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Axis axis (Artiodactyla: Cervidae)

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Abstract: *Axis axis* (Erxleben, 1777) is an Old World deer commonly known as chital, Indian spotted deer, or axis deer. It is one of five species in the genus *Axis* and is native to the Indian subcontinent, occurring in India, Nepal, Bhutan, Bangladesh, and Sri Lanka. Free-ranging and confined populations of *A. axis* have been established in Europe, Australia, and both North and South America. Globally, it is considered "Least Concern" (LC) by the International Union for Conservation of Nature and Natural Resources.

Key words: axis deer, cerf axis, cervid, chital, Indian spotted deer

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Axis Gray, 1825

Cervus: Erxleben, 1777:312. Part.

Axis: Gray, 1825:342. Described as a member of the tribe Cervina to contain *Muntjaccus*, *Coassus*, *Capreolus*, *Axis*, *Cervus*, *Dama*, *Tarandus*, and *Alus*; (see "Nomenclatural Notes").

Axis: Hamilton-Smith, 1827b:312. Described as a subgenus of *Cervus* Linnaeus, 1758, to contain *C. axis*, *C. porcinus*, and *C. pumilio*; type species *Cervus axis* Erxleben, 1777, by subsequent designation (Kretzoi and Kretzoi 2000a:42, 2000b:446).

Hippelaphi Sundevall, 1846:177. Part; incorrect subsequent spelling of *Hippelaphus* Bonaparte, 1837; described as a subgenus of *Cervus* Linnaeus, 1758, to contain *C. japonicus*, *C. duvaucelli*, *C. aristotelis*, *C. equinus*, *C. hippelaphus, C. moluccenis*, *C. peroni*, *C. kuhlii*, *C. philippinus*, *C. mariannus*, *C. lepidus*, *C. axis*, *C. pseudaxis*, and *C. nudipalpebra*.

Hyelaphus Sundevall, 1846:180. Described as subgenus of *Cervus* Linnaeus, 1758, to contain *C. porcinus*.

Melanaxis Heude, 1888:8. Type species *Cervus alfredi* Sclater, 1870, by original designation.

Chital Griffith, 1928:206. Nomen dubuim.

Fig. 1.—Adult male *Axis axis*. Photograph by Paul Wild used with permission.

Context and Content. Order Artiodactyla, suborder Ruminantia, infraorder Pecora, family Cervidae, subfamily Cervinae, tribe Cervini, genus *Axis*. There are five species of *Axis* (Groves and Grubb 2011). Antler structure and development are similar among species and therefore not a useful characteristic for distinguishing species within *Axis*. In wild populations, geographical distributions can be used to differentiate *A. kuhlii* (Bawean Island, Indonesia) and *A. calamianensis* (Calamian Islands, Philippines) from each other and from other species of *Axis* (Groves and Grubb 2011). Coat patterns and geographical distribution were used to develop the following general key.

1. Distinct dorsal stripe extending from shoulders to base of tail 2
   Indistinct, or lacking, dorsal stripe 3
2. Coat marked by distinct white spots .... *A. axis*
   Coat lacking distinct spotted pattern .... *A. calamianensis*
3. Lips lighter in color than face; accentuated by dark band extending from the corner of the mouth up toward nose .... *A. kuhlii*
   Lips and face similarly colored; lacking distinct facial markings 4
4. Species found from Pakistan to Myanmar .... *A. porcinus*
   Species found from Thailand, Cambodia, and Vietnam .... *A. annamiticus*

Axis axis (Erxleben, 1777)

Chital

[*Cervus*] *Axis* Erxleben, 1777:312. Type locality "habitat ad ripas Gangis, vulgaris; in Iaua [sic], Ceylona [= common habitat on the banks of the Ganges; on "Illa Iana," Ceylon (= Sri Lanka)]."

C[*ervus*]. *Axis maculatus* Kerr, 1792:300. Type locality "banks of the Ganges and the island of Ceylon (= Sri Lanka)."

Cervus axis: Hamilton-Smith, 1827a:117. Name combination.

Cervus axis var. *ceylonensis* J. B. Fischer, 1829:619 (page numbered as 419 due to error). Type locality "*In campis prope Surpat Indiae orinetalis et in sylvis densis Indiae orientalis insularumque Ceylon, Javae et Sumatrae.*"

Cervus axis var. *indicus* J. B. Fischer, 1829:619 (page numbered as 419 due to error). Type locality "*In campis prope Surpat Indiae orinetalis et in sylvis densis Indiae orientalis insularumque Ceylon, Javae et Sumatrae.*"

Cervus nudipalpebra Ogilby, 1831:136. Type locality "Banks of the Ganges."

Axis maculatus: Jardine, 1835:un-numbered page (in Table of Contents). Name combination.

Axis aculatus Jardine, 1835:167. Incorrect subsequent spelling of *Cervus axis maculatus* Kerr, 1792.

Cervus (*Axis*) *major* Hodgson, 1841:914. Type locality "Nepal."

Cervus (*Axis*) *minor* Hodgson, 1841:914. Type locality "Nepal."

Axis maculata: Gray, 1843:178. Name combination and unjustified emendation of *Cervus axis maculatus* Kerr, 1792.

C[*ervus* (*Hippelaphi*)]. *axis*: Sundevall, 1846:177, 180. Name combination.

C[*ervus*]. *axi* Sundevall, 1846:180. Incorrect subsequent spelling of *Cervus axis* Erxleben, 1777.

Axis maculatus: Jerdon, 1867:260. Correction of gender agreement.

Hyelaphus maculatus: Fitzinger, 1874:259. Name combination.

Axis maculata ceylonensis: Fitzinger, 1874:269. Name combination.

Axis nudipalpebra: Fitzinger, 1874:270. Name combination.

Cervus (*Rusa*) *axis zeylanicus* Lydekker, 1905:947. Type locality "Ceylon (= Sri Lanka)."

Axis axis: R. I. Pocock, 1923:184. First use of current name combination.

Chital cervus axis: A. S. Griffith, 1928:206. Name combination.

Cervus axis maculates Groves, 2003:351. Incorrect subsequent spelling of *Cervus axis maculatus* Kerr, 1792:300.

Context and Content. Context as for genus. *Axis axis* is monotypic.

