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MAMMALIAN SPECIES 843:1–11

Tetracerus quadricornis (Artiodactyla: Bovidae)

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Abstract: *Tetracerus quadricornis* (de Blainville, 1816) is 1 of the smallest Asian bovids and commonly is called the four-horned antelope or chousingha. It is endemic to Peninsular India and small parts of lowland Nepal. *T. quadricornis* is a sexually dimorphic boselaphid of small stature; only males have horns, with 2 of the 3 recognized subspecies having 2 anterior and 2 posterior smooth, sharp horns, unique among wild horned mammals. *Tetracerus* is monotypic. It prefers dry deciduous forested habitat and hilly terrain and is secretive and little studied. This diminutive species is considered Vulnerable by the International Union for Conservation of Nature and Natural Resources, and it is very uncommon in captivity. DOI: 10.1644/843.1.

Key words: chauka, chousingha, four-horned antelope, India, ruminant, ungulate, vulnerable species

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Tetracerus É. Geoffroy Saint-Hilaire and F. Cuvier, 1824

Cerophorus de Blainville, 1816:74. Part.

Cervicapra: de Blainville, 1816:75, 78. Part; preoccupied by *Cervicapra* Sparrman, 1780.

Antilope: Desmarest, 1816:193. Part.

Tetracerus É. Geoffroy Saint-Hilaire and F. Cuvier, 1824:unnumbered page associated with pl. 383, vol. vi, livr. 44. Type species *Tetracerus striaticornis* É. Geoffroy Saint-Hilaire and F. Cuvier, 1824, by original designation (see "Nomenclatural Notes").

Tetracerus Hardwicke, 1825:520. Type species *Antilope chickara* Hardwicke, 1825; preoccupied by *Tetracerus* É. Geoffroy Saint-Hilaire and F. Cuvier, 1824.

Tetraceros Brookes, 1828:64. Incorrect subsequent spelling of *Tetracerus* É. Geoffroy Saint-Hilaire and F. Cuvier, 1824.

Cervus: É. Geoffroy Saint-Hilaire and F. Cuvier, 1832:unnumbered page associated with pl. 364, vol. vii, livr. 65. Part.

Grimmia Laurillard, 1839:624. Part.

Styloceros: Lesson, 1842:174. Part; incorrect subsequent spelling of *Stylocerus* Hamilton-Smith, 1827.

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



Fig. 1.—Male *Tetracerus quadricornis* illustrating the 4 horns typical of adult males of 2 subspecies; note enlarged preorbital gland extending below the eye. Photograph by K. Sharma.

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Tetracerus quadricornis (de Blainville, 1816)
Four-horned Antelope

[*Cerophorus* (*Cervicapra*)] *Quadricornis* de Blainville, 1816:75, 78–79. Type locality "l'Inde."

Antilope quadricornis: Desmarest, 1816:193. Name combination.

[*Tetracerus*] *Striaticornis* É. Geoffroy Saint-Hilaire and F. Cuvier, 1824:unnumbered page associated with pl. 383, vol. vi, livr. 44. Type locality unknown; references in text to "Nepaul" [= Nepal] and "Bengale," northeastern India (see "Nomenclatural Notes").

[*Tetracerus*] *Undicornis* É. Geoffroy Saint-Hilaire and F. Cuvier, 1824:unnumbered page associated with pl. 383, vol. vi, livr. 44. Nomen nudum (see "Nomenclatural Notes").

Antilope [(*Cervicapra*)] *Chickara* Hardwicke, 1825:520. Type locality "western provinces of Bengal, Bihar and Orissa," India.

A[*ntilope* (*Tetracerus*)]. *chickara*: Hamilton-Smith, 1827:343. Name combination.

A[*ntilope* (*Tetracerus*)]. *quadricornis*: Hamilton-Smith, 1827:343. Name combination.

A[*ntilope*]. *Chikara* J. B. Fischer, 1829:471. Incorrect subsequent spelling of *Antilope chickara* Hardwicke, 1825.

[*Cervus*] *Labipes* É. Geoffroy Saint-Hilaire and F. Cuvier, 1832:unnumbered page associated with pl. 364, vol. vii, livr. 65. Type locality "des Mariannes," islands in the Philippine Sea but not from islands known today as the Northern Marianas Islands.

Antilope chicara Kaup 1835:179. Incorrect subsequent spelling of *Antilope chickara* Hardwicke, 1825.

A[*ntilope*]. *Tetracornis* Hodgson, 1836:524, pt. 6, pl. I. Type locality "Taraï [= lowland Nepal]."

Tetracerus chickara: Jardine, 1836:224. Name combination.

T[*etracerus*]. *quadricornes* Jardine, 1836:225. Incorrect subsequent spelling of *Cerophorus quadricornis* de Blainville, 1816.

Antilope (*Grimmia*) *quadricornis*: Laurillard, 1839:624. Name combination.

