecific (while stationary, walking, or running toward opponent) and rush threat from a normal stance or after a lateral display with lowered neck, head toward the ground, and horns horizontal (contact and goring of the thighs or flank are common, and chases of ≤ 750 m have been observed—Fall 1972; Sheffield et al. 1983). While displaying, males may circle one another crouched and with a stiff posture (Cowan and Geist 1961; Fall 1972).

Two types of fights occur between males: head butting with horns and neck fighting, either in standing or kneeling positions (Lundrigan 1996; Walther 1958). Neck fighting of male *B. tragocamelus* is relatively unique among ungulates (Sheffield et al. 1983). Neck fighting occurs most often in bachelor herds among subadults and yearlings (also noted in captive calves—Oguya and Eltringham 1991); although intense, these interactions appear to be mock fights (Fall 1972). The thick dermal shield on the neck and chest of male *B. tragocamelus* is protective, but fighting of either type can result in serious goring and mortality. Puncture wounds and even protruding viscera have been observed; 40 mature males collected for dietary studies in southern Texas had noticeable scars on their neck and shoulders (Sheffield et al. 1983). Female *B. tragocamelus* also neck fight and display intrasexual agonistic behavior by rushing; head butting other females on their shoulders, flanks, or sides; and threatening with flattened ears and stretched neck (Fall 1972; Sheffield et al. 1983).

During breeding, generally only 1 mature male accompanies a female group at a time, sometimes for only a few hours (Fall 1972). Even during the breeding season, female

groups usually do not have a breeding male present; males display no attempt at harem formation or defense of a spatially defined breeding territory (Fall 1972; Sheffield et al. 1983). Courtship is simple and may last 45 min: breeding male approaches a female stiffly, body stretched lengthwise, and tail erect with the tuft at a right-angle kink; female typically holds her head close to ground and meanders forward (Fig. 6); male licks and nuzzles the female's perineum; if receptive, female raises her tail and elicits a flehmen (lip curl) response from the male, who then rests his chin on her rump, pushes his chest forward to touch her, and mounts; copulation is terminated by the female; no postcopulation display is noted (Fall 1972; Sheffield et al. 1983).

Free-ranging female *B. tragocamelus* become solitary as parturition approaches and keep neonates hidden from other conspecifics for about 1 month (Fall 1972; Sheffield et al. 1983). Even in captivity, neonates are hidden if possible (Lacey 1969); parturition of 1 twin took place in a standing position and the other, 25 min later, in a lying position; neonates stood after 20–40 min (Goldman and Stevens 1980). Neonates nurse from a reverse parallel position, and females often terminate nursing by stepping over their calf (Fall 1972; Sheffield et al. 1983). Average nursing bouts can last 7 min in captivity, and calves show interest in forage during their 4th week (Goldman and Stevens 1980). Play behavior is apparent but not frequent among calves; activities include bounding with a spring start and landing stiff-legged, chasing (Goldman and Stevens 1980), and play-fighting (rudimentary neck fighting) with erect tails as early as 3 months old (Fall 1972; Sheffield et al. 1983).

Communication.—*Boselaphus tragocamelus* is normally quiet, but early accounts describe vocalizations like “a creaking ... of a Child's Rattle, or Croaking of some Birds” (Parsons 1745:467). All age classes < 5 months of both sexes use a forceful “guttural, coughing roar (‘bwooh’) when alerted” that lasts only 0.5 s, can be heard from 500 m, and occasionally is responded to in-kind by other herds ≤ 500 m away; pitch of this vocalization is lowest for males and highest for calves (Fall 1972; Sheffield et al. 1983:35). Aggressive bulls occasionally display a “low-pitched belching moan” while chasing one another (Fall 1972; Sheffield et al. 1983:35). In captivity, females display a “low guttural clicking” while neonates nurse (Goldman and Stevens 1980) and call while in estrus (Lacey 1969).