Nomenclatural Notes. Although Hamilton-Smith (1827b) is usually considered the authority of the genus *Axis* (e.g., Grubb 2005; Groves and Grubb 2011), Kretzoi and Kretzoi (2000a, 2000b) refer to "de Blainville 1816 -?-" as the authority with the annotation "fide [trust in] Gray 1825." Gray (1825) predates Hamilton-Smith (1827b), and used *Axis* as one of eight genera in his tribe Cervina and presented it as "Axis, *Blainv.*" Uncertain of the true publication date of de Blainville in which *Axis* was presented, Kretzoi and Kretzoi (2000a, 2000b) trusted Gray's reference to an earlier publication and guessed that the year 1816 was correct. The 1816 publication by de Blainville represents his earliest classification of "ruminans" but does not include the name *Axis*. Later, de Blainville (1822) published a detailed classification of *Cervus*, in which he grouped 10 Asian species under the vernacular name "Axis." He did present one of those species as "L'Axis unicolor, *A. unicolor*," possibly the first use of "*A*[*xis*]" as a genus or a lapsus. Despite de Blainville's (1822) usage of "Axis" as a vernacular name and potential for "*A. unicolor*" to be a reference to "Axis" as a genus, his intent is unclear. Thus, the most straightforward first use of *Axis* as a genus is Gray (1825), and therefore he is considered the authority.

DIAGNOSIS

The subfamily Cervinae consists of nine genera found almost entirely in Eurasia; seven of the nine genera in Cervinae are currently in the tribe Cervini: *Axis*, *Cervus*, *Dama*, *Elaphurus*, *Przewalskium*, *Rucervus*, and *Rusa* (Groves and Grubb 2011). Among the five species of *Axis* (*axis*, *annamiticus* [Indochina hog deer], *calamianensis* [Calamian deer], *kuhlii* [Bawean deer], and *porcinus* [Indian hog deer]), distribution differentiates *Axis axis* from all congeneric species. In areas where *A. axis* has been introduced, adults can be differentiated from co-occurring species, excluding *Dama dama* (common fallow deer), by their spotted coat. Where *A. axis* co-occurs with common fallow deer, adult *A. axis* may be differentiated from the common fallow deer by its more reddish coat, stronger dorsal stripe, and palmate antlers in the male.

GENERAL CHARACTERS

Axis axis is a medium-sized, heavily spotted deer standing 0.6–1.0 m at the shoulder with an average overall body length of 1.5 m (Walker 1964), and is the third largest ungulate on the Indian subcontinent (Karanth and Sunquist 1992; Khan et al. 1995) with *Boselaphus tragocamelus* (nilgai—Leslie 2008) and *Rusa unicolor* (sambar—Leslie 2011) being the largest and second largest ungulates, respectively, on the Indian subcontinent. *A. axis* has white spots, often aligning in longitudinal rows, on its flanks and back over a reddish coat, with a dark brown-to-black stripe running from the base of the neck to the base of the tail; inner legs, belly, throat patch, and underside of the tail are white (Walker 1964; Ables et al. 1977). Males grow large, simple antlers, typically with three tines per side; each triad has a relatively short, forward-curved brow tine, an elongated frontal tine, and the long tip of the main shaft forms the third tine (Fig. 1; Grubb 1990).

DISTRIBUTION

Axis axis is native to south Asia, occurring between 8 and 30°N in Bhutan, Bangladesh, India, Nepal, Pakistan, and Sri Lanka (Prater 1934; Schaller 1967; Duckworth et al. 2015), with the Himalayan foothills forming the northern boundary of distribution (Walker 1975). Free-living and captive populations have been established in Australia, the continental United States (Graf and Nichols 1966; Ables et al. 1977; Brooks 2006), the Hawaiian Islands (Tomich 1986), and South America (Petrides 1975; Crespo 1982; Lever 1985; Navas 1987; Carpinetti and Merino 1999; Sponchiado et al. 2011), and Europe (Grubb 2005; Fig. 2).

FOSSIL RECORD

Artiodactyls first appear in the fossil record in the Eocene epoch with widespread occurrences throughout North American and Eurasian deposits 46 million years ago (Rose 1982, 1996). Tectonic uplifts forming the Himalayas and Alps during the Oligocene epoch lead to significant diversification of deer-like forms with the emergence of Cervids during the late Oligocene; the Cervinae subfamily dates from the central Asian fossil records 7–9 million years ago, during the late Miocene (Bubenik 1990; Petronio et al. 2007).

The first recognizable Cervini forms are from early and middle Pliocene deposits of central and western Asia (Teilhard de Chardin and Trassaert 1937; Flynn et al. 1991; Di Stefano and Petronio 2002). Current evolutionary evidence suggests that *Axis* diverged from *Cervus* about 6 million years ago with an additional divergence between *Axis* and *Rucervus* about 5 million years ago (Pitra et al. 2004), representing the earliest divergence in tribe Cervini (Gilbert et al. 2006).

Axis shansius is the first recorded fossil specimen of *Axis*, identified from the Yushé Basin, southern Shansi, China (Teilhard de Chardin and Trassaert 1937), and is the earliest fossil specimen recorded in the *Axis* lineage (Di Stefano and Petronio 2002). *A. shansius* has been located throughout Eurasia including China (Teilhard de Chardin and Trassaert 1937), Russia (Vislobokova et al. 1995), and the Guide Basin, Tibet (Pares et al. 2003). Within the Plio-Pleistocene deposits, species of *Axis* and *Rusa* were characterized in zone II of the Yushé series and classified into the Indo-Malayan group (Teilhard de Chardin and Trassaert 1937; Otsuka 1969). *Axis* fossils are characteristic of the Nihowan and Kuchinotsu fauna assemblages of Japan (Otsuka 1969), with *A. japonicus* (Otsuka 1967) having a less intimate relationship to the Chinese *Axis* species described by Teilhard de Chardin and Trassaert (1937). *A. japonicus* is thought to be more closely related to the Trinil and Djetis faunas of Java and might be an ancestral form to *A. javanicus* and *A. lydekkeri* (Otsuka 1969).

