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Author: Leslie, David M.

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Procapra picticaudata (Artiodactyla: Bovidae)

DAVID M. LESLIE, JR.

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

Abstract: *Procapra picticaudata* Hodgson, 1846, is commonly called the Tibetan gazelle, goa (= Tibetan), or zang yuan ling (= Chinese) and is monotypic. It is a high-elevation specialist endemic to the Tibetan Plateau where it prefers alpine meadow and alpine steppe but uses other lower-elevation plains and valleys. It is partial to good grasslands with high diversity of forbs. There have been no systematic estimates of total numbers of *P. picticaudata*. Populations are currently widespread but have been reduced from historic levels and are vulnerable because of poaching in remote areas and competition with livestock of pastoralists. *P. picticaudata* is uncommon in zoos and private collections. It is a threatened Class II species in China and considered "Near Threatened" by the International Union for Conservation of Nature and Natural Resources. DOI: 10.1644/861.1.

Key words: China, conservation, Gansu, India, Qinghai, Sichuan, threatened species, Tibet, Tibetan Plateau ungulate, Xinjiang

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Procapra picticaudata Hodgson, 1846
Tibetan Gazelle

P[*rocapra*]. *picticaudata* Hodgson, 1846:334, pl. 2. Type locality "plains of Tibet, amid ravines and low barren hills;" restricted to "the district north of Sikkim, where most of Hodgson's specimens were obtained after 1844" by Groves (1967:148); first use of current name combination.

A[*ntilope*]. *picticaudata*: Wagner, 1855:408. Name combination.

Procapra picticauda Gray, 1867:245, fig. 2. Incorrect subsequent spelling of *Procapra picticaudata* Hodgson, 1846.

Gazella picticaudata: Brooke, 1873:547. Name combination.

Procapra picticanda Stein-Nordheim, 1884:110. Incorrect subsequent spelling of *Procapra picticaudata* Hodgson, 1846.

Gacella picticaudata: Elliot, 1907:76. Name combination.

Gazella (*Procapra*) *picticaudata*: Ward, Lydekker, and Burlace, 1914:238. Name combination.

Procapra (*Procapra*) *picticaudata*: Groves, 1967:148. Name combination.

Procapra prze picticaudata: Y.-M. Li, Gao, X. Li, Wang, and Niemelä, 2000:906, table 1. Name combination.

CONTEXT AND CONTENT. Order Artiodactyla, suborder Ruminantia, family Bovidae, subfamily Antilopinae, tribe Antilopini. *Procapra picticaudata* is monotypic (Grubb 2005; MacKinnon 2008), although interpopulational differences in horn spread and body size have been noted (Groves 1967;

Fig. 1.—Mature male *Procapra picticaudata* in a lowland plain of the Chang Tang Nature Reserve, Tibet. Photograph by G. B. Schaller used with permission.

Schaller 1998). Groves (1967) identified 3 demes: a Ladakh deme in northwestern Tibet (largest relative to size), a southern Tibet deme, and a Sichuan deme. Most morphological and phylogenetic analyses recognize *Procapra* in western China, Mongolia, and southern Russia as an independent, gazellelike lineage with unique characteristics (narrow nasals [Pilgrim 1939]; modestly patterned pelage, hornless females [Groves 1967]; and presumed primitive karyotype [Effron et al. 1976; Groves 2000; Leslie et al. 2010; Orlov et al. 1978; Sokolov and Lushchekina 1997]). Some taxonomists have included these western Asian species in *Gazella* (Brooke 1873; Sclater and Thomas 1898; Ward et al. 1914), or at least considered them to have arisen from an old lineage of *Gazella* (Heptner et al. 1989). *Procapra* has been used generically, and sometimes subgenerically, to distinguish *picticaudata*, *gutturosa*, and *przewalskii* from other gazelles. Some have grouped *picticaudata* and *przewalskii* as a single species (Allen 1940; Ellerman and Morrison-Scott 1966), but Stroganov (1949) and Groves (1967) gave specific status to *picticaudata* and *przewalskii*. Recent genetic studies of ribosomal DNA support the longstanding monophyly of these 3 species under *Procapra* (Lei et al. 2003). Groves (2000) aligned *Procapra* and *Saiga* in a single clade of Antilopini based largely on unique skull and dental characteristics but stopped short of designating subtribes among Antilopini.

