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Source: Mammalian Species, 2008(817) : 1-13

Published By: American Society of Mammalogists

URL: <https://doi.org/10.1644/817.1>

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Pantholops hodgsonii (Artiodactyla: Bovidae)

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Abstract: *Pantholops hodgsonii* (Abel, 1826) is a bovid commonly called the chiru or Tibetan antelope. *Pantholops* is monotypic. This species inhabits high-elevation alpine and desert steppe with flat to rolling terrain in the Tibetan Plateau and only recently has been studied in any detail. At least 5 populations of *P. hodgsonii* are migratory, some moving up to 300–400 km; others are nonmigratory. This species is endangered because of exploitation and competition with domestic livestock of pastoralists; extant populations probably number about 100,000. It is virtually unknown in zoos, but young have been born and orphans have been reared successfully in a 200-ha fenced enclosure in native habitat. DOI: 10.1644/817.1.

Key words: Chang Tang, China, chiru, endangered species, nomadic pastoralist, Qinghai, Tibet, Tibetan antelope, ungulate, Xinjiang

Published 9 October 2008 by the American Society of Mammalogists
Synonymies completed 14 April 2008

www.mammalogy.org



Pantholops Hodgson, 1834

Antelope Abel, 1826:234. Incorrect subsequent spelling of, but not *Antilope* Pallas, 1766.

Oryx Hamilton-Smith, 1827:196. Part; used as a subgenus of *Antilope* Pallas, 1766.

Pantholops Hodgson, 1834:81. Part; proposed as a subgenus of *Antilope* Pallas, 1766; type species *Antilope hodgsonii* Abel, 1826, by monotypy.

Pantholops: Hodgson, 1838:153. First use as a genus.

Kemas: Gray, 1843:157. Not *Kemas* Ogilby, 1837.

Pantolops Stein-Nordheim, 1884:109. Incorrect subsequent spelling of *Pantholops* Hodgson, 1834.

CONTEXT AND CONTENT. Order Artiodactyla, suborder Ruminantia, family Bovidae, subfamily Caprinae, tribe variously Pantholopini or Saigini. *Pantholops* is monotypic. Hodgson (1834) aligned *P. hodgsonii* with the “Antilopine” and “Gazelline” groups, but Gray (1872) created a new family, Pantholopidae, because of its “peculiarities” (Pocock 1910:899). Current molecular and morphological studies align *P. hodgsonii* most closely with Caprinae (e.g., Gatsey et al. 1997; Gentry 1992), although some contend that additional genetic resolution needs to be achieved (Lei et al. 2003; Schaller and Amato 1998). Based on behavior and various morphological characteristics, Vrba and Schaller (2000:220) concluded that *Pantholops* “has no close recent relatives and represents an ancient lineage that diverged during the Miocene from the closest living forms [Caprinae].” Grubb (2005) placed *P. hodgsonii* in the subfamily Caprinae.



Fig. 1.—Mature male *Pantholops hodgsonii* in nuptial pelage, Qinghai Province, China, November 2006. Photograph by G. B. Schaller.

***Pantholops hodgsonii* (Abel, 1826)**
Chiru or Tibetan Antelope

- Antelope hodgsonii* Abel, 1826:233–234. Type locality “Tingri Maidan, a fine plain or valley, through which the Arrun flows ... beyond the snows made by Kooti pass [= Tibet].”
- A[ntilope (Oryx)]. kemas?* Hamilton-Smith, 1827:196, 199. Type locality “Chandang, north-west of Digurgu, in the Himalaya mountains;” described as the “Unicorn Chiru of Bhote, in all likelihood, the Unicorn of the ancient Persians.”
- Antilope [(Antilope)] chiru* Lesson, 1827:371. Type locality “les habitans du Népal [= Nepal].”
- Antilope [(Pantholops)] hodgsonii*: Hodgson, 1834:81. Name combination.
- Antilope Hodgesonii* Hodgson, 1838:154. Incorrect subsequent spelling of *Antilope hodgsonii* Abel, 1826.
- Pantholops hodgsonii* Hodgson, 1842:282. First use of current name combination.
- Kemas hodgsonii*: Gray, 1843:157. Name combination and incorrect subsequent spelling of *Antilope hodgsonii* Abel, 1826.

CONTEXT AND CONTENT. Context as for genus. *P. hodgsonii* is monotypic.

NOMENCLATURE NOTES. According to Sclater and Thomas (1887), the 1st description of this species was published by C. Abel in the *Calcutta Government Gazette* in 1826 and was formalized in his correspondence to *The Philosophical Magazine and Journal* in the same year. We were unable to locate the “article” in the *Gazette*, and following other zoologists who seemingly had the same difficulty and constructed synonymies of *P. hodgsonii* without it, we provide reference only to the article in the *Philosophical Magazine*. In the mid-1820s, specimens and descriptions of this species were being shared by naturalists such as Abel, Hodgson, Lesson, and Hamilton-Smith with follow-up “publications” and correspondences that overlapped one another in time (Sclater and Thomas 1887). We defer to the summary of Sclater and Thomas (1887:46–47) of the nomenclature sequence of events and rely on Abel’s correspondence in the *Philosophical Magazine* as the starting point of this synonymy.

DIAGNOSIS

Pantholops hodgsonii is the only completely endemic species of large mammal on the Tibetan Plateau (Schaller 1998); it has no congeners and is unique among ungulates of comparable size. Unlike other caprids, female *P. hodgsonii* do not have horns (Pilgrim 1939). Enlarged snout and fine undercoat of the pelage of both sexes and long upright

lyre-shaped horns of males (Fig. 1) distinguish *P. hodgsonii* from other ungulates, particularly the sympatric *Procapra picticaudata* (Tibetan gazelle—Schaller 1998) and other Asiatic gazelles, such as *Gazella subgutturosa* (goitered gazelle—Kingswood and Blank 1996) and *Procapra gutturosa* (Mongolian gazelle—Sokolov and Lushchekina 1997).