Fossil remains from the Khok Sung site, Thailand, are the first reported for *A. axis* in Southeast Asia (Suraprasit et al. 2016). Most *A. axis* fossils are known from the upper Pleistocene to Holocene deposits in India including the Narmanda Valley (Badam and Sankhyan 2009), Son Valley (Badam 2002), Manjra Valley (Badam et al. 1984), the Kurnool cave-complex in the Nandyal Basin (Chuahan 2008), and the Tarafeni Valley in West Bengal (Dassarma et al. 1982; Basak et al. 1998).

FORM AND FUNCTION

Form.—The skull of *Axis axis* is composed of two major regions: the facial and cranial parts (Fig. 3). The shape is dolichocephalic with the facial portion being longer than the cranial portion, forming a roughly triangular shape (Ramswarup et al. 2014). The maximum skull length is 25.5 cm, and maximum skull width is 10.2 cm. The dental formula for *A. axis* is: i 0/3, c 0/1, p 3/3. m 3/3, total 32; canines are incisiform as in all Artiodactyla (Ungar 2010).

The pelvic girdle (os-coxae) consists of two parts meeting at the pelvic symphysis in the midline and is described as a flat irregular bone (Yadav et al. 2012). A detailed description of the pelvic bones is provided by Yadav et al. (2012).

Heart morphology of *A. axis* resembles that of an adult goat, having two surfaces: a broad base and narrow apex ($n = 4$—Gupta et al. 2015). Mean heart weight (± *SE*) was 353.75 ± 2.39 g with a length from base to apex of 13.51 ± 0.04 cm (Gupta et al. 2015). Diameter was 9.80 ± 0.04 cm (sagittal) and 7.58 ±

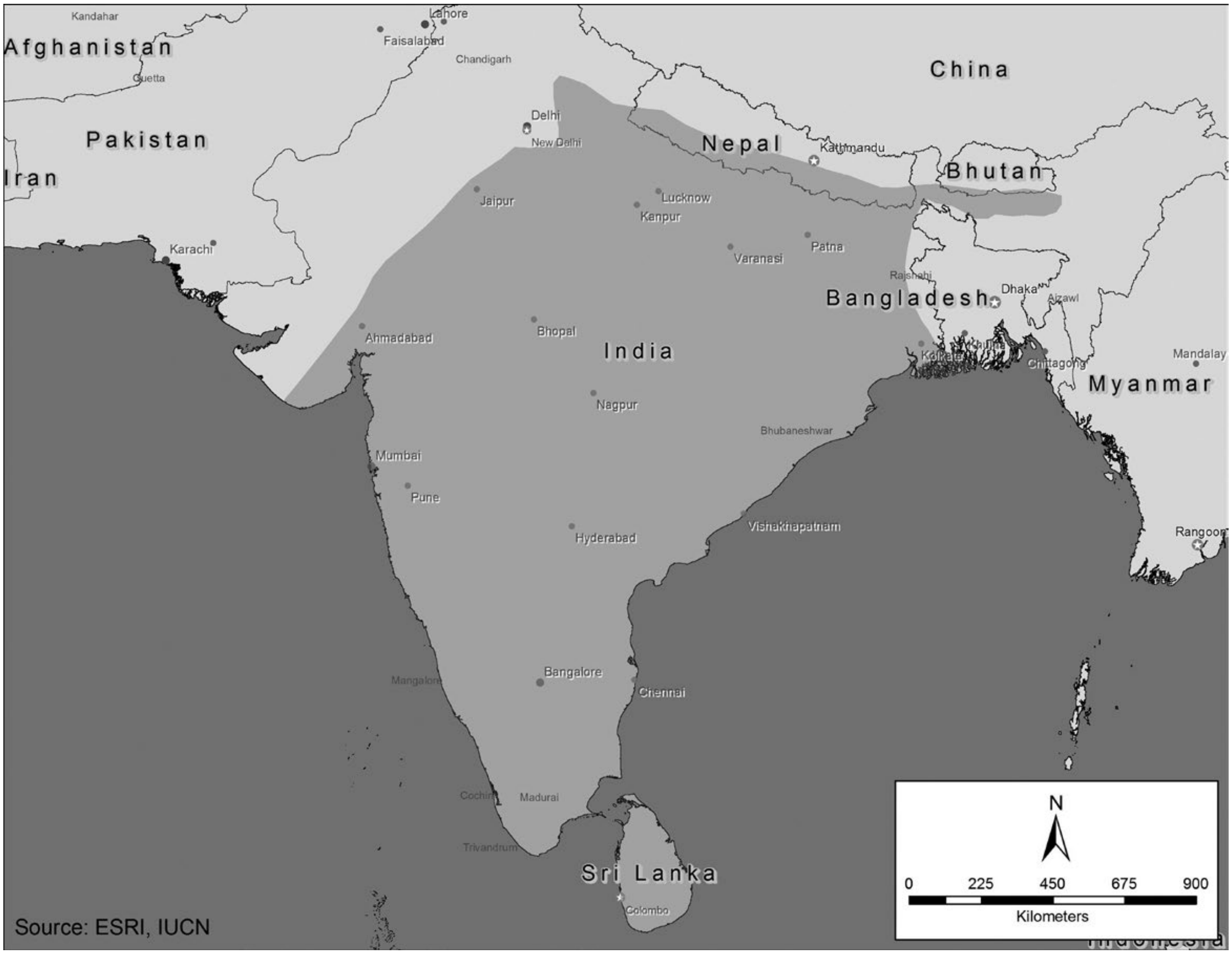

Fig. 2.—Geographic distribution of the native populations of *Axis axis*.

0.04 cm (transverse); circumference was 24.12 ± 0.42 cm (coronary groove), 19.00 ± 0.40 cm (middle of heart), and 10.65 ± 0.06 cm (junction of left and right longitudinal grooves—Gupta et al. 2015).

The tongue of *A. axis* is fairly elongated and terminates in an oval tip (Erdoğan and Pérez 2014). Mean (± *SE*) tongue length from root to apex is 123.89 ± 3.10 mm, and it is uniformly wide along its length: 26.04 ± 0.57 mm (apex), 28.41 ± 1.08 mm (body), 35.23 ± 1.39 mm (torus), and 32.43 ± 0.46 mm (radix). The greatest thickness is 34.24 ± 0.87 mm and found at the torus. Three mechanical papillae (filiform, lenticular, and conical) and two gustatory papillae (circumvallate and fungiform) are found on the dorsal surface of the tongue (*n* = 5—Erdoğan and Pérez 2014).