Boselaphus tragocamelus of both sexes and all age classes defecate repeatedly in conspicuous fecal piles, often > 3 m and up to 6 m in diameter, within their home range; this type of scent-marking likely has social or communicative implications (Blanford 1888; Brander 1923; Dharmakumar-sinhji 1959; Fall 1972; Prater 1980; Schaller 1967; Sheffield et al. 1983). In southern Texas, fecal piles are most frequent “on bare or open ground along roads, game trails, and at trail intersections” (Sheffield et al. 1983:33), suggesting a form of advertising. Fresh feces are added to a pile, on

average, every 3.7 days (Sheffield et al. 1983). By manipulating fecal piles, Fall (1972) demonstrated that odor and presence of feces are more important than characteristics of the site of defecation. Fecal piles are sometimes established on carcasses of dead animals (Sheffield et al. 1983).

Defecation postures of *B. tragocamelus* are characteristic and exaggerated (Fig. 1); males stand with their rear legs spread 0.6–1.0 m, rump lowered, tail erect at least above horizontal and often near vertical, and head and neck erect and forward; the position is maintained for ≥ 10 s after defecation; forward spraying of urine by males often accompanies defecation (Fall 1972). Females defecate in a similar but less exaggerated posture than males and, unlike males, will defecate while walking (Fall 1972:101). As is common in ungulates, contagious defecations usually occur when individuals arise from a bedded position (Fall 1972). *B. tragocamelus* beds in the typical bovine position but often in sparsely vegetated areas without shade even during the heat of the day, typically separated by 5–10 m (Fall 1972; Sheffield et al. 1983). Position of ungular glands on the legs may serve to scent-mark bedding sites (Gosling 1985; Pocock 1910).

Miscellaneous behavior.—*Boselaphus tragocamelus* can be very wary (Fall 1972; Schaller 1967; Sheffield et al. 1983), likely related to harassment. In contrast, early accounts from Hindu-dominated areas in India where the species was not hunted or harassed described them as very tame (Blanford 1888; Lydekker 1894; Sclater and Thomas 1900); tame individuals have been used in feeding and nutritional evaluations (Berwick 1974; Sheffield et al. 1983). In southern Texas, males and females are equally likely to flee approaching research vehicles; mean flight distance was about 300 m, but a galloping flight response (up to 48 km/h—Fall 1972:97) was apparent even up to 700 m; individuals did not seek cover but ran opposite of the disturbance (Sheffield et al. 1983).

GENETICS

Boselaphus tragocamelus has a diploid chromosome number (2n) of 46: female fundamental number (FN) = 60, male FN = 59, autosomal arm number = 56 with 16 acrocentric and 6 biarmed autosomal pairs (Gallagher et al. 1998; Wurstor and Benirschke 1968). Compared with a standard cattle karyotype, 6 biarmed elements of *B. tragocamelus* are derived from centric fusion between acrocentric chromosomes (1;5, 2;3, 6;13, 8;12, 19;27, 24;25—Gallagher et al. 1998). G-, Q-, and C-band karyotypes are present, chromosome 25 is centrically fused to 24, and chromosome 16 is acrocentric (Gallagher et al. 1998). The X chromosome is compound metacentric, and the Y chromosome is compound acrocentric (Gallagher et al. 1999). Internal telomeric sequences are evident on the Y and X chromosome indicating past translocation events with autosomes (Petit et al. 1999).

DNA sequence conservation occurs in *B. tragocamelus* (Pépin et al. 1995). Gallagher et al. (1998) concluded that *B. tragocamelus* was karyotypically derived with conditions unique to species of Bovinae; some derived chromosomal conditions common to *B. tragocamelus*, the African buffalo (*Syncerus caffer*), and some Tragelaphini could be convergent. Gene sequences for interleukin 2 (Das et al. 2006), Toll-like receptor 3 (Dhara et al. 2007), and prion protein gene (Seabury et al. 2004) suggest that *B. tragocamelus* shares a common lineage with water buffalo (*B. bubalis*) and kudu (*Tragelaphus*) more than with domestic cattle. A unique T→C transition exists at position 345 of the mitochondrial 16S rRNA gene in *B. tragocamelus* that can be used forensically to differentiate it from 23 species in 7 subfamilies of Bovidae and various species in families Equidae, Rhinocerotidae, Felidae, and Hominidae (Guha and Kashyap 2003).