The related, but allopatric, *Saiga tatarica* (saiga antelope—Sokolov 1974) is of comparable mass, except the horns are straighter and about 2 times longer in *P. hodgsonii*. Although both species have pronounced nasal cavities, those of saiga antelope result in unique “large lacrimal bones forming lateral sides of nasal foramen” (Sokolov 1974:1). *P. hodgsonii* has short and broad nasals with large nasal apertures (Pilgrim 1939).

GENERAL CHARACTERS

Sexes of *Pantholops hodgsonii* are distinguished by the larger mass of males and male-only slender black horns of “wavy triple curvature, with circular rings towards their base, which project more before than behind” (Abel 1826:233) and are often lyre-shaped (Roosevelt and Roosevelt 1926) with “rapier-like tips” (Schaller 1998:43). Hodgson’s (1833) early description has been amended through time: somewhat chunky with slender legs; no preorbital glands or associated lachrymal fossa and no pedal glands (Blanford 1888; Pocock 1910); large inguinal glands, developed to fist size in males (Prater 1980; Rawling 1905), and removed from mammae (Pocock 1910); pelage dense, woolly, and fine (Blanford 1888); coloration pale fawn with pink to red to brown hints ventrally, fading to a whitish on belly (Roosevelt and Roosevelt 1926; Sclater and Thomas 1887); as rut approaches, males ≥ 3.5 years of age attain “a striking white” nuptial pelage (Fig. 1) that contrasts an almost black face; muzzle conspicuously swollen by walnut-sized lateral nasal chambers, more so in males (Hodgson 1833; Prater 1980); coloration of muzzle swelling in males varies from grayish brown in Tibet and Qinghai Province, China, to white in Xinjiang Province, providing a sharp contrast to the black face (Schaller 1998); legs grayish but males have black stripes running down the front of all 4 (Lydekker and Blaine 1914; Sclater and Thomas 1887) that are particularly obvious during rut; no distinct rump patch in either sex; ears short, somewhat pointed, and white on the back; tail short (13–14 cm—Schaller 1998), not tufted, and colored like the rump and back.

Dentition of adult *P. hodgsonii* is not completely clear, but it is reduced by the loss of a pair of upper and lower premolars: i 0/3, c 0/1, p 2/2, m 3/3, total 28 (Fig. 2). Pilgrim (1939) contended that P2 and p2 were missing. In contrast, adult specimens of *P. hodgsonii* in the American Museum of Natural History, New York, and the mature male in Fig. 2 appear to lack P4 and p4 (N. Solounias, in litt.). Lydekker and Blaine (1914) contended that the missing pair of



Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of adult male *Pantholops hodgsonii* (British Museum [Natural History], specimen 1843.112.100). Greatest length of skull is 256 mm, but note that the tip of nasals is broken off.

premolars in *P. hodgsonii* was similar in saiga, which lacks the anterior lower premolars; loss of such dentition through time could be related to diet (N. Solounias, in litt.). Canines are incisoriform. Upper molars have pronounced external folds; lobes are concave between and almost without medial ribs (Pilgrim 1939). Deciduous teeth are replaced first with permanent incisors beginning at about 12 months of age, 3rd molars begin to emerge at 12 months of age, and full permanent dentition is attained at 28–30 months (Schaller

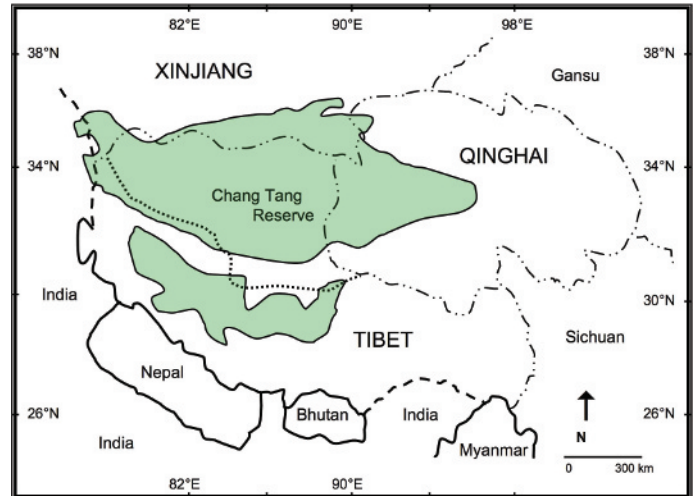


Fig. 3.—Current distribution of *Pantholops hodgsonii* in the Tibetan Plateau of the Chinese provinces of Tibet, Qinghai, and Xinjiang, modified from Schaller (1998) by reducing the eastern range in central Qinghai by about 150 km; boundaries of the Chang Tang Reserve depicted by the dotted line on the south and the provincial demarcation between Tibet and Xinjiang on the north; disputed boundaries between China and India depicted with heavy dashed line.

1998). After 2.5 years, age of *P. hodgsonii* can be determined only by general wear in the center of molar cusps, which begins on the 1st molar and progresses to the 3rd molar as an individual ages; aging by counts of cementum annuli has not been satisfactory (Schaller 1998).

DISTRIBUTION

Pantholops hodgsonii is endemic to the Tibetan Plateau (Fig. 3) at elevations of 3,250–5,500 m (Blanford 1888; Bower 1894; Fox and Bårdsen 2005; Schaller 1998). It presently occurs, almost exclusively, in about 800,000 km² of the Chinese provinces of Tibet (Xizang), Xinjiang, and Qinghai (Harris and Miller 1995; Ruan et al. 2005; Schaller 1998; Schaller et al. 1991) and in very small numbers in the Ladakh district of northwestern India, mainly during summer (Fox et al. 1991; Mishra et al. 2001; Ul-Haq 2002). Despite Lesson's (1827) type locality, *P. hodgsonii* rarely occurred in Nepal (Groves 2003; Heinen and Yonzon 1994; Schaller 1977, 1998).