Antilope Sub-4-cornutus Elliot, 1839:225. Type locality "undulating hills of the Mulnad [= Malnad]," Karnataka, southern India.

Antilope chicarra É. Geoffroy Saint-Hilaire and F. Cuvier, 1842:3. Incorrect subsequent spelling of *Antilope chickara* Hardwicke, 1825.

Tetraceros chickera Blyth 1842:451. Incorrect subsequent spelling of *Antilope chickara* Hardwicke, 1825.

Ant[*ilope*]. *subquadricornutus* Blyth 1842:452. Justified emendation of *sub-4-cornutus* Elliot, 1839.

Cervus [(*Styloceros*)] *labipes*: Lesson, 1842:174. Name combination.

Tetracerus quadricornis: Gray, 1843:159. First use of current name combination.

Tetracerus subquadricornis Gray, 1843:159. Type locality "Madras," India.

T[*etracerus*]. *subquadricornutus*: Hodgson, 1847:89. Name combination.

T[*etracerus*]. *iodes* Hodgson, 1847:90. Type locality "Saul forests [India] beneath the Sub-Himalayas."

T[*etracerus*]. *paccerois* Hodgson, 1847:90. Type locality "Saul forests," India.

Tetracerus paccervis Gray, 1852. Incorrect subsequent spelling of *Tetracerus paccerois* Hodgson, 1847.

T[*etraceros*]. *q*[*uadricornis*]. *typicus* Sclater and Thomas, 1895:215. Usage is equivalent to *Tetracerus quadricornis quadricornis* and not intended as a new name.

T[*etraceros*]. *q*[*uadricornis*]. *subquadricornutus*: Sclater and Thomas, 1895:215. Name combination.

Cervus latipes Sclater and Thomas, 1895:216. Incorrect subsequent spelling of *Cervus labipes* É. Geoffroy Saint-Hilaire and F. Cuvier, 1832.

CONTEXT AND CONTENT. Context as for genus. Groves (2003:353–354) recognized 3 subspecies based on body size, shape of nasals, color and color pattern, length of tail, and number of horns in adult males (Fig. 1); molecular investigations have not been conducted:

T. q. iodes Hodgson, 1847. See above.
T. q. quadricornis (de Blainville, 1816). See above.
T. q. subquadricornis Gray, 1843. See above.

Some concern exists over whether subspecific characters include presence or absence of anterior horns because males 10–14 months of age that do not yet have developed anterior horns may be confused for adult males that can be of comparable size (Sharma et al. 2005).

NOMENCLATURAL NOTES. The authority and date for *Tetracerus* have been reported as either Leach, 1825 (Gray 1850; Grubb 2005) or Hardwicke, 1825 (Sclater and Thomas 1895). Confusion exists because *Tetracerus* was attributed to W. E. Leach (1790–1836) in a note (perhaps authored by an editor) at the end of the publication by Hardwicke (1825:524), based on text read to the Linnean Society of London on 18 February and 17 June 1823. Leach never published this specific nomenclatural act (as far as we can determine), but he did publish other taxonomic volumes (Brewer 1884) and perhaps organized certain specimens under *Tetracerus* that became generally known during his tenure at the British Museum (Natural History), which ended in 1821 (Lee 1909).

Attributing *Tetracerus* to Leach would be permitted under Article 50.1.1 of the *International Code of Zoological Nomenclature* (International Commission on Zoological Nomenclature 1999) if the attribution to Leach was clear in someone else's publication and if Leach previously satisfied 2 of the 3 criteria of availability by offering a name, a description or indication, or a publication (A. L. Gardner, United States Geological Survey, pers. comm.).

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The last 2 conditions were not met in Hardwicke's (1825) publication, indicating that Hardwicke himself should be given authority for *Tetracerus*. A year earlier than Hardwicke (1825), however, É. Geoffroy Saint-Hilaire and F. Cuvier (1824) also credited Leach with naming *Tetracerus* (Sclater and Thomas 1895) and provided its 1st published affiliation with *striaticornis*, often attributed to Brookes, 1828 (Grubb 2005:697). Nevertheless, É. Geoffroy Saint-Hilaire and F. Cuvier's (1824) publication also did not meet the conditions given above.

Credit for *Tetracerus* was contentious at the time. Sclater and Thomas (1895:217–218) sided with their "countryman," Hardwicke, who claimed priority in 3 letters to the Linnean Society in January 1825 (*Linnean Online Library Catalogue*; http://linnean.org). Hardwicke accused A. Devaucelle (also occurs in print as Devaucel, Duvaucel, and Du Vaucel) of Chandernagore, a French naturalist whom he associated with in India prior to these publications, of plagiarism by giving his drawings and descriptions to É. Geoffroy Saint-Hilaire and F. Cuvier, who subsequently used the information in their classic *Historie Naturelle des Mammifères*. Although historically interesting, Hardwicke's accusations cannot be resolved now and, more importantly, are not relevant to current nomenclatural standards (International Commission on Zoological Nomenclature 1999).