Nomenclatural Notes. As with a comparable error in the nomenclature of the chiru (*Pantholops hodgsonii*—Leslie and Schaller 2008), I attributed the incorrect spelling, *picticanda*, to Stein-Nordheim (1884) because he translated Przewalski's *Reisen in Tibet* and the misspelling did not occur in the original Russian version. The etymology of *Procapra picticaudata* is Latin meaning before goat and painted tail. Along with Tibetan gazelle, other common names include rágóá, góá, and gowa (Tibetan—Hodgson 1846; Teichman 1922), ata-dzeren (little antelope in Mongolian—Przewalski 1876; Sclater and Thomas 1898), raakon (Sikkim, India—Ushaganguli-Lachungpa 1997), gazelle du Tibet (French), and gacela del Tibet (Spanish—Mallon and Bhatnagar 2008). Some translations of Chinese and Kazak (= ak-kut) names for *P. picticaudata* include "white behind," in reference to the "distinctively large and furry white rump patch" (Harris 2008:164).

DIAGNOSIS

The 3 species of *Procapra* and 1 species of *Gazella* that occur in western China, Mongolia, and southern Russia could be confused (Grubb 2005; MacKinnon 2008): *P. picticaudata* (Fig. 1; Hodgson 1846), Przewalski's gazelle (*P. przewalskii*—Leslie et al. 2010; Sclater and Thomas 1898), Mongolian gazelle (*P. gutturosa*—Sokolov and Lushchekina 1997), and goitered gazelle (*Gazella subgutturosa*—Kingswood and Blank 1996). Several keys for *Procapra* have been published (Lydekker and Blaine 1914; MacKinnon 2008; Sokolov and Lushchekina 1997), and Leslie et al. (2010) summarized physical differences among species. *P. picticaudata* mainly occurs south of where *G. subgutturosa* occurs, and the 2 species are unlikely sympatric because of disparate habitat preferences (Schaller 1998). *P. gutturosa* and the highly endangered *P. przewalskii* (Jiang et al. 2000; Jiang and Wung 2001; Leslie et al. 2010; Mallon and Bhatnagar 2008) can be sympatric, or at least parapatric, with *P. picticaudata* only in the Chinese provinces of Qinghai and Gansu (MacKinnon 2008; Schaller 1998).

GENERAL CHARACTERS

Except for male-only horns, sexes of *Procapra picticaudata* are not strikingly dimorphic relative to mass and coloration (Schaller 1998). General measurements of *P. picticaudata* for sexes combined are body mass, 13–16 kg; shoulder height, 54–65 cm; and head and body length, 91–105 cm (MacKinnon 2008; Schaller 1998). Like other *Procapra* species, horns of male *P. picticaudata* arise between the orbits (Hodgson 1846) and form a similar upward and then downward arch (Fig. 2). Unlike other *Procapra* species, horns of male *P. picticaudata* are relatively straight and diverge little at the tips and are slender and ridged from the base to the distal one-fourth (Schaller 1998:figure 6.2) with 25–30 full rings in adult males (Blanford 1888; Hodgson 1846).

Procapra picticaudata was initially described as having "exquisite grace and delicacy of form" (Hodgson 1846:335) and being "remarkable for its diminutive size" (Przewalski 1876:208). The 1st description of *P. picticaudata* was provided by Hodgson (1846) and amended by Przewalski (1876), Blanford (1888), Sclater and Thomas (1898), Lydekker and Blaine (1914), and Allen (1940): small, slender, but compact body with long and fine limbs; coloration grizzled by light tips of hair and varying dorsally from light sandy fawn in winter to gray or slate gray in summer, and white ventrally (Blanford 1888); rufous brown posteriorly on the edges of a whitish, heart-shaped rump patch (Sclater and Thomas 1898) surrounding a short, black-tipped tail (80–90 mm—Feng et al. 1986; Li et al. 1989; Schaller 1998), which is bare on the underside; no lateral or face markings; muzzle with hairs "elongated … to form a sort of lateral tuft, which extends backwards under the eyes" (Sclater and Thomas 1898:72); little to "no trace of moist rhinarium" (Allen 1940; Groves 2000; Hodgson 1846; Pocock 1918:128); large eyes; long, narrow, pointed ears; main hooves anteriorly compressed and posteriorly wide and rounded; dew claws "large, but obtuse" (Hodgson 1846:336); lacking metatarsal, inguinal, and preorbital glands, and associated lachrymal fossa but having 4 small interdigital glands and postcornual sinus (Pocock 1910, 1918); and small testes in a "neat hairy scrotum" (Hodgson 1846:337).