The 300,000-km² Chang Tang (= northern plain in Tibetan) Reserve, located in north-central Tibet, was established as a nature reserve in 1993 and upgraded to a national reserve in 1999. It is roughly the size of New Mexico (United States) or Germany, making it the second largest such reserve in the world, and conserves *P. hodgsonii* and other Tibetan biota. Relative to conservation, important contiguous reserves to the north in Xinjiang include West Kunlun Reserve (30,000 km²), Mid-Kunlun Reserve (32,000 km²),

and Arjin Shan Reserve (45,000 km²). Kekexili Reserve (45,000 km²) and Sanjiangyuan Reserve (150,000 km²) occur east of Chang Tang in Qinghai, but *P. hodgsonii* only occurs in the western part of Sanjiangyuan. This network of reserves is important because migratory populations move north and south between Tibet and Xinjiang and west and east between Tibet and Qinghai. Nevertheless, extant populations are still threatened by human activities, including illegal harvest and competition with domestic sheep and goats (e.g., Harris 2008; Qiu and Feng 2004; Schaller 1998), and these threats have changed somewhat in the past 10–15 years (see “Conservation” section).

FOSSIL RECORD

Generally, *Pantholops* and closely related taxa are rare in the fossil record, perhaps because geological processes on the Tibetan Plateau are not conducive to fossilization (Pilgrim 1939). Miocene *Qurlignoria* from the Qaidam Basin, China, is thought to be an extinct type of *Pantholops* (Gentry 1968, 1992:24). A “slightly smaller” extinct species, *P. hundesiensis*, is described from Hundes, Tibet, and is dated variously from the middle Pleistocene (Pilgrim 1939:61) about 1 million years ago to the late Pliocene (Lydekker 1901) about 2 million years ago. *P. hundesiensis* had a longer parietal and narrower skull, including frontals at the orbits, braincase, and occipitals, than extant *P. hodgsonii* (Pilgrim 1939).

Pantholops hodgsonii is featured convincingly to some (Bate 1950), but not others (Guthrie 2000), in the 17,000-year-old Lascaux cave paintings of central France, leading to speculation that the species occurred westward into Europe through the upper Paleolithic, as did the saiga antelope, now considered an Asian steppe mammal (Sokolov 1974). Among Tibetan medicinal uses of *P. hodgsonii*, ground horns have been used for easing child birth and treating diarrhea, blood diseases, and ulcers (Wright and Kumar 1997), likely for several thousand years and currently by 95% of “amchis,” or shamans (Kala 2005).

FORM AND FUNCTION

Fine undercoat fibers (7–<10 μm in diameter) of *Pantholops hodgsonii* examined by Rollins and Hall (1999—collection site on the body not stated) were dark brown, but they can range from brown to beige and even white on the belly (Schaller 1998; Wright and Kumar 1997). Fibers have no medulla but do have internal voids; long guard hairs are “nearly snow white” with larger diameters (50–100 μm) than those of goats (50–60 μm—Rollins and Hall 1999:857). Under electron microscopy, guard hairs of *P. hodgsonii* show very thin walls and unique benzene-ring-like patterning; the rounded shape of the large medullar cells in the guard hairs permits forensic differentiation from goats (Donn and Yates 2002).

Mean (\pm SD) body mass (kg) and mean shoulder heights (cm) of *P. hodgsonii* are: 4 month olds, 15.5 \pm 0.9 (n = 3), 63.4 \pm 2.4 (n = 7); 16-month-old females, 20.9 (n = 1), 67.0 \pm 2.8 (n = 2); 16-month-old males, 25.5 \pm 1.9 (n = 2), 76.8 \pm 1.6 (n = 3); adult females, 25.9 \pm 2.9 (n = 9), 74.4 \pm 2.2 (n = 8); adult males, 38.8 \pm 2.5 (n = 2), 83.0 \pm 1.4 (n = 2—Schaller 1998; Schaller and Ren 1988). Skeletal characteristics of *P. hodgsonii* compared with other Bovidae suggest affinity with Caprinae (Gentry 1992). Horns on males are remarkably uniform, 54–60 cm in length with >70 cm being extreme (Sclater and Thomas 1887) and have no age rings (Fig. 3). Adult male horn tip-to-tip intervals (19–46 cm—Lydekker and Blaine 1914; Schaller 1998) display the greatest variation but are not correlated with age. Basal circumference of horns averages 12 cm, but, unlike caprids, there is no evidence that horns continue to grow after males reach adulthood at about 3.5 years of age (Schaller 1998).

Specific skull measurements are lacking (Fig. 3). Pilgrim (1939:59) provided a general description of the skull: rather long slender braincase; frontals almost flat; orbital roof expanded laterally; supraorbital foramina almost flush with surface; no lachrymal fossa; horn cores long, slender, upright, and compressed laterally; parietal relatively long; basioccipital narrow and subtriangular and rectangular; and auditory bulla long, slender, and not inflated.

The purpose of the walnut-sized bulbous nasal sacs on the muzzle of female and male *P. hodgsonii* (Pocock 1910) has been a matter of speculation. In his early description, Hodgson (1833:110) stated that the “nasal tumours” are “a round, firm, elastic swelling on each lip” that serve as “supplementary nostrils, designed to assist this exceedingly fleet animal in breathing when he is exerting all his speed [at high elevations].” Nasal sacs, which are particularly swollen in males (Prater 1980), may play a role in vocalizations during rut (Schaller 1998).

ONTOGENY AND REPRODUCTION

Age at sexual maturity of *Pantholops hodgsonii* is not clearly understood but, as in other ungulates of comparable size, it probably occurs at 1.5–2.5 years of age with gestation of about 6–6.5 months (Grzimek 1990; Schaller 1998). Two mammae are present (Hodgson 1834; Schaller 1998). Neonates are precocial, can arise and nurse 12–15 min postpartum (Fig. 4), can follow their mother 1 h postpartum (Schaller et al. 2006), and are capable of outrunning ponies during their 1st day of life (Rawling 1905:53–54). Offspring grow rapidly: 15-month-old females are almost indistinguishable from adult females and males are identified by their developing horns. Males begin to leave their mothers at 10–11 months of age; some females also leave their mothers at about this age, but most remain until just before new offspring are born (Schaller 1998). Given the endangered



Fig. 4.—One-month-old *Pantholops hodgsonii* suckling in early August (top), and a newborn calf laying in open steppe habitat in late July (bottom), Tibet. Photographs by G. B. Schaller.

status of *P. hodgsonii*, cloning has been investigated using goat and rabbit oocytes, with some blastocyst development noted (Zhao et al. 2006, 2007).