Because neither publication by É. Geoffroy Saint-Hilaire and F. Cuvier (1824) or Hardwicke (1825) satisfied criteria needed to attribute *Tetracerus* to Leach, 1825 (Grubb 2005), we changed the authority and date to É. Geoffroy Saint-Hilaire and F. Cuvier, 1824, and also credited them with the 1st use of *striaticornis*. Furthermore, we added *undicornis* É. Geoffroy Saint-Hilaire and Cuvier, 1824, in the synonymy as a nomen nudum (Article 12.1—International Commission on Zoological Nomenclature 1999) because the publication specifically stated that the species description was of *striaticornis*, not *undicornis* for which no description was (or has been) provided. Throughout most of the early 1800s, it was not clear how many species should be assigned to *Tetracerus* because of geographic variation in size and presence (or absence) of the 4 horns. Although zoologists named multiple species of *Tetracerus* through the 1800s, the genus is now considered monotypic, currently with 3 named subspecies (Groves 2003).

The repetitive etymology of *Tetracerus quadricornis* in Greek and Latin is four (*Tetra*, Greek)-horned (*keras*, Greek) and four (*quadri*, Latin)-horned (*cornu*, Latin). Common names of *T. quadricornis* vary depending on language and country of origin (International Union for Conservation of Nature and Natural Resources 2008; Prater 1980): chousingha, chowsingha, or chausingha (Hindi meaning 4 horns), doda (Hindi), nari komboo marn (Tamil), kondu kuri (Kannada), ghutri (central India), chauka (Nepal), four-horned antelope (English), antilope à quatre cornes or tétracère (French), and antílope de cuatro cuernos (Spanish). Hardwicke's (1825) specific epithet *chickara* led to some early confusion (Blanford 1888; Elliot 1839; Sclater and Thomas 1895) because the common name for the Indian gazelle (*Gazella bennettii*) is chinkara.

DIAGNOSIS

Tetracerus quadricornis is 1 of the most diminutive Asian bovids and has no congeners. It is easily distinguished from the only other species in the tribe Boselaphini, the sympatric nilgai (*Boselaphus tragocamelus*—Leslie 2008), by its considerably smaller mass (1:9) and height (1:2) and frequent presence of 4 male-only horns (2 posterior and 2 anterior, but lacking in *T. q. subquadricornis* according to Groves [2003]). Aside from some breeds of domestic sheep, *T. quadricornis* is the only extant mammal with 4 horns (Figs. 1 and 2).

Relative to their mass, stature, coloration, and habitat preferences, *T. quadricornis* may be confused with the Indian muntjac (*Muntiacus muntjak*) and hog deer (*Axis porcinus*—Nowak 1991). Unlike *T. quadricornis*, however, males of the latter 2 species have antlers that are shed annually, and both sexes have upper canines. The male Indian muntjac is distinguished further by bony facial ridges that give rise to pedicels to support small antlers. All 3 species are generally solitary, prefer dense vegetative cover, and remain close to water, albeit range overlap in India is minimal. "Jerky" movements of *T. quadricornis* distinguish it from other comparably sized ungulates in its native range (Blanford 1888:521; Nowak 1991). Although the Indian gazelle can be of comparable mass (Berwick 1974; Krishnan 1972), the white and brown patterning of its pelage and large ringed horns differentiate it from *T. quadricornis*.

GENERAL CHARACTERS

Male-only horns distinguish sexes of *Tetracerus quadricornis* (Fig. 1) at maturity; mass is comparable. De Blainville's (1816) initial description focused on the 4 horns and the unique frontal bone of the skull from which they arise. Blanford (1888), Lydekker and Blaine (1914), Prater (1980), and Groves (2003) expanded the species' description: anterior and posterior horns of some males unique among wild ungulates, otherwise general description the same for both sexes; small size and delicate build; pelage thin, short, and lighter in summer but thick, coarse, and darker in winter; color variable, perhaps among currently described subspecies (Groves 2003:354), from dull rufous-red and pale brown to yellow-creamy fawn in summer to brown in winter, with lighter or whitish ventral and inner leg markings without clear demarcation; white ring and tuft of hair on

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Fig. 2.—Dorsal, ventral, and lateral views of skull (British Museum [Natural History] BMNH specimen 1902.8.14.3) and lateral view of mandible (BMNH 1856.9.22.1) of adult male *Tetracerus quadricornis*. Greatest length of skull is 179 mm.

lower legs, sometimes not obvious; muzzle, back of ears, and anterior strips down legs blackish; occasional pair of white spots on each cheek, similar to *B. tragocamelus* (Leslie 2008); tail short and compressed; large preorbital glands elongated (Fig. 1) and well developed, unguinal glands above dew-