Mean (± *SE*) solar surface (*n* = 4) of the fore hoof was 6.56 ± 0.024 cm long laterally, with maximum solar surface width of 2.09 ± 0.013 cm; mean (± *SE*) maximum lateral surface was 3.28 ± 0.014 cm; and mean (± *SE*) maximum coronet was 0.58 ± 0.014 cm (Tomar et al. 2011). Mean (± *SE*) interdigital border was 3.48 ± 0.014 cm long, and mean (± *SE*) posterior hoof surface was 1.39 ± 0.013 cm. Mean (± *SE*) hoof angle was 45.0 ± 0.41°. Mean (± *SE*) solar surface of the hind hooves was 5.79 ± 0.013 cm long laterally, with maximum solar surface width of 1.73 ± 0.014 cm; mean (± *SE*) maximum lateral surface was 3.40 ± 0.02 cm; and mean (± *SE*) maximum coronet was 1.23 ± 0.014 cm. Mean (± *SE*) interdigital border was 3.41 ± 0.013 cm long, and mean (± *SE*) posterior hoof surface was 1.89 ± 0.013 cm (Tomar et al. 2011).

Function.—Mean (± *SE*) rectal temperature was 39.2 ± 0.4°C, mean (± *SE*) heart rate was 75.5 ± 6.5 beats/min, and mean (± *SE*) respiratory rate was 62.1 ± 4.2 breaths/min, based on eight chemically immobilized captive *A. axis* (Arnemo et al. 1993). Basic hematology of captive *Axis axis* was: hemoglobin, 109.0–171.2 g/l; mean corpuscular hemoglobin concentration, 327–368 g/l; red blood cells 10.22–14.27 × 10^{12}/l; hematocrit (ratio of red blood cell volume to total blood volume), 0.34–0.47 l/l; white blood cell count, 3.92–8.40 × 10^9/l; and mean corpuscular volume, 10.94–12.47 pg (Chapple et al. 1991). Serum constituent ranges were: protein, 56.3–70.2 g/l; albumin, 27.5–38.3 g/l; alkaline phosphatase, 118–2,493 U/l; creatine kinase, 294–7,400 U/l; calcium, 2.3–2.7 mmol/l; and phosphorus, 2.2–2.7 mmol/l (*n* = 37—Chapple et al. 1991).

Fig. 3.—Dorsal, ventral, and lateral view of skull and lateral view of mandible of adult male *Axis axis* (DMNS [Denver Museum of Nature & Science] ZM.6800) from San Diego Zoo, San Diego, California. Photograph by René O'Connell, Image Archivist, Denver Museum of Nature & Science used with permission.

As a tropical or subtropical species the antler cycle in *A. axis* does not appear to be correlated to photoperiod as it is with temperate cervid species (Grubb 1990). Increases in plasma testosterone levels have been positively correlated with promotion of antler development, and decreasing plasma testosterone levels begin the mineralization process and lead to the ultimate shedding of antlers at completion of the antler growth cycle (Goss and Rosen 1973).

Testis volume (± *SE*) was greater in hard-antlered males (118.8 ± 4.6 cm^3) than velvet-antlered males (74.6 ± 4.4 cm^3—Umapathy et al. 2007). Serum testosterone (± *SE*) was also greater in hard-antlered males (1.2 ± 0.1 ng/ml) than velvet-antlered males (0.6 ± 0.1 ng/ml—Umapathy et al. 2007). Hard-antlered males additionally had higher semen volume (± *SE*; 4.1 ± 9.6 ml) and sperm concentration (338.3 ± 24.9 × 10^6 ml^{-1}) compared to velvet-antlered males semen volume (3.2 ± 0.2 ml) and sperm concentration (57.3 ± 12.4 × 10^6 ml^{-1}—Umapathy et al. 2007). Morphologically abnormal sperm were more prevalent (± *SE*) in velvet-antlered males (43.8 ± 4.1%) than hard-antlered males (20.9 ± 1.9%—Umapathy et al. 2007). Motile sperm percentages (± *SE*) were more than double in the ejaculate of hard-antlered males (66.5 ± 1.5%) than velvet-antlered males (29.9 ± 4.9%—Umapathy et al. 2007). In a study of captive *A. axis*, motile spermatozoa were collected during all phases of the antler development cycle (Loudon and Curlewis 1988).

ONTOGENY AND REPRODUCTION

Ontogeny.—A sigmoid growth curve for weight characterizes fetal development of *Axis axis* (Chapple 1989). Conversely, increases in fetal length are approximately linear at about 13 mm/week. Parturition can occur throughout the year, with birth peaks varying widely by geographic location (Ables et al. 1977; Dinerstein 1980; Mylrea et al. 1999; Ahrestani et al. 2012). The male:female birth ratio of *A. axis* is about 7:10 (Mukhopadhayay 2001). Mean birth weight (± *SD*) is 3.53 ± 0.52 kg (range 2.5–4.7 kg) with mean male fawn weight (3.71 ± 0.47 kg) slightly larger than female fawn weight (3.37 ± 0.47 kg) at birth (Chapple 1989; Willard et al. 1998; Azad et al. 2005). Average daily weight gains from birth to day 280 were 106.0–148.2 g/day for males and 105.0–119.3 g/day for females (Willard et al. 1998). Fawns regularly are left hidden by does for extended periods, with their mothers returning to allow suckling (Schaller 1967). Mean duration of nursing ranges from 44 to 69 s based on 382 observations (Schaller1967). Fawns are known to consume solid foods as early as 3 weeks of age (Khanpara and Vachhrajani 2007), with weaning at 12–20 weeks of age and complete weaning at 6 months of age (Graf and Nichols 1966; Chapple 1989; Azad et al. 2005).