CONSERVATION

Boselaphus tragocamelus is a species of least conservation concern in its native range (International Union for Conservation of Nature and Natural Resources 2006). Numbers in India total about 100,000 but have always been low in lowland Nepal (Adams 1858; Dinerstein 1979); this species is rare in Pakistan (Mirza and Khan 1975) and extinct in Bangladesh (Mallon 2003; Rahmani 2001). About 37,000 exotic *B. tragocamelus* occur in southern Texas (International Union for Conservation of Nature and Natural Resources 2006; M. Traweek and R. Welch, in litt.); the species can be harvested throughout the year with no limit on numbers if the hunter has a valid hunting license from the state of Texas. Recent concern has been expressed over the negative impact of heavily used trails of *B. tragocamelus* that may open up dense shrubby habitats that are critical for the endangered ocelot (*Leopardus pardalis*) and jaguaroni (*Puma yagouaroundi*) in extreme southern Texas (B. R. Winton, in litt.). Numbers of exotic *B. tragocamelus* in Mexico are unknown, but they currently range over 44,500 ha in 5 states (J. Álvarez-Romero, in litt.).

Boselaphus tragocamelus can jump fences 2.1–2.5 m high (Sharma 1981; Sheffield et al. 1983), so exotic populations in the United States, Mexico, and South Africa thought to be contained within fenced private properties likely have, or will, disperse. The species is often a serious agricultural pest in India (Bohra et al. 1992; Chauhan and Sawarkar 1989; Goyal and Rajpurohit 1999; International Union for Conservation of Nature and Natural Resources 2006; Mathai 1999; Prajapati and Singh 1994; Sekhar 1998; Sharma 1981) and is responsible for depredation of wheat (*Triticum*), sorghum (*Sorghum*), mung (*Phaseolus*), and mustard (*Brassica*—Sharma 1981). Legal protection in India is often waved to minimize depredation complaints (International Union for Conservation of Nature and Natural Resources 2006).

REMARKS

Perhaps as a reflection of the primitive lineage and mixed appearance of *B. tragocamelus*, its scientific name translates, in Latin and Greek, to the ox (*bos*, Latin)—deer (*elaphos*, Greek) and goat (*tragos*, Greek)—camel (*kamelos*, Greek). The various common names of *B. tragocamelus* are equally mixed in meaning and origin: nilgai (roots are Hindustani nil meaning blue and gai meaning bovine, and Sanskrit gabhih meaning female bovine, or Persian gaw meaning cow), nylghai (Pilgrim 1939), nylghiae, neel-ghae (Ogilby 1837), nylghau (Gray 1850), nilgo, nilgau (International Union for Conservation of Nature and Natural Resources 2006), white-footed antelope (Pennant 1771), and blue bull or bluebuck with clear relevance to the coloration of mature males. The various references to cow and bull have led to local Hindu beliefs that *B. tragocamelus* is sacred (International Union for Conservation of Nature and Natural Resources 2006; Prater 1980) and should be protected from hunting in India.

Early accounts about the palatability of the flesh of *B. tragocamelus* were less than flattering (Sclater and Thomas 1900). However, flesh of adult females is of comparable texture and tenderness to beef but is less flavorful and lower in fat (by 2 times) and cholesterol (Tegarden 1988). In various formulations of hot dogs for human consumption (presumably the American market), taste panels preferred the flavor of hot dogs with 33% *B. tragocamelus* (Eggen et al. 1973).

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