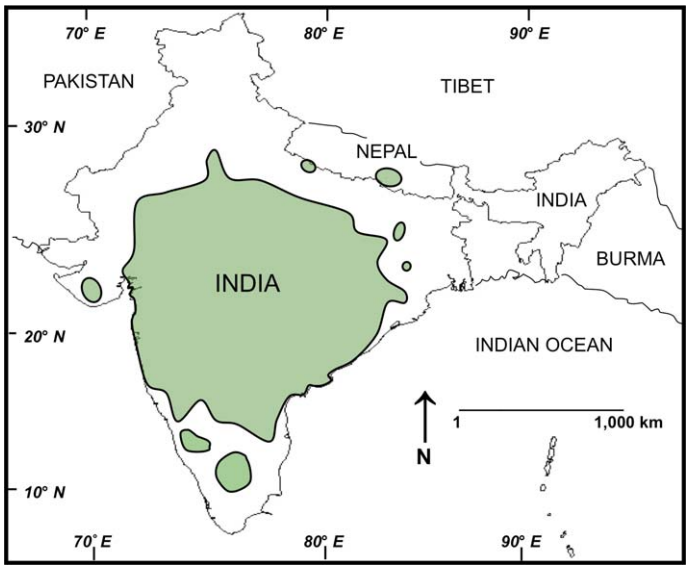


Fig. 3.—Distribution of *Tetracerus quadricornis* in India and Nepal; densities tend to be highest in central parts of the main range in India (Sharma 2006).

claws on rear legs, but no inguinal glands (Gosling 1985; Pocock 1910).

DISTRIBUTION

Tetracerus quadricornis is endemic to the Peninsular Indian and Indus divisions of the Indian Subregion in the Asian Indomalayan Region (Corbet and Hill 1992) and occurs only in India and Nepal (Fig. 3; Chesemore 1970; Krishnan 1972; Prater 1980; Rahmani 2001; Rice 1991; Sharma et al. 2005; Singh and Swain 2003). Extant populations of *T. quadricornis* are fragmented by human activities, but the species is most abundant in the central states of India (Fig. 3). Isolated populations exist in Gir Wildlife Sanctuary in western India (Sharma et al. 2005:15, figure 4.i; Singh 2001), 2 areas in southern India, 1 in northern India, 2 areas northeast of the central range, and 1 area in Nepal (Sharma 2006).

FOSSIL RECORD

Fossils related to extant tribe Boselaphini are well represented in Africa and Eurasia from the Miocene and represent the earliest bovids that arose 16–18 million years ago (Gentry 1978; Ginsburg and Heintz 1968; Solounias 1990). Pilgrim (1939:138) considered extant *Tetracerus* the most direct descendant of the primitive and extinct *Eostragus* (Ginsburg and Heintz 1968). Living Boselaphini (*T. quadricornis* and *B. tragocamelus*) are Miocene relicts and most related to early bovids (Pilgrim 1939; Pitra et al. 1997; Prothero and Schoch 2002), with horn morphology

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(straight and circular in cross section) representing the primitive condition (Geist 1966; Janis 1982; Lundrigan 1996). *Tetracerus*, *Boselaphus*, and related fossil forms share similar primitive horn-core ontogeny (Solounias 1990).

The artiodactylan fossil fauna of India is rich and includes extinct genera closely related to *T. quadricornis* (Colbert 1935; Pilgrim 1937, 1939). India may have been the ''developmental centre,'' or close to it, of Bovidae 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). Bovids differentiated considerably during the Middle Miocene about 15 million years ago, and Bovini and Boselaphini likely arose 8–9 million years ago in Asia south of the Himalaya Mountains (Bibi 2007; Hassanin and Ropiquet 2004). Seven boselaphine-like genera (*Boselaphus*, *Duboisia*, *Perimia*, *Proboselaphus*, *Selenoportax*, *Sivaportax*, and *Tetracerus*), based largely on their similar ''circular or equilaterally triangular cross-section[s]'' of their horn cores, are represented in the fossil record of India (Pilgrim 1939:191). *Boselaphus*, *Duboisia*, and *Sivaportax* are related most closely to *Tetracerus* (Pilgrim 1939).

Unlike *T. quadricornis*, females of many related fossilized boselaphines had horns with similar morphology and developmental processes as other bovids (e.g., Hooijer 1958; Kostopoulus 2005). Late Miocene boselaphine fossils from the eastern Mediterranean region are common (Kostopoulus 2005; Kostopoulus and Koufos 2006). Boselaphine-like fossils from the Pleistocene have been found eastward from India to Burma (Blanford 1888; Colbert 1943). Human use of *T. quadricornis* is evident in the Mesolithic of southern India 5,000–8,000 years ago (Murty 1985) and the Chalcolithic of eastern India about 3,000 years ago (Badam et al. 2001).

FORM AND FUNCTION

Few published records of mass and stature exist for *Tetracerus quadricornis.* Generally, adults weigh 17–22 kg (Elliot 1839; Nowak 1991; Sharma and Rahmani 2004) and stand 55–64 cm at the shoulder (Nowak 1991; Sclater and Thomas 1895; Sharma and Rahmani 2004). *T. quadricornis* can be anesthetized with ketamine (>8–12 mg/kg body weight—Shashidhar 1981).