Axis axis can conceive at about 9 months of age under the optimal nutritional conditions of captive rearing (Raman 1998), but estrus can be delayed as long as 2–3 years under suboptimal nutritional conditions. Estrus occurs after a female reaches 50% of mature body weight. Estrus is typically signaled by continual tail flipping and marked restlessness of females (Chapple 1989). All males over 1 year of age with hard antlers produced sufficient sperm to breed, with a positive relationship between the testes:body size ratio and quantity of sperm (Umapathy et al. 2007). Testicular volume mirrors the antler development cycle, with peak testicular volume occurring while males are in hard antler and minimum testicular volumes occurring after antlers are shed (Loudon and Curlewis 1988; Umapathy et al. 2007).

Reproduction.—Breeding periods for *Axis axis* vary widely and can be classified as aseasonal. Regionally, breeding seasons appear to be influenced primarily by weather and climatic conditions (Delany and Happold 1979; Robbins et al. 1987; Sempéré 1990). Breeding condition of males appears to influence timing of primary breeding season. In its native distribution, northern Indian populations breed in October–April, whereas southern Indian populations breed in April–August (Raman 1998). Introduced *A. axis* in Texas commonly breed in May–August, whereas those is Hawaii breed in April–August (Ables et al. 1977). Estrus lasts for 12–30 h or until a female mates. Reports of the length of the interestrous period are 17–56 days, with 17–21 days being most common. Synchronization of estrous cycles is common among females in the same social unit. When calculated from progesterone profiles in two studies (n = 61), interestrous periods were 18 days averaged (Chapple et al. 1993; Mylrea et al. 1999). Serum progesterone levels were 2.7–26 nmol/l. One study reported a female entering estrus 11 times in a 12-month period. Gestation lasts 228–239 days (English 1992), and the average first postpartum estrus occurs 20 days after birth, with as few as 10 days recorded. Twinning is rare, with an average of about 1.03 neonates/female, and litters with triplets have not been documented. Male:female birth ratios are about 1:1 (English 1992). Longevity in the wild varies with 9–13 years typical, in captive populations longevity can exceed 20 years (Weigl 2005).

ECOLOGY

Population characteristics.—Male:female ratios ranged from 0.4:1 to 0.93:1 in Bandipur Tiger Reserve between August 1976 and July 1978 (Johnsingh 1983). Sex ratios in Corbett National Park were reported as about 1:1 (De and Spillett 1966). Densities of *Axis axis* were 10.7–19.7 individuals/km^2 in Nepal (Wegge and Storaas 2009), with typical densities from 4.51 to 51.3 individuals/km^2 across India (Joslin 1973; Berwick 1974; Haque 1990; Karanth and Sunquist 1995; Khan et al. 1996; Raman 1997; Biswas and Sankar 2002; Jathanna et al. 2003), and ≥ 200 individuals/km^2 in forested habitats in southern India (Raman 1997). Few density estimates of introduced *A. axis* populations are available, with most estimated to be within the typical range reported for India (Hawaii Invasive Species Council 2016). Densities of *A. axis* on Maui, Hawaii were 9.5–27.2 individuals/km^2 between 2013 and 2016 (Hawaii Invasive Species Council 2016). In Texas, population densities are currently unknown, and based on our anecdotal observations from 2001 to 2019 vary substantially by county, ranch size, and hunting valuation.

Space use.—*Axis axis* is typically associated with open grass-shrub and mixed forest habitats in India (Graf and Nichols 1966; Mishra 1982), Nepal (Dinerstein 1979; Mishra 1982; Sharma and Chalise 2014), but within its native range *A. axis* occupies areas ranging from semidesert to rainforest (Graf and Nichols 1966; Bhat and Rawat 1995; Raman 1997). *A. axis* was observed more frequently in savannah (grassland) than in other habitat types in the Royal Karnali-Bardia Wildlife Reserve, Nepal (Dinerstein 1979), but radiocollared individuals were located in Riverine Forest habitats in greater proportion than available in the Royal Chitwan National Park, Nepal (Mishra 1982). In central Nepal, *A. axis* preferentially selected grassland and Bheller (*Trewia nudiflora*)–Sisoo (*Dalbergia sisoo*) Mixed Forest habitats over other available habitats (Sharma and Chalise 2014).

Movement and concentration patterns of *A. axis* are location-specific and seasonally dependent (Mishra 1982). In the Bandipur Tiger Reserve, *A. axis* was reported to aggregate after rains, with large herd breakup reported in the Wilpattu (Eisenberg and Lockhart 1972; Johnsingh 1983). Other factors associated with daily and seasonal movements include temperature (Bhat and Rawat 1995), weather (Graf and Nichols 1966; Ables et al. 1977; Bhat and Rawat 1995), forage availability (Balasubramaniam et al. 1980; Sheikh et al. 2011), water availability, and disturbance (De and Spillett 1966; Raman 1997; Sheikh et al. 2011).

Home range sizes vary by location and sex, with males having larger home ranges (204–648 ha) than females (135–648 ha—Schaller 1967; Ables et al. 1977; Moe and Wegge 1994). Male home range sizes in the Royal Chitwan National Park, Nepal were larger than female home ranges for all seasons (Mishra 1982). Mean home range (no *SE* or *SD* provided) during the pre-monsoon for adult males was reported as 220.5 ha compared to 142.6 ha for females during the same period (Mishra 1982), with monsoon home ranges of 146.9 ha and 110.2 ha, and post-monsoon home ranges of 154.5 ha and 126.5 ha reported for adult males and females, respectively (Mishra 1982). Similar patterns were reported for annual home ranges of adult male (301.41 ha) versus adult female (210.9 ha) in Nepal (Mishra 1982). Conversely, the reported annual home range of yearling females (290.4 ha) was larger than yearling males (229.13 ha) in Nepal (Mishra 1982). In India, home range sizes were typically larger during the monsoon period than the cool-dry season, with the pattern of males using larger areas than females holding true (Moe and Wegge 1994).