In Tibet, migratory females move south to north to their calving grounds in May–June, give birth to a single offspring in late June–early July, and return south almost immediately in late July–early August to their autumn–winter range (Schaller 1998). At least 1 population migrates east to west in Qinghai. Little information exists on the number of resident populations. Ratios of young-of-the-year to adult females vary, but under normal conditions, are 30–50 offspring: 100 adult females 1–2 months postpartum (Schaller 1998). Years of near complete reproductive failure occur from extreme weather before, during, and after parturition (Schaller 1998; Schaller et al. 2006).

ECOLOGY

Population characteristics.—Densities of *Pantholops hodgsonii* are difficult to estimate because of the expansive nature of the Tibetan Plateau and variable intersexual herding behavior, movements (migratory or resident), and space use at different times of the year. Weather, particularly

snow (Schaller and Ren 1988), affects grouping behavior and area occupied, often confining populations to limited areas. These factors and demarcation and size of survey areas greatly influence density estimates, so the many published figures (e.g., Achuff and Petocz 1988; Fox and Bårdsen 2005; Schaller 1998; Schaller and Ren 1988) should not be construed to represent the entire metapopulation of *P. hodgsonii*. For example, during a recent winter survey of 3,384 km² across the Chang Tang (Tibet), Kekexili, and Sanjiangyuan (Qinghai) nature reserves during the rutting season in November–December, densities of *P. hodgsonii* varied considerably by location, ranging from 0.03 to 9.21 individuals/km² with an overall density of 1.77 individuals/km² (Schaller et al. 2007). Regardless of site-specific estimates, overall densities of *P. hodgsonii* are clearly lower now than they were historically (Schaller 1998).

Human presence affects densities of *P. hodgsonii*. In Chang Tang Nature Reserve in April 1999, October 2000, and October 2002, densities decreased as human presence (indexed by herd and tent counts) increased: low human influence, 8.15–10.98 *P. hodgsonii*/km²; medium, 1.07–1.74 *P. hodgsonii*/km²; and overall, 3.30 *P. hodgsonii*/km² (Fox and Bårdsen 2005). Similarly, encounter rates of *P. hodgsonii* decreased from 0.59–1.28 individuals/km² with low human influence to 0.15–0.33 individuals/km² with medium human influence and 0.06 individuals/km² with high human influence (Fox and Bårdsen 2005).

As with other ungulates of comparable size, maximum life span of *P. hodgsonii* in the wild is likely 10+ years. Schaller (1998:68) examined 88 jaws from Tuotuohe, Qinghai, and only 3 individuals were “old,” which suggested that few *P. hodgsonii* “reach an advanced age.” No individuals have been maintained long enough in captivity to document longevity (Su et al. 2003). Monthly adult sex ratios suggest differential mortality of males, not uncommon to ungulates. For example, winter sex ratios of migratory *P. hodgsonii* in Chang Tang, where females and males occupy the same area, are 35–75 males: 100 females (Schaller 1998). Ratios of young *P. hodgsonii* to adult females suggest that typically up to two-thirds of individuals of ≤2 years of age die (Schaller 1998). Extreme weather, even a single snowfall event (Schaller and Ren 1988), can result in disproportionate death of young, subadults, and females, presumably from malnutrition.

Space use.—*Pantholops hodgsonii* occupies open high-elevation alpine and desert steppe habitats with flat to rolling terrain, and it infrequently occurs in mountainous terrain (Hodgson 1833; Schaller 1998; Schaller et al. 2006). Occupied habitats often have sparse vegetative cover (e.g., only about 10–15% in Chang Tang—Schaller and Ren 1988) with low primary productivity (80–160 kg/ha dry matter—Schaller 1998; Schaller et al. 2005). In the Chang Tang Nature Reserve, overall encounter rates of *P. hodgsonii* under low levels of human influence in April and October were twice as high at elevations > 4,900 m (0.94 individuals/

km²) than at elevations of 4,700–4,900 m (0.46 individuals/km²—Fox and Bårdsen 2005).

Extant populations of *P. hodgsonii* are either migratory or sedentary (perhaps facultative), and both types generally display sexual segregation during the nonrutting period from January through October (Bower 1894; Schaller 1998). Deep snows can cause *P. hodgsonii* to modify traditional migratory movements in search of forage and as a means of avoidance; it is not suited for efficient travel through snow with a supporting area (= total mass/hoof area) of 411 g/cm² (Schaller 1998). Oddly, migratory individuals of both sexes often leave winter ranges just when forage quality is beginning to increase in spring and move north into areas where vegetation is still dormant and apparently of lower quality (Schaller 1998). Satellite imagery between 2000 and 2004 in Xinjiang showed that primary production was more than twice as high on winter range of *P. hodgsonii* as on calving grounds when females arrived to give birth (Schaller et al. 2006), in contrast to space used by Mongolian gazelles (Leimgruber et al. 2001; Sokolov and Lushchekina 1997). Such northward migration to calve seems ill-timed relative to phenology, weather, stage of pregnancy, and ease of movement. This behavior could be vestigial from times when glacial and vegetative patterns established traditional migratory patterns that are still followed (Schaller 1998). Females also may be moving to calving grounds with low numbers of predators and other ungulates and less insect harassment (Schaller et al. 2006).

Migratory females move greater distances than males, particularly in late spring–early summer when they can travel 300–400 km north to traditional calving grounds (Schaller 1998; Schaller et al. 2006). Movement patterns of male *P. hodgsonii* are more diverse and leisurely than females, seemingly taking advantage of favorable forage availability, particularly in spring. Some males move up in elevation in spring, apparently following new growth of vegetation. Other males move little between winter, summer, and rutting areas; others move short distances between winter and summer ranges; still others move northward after winter and disperse widely, returning to rut in autumn.