The frontal–parietal profile of the skull of *T. quadricornis* is ''slightly and gently rounded, the occipital meeting the parietal at a right angle'' with large lachrymal fossae (Fig. 2; Blanford 1888:519; Lydekker and Blaine 1914). Male-only horns characteristically arise close together just behind the orbits directed upward. They are nearly straight with no arch, black, generally smooth, and sharp.

Mean (± *SE*) skull and horn characteristics (mm) of males of the 3 subspecies of *T. quadricornis* outlined by Groves (2003:354) are: *T. q. quadricornis* with 4 horns: skull length, 192.9 ± 5.47 (n = 11); nasal breadth, 17.2 ± 1.38 (17); posterior horn length, 90.7 ± 10.61 (23); anterior horn length, 48.6 ± 3.78 (7) in Rajasthan, India, and 31.7 ± 11.31 (11) elsewhere; *T. q. iodes* with 4 horns: skull length, 191.0 (1); nasal breadth, 18.7 ± 2.52 (3); posterior horn length, 73.5 ± 4.73 (4); anterior horn length, 20.7 ± 5.69 (3); and *T. q. subquadricornis* with 2 horns: skull length, 187.0 ± 3.0 (3); nasal breadth, 19.7 ± 1.15 (3); posterior horn length, 83.5 ± 13.18 (4). Anterior horns are sometimes represented by only hairless raised bumps (Nowak 1991; Phythian-Adams 1951; Prater 1980). Other skull measurements of a male *T. quadricornis* are (mm): width of zygomatic arches, 78; width of skull orbits, 80; width of braincase, 56; circumference of horn core at base, 42; length of lachrymal, 39 (British Museum [Natural History] specimen 1858.5.4.41—Pilgrim 1939:171).

Dentition of adult *T. quadricornis* is typical of bovids: i 0/3, c 0/1, p 3/3, m 3/3, total 32. Canines are incisoriform, and upper molars are short with quadrangular crowns and selenodont cusps and lack additional columns on the inner side (Lydekker and Blaine 1914). Selected dental measurements from a male are (mm): length of premolar series, 27; length of molar series, 35; height of M3, 15; anterior-to-posterior diameter of M3, 14 (specimen number not given—Pilgrim 1939:155).

Specific aging techniques have not been developed for *T. quadricornis*. Sharma et al. (2005) classified males in Panna National Park in 4 age classes based on presence and lengths of anterior horns of 1 of the subspecies characterized by 4 horns: class 1 = young-of-the-year < 66% of adult body mass; class 2 = juvenile males with no evidence of anterior horns, which start to develop at 10–14 months of age in captivity; class 3 = males with anterior horns ≤ 33% of the length of the posterior horns; and class 4 = oldest males with anterior horns ≥ 33% of the posterior horns. Most male *T. quadricornis* in Panna National Park, India, had anterior horns 25–66% the length of their posterior horns, but some males had anterior and posterior horns of equal length (Sharma et al. 2005). ''Dark interior [lines] of the ear face'' may automimic posterior horns of male *T. quadricornis* (Fig. 4), enhancing threat signals (Guthrie and Petocz 1970:586).

ONTOGENY AND REPRODUCTION

The female reproductive tract of *Tetracerus quadricornis* contains 2 uterine compartments separated by a median anterior-to-posterior septum and small fallopian tubes relative to other ungulates (Weldon 1884). Placental cotyledons number 22–30, about one-half that noted in other antelopes; the fetal chorion has vascular ridges similar to those of the pig (*Sus scrofa*); and fetuses have a uniserial psalterium (= developing omasum—Weldon 1884). Four inguinal mammae are present in females.

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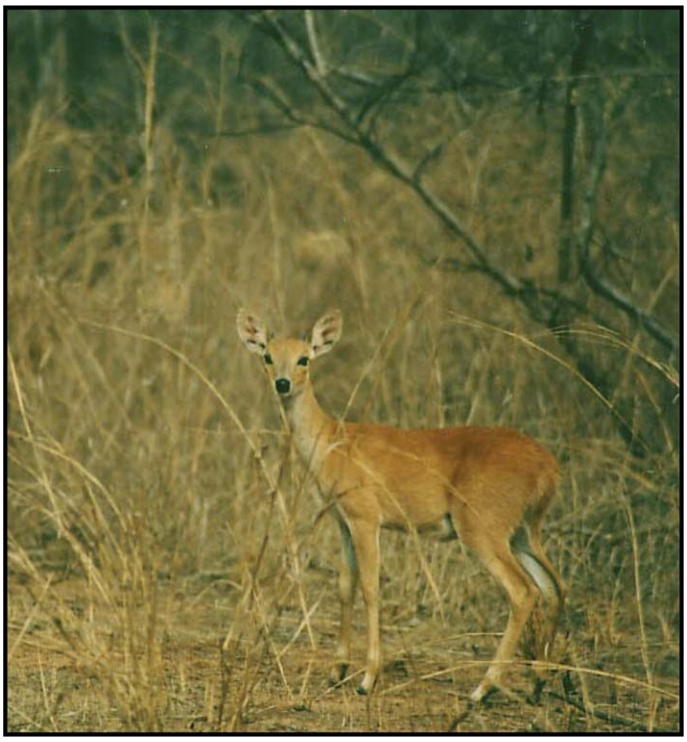