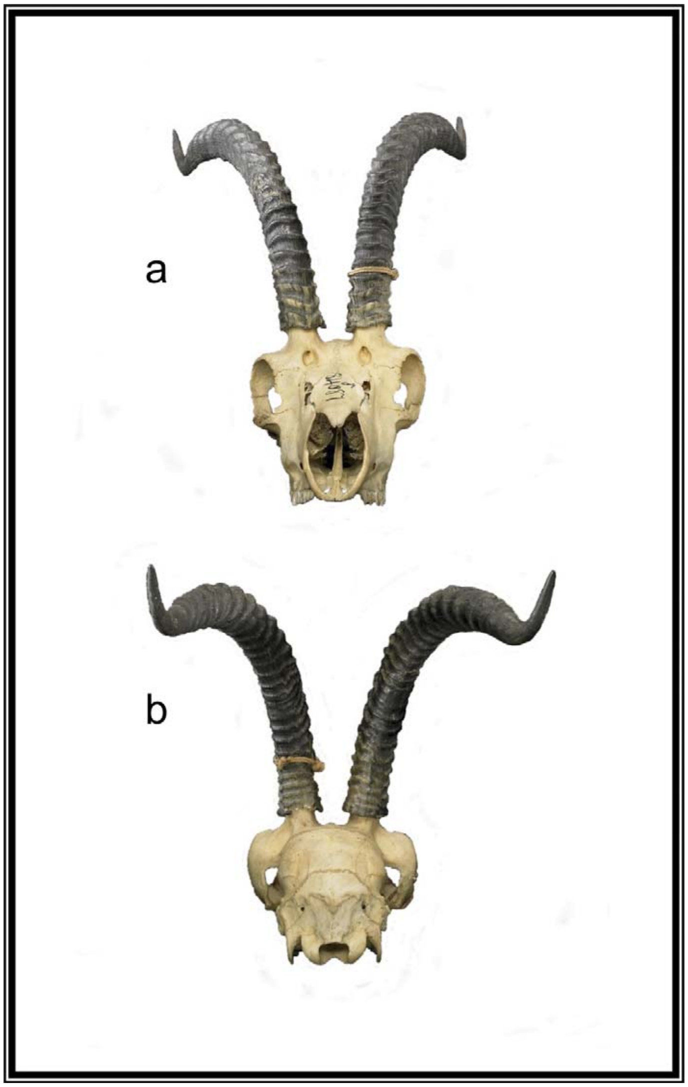

Fig. 2.—a) Anterior and b) posterior views of the skull of an adult male *Procapra picticaudata* (Smithsonian Institution's National Museum of Natural History, specimen 84087, collected in the Ladakh District, India, by W. L. Abbott in 1897) illustrating close proximity of the horns at their point of origin on top of the skull and their near vertical rise between the orbits.

DISTRIBUTION

Procapra picticaudata is considered endemic to the Tibetan Plateau (Fig. 3) at elevations of about 3,000–5,750 m (MacKinnon 2008) and is 1 of the most geographically widespread ungulates on the plateau (Harris and Loggers 2004; Jiang and Wung 2001; Schaller 1997, 1998; Schaller and Gu 1994). More than 99% of extant *P. picticaudata* occur in scattered populations in the Chinese provinces of Gansu, Qinghai, Sichuan, Tibet, and Xinjiang (Jiang and Wung 2001; MacKinnon 2008; Mallon and Bhatnagar 2008; Schaller 1998). As few as 50–100 individuals remain in India in the Ladakh region and seasonally in Sikkim (Bhatnagar et al. 2006, 2007; Fox et al. 1991; Namgail et al. 2008; Ushaganguli-Lachungpa 1997).