Diets.—*Pantholops hodgsonii* is an herbivorous ruminant. Foraging preferences are understood mainly from limited microhistological analyses of feces (Cao et al. 2008; Harris and Miller 1995; Schaller 1998). *P. hodgsonii* is a mixed feeder (Cao et al. 2008), seasonally eating grasses, sedges, forbs, and select parts of dwarf woody vegetation, although dietary diversity is constrained substantially by limited forage availability and diversity on the Tibetan Plateau (Schaller 1998). In Chang Tang Nature Reserve, annual percent use of various plants is graminoids: *Stipa*, 3.7–47.3%; *Kobresia*, 1.1–33.1%; *Carex moorcroftii*, 0.5–22.8%; herbaceous plants: *Potentilla bifurca*, 0.3–31.1%, *Leontopodium*, 0.2–11.9%; and dwarf shrubs: *Ceratoides compacta*, 0.2–63.5%, *Ajania fruticososa*, 21.2% (Schaller 1998).



Fig. 5.—Adult male *Pantholops hodgsonii* pawing for scant forage (top), and adult male and female foraging in snow (bottom), Qinghai, late October. Photographs by G. B. Schaller.

Overall, grasses and sedges represent 33–66% of the diet, being most abundant in winter diets when *P. hodgsonii* will dig through snow to obtain forage (Schaller 1998; Fig. 5). Seasonally, the grass *Stipa* is important in winter; the sedge *Kobresia* is eaten most often in alpine meadows and steppe habitats in summer; and the dwarf shrub *C. compacta* is eaten most often in desert steppe (63.5%) and less so in alpine steppe (Schaller 1998). In Kekexili Nature Reserve, Qinghai, the grass *Poa* accounts for 36.9% of summer diets and 26.3% of winter diets (Cao et al. 2008). Summer diets of spatially segregated male and female *P. hodgsonii* in Yeniugou, Qinghai, were somewhat disparate; males selected *Kobresia* and forbs, and females selected forbs, notably *Potentilla*, and avoided grasses and sedges (Harris and Miller 1995). On calving grounds in desert steppe in the western Kunlun Mountains of Xinjiang, ruminal contents of adult females had 57% *C. compacta* and 43% grasses and sedges, principally *C. moorcroftii* (Schaller et al. 2006).

Nutritionally, diets of *P. hodgsonii* probably are deficient in protein (<6%) from October to May because of low forage quality on the Tibetan Plateau. During the

growing season from June to August, forages eaten by *P. hodgsonii* have crude protein levels of 3.3–20.8% (Schaller 1998). On calving grounds, the dwarf shrub *Ceratoides* contained more protein (22.7–27.0%) than did grasses (13.2%), but the latter were preferred by female *P. hodgsonii* (Schaller et al. 2006). Forage may be deficient in minerals such as phosphorus and potassium depending on local soil fertility (Schaller 1998).

Diseases and parasites.—Although no known pathogen or disease singularly limits contemporary populations of *P. hodgsonii*, early accounts by visitors and pastoralists suggest that large disease-related die-offs occurred (Rockhill 1894), perhaps from hemorrhagic septicemia. Severe bacterial lung infections resulting in pneumonia were found in 1 dead and 1 near-dead female *P. hodgsonii* in Chang Tang Reserve in late summer (Schaller 1998). Feces of *P. hodgsonii* from Chang Tang Reserve contained light-to-moderate levels of 2 species of protozoan (also found in other Tibetan ungulates) and the nematode *Enterobius*, unique to *P. hodgsonii* (Schaller 1998).

Ectoparasites include ≥ 2 species of oestrid flies: larvae of 1 species burrow under the skin and consume flesh on the rump and lower back before emerging and the other species infects nasal sinuses and the throat (Schaller 1998). Harassment by these flies can cause *P. hodgsonii* to stand in groups of 50+ in knee-deep water or on mudflats, ice patches, and high ridges and perhaps to dig its characteristic summer “bowl-shaped hollows” in sand and silt for near-total concealment (Schaller 1998:64–65). The latter behavior also had been thought to involve predator avoidance (Rawling 1905).

Interspecific interactions.—The Tibetan Plateau has a rich ungulate fauna (Sclater 1896), although it has been diminished by human activities. *P. hodgsonii* can be sympatric with *P. picticaudata* (Tibetan gazelle), *Bos mutus* (wild yak—Schaller and Liu 1996), *Equus kiang* (Tibetan wild ass or kiang), *Pseudois nayaur* (blue sheep or bharal—Wang and Hoffman 1987), *Ovis ammon hodgsoni* (Tibetan argali—Fedosenko and Blank 2005), and occasionally others, such as *Przewalskium albirostris* (white-lipped deer—Harris and Miller 1995; MacKinnon 2008; Schaller 1998). As in mixed ungulate assemblages elsewhere, Tibetan species likely partition food and space, relative to size and digestive capabilities, to minimize competition (Harris and Miller 1995; Schaller 1998; Schaller et al. 1991). For example, *P. hodgsonii* shares flatlands with Tibetan gazelle, but yak and argali tend to use hilly to mountainous areas, and the wild ass uses both (Schaller et al. 1991). During periods of sexual segregation in Yiniugou, Qinghai, female *P. hodgsonii* and male Tibetan gazelles use high-elevation habitats, in contrast to male *P. hodgsonii* and female Tibetan gazelles, which use lower-elevation habitats (Harris and Miller 1995).

Scant information exists on predator–prey dynamics on the Tibetan Plateau, and current dynamics are a product of reduced populations of both due to various human activities.