Fig. 4.—Male *Tetracerus quadricornis* in typical habitat of dry deciduous forest edge, Panna National Park, central India; note inner ear markings that may serve to automimic posterior horns in adult males and enhance threat displays (Guthrie and Petocz 1970). Photograph by K. Sharma.

Age at sexual maturity of wild *T. quadricornis* is not clearly understood (Grzimek 1990), but 2 captive females had their 1st offspring at 21 months of age (Acharjyo and Misra 1975a, 1975b). Gestation is about 8 months—long for such a small ungulate (Shull 1958); Asdell's (1946) assertion of a 183-day gestation seems to be an underestimate (Crandall 1964). Interparturition intervals of 1 captive female were 285 and 327 days (Acharjyo and Misra 1975a). Of 64 captive births in Paris, France, 59% were twins and 41% were single births; sex ratio at birth was generally equal; and parturition extended from August through May (Mauget et al. 2000). In captivity in native India, average litter size was 1.6 (Acharjyo and Mohapatra 1980), and 7 neonates were 0.74–1.1 kg at birth, 42–46 cm in total length, with shoulder heights of 24.0–27.5 cm (Acharjyo and Misra 1975a, 1981).

Parturition can occur throughout the year in the wild, but newborns are noted most often in October–November in India (Sharma at al. 2005; Shull 1958). Most newborn sightings are of twins, but later, most sightings are of single offspring suggesting regular loss of 1 offspring (Sharma et al. 2005). Offspring remain with their mothers for about 1 year, and an adult female can be seen with her young-of-the-year and a juvenile, presumably hers (Sharma et al. 2005). Breeding likely peaks in June–July when the chance of seeing pairs of females and males is highest (Sharma et al. 2005:32, figure 7.iv).

ECOLOGY

Population characteristics.—Densities of *Tetracerus quadricornis* in India are generally low and vary depending on habitat conditions, competition with domestic livestock, predation, and degree of protection. Specific densities reported in India are: 0.22–0.75 individuals/km^2, Gir Lion Sanctuary (Berwick 1974; Berwick and Jordan 1971; Khan 1997; Khan et al. 1996; Rice 1991); 0.29–0.80 individuals/km^2, Pench Tiger Reserve, and 0.29–2.70 individuals/km^2, Panna National Park (Biswas and Sankar 2002; Rice 1991; Sharma et al. 2005; Shukla 1997); 0.80 individuals/km^2, Nagarhole National Park (Karanth and Sunquist 1992); 1.28 individuals/km^2, Dhaknakolkaz Wildlife Sanctuary (Rice 1991); and 2.05 individuals/km^2, Kanha National Park (Schaller 1967). No density estimates of *T. quadricornis* are available from Nepal (Heinen and Yonzon 1994).

Maximum life span of *T. quadricornis* in captivity is generally $\leq$10 years (Grzimek 1990; Jones 1982), but 1 individual lived 17 years and 5 months (Weigl 2005). In captivity, 59% of offspring died in their 1st year (Mauget et al. 2000), perhaps reflecting uncertain husbandry techniques. No information exists on survival of offspring in the wild (Berwick 1974), but it is likely less. In Gir National Park and Wildlife Sanctuary, India, female : male ratios were 1:0.62 in winter and 1:0.71 during the hot-dry season; female : offspring (<1 year) ratios were 1:046 in winter and 1:0.14 during the hot-dry season (Berwick 1974). Monthly sex ratios in Panna National Park ranged from 1:0.37 in November to 1:1.45 in July (annual average = 1:0.72), the larger ratio perhaps reflecting greater visibility of males during the breeding season (Sharma et al. 2005). Female and male *T. quadricornis* are similar in size and color, but behavioral differences permit estimation of detection probabilities; using such detection probabilities, Sharma (2006) estimated a year-round sex ratio of 1:0.69.

Space use.—In India, *Tetracerus quadricornis* is a habitat generalist (Berwick 1974; Sharma 2006) but is observed mostly in dry deciduous mixed forest with ''thickets and clusters of trees even within open dry patches,'' hilly terrain, and limited human disturbance (Prater 1980; Sharma 2006; Sharma et al. 2005:37; Singh 2001). In Panna National Park, India, *T. quadricornis* avoids disturbed areas and uses all other habitats in proportion to their availabilities; height of grassy vegetation is associated with an index of wariness and provides protection from predators (Sharma et al. 2005).