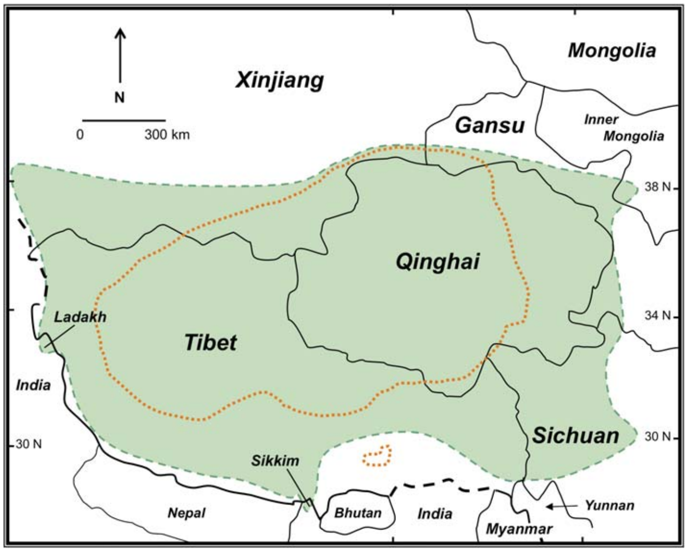

Fig. 3.—Distribution of *Procapra picticaudata* in Chinese provinces of Tibet, Xinjiang, Gansu, Qinghai, and Sichuan and limited distribution in the Ladakh and Sikkim districts of India (green shading generalized from Jiang and Wung [2001], Schaller [1998], and MacKinnon [2008]); areas outlined by the orange dashed line represent specific observations from Schaller (1998: figure 6.3). Dashed lines in the darker southern international boundary indicate areas disputed between China and India.

No systematic range-wide surveys of *P. picticaudata* have been conducted, but some published estimates of total numbers ranged from 20,000 to about 180,000 in the 1980s and early 1990s (Jiang and Wung 2001). Numbers of *P. picticaudata* appeared to be highest in, and east and south of, the Chang Tang Nature Reserve, but the species is largely absent in its desert-like northern parts (G. B. Schaller, pers. comm.). There may have been about 100,000 individuals range-wide in the early 1990s, and currently, range-wide numbers appear higher than in the 1990s with enhanced protection (G. B. Schaller, pers. comm.). Nevertheless, declining numbers and distribution of *P. picticaudata* prompted the International Union for Conservation of Nature and Natural Resources to reclassify the species from "Least Concern" in 2007 to "Near Threatened" in 2008 (Mallon and Bhatnagar 2008).

FOSSIL RECORD

The mammalian fossil record of the Tibetan Plateau is limited, perhaps because geological processes are not conducive to fossilization (Pilgrim 1939) and relatively limited investigation. Distinct antelope-like species were abundant in Eurasia during the late Miocene 13–15 million years ago (e.g., Korotkevich 1968), and central Asia was considered by Pilgrim (1939) to be the evolutionary center of gazellelike forms. *Procapra* apparently did not appear as a distinct genus in Asian fauna until the late Pliocene (Heptner et al. 1989; Sokolov and Lushchekina 1997) or early Pleistocene (Carroll 1988; Savage and Russell 1983).

Isotopic analyses of fossil and living herbivores from the east Kunlun Mountains in the northern Tibetan Plateau suggest that the climate was milder and wetter and habitat diversity was greater in the Pliocene 2–3 million years ago than they are now (Wang et al. 2008); such conditions could have led to emergence and diversification of *Procapra*. Specific fossil material of *Procapra* is limited (Korotkevich 1968). The group is purported to have arisen from a now-extinct species similar to *Gazella sinensis* of the late Pliocene and *G. paragutturosa* of the early Pleistocene (Sokolov 1959, not seen, cited in Sokolov and Lushchekina 1997). Recent evidence suggests that Epipaleolithic and early Neolithic humans hunted *Procapra* species near Qinghai Lake, Qinghai, China (Rhode at al. 2007).