At present, *P. hodgsonii* does not constitute a large percentage of prey in any predator’s annual diet, but it can be seasonally important. Many *P. hodgsonii* probably are scavenged after dying from other causes (Schaller 1998; Schaller et al. 2006). Scavengers included *Ursus arctos pruinosus* (Tibetan brown bear, also a predator), *Vulpes ferrilata* (Tibetan sand fox), *Buteo hemilasius* (upland buzzards), *Corvus corax* (ravens), and other avian species (Lian et al. 2007; Schaller 1998). In Kekexili Nature Reserve, analysis of brown bear feces suggested a summer diet consisting of 17% *P. hodgsonii*, presumably, mostly from scavenging dead calves (Xu et al. 2006). Forty-nine legs from 36 individual (based on DNA analyses) *P. hodgsonii* calves were found at 1 upland buzzard nest; calves presumably died from other causes (Lian et al. 2007). *Aquila chrysaetos* (golden eagles) or *Aegypius monachus* (cinereous vultures) were suspected predators of newborn calves in Xinjiang (Schaller et al. 2006). One of us (GBS) observed upland buzzards using horns and leg bones of *P. hodgsonii* to construct their nests, likely because of the scarcity of branches for nesting material.

Canis lupus (wolf) preys on *P. hodgsonii*. Schaller (1998) observed a large wolf pursuing about 50 *P. hodgsonii* and successfully killing a pregnant female; 8 fresh wolf kills were noted elsewhere on different occasions. Wolf feces in Kunlun Shan, Xinjiang, contained 9.6% *P. hodgsonii* (Schaller 1998), and on calving grounds in Xinjiang, feces contained 54% (Schaller et al. 2006). Lian et al. (2007) observed 17 instances of wolves attacking and killing *P. hodgsonii* during seasonal migration in Kekexili Nature Reserve, Qinghai, when individuals were concentrated in herds. *Vulpes vulpes* (red fox) on calving grounds had 10% *P. hodgsonii* in their feces. Schaller (1998) reported 1 case of predation by *Lynx lynx* (lynx) and 1 case of *P. hodgsonii* in feces of *Uncia uncia* (snow leopard) in Chang Tang Nature Reserve. Domestic dogs killed 19 mostly young and yearling *P. hodgsonii* that were malnourished and impeded by deep snow near a highway in Qinghai (Schaller 1998). Presumably in response to predation risk, vigilance by *P. hodgsonii* decreased and time spent foraging increased as group size increased to 30 individuals (Lian et al. 2007).

BEHAVIOR

Grouping behavior.—*Pantholops hodgsonii* is a herding ungulate, and grouping behavior varies considerably depending on sex, time of year, migratory patterns, weather, and insect harassment; probably the only long-lasting association is between a female and her young-of-the-year into its 2nd year (Lian et al. 2005, 2007; Schaller 1998; Schaller et al. 2006). Other group types included adult and yearling males, female and offspring, and mixed; males and females also occur singly (Lian et al. 2005; Schaller 1998).



Fig. 6.—Mature male *Pantholops hodgsonii* tending a harem in December with a typical Tibetan backdrop (top), and mature males sparring, Qinghai, late October (bottom). Photographs by G. B. Schaller.

Among 1,000 male *P. hodgsonii* dispersed in the Aru Basin of the Chang Tang Nature Reserve in summer 1992, mean group size was 6.6 individuals (range: 1–82 individuals, 50% of groups 2–20 individuals); during autumn and spring migration, female herds can exceed 1,000 individuals, but they disperse into small groups of generally ≤ 20 individuals, with as many as 15–20% of females occurring singly (Schaller 1998). Yearling males begin to leave their mothers at 10–11 months of age and associate more regularly with males of their own age or older (Schaller 1998).

Reproductive behavior.—All male *P. hodgsonii* attain comparable body and horn size at about 3.5 years of age, and unlike related caprids, they lack a “graded system of rank” based on horn length (Schaller 1998:266). Mature male *P. hodgsonii* are not territorial but form harems (Fig. 6) with 1–4 females in 70% of harems, 5–8 females in 25% of harems, and >9 females in 5% of harems in Chang Tang Nature Reserve ($n = 312$ harems—Schaller 1998). Lian et al. (2005) noted harems each with 2–12 females during rut in the Kekexili region of Qinghai.

Male *P. hodgsonii* tend to space themselves individually throughout rutting areas and avoid serious horn-to-horn

combat with various head-up (28% of 54 interactions), neck-low (28%), and exaggerated head-down (18%) displays and chases (22%); only 4% of male-to-male interactions during rut were sparring (Schaller 1998; Fig. 6). During 6 extensive surveys by GBS in the range of *P. hodgsonii* during the November–December rut, only 1 mature male was found with what appeared to be a fatal puncture wound to the abdomen. Most aggressive interactions involve 1 male trotting or lunging with head down and horns aimed at a rival; such behavior often terminates the interaction, but as rut intensifies, chases of up to 1 km are not uncommon (Schaller 1998). In contrast, early accounts claimed that rutting males fought with vigor, often resulting in serious injury and death (Rawling 1905). Vocalizations of rutting males may involve the enlarged nasal sinuses that serve as “resonators” and include “growl or croak like muffled toads” (Schaller 1998:263) or “deep-toned roar[s] of rage and defiance” (Rawling 1905:311).

Courtship and mating of *P. hodgsonii* are abrupt and brief, with cursory displays and contacts (Schaller 1998). Early in rut, males spend considerable time chasing females to maintain a harem, and females seem disinterested; as rut progresses, females tolerate closer proximity of males and may circle back toward them when chased. When the female is receptive, the male approaches her with his head up and in a distinctive walking gait with stiff forelegs raised high (Schaller 1998). While in close proximity to females, male *P. hodgsonii* do not display many of the courting behaviors common among ungulates; front-leg kicks that skim a female’s thigh are common, but crouching, low-stretch behavior upon approach and vulva sniffing, nuzzling, and licking were not observed (Schaller 1998). Occasionally, males display a lip-curl after inspecting an area where a female had previously urinated or defecated. A male copulates by rearing upright, balancing on its hind legs, with minimal contact with its mate (Schaller 1998).