Despite occupying dry forests (Fig. 4), local distributions of *T. quadricornis* are constrained by daily need for free water (Blanford 1888:521; Krishnan 1972; Prater 1980). *T.*

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quadricornis is nonmigratory, and although little is known about its space use, it is likely sedentary (Krishnan 1972) with individuals possibly occupying exclusive home ranges (Sharma and Rahmani 2004).

Diet.—*Tetracerus quadricornis* is herbivorous with a ruminal digestive system. Foraging preferences of *T. quadricornis* are understood only from limited direct observations of wild individuals (Sharma et al. 2005) and research with tamed animals under conditions that may or may not have reflected their native habitat preferences (Solanki and Naik 1998 cf. Berwick 1974). As a small antelope (Jarman 1974), *T. quadricornis* forages selectively and eats nutritious plant parts such as fruits, flowers, and fresh leaves (Berwick 1974; Sharma et al. 2005).

In tame-animal trials on grazing plots dominated by grasses and forbs in India, *T. quadricornis* preferred, in descending order, legumes, other herbaceous species, woody species, and grasses—generally reflecting selection of the most nutritious forage available (Solanki and Naik 1998). In those trials, *T. quadricornis* selected a diet containing 59.9% legumes: 40.0% *Alysicarpus elsinoideys*, 10.5% *Indiofera cordifolia*, and 9.4% *A. bupleurifolius*. In Gir National Forest, mixed ungulate assemblages partition their food selection, but all depend on woody species during the hot-dry season (Berwick 1974). *T. quadricornis* preferred woody species in all cafeteria and field experiments (ranked in order of percent occurrence from highest to lowest): *Ziziphus mauritiana*, *Bauhinia racemosa*, *Emblica officinalis*, *Acacia leucophloea*, *Terminalia tomentosa*, *Bosewellia serrata*, *Soymida febrifuga*, and *Lannea coromandelica* (Berwick 1974). Sharma (2006) demonstrated preference for *Z. mauritiana*, *A. nilotica*, *A. leucophloea*, *A. catechu*, *E. officinalis*, and *Dendrocalamus strictus*. Fruits of *Emblica* and *Terminalia* were consumed by all Indian ruminants examined by Berwick (1974).

Diseases and parasites.—*Tetracerus quadricornis* likely harbors similar disease agents and parasites as other Indian antelopes (Leslie 2008), but published information specific to *T. quadricornis* is lacking. No particular pathogen or disease has been reported to singularly limit population levels. Sarcocystotic cysts with associated pathology of the heart muscle (Acharjyo and Rao 1988; Rao and Acharjyo 1984), rinderpest (Mathur et al. 1975), pulmonary tuberculosis and the liver fluke *Fasciola gigantica* (Rao and Acharjyo 1996), and an unidentified parasite of the aorta (Rao and Acharjyo 1984) have been reported for *T. quadricornis* in captivity.

Interspecific interactions.—India has a rich ungulate fauna (Sclater 1896), although it has been diminished by human activities in some areas (Bagchi 2006). Distributional and habitat overlap can be substantial among *Tetracerus quadricornis*, nilgai, and sambar (*Rusa unicolor*) and less so with Indian gazelle and chital (*Axis axis*); overlap with hog deer and blackbuck (*Antilope cervicapra*) is very uncommon and with Indian muntjac almost nonexistent because the latter dwells exclusively in moist deciduous and evergreen forests (Bagchi 2006; Berwick 1974; Schaller 1967; Sharma et al. 2005). In Panna National Park, common use of fecal piles by *T. quadricornis*, nilgai, and Indian gazelle suggests the greatest niche separation between *T. quadricornis* and Indian gazelle (Sharma et al. 2005).

The endangered Indian tiger (*Panthera tigris tigris*) preys on *T. quadricornis*, although it constitutes only 1.8% of prey items in Pench National Park (Biswas and Sankar 2002), 2.8% in Panna National Park (Chundawat et al. 2006), 3.4% in Sariska Tiger Reserve (Sankar and Johnsingh 2002), and 4.2–15.8% in Nagarjunasagar Srisailam Tiger Reserve (Reddy et al. 2004). *T. quadricornis* comprised 2.0% and 5.0% of the prey of the leopard (*Panthera pardus*) in Nagarahole National Park (Karanth and Sunquist 1995) and Gir National Park (Mukherjee et al. 1994), respectively, but there was no evidence of such predation in Sariska Tiger Reserve (Sankar and Johnsingh 2002). Dhole (*Cuon alpinus*) scats contained 2% remains of *T. quadricornis* in Nagarahole National Park, India (Karanth and Sunquist 1995). Other large mammalian predators of the Indian Peninsula, such as the endangered Indian wolf (*Canis lupus pallipes*) and striped hyenas (*Hyaena hyaena*), have not been noted to prey on *T. quadricornis*.