FORM AND FUNCTION

The skull of *Procapra picticaudata* is "lightly built, with very prominent, almost tubular orbits, the distance from their rim to the brain case being equal to a third of the distance across the frontoparietal suture" (Fig. 4; Allen 1940:1218). Early descriptions of *P. picticaudata* included various skull measurements from individual specimens (Allen 1940; Lydekker and Blaine 1914; Sclater and Thomas 1898). Groves (1967) provided comprehensive skull measurements (mm, range) from samples of 1–19 male and 1–15 female *P. picticaudata* from various locations on the Tibetan Plateau: length of nasals, 59.2–63.4 and 55.0–61.9; greatest length, 180.6–187.3 and 177.0–185.0; greatest breadth, 91.0–94.7 and 84.0–88.0; and braincase length, 99.2–102.0 and 94.2–98.0. Similar skull measurements were provided by Feng et al. (1986) and Li et al. (1989). Horn measurements (mm, range) of the same sample of males were: length, 261.2–276.0; tip-to-tip, 96.5–136.6; and greatest width across horns, 122.5–152.4; considerable variation by location was noted (Groves 1967). Schaller (1998) reported adult horn lengths (mm) of 260–322 ($n = 21$) and tip-to-tip lengths of 103–168 ($n = 10$).

The dental formula of *P. picticaudata* is i 0/3, c 0/1, p 2/3, m 3/3, total 30 (Heptner et al. 1989); adult dentition is reduced by the loss of P1 (Groves 2000; Heptner et al. 1989). Groves (2000) evaluated variation of teeth among Antilopini and noted similarity between *Procapra* and *Saiga. Procapra* species have unreduced P2; prominent antero-external style and lingual fold of P3; mesial and distal closure of the lingual wall of P4; buccal midwall convexities of molars not developed into stylids but very angular; and distal lobe of M3 small and simple (Groves 2000). No aging techniques based on tooth eruption and wear in *P. picticaudata* have been reported, but yearling males can be distinguished from females and older males based on their 10-cm horns at 12 months of age (Schaller 1998).