Miscellaneous behavior.—*Pantholops hodgsonii* is virtually unknown in zoos. Some *P. hodgsonii* have been born and orphans have been reared successfully in a 200-ha fenced enclosure in native habitat in Qinghai; one of us (GBS) noted 4 adult males, 1 yearling male, 5 females, and 9 orphaned young lived in that enclosure in November 2007. One *P. hodgsonii* lived among a Tibetan herdsman’s sheep and goats for 17 months (Su et al. 2003).

GENETICS

All chromosomes of *Pantholops hodgsonii* are acrocentric with a diploid number ($2n$) = 60 (Zhao et al. 2006). Analyses of 12S and 16S rRNA mitochondrial (Kuznetsova et al. 2002), the entire cytochrome-*b* (Xu et al. 2005), and hemoglobin alpha-chain (Yang et al. 2007) genes suggest phylogenetic affinity of *P. hodgsonii* with *Ovis* and various caprids (e.g., *Capra hircus*). Evaluation of the entire control

region of the mitochondrial DNA suggests closer affinity to domestic sheep than to domestic goats, both of Tibetan breeds (Feng et al. 2008). Combined rDNA and morphological analyses suggest placement of *P. hodgsonii* as a sister clade to Caprinae (Gatesy et al. 1997). Positive selection for the cytochrome-*c* oxidase subunit I gene in *P. hodgsonii* and the yak may reflect an adaptation for living at high elevations (Xu et al. 2005).

Three extant populations of *P. hodgsonii* have levels of mitochondrial DNA nucleotide diversity ($\pi = 2.18\%$) comparable to that of other antelopes and show high levels of gene flow among them relative to migration routes, calving grounds, and early expansion from ancestral populations (Ruan et al. 2005). In Qinghai, genetic assessments of a population of *P. hodgsonii* showed that 9 of 25 microstallite loci examined had high levels of genetic diversity, with 7–12 alleles per locus (Zhou et al. 2007). Forensically, partial DNA fragments of cytochrome *b* in fibers from the pelage of *P. hodgsonii* can be differentiated from those in fibers of sheep and goats (Lee et al. 2006).

CONSERVATION

Pantholops hodgsonii is a Class I protected species in China, and hunting has been prohibited since the early 1990s (Schaller 1998). *P. hodgsonii* also is protected as endangered in India and Nepal (Wright and Kumar 1997) and by laws and conventions of, for example, the International Union for Conservation of Nature and Natural Resources (2006), Appendix I of the Convention on International Trade of Endangered Species (2007), the European Union's (2008) Council Resolution restricting trade, and the United States Fish and Wildlife Service (2006). From a high of perhaps a million or more, the range-wide population was estimated at only 65,000–72,500 in the mid-1990s (Schaller 1998) and currently may be about 100,000, but no adequate census of the total number of *P. hodgsonii* has ever been conducted. Schaller et al. (2005) noted increased numbers of *P. hodgsonii* in some areas of Chang Tang between the 1990s and 2003, but recent local extirpations of subpopulations also have been noted (Harris and Loggers 2004; Harris et al. 1999). Clearly, the great herds of *P. hodgsonii* and other Tibetan ungulates are a distant memory, and substantial conservation challenges have emerged with changing governmental policies and their impact on culture and ecology.

Based on lithic assemblages with specialized blade technology from the northern Chang Tang (Schaller 1998), humans probably have occupied the Tibetan Plateau since the late Pleistocene–early Holocene 15,000–25,000 years ago (Brantingham et al. 2001). Given sparse resources for subsistence on the Plateau, humans have been dependent on hunting ungulates to varying degrees since initial occupation (Ekvall 1968; Huber 2005). Traditional hunting techniques for *P. hodgsonii* vary by season (Huber 2005) and



Fig. 7.—Poacher's camp with a pile of carcasses and heads of *Pantholops hodgsonii* in Tibet, December (top), and nomad tents and herds of sheep and goats occupy traditional range of *P. hodgsonii* in western Tibet, July (bottom). Photographs by G. B. Schaller.

include leghold traps made with a circular base of horn, soaked until pliable (Goldstein and Beall 1990), and pegs of bone (Bower 1894) or wood (Rawling 1905) that radiate toward the center of the base; such traps are placed over a hole for deep penetration of a leg and do not permit a captured animal from withdrawing its leg after stepping through it. Drive lines with diversionary barriers also were used to funnel *P. hodgsonii* toward waiting hunters and leghold traps; *P. hodgsonii* is reluctant to cross barriers of even low stature (J. L. Fox and D. Tsechoe, in litt.; Huber 2005).

Since the mid-1900s, significant changes have occurred in the traditional lifestyles of Tibetan pastoralists (Fig. 7) and their grazing livestock, primarily sheep and goats followed by domestic yaks and horses (Ekvall 1968; Goldstein and Beall 1990; Harris 2008; Miller 2000; Schaller 1998; Yan et al. 2005). Before that time, pastoralists were relatively limited in their movements, bound by heredity to a monastery or elite family, and operated under a triennial pasture-allocation system based on numbers of family

members and livestock (Goldstein and Beall 1990; Miller 2000; Schaller 1998; Schaller et al. 2005). In the 1950s, roads began to penetrate the Plateau, and in the late 1960s, the government of China abolished most private property rights, established cooperatives, and began ongoing relocation of families. In the early 1980s, cooperatives were changed to a household-responsibility system (Banks 2003; Banks et al. 2003) with livestock becoming private again. Most recently, parcels of previously communal land have been divided into household-based rangeland used by a single family or a group of related families on 30- to 70-year leases, which effectively turned the nomad into a sedentary private rancher (Schaller et al. 2005).