BEHAVIOR

Tetracerus quadricornis is a shy, nonherding ungulate and occurs solitarily or in groups of ≤4 individuals throughout the year. In Nagarhole National Park, India, 80% of observations of *T. quadricornis* were of solitary individuals, and maximum group size was 2 individuals (Karanth and Sunquist 1992). In Gir National Forest, India, maximum group size was 4 but averaged 1.5–1.6 individuals (Berwick 1974); mean group sizes were generally ≤1.2 individuals (Khan et al. 1996). In Panna National Park, India, 69% of individuals were solitary throughout the year, followed by 24% in groups of 2; mean group size increased seasonally, but marginally, from 1.1 individuals in November to 1.6 individuals in May, reflecting an increased chance of female–male association during the breeding season (Sharma et al. 2005).

Few observations of breeding behavior of wild *T. quadricornis* exist (Fig. 5). Male–female pairs increase in frequency in May–July in Panna National Park suggesting breeding activity, but only two 1- to 2-s copulatory bouts were observed (Sharma et al. 2005). In captivity, Shull (1958:10) described mating behavior that included a precopulatory ''period of play, kneeling on their front knees facing each other, interlocking their necks [the latter 2 behaviors reminiscent of the related nilgai—Leslie 2008] and pushing with all their strength.'' That was followed by ''drill-like'' strutting behavior by the male and then copulation (Shull 1958).

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Fig. 5.—Male (left) and female (right) *Tetracerus quadricornis* associate irregularly and are seen together most often during rut in May–July, Panna National Park, central India. Photograph by K. Sharma.

Alarm calls of *T. quadricornis* are described as a ''husky pronk'' or ''sharp bark'' (Phythian-Adams 1951:5); males make a distinct ''cough'' sound around females, and females make ''soft calls'' to locate hidden neonates (Sharma 2006; Sharma et al. 2005). Both sexes of *T. quadricornis* defecate repeatedly at the same location (Blanford 1888; Sharma et al. 2005). Nonrandom clustering of fecal piles of *T. quadricornis* in some areas suggests a form of communication or advertisement (Sharma et al. 2005), similar to behavior of *B. tragocamelus* (Leslie 2008). Male and female *T. quadricornis* use their large preorbital scent glands (Pocock 1910; Fig. 1) to mark vegetation, leaving a white crystallized film (Sharma et al. 2005).

Tetracerus quadricornis is secretive and very wary in present-day India—described as ''wideawake'' by Phythian-Adams (1951). It will often freeze rather than flee when a threat approaches (Sharma et al. 2005), but it also will make ''conspicuous leaps followed by quiet stealthy movements'' (Sharma and Rahmani 2004:unnumbered page). *T. quadricornis* is easily tamed when young (Prater 1980). Berwick (1974) used tame individuals for his feeding preference evaluations in Gir National Forest, India. Males can be bold in captivity and can cause serious injury by goring a handler with their horns (Shull 1958); 1 captive male was described as a ''little unruly antelope'' (Shashidhar 1981:8), and during breeding, males have been described as ''exceedingly wild and mischievous'' (Jardine 1836:224–225).

GENETICS

Tetracerus quadricornis has a diploid chromosome number (2n) of 38 and fundamental number (FN) of 38 with 36 acrocentric and subacrocentric autosomes and no metacentric or submetacentric autosomes (Wurster and Benirschke 1968). The X chromosome is medium-sized acrocentric, and the Y chromosome is small metacentric (Wurster and Benirschke 1968). Analyses of 12S and 16S rRNA mitochondrial genes confirm the phylogenetic affinity of *T. quadricornis* and the nilgai, and affinities with the domestic yak (*Bos grunniens*—Leslie and Schaller 2009), domestic cow (*B. taurus*), and American bison (*Bison bison*—Kuznetsova et al. 2002). Given habitat fragmentation, isolation, and small sizes of populations of *T. quadricornis*, loss of genetic diversity is of concern (Rice 1991).

CONSERVATION

Because of the unique pairs of anterior and posterior horns, *Tetracerus quadricornis* has been prized as a hunting trophy; some sportsman consider its meat dry and not as palatable as that of other antelopes (Blanford 1888; Nowak 1991), but at least 1 claimed it to be ''the best of any antelope or deer'' (Phythian-Adams 1951:5). Currently, *T. quadricornis* is protected in Nepal (Heinen and Yonzon 1994) and India (e.g., Indian Wildlife Protection Act of 1972—Sharma et al. 2005) and considered Vulnerable with decreasing population trends on the *Red List of Threatened Species* of the International Union for Conservation of Nature and Natural Resources (2008).

The rangewide population is estimated at only 10,000 (Mallon 2003). Many populations are protected in various sanctuaries and national parks in India (Rice 1991) and Nepal (Chaudhary 2000; Heinen and Yonzon 1994), but adding to basic knowledge of this little-studied species (Bagchi 2006; Sharma et al. 2005), minimizing habitat loss from human activities (Awasthi et al. 1994; Chhangani 2001; Khan 1995; Singh 2001), and maintaining connectivity among protected areas (Ravan et al. 2005) are ongoing conservation challenges.

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