Diet.—*Axis axis* is a versatile feeder, as is evident from the broad distribution of habitats in which it is found (Schaller 1967; Eisenberg and Lockhart 1972; Krishna 1972; Khan 1994; Moe and Wegge 1994). Preferred native browse species in peninsular India included mallow-leaved crossberry (*Grewia aspera*), bran plant (*G. hirsuta*), East-Indian screw tree (*Helicteres isora*), orange climber (*Toddalia aculeate*), wood apple (*Pleiospermium alata*), Indian pavetta (*Pavetta indica*), and true indigo (*Indigofera*—Krishna 1972). Although primarily a grazing species, *A. axis* is known to browse when necessary (Dinerstein 1979), with *Acacia* and *Zizyphus* fruits identified as the primary winter food item in the dry deciduous forests of Gir, India (Khan et al. 1996) and with up to 75% of all winter food items consumed classified as browse (Dave 2008). Fruits of orange climber, Bengal quince (*Aegle marmelos*), cluster fig tree (*Ficus glomerata*), and madanphala (*Randia dumetorum*) are preferred food items when available (Krishna 1972). Osteophagia has been recorded in Wilpattu National Park, Sri Lanka (Barrette 1985).

Diseases and parasites.—*Axis axis* is susceptible to foot-and-mouth disease (*Aphthae epizooticae*) with mortalities reported in the Bandipur Forest Reserve (Neginhal 1974), and Nandankanan Biological Park (Kar et al. 1983). Foot-and-mouth-related mortality rates are 1.03–50% (Kar et al. 1983; Acharjyo and Rao 1992). *Myxovirus parainfluenza* 3 is known from the Kanha Park, Madhya Predesh, India (Shah et al. 1965). *A. axis* is considered highly susceptible to malignant catarrhal fever (Haigh et al. 2002) and it is a confirmed mortality source for *A. axis* herds in Texas (Clark et al. 1970). Pneumonia (viral and bacterial)-related mortalities have been reported across India with mortality rates of 6–15.4% (Acharjyo and Rao 1986; Arora and Goyal 1987; Acharjyo and Rao 1987; Chakraborty et al. 1995).

Pasteurellosis (*Pasturella multocida*) in *A. axis* has been reported worldwide (Campbell and Saini 1991; Ravishankar et al. 2004; Rajagopal et al. 2010). Mortality rates associated with pasteurellosis range from 20% (Rajagopal et al. 2010) to 47.1% (Ravishankar et al. 2004). *A. axis* is susceptible to multiple strains of tuberculosis (*Mycobacterium tuberculosis*—Sengupta 1974; Singh et al. 1981; *M. bovis*—O'Brien et al. 2001; *M. paratuberculosis*—de Lisle et al. 1993). Tuberculosis-related mortality rates are 11.3–47.2% (Rathmore and Khera 1984; Acharjyo and Rao 1987; Arora and Goyal 1987; Rao and Acharjyo 1992, 1996). Acute anthrax (*Bacillus anthracis*) infections in *A. axis* have occurred in the Lower Assam (Sinha 1975), West Bengal (Rathmore and Khera 1984), and Rajasthan, India (Mehrotra et al. 2000; Jana and Ghosh 2001). *Escherichia coli* infections are known from India, with mortality rates of approximately 3% reported (Chakraborty 1992; Rao and Acharjyo 1992). *Yersinia pseudotuberculosis* is a major mortality source of farmed *A. axis* in Australia (Jerrett et al. 1990). *Lysteria* infection in *A. axis* has been reported in captive Indian herds (Sarangi and Panda 2013). The prevalence of *Brucella abortus* infections of wild *A. axis* in their native range is undocumented, with clinical studies conducted in Texas indicating *A. axis* is susceptible to infection (Davis et al. 1984).

Endoparasitic infections include trematodes (*Fasciola gigantica*—Guar et al. 1979; *Muellerius capillaris*—Ramaswamy and Arora 1991; *Calicophoron cauliorchis*—De and Spillett 1966), nematodes (*Oesophagostomum venulosum*—Richardson and Demarais 1992; *Haemonchus contortus*—McKenzie and Davidson 1989; *Capillaria bovis*—McKenzie and Davidson 1989; *Cooperia punctata*—McKenzie and Davidson 1989; *Gongylonema pulchrum*—McKenzie and Davidson 1989; *Trichostrongylus axei*—McKenzie and Davidson 1989; *Muellerius capillaris*—Ramaswamy and Arora 1991; *Trichuris*—McKenzie and Davidson 1989), cestodes (*Moniezia benedeni*—McKenzie and Davidson 1989), and protozoan (*Sarcocystis*—Jog et al. 2005; *Neospora caninum*—Basso et al. 2014; *Babesia bovis*—Garcia-Vazquez et al. 2015; *B. bigemina*—Garcia-Vazquez et al. 2015).

Ectoparasites reported from India include the following ticks: *Haemaphysalis turturis* (Dhanda et al. 1970), *H. ramachandrai* (Dhanda et al. 1970), *H.* [*Kaiseriana*] *bispinosa* (Kumar et al. 2018), *Rhipicephals* [*Boophilus*] *annualtus* (Kumar et al. 2018), and *R. haemaphysaloides* (Kumar et al. 2018). North American ectoparasites reported from introduced *A. axis* populations include ticks, *Amblyomma americanum* (Richardson and Demarais 1992), *Dermacentor albipictus* (Richardson and Demarais 1992), and *Ixodes scapularis* (Richardson and Demarais 1992), a deer ked *Lipoptena mazamae* (Richardson and Demarais 1992), and a louse *Bovicola tibialis* (Mertins et al. 2011).

Interspecific interactions.—Predation is the major mortality source for all age classes of *Axis axis*, with disease and accidents (e.g., vehicular strike and conspecific goring) also reported (Johnsingh 1983). *A. axis* is a preferred prey of tiger (*Panthera tigris*—Karanth and Sunquist 2000; Biswas and Sankar 2002; Ramesh et al. 2009; Roy et al. 2016), leopard (*Panthera pardus*—Eisenberg and Lockhart 1972; Karanth and Sunquist 2000; Odden and Wegge 2009; Ramesh et al. 2009), and dhole (*Cuon alpinus*—Karanth and Sunquist 2000; Andheria et al. 2007) in southwestern India (Sharatchandra and Gadgil 1978; Karanth and Sunquist 1995; Andheria et al. 2007). The percent composition of *A. axis* in diets of tigers in India ranges from 31.2% in Nagarhole (Karanth and Sunquist 1995) to 77.7% in Bardia (Stoen and Wegge 1996). Other known predators include: eagles (De and Spillett 1966), golden jackal (*Canis aureus*—Majumder et al. 2011), striped hyena (*Hyaena hyaena*—Alam and Khan 2015), wild pig (*Sus scrofa*—Behera and Gupta 2007), and red fox (*Vulpes vulpes*—English 1992).