Some of these changes have improved the socioeconomic status of pastoralists (e.g., dwelling in houses instead of tents, using electricity from solar panels, and traveling by motorcycles instead of horses), but others have modified traditional ways of life and affected wildlife adversely (Fox et al. 2004; Harris 2008). Reminiscent of the western United States in the 1800s, land “ownership” has led to construction of fences to delineate household and rangeland boundaries (Miller 2000). This in turn limits movements of domestic animals and hinders movements of wild ones, in the latter sometimes causing mortality from entanglement in fences. Roads encroach into heretofore remote areas, which can lead to increased poaching and affect wildlife movement (Yin et al. 2006). Improvements invariably increase densities of humans and domestic livestock—often on the most productive rangeland (Schaller et al. 2005), and they can cause unintentional habitat degradation (Banks 2003; Banks et al. 2003) and reduced carrying capacity for wildlife (Schaller 1998). Wildlife in the Chang Tang region now shares rangeland with >8 million head of livestock (Harris 2008).

Although legal actions are in place to protect *P. hodgsonii*, many challenges remain. Notably, illegal trade in the hides of *P. hodgsonii* is an ongoing threat because of the black market for its wool (Wright and Kumar 1997), which is finer than cashmere and used to make expensive “shahtoosh” shawls and scarves (Li et al. 2000; Næss et al. 2004; Schaller 1998; Traffic Network 1999). Shahtoosh is Persian for “from nature and fit for a king,” or shortened to “king of wools” (Traffic Network 1999:1). The only way to get wool from *P. hodgsonii* is by killing, and it can take 3–5 hides to make a single shawl. Wool cannot be sheared or combed because the fibers are very short and attached to the base of guard hairs, making husbandry infeasible.

According to the Chinese government, about 20,000 *P. hodgsonii* were poached annually in the late 1990s, primarily to make shahtoosh shawls and scarves (Schaller et al. 2005; Traffic Network 1999; Fig. 7). Such garments can sell for U.S.\$1,000–5,000 a piece (Traffic Network 1999) and sometimes as much as U.S.\$15,000–17,600 depending on length (Schaller et al. 2005; Wright and Kumar 1997).

Amazingly, black-market bartering, with profit margins approaching 600%, often results in movement of bones and other parts of endangered Indian tigers (*Panthera tigris*) to Asian markets in exchange for wool of *P. hodgsonii* that moves illegally into Nepal and India (Wright and Kumar 1997). Legal inroads have been made in thwarting traditional black-market routes and worldwide demand for shahtoosh garments (Traffic Network 1999), but continued vigilance and education are needed (Donn and Yates 2002; Wright and Kumar 1997).

Current conservation challenges for *P. hodgsonii* include minimizing habitat degradation from pastoralist activities (e.g., overgrazing by domestic species) and threats from development (e.g., road, fences, and mining) that disrupt movement of wildlife; eliminating poaching and trade in hides; and establishing and appropriately managing reserves to protect extant populations of all Tibetan fauna. Remarkable progress has been made by the Chinese government in expanding the contiguous reserve network in the Chang Tang region, which already includes about 600,000 km² and all the migratory routes of *P. hodgsonii*. The challenge will be to manage the reserve network well. Basic ecological insights on *P. hodgsonii* and associated fauna and flora of the Tibetan Plateau are still needed to establish the most effective and lasting conservation strategies.

REMARKS

The etymology of *Pantholops hodgsonii* is “all” (*pans*, Greek) “antelope” (*antholops*, Greek), which is now misleading because of its phylogenetic affiliation with Caprinae. Along with chiru (= Tibetan for antelope), other common names of *P. hodgsonii* include tsus (male), chus (female), chuhu, tso, tsi, and tsod (Tibetan), orongo or orong (Mongolian), zangling yang (Chinese), and Tibetan antelope (English). The importance of *P. hodgsonii* to native Tibetans is reflected in their year-specific names given to females and males, in part based on dentition and horn growth; for example, 1-year-old, gtsod-ris, ris-thog, or ri'u both sexes; 2-year-old, tshe-ris-ma and ra-bzhi for females, sgam-gtsod and rna-bzhi for males; 4-year-old, so-drug meaning 6 teeth, both sexes; and 8+ years old, chib-gsum, both sexes, meaning 3 units of measurement, likely related to horn growth in males (Huber 2005).

When viewed in profile, the upright and symmetrical horns on adult male *P. hodgsonii* led to early descriptions like “Unicorn of the ancient Persians” (Abel 1826; Hamilton-Smith 1827:196; Prater 1980). *P. hodgsonii* was once prized by explorers of the Tibetan highland for its excellent meat and ease of hunting (Bower 1894; Roosevelt and Roosevelt 1926; Sclater and Thomas 1887). A caricature of a chiru, named Yingying, was used as 1 of 5 mascots for the 2008 Summer Olympics in Beijing, China.

ACKNOWLEDGMENTS

We are particularly grateful to N. Solounias, New York Institute of Technology, for graciously examining skull specimens in the American Museum of Natural History to assess premolar dentition. We also thank J. A. Jenks, W. P. Smith, and W. D. Walter for comments on this account; A. L. Fettes and the entire staff of Interlibrary Loan Services, Oklahoma State University, and D. Wingreen-Mason, Cullman Collection, Smithsonian Libraries, Washington, D.C., for providing electronic copies of many seminal pages from rare literature; and K. Anderson and L. Tomsett of the British Museum (Natural History) for their able assistance with preparation of the skull images. The Oklahoma Cooperative Fish and Wildlife Research Unit (Oklahoma State University, Oklahoma Department of Wildlife Conservation, United States Geological Survey, United States Fish and Wildlife Service, and Wildlife Management Institute cooperating) provided technical support during the preparation of this account. G. B. Schaller's work was sponsored by the Wildlife Conservation Society, and in China, the cooperation of the State Forestry Administration, the Forestry Departments of Tibet, Qinghai, and Xinjiang, and the Tibet Plateau Institute of Biology was greatly appreciated. Since 1895, the Wildlife Conservation Society (www.wcs.org) has been dedicated to preserving biodiversity, teaching ecology, and inspiring care of our wildlife heritage.

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Associate editors of this account were DAVID A. ZEGERS and PAMELA OWEN. Synonymies were reviewed by ALFRED L. GARDNER and COLIN P. GROVES. Editor was MEREDITH J. HAMILTON.