In Sri Lanka and southern India, *A. axis* forms feeding associations with troops of tufted gray langur (*Semnopithecus priam*) and it associates with northern plains gray langur (*S. entellus*) in northern and western India (Fig. 4). The association provides *A. axis* with access to dropped food items (e.g., browse and fruit) beyond its reach (Ramesh et al. 2012a). Both species benefit from the antipredator behaviors of the other species (De and Spillett 1966; Eisenberg and Lockhart 1972; Mishra 1982); the primary relationship is an asymmetrical mutualism, with langurs primarily benefitting from *A. axis* alarm calls (Newton 1989). Langurs have been observed grooming *A. axis* in Kanha National Park, India (Boyce et al. 1982).

Axis axis co-occurs with livestock (e.g., cattle, buffalo [*Bubalus arnee*], goats, and sheep) in its native and introduced ranges. Dietary overlap with livestock is dependent on location and type of livestock present, with long-term livestock grazing decreasing densities of *A. axis* up to 62% (Dave and Jhala 2011). Dietary overlap between *A. axis* and domestic cattle and buffalo in the Gir Forest, India was comparatively low (< 35%) during all

Fig. 4.—Feeding association of *Axis axis* and *Semnopithecus* in India. Photo by Paul Wild used with permission.

seasons, due primarily to differences in seasonal habitat use. The maximum dietary overlap (> 60%) was observed during summer months when forage was limited and browsing predominated (Dave 2008). In Point Reyes National Seashore (California) dietary overlap was more significant with fallow deer than with cattle (Elliot and Barrett 1985; Dave and Jhala 2011).

HUSBANDRY

Australian deer farmers encountered problems during early efforts at commercially raising *Axis axis* including losses from trauma, post-capture, myopathy, and high perinatal mortality (Tuckwell 1999). Many of these problems were attributed to the nervous nature of *A. axis* in captivity (English 1992). Despite its nervous nature and a tendency to panic, *A. axis* produces high-quality venison (Anderson 1978), providing economic incentives for ranchers to improve their husbandry practices. Initial husbandry practices focused on mixed-sex and age cohorts to increase production through unrestricted mating periods, reduced anthropogenic interactions for the first 3 months post-calving, and segregation of females, males, and juveniles (English 1992).

To address major husbandry issues encountered by Australian deer farmers, three husbandry practices were identified to improve restraint and handling procedures for farmed *A. axis*: (1) separation of *A. axis* into like groups (e.g., female herds, growing juveniles, and males); (2) good stockmanship, including increased behavioral knowledge, use of coercion as opposed to driving animals; and (3) group training and taming (Harthoorn 1981) to achieve a system of regular and gradual habituation of *A. axis* to human presence within paddocks through the use supplemental feeding (English 1992).

BEHAVIOR

Grouping behavior.—*Axis axis* is gregarious and forms groups consisting of both sexes and multiple age classes throughout the year (Schaller 1967; Eisenberg and Lockhart 1972; Krishna 1972; Mayze and Moore 1990), with group sizes ranging from a single individual to multiple hundreds (Jarman 1974; Srinivasulu 2001; Biswas and Sankar 2002; Ramesh et al. 2012b). The basic social structure is considered a matriarchal family group consisting of an adult female and her offspring from the current and previous years (Ables et al. 1977; Putman 1988; Ramesh et al. 2012b). The herd social structure is relatively loose, typically consisting of two or more family groups (Ramesh et al. 2012b), with individuals readily splitting from and joining other groups (Mishra 1982). Hard-antlered males typically occupy the center of each herd with females and young found on the periphery. Males in velvet often form bachelor herds, maintaining close affiliations with female and mixed-sex groups (Graf and Nichols 1966). *A. axis* often forms tight groups when predators are detected (Sharatchandra and Gadgil 1978), which has been shown to reduce predation attempts particularly by dholes (Johnsingh 1983).

Group size varies significantly by season, habitat, and location (Mishra 1982; Karanth and Sunquist 1992; Raman et al. 1997). Mean reported group size ranges from 1.2 to 18.5 (Raman 1997; Bagchi et al. 2008; Dave and Jhala 2011). Across habitat types group sizes are typically smaller in summer than during the monsoon season (India only) or winter (all populations—Ables et al. 1977; Raman 1997; Srinivasulu 2001; Dave and Jhala 2011; Ramesh et al. 2012b). Group size (mean ± *SE*) in the Ranthambhore Tiger Reserve ranged from 4.5 ± 0.4 to 4.7 ± 0.4 individuals in summer and winter, respectively, with typical group sizes reported of 7.9 and 9.2 for the same periods (Bagchi et al. 2008).

In the Mudumalai Tiger Reserve of the Western Ghats, southwestern India seasonal group sizes ranged from a single individual to 131 members with an overall mean (± *SE*) group size of 13.1 ± 0.5, and group size ranging by season from 10.0 ± 0.6 in the dry season to 14.8 ± 0.8 in the monsoon (Ramesh et al. 2012b). Similar group sizes were reported for the Nallamala Hills, Eastern Ghats, India, with a mean group size of 11.96 individuals, with significant variation between seasons with mean (± *SE*) of 6.1 ± 1.2 in summer, 14.75 ± 4.02 in the monsoon season, and 27.0 ± 4.07 in winter (Srinivasulu 2001).

Reproductive behavior.—*Axis axis*, as a tropical or subtropical species, is considered to have an aseasonal reproductive cycle (Loudon and Curlewis 1988). Hard-antlered males are present throughout the year, supporting the idea of year-round reproductive potential; however, seasonally distinct peaks were observed in the Royal Chitwan National Park, Nepal (Mishra 1982), Rajasthan, India (Sankar 1994), Guindy National Park, Tamil Nadu, India (Raman 1998), and the Western Ghat, southern India (Ramesh et al. 2013). Courtship and other mating behaviors of *A. axis* begin with males performing a low stretch, which is described as the nose pointing forward with the head and neck held at or near horizontal with rapid tongue flicks and antlers obscured. During this phase, the penis is unsheathed and pulsates in the sagittal plane, both up and down, and in and out. During the low stretch, females in estrous withdraw before being touched by an approaching male while voiding small amounts of urine (Barrette 1987). The second phase of courtship includes the male Flehmen or lip curl (Barrette 1987). The third courtship phase, guarding, is a conspicuous behavior during which the male's head is held high with a stiff neck and stiff tail curled over the back. Males march in a stiff-legged manner, lifting feet high, and stamping. In the guarding phase, the penis is never visible, and grazing has not been observed. Males attend females during the guarding phase, without directly facing the female, and are typically positioned a few steps ahead of the female, either parallel or slightly blocking her forward movement. Males repeatedly test urine and perform the lip curl during this phase, followed by more guarding behavior. Mating during the guarding phase is rare (Barrette 1987). The fourth courtship phase begins with the first physical contact between the sexes, with the female allowing the male to lick the vulva. During this behavior the female either immediately breaks contact or stands for several seconds and urinates while the male actively licks the vulva and drinks the urine (Barrette 1987). Chin-on-rump is the fifth courtship behavior. If the female does not move away during the vulva-licking phase, the male eventually places his chin on her rump, flicking his tongue and licking the female's rump. This phase of courtship can proceed for over an hour and immediately precedes mounting; it is not a reliable indication that mating has taken place. Chest-licking is a more reliable indicator of imminent mating. During this phase the sexes are side-by-side, with the male twisting his head to lick the ventral side of the lower neck, chest, and inside foreleg on the opposite side. After the chest-licking phase has been initiated, mating generally occurs within a few minutes. The male will stop licking and move around the standing female, place his head on the rump, and mount. The mount is initiated by the head-on-rump behavior, with the male sliding his chin from the female's rump to her withers, while flicking his tongue. The male may attempt to mount the female 2–16 times before ejaculation occurs, with each mount lasting 5–10 s (Barrette 1987).

Communication.—Eisenberg and Lockhart (1972) described two classes of auditory communication among *Axis axis*: true vocalizations and sounds produced by the body itself (e.g., hoof stamping, antler raking). True vocalizations included alarm call, challenge or long call of the buck, growl, scream note, and bleat. The alarm call is described as a sharp, repeated note given in response to a predator. The alarm call is typically accompanied by piloerection, an upright tail position, and physical orientation to the disturbance source. Tonal differences were detected between the sexes, with male alarm calls generally deeper in tone compared to females. The challenge or long call is generally given by males in full rut and consists of a high-pitched note repeated in a burst of six or seven. The growl vocalization is low and inaudible unless nearby and is typically given by males exhibiting aggressive behavior. The scream note is produced by both sexes when captured by predators or in high-stress situations. Bleat calls are given by fawns and females. Bleats are typically given by a fawn attempting to locate its mother when she is out of visual contact. Females bleat in response to fawn bleats or to entice fawns to follow during herd movements. Signposting, or marking behavior, is weakly developed, not highly organized and of relatively low value (Ables et al. 1977).

GENETICS

The diploid number (2n) for *Axis axis* is 66 chromosomes, with 32 pairs of autosomes and a single sex chromosome pair (Hsu and Benirschke 1974; Shanthi et al. 2008). Four autosomes are considered metacentric, 60 autosomes are considered acrocentric, and both the X and Y sex chromosomes are acrocentric (Hsu and Benirschke 1974). Karyotype and idiogram analyses reported the fundamental number (FN) of chromosomes to be 70 for males and females (Khongcharoensuk et al. 2017). The same study refined autosomal classification as two large metacentric, two large submetacentric, two large telocentric, six medium telocentric, and 52 small telocentric chromosomes (Khongcharoensuk et al. 2017). The X chromosome is a large telocentric chromosome, and the Y chromosome a small telocentric chromosome (Khongcharoensuk et al. 2017).

Ten polymorphic microsatellite loci were isolated from *A. axis* (*n* = 22) at the Nehru Zoological Park, Hyderabad, India; with each loci exhibiting a high level of allelic diversity per locus (Guar et al. 2003; Shrivastava et al. 2013). Genetic distance, as measured at 18 loci, between *A. axis* and nine other species of cervid ranged from 0.51 (common fallow deer) to 0.95 (sika deer, *Cervus nippon*—Emerson and Tate 1993).

No significant genetic disorders have been reported for *A. axis*. There are however reports of genetic coat variations including albinism (Atkinson 1932; Prabu et al. 2013; Pradhan et al. 2014; Sayyad et al. 2015) and melanism (Anwar et al. 2015) from India. Hybridization is rare and has only been reported between sika deer and *A. axis* within a captive herd in Tennessee, United States (Asher et al. 1999).

CONSERVATION

Populations of *Axis axis* throughout India are considered stable, with a large distribution area and multiple large populations. The species is classified as "Least Concern" (LC) by the International Union for Conservation of Nature and Natural Resources, with no range-wide threats to long-term population stability identified as a significant conservation concern (Duckworth et al. 2015). Like other large mammalian fauna of India, habitat conversion, poaching (Menon 2003; Sankar and Acharya 2004; Bali et al. 2007), and anthropogenic conflict (e.g., crop damage and competition with livestock) might represent future areas of conflict beyond a local scale (Menon 2003; Sankar and Acharya 2004). *A. axis* is "Protected" under Schedule III of the Indian Wildlife Protection Act (Sankar and Acharya 2004) and Bangladesh Wildlife Act (Duckworth et al. 2015).

Introduced, free-ranging populations of *A. axis* are considered an invasive and pest species in all jurisdictions, excluding Texas where the species is listed as "exotic" and treated similar to livestock. Free-ranging *A. axis* have been classified as a Class 2 pest animal under the Australian Land Protection Act 2003, with a broad range of population management strategies occurring between states (Nugent et al. 2011). Conservation and management concerns of *A. axis* in South American countries relate more specifically to the species potential impacts to native fauna via competition and displacement (Veblin et al. 1992; Nuñez et al. 2008).

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Associate Editor was Robert K. Rose. Terrence Demos, David M. Leslie, Jr., and Ryan Norris reviewed the synonymies. Editor was Meredith J. Hamilton.