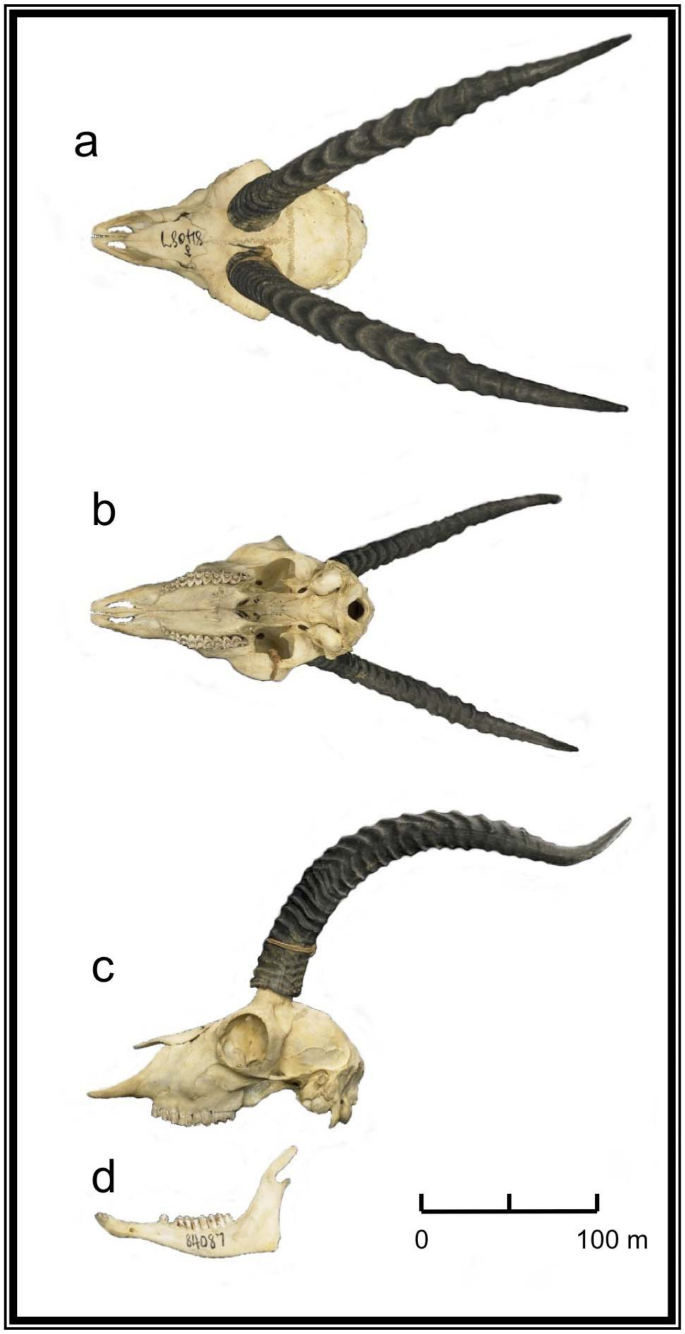

Fig. 4.—a) Dorsal, b) ventral, and c) lateral views of skull and d) lateral view of mandible of an adult male *Procapra picticaudata* (Smithsonian Institution's National Museum of Natural History, specimen 84087) collected in the Ladakh District, India, by W. L. Abbott in 1897. Greatest length of skull is 195.0 mm.

Procapra picticaudata lives in high-elevation areas with associated low temperatures, intense solar radiation, and limited oxygen availability. No particular adaptations of *P.*

picticaudata to living in such extremes have been studied, as they have been for other large mammals in western Asia such as the wild yak (*Bos mutus*—Leslie and Schaller 2009) and the Mongolian gazelle (Sokolov and Lushchekina 1997), a species occurring at lower elevations than *P. picticaudata*. Like the white-lipped deer (*Przewalskium albirostre*—Leslie 2010), *P. picticaudata* lacks an undercoat; the pelage is composed of only guard hairs, "neither fine nor very coarse," about 38 mm in length, and thick and close in winter (Hodgson 1846:336).

Procapra picticaudata is generally crepuscular in its daily activity with 2 feeding and moving periods early and late in the day and resting–bedding during midday (Lu and Wang 2004), although feeding throughout the day is not uncommon (D. Mallon, pers. comm.). Activity budgets varied between female and male groups in the Upper Buha River Valley, Qinghai, in June–September: percent of time spent feeding, male = 58%, female = 38%; bedding (rest and rumination), male = 35%, female = 37%; moving (walking and running), male = 9%, female = 10%; and standing, male = 8%, female = 10% (data extrapolated from Li and Jiang 2007:figure 1).

No specific studies of the senses of *P. picticaudata* have been conducted, but Przewalski (1876) believed that their vision was poor. In contrast, Rawling (1905:314) commented on their "well-developed" senses including "hearing, scent and sight," and contemporary observations suggest very good eyesight (R. Harris, pers. comm.; D. Mallon, pers. comm.). *P. picticaudata* is exceptionally fleet footed and swift and "bounds like an India-rubber ball, and when startled seems absolutely to fly" (Przewalski 1876:209).

ONTOGENY AND REPRODUCTION

Age at sexual maturity of *Procapra picticaudata* is unknown, but if it is comparable to the related goitered gazelle (Kingswood and Blank 1996) and the Mongolian gazelle (Miyashita and Nagase 1981; Nowak 1991; Sokolov and Lushchekina 1997), it occurs at 1.5 years of age for females. Gestation is 5.5–6.0 months (Schaller 1998). Two mammae are present (Hodgson 1846). Parturition generally occurs from July to early August (Schaller 1998). Although MacKinnon (2008:471) stated that *P. picticaudata* "occasionally twin[s]," single offspring appear to be the rule; no multiple births were noted by Schaller (1998). No information on the physical attributes of neonates is available. Pregnant female *P. picticaudata* separate themselves from other females, seek a secluded place to give birth—often moving up in elevation, and hide their neonates for up to 2 weeks (Fig. 5; Schaller 1998). Declining female group size during the parturition period supports this pattern (Li and Jiang 2006).

Schaller (1998) provided the best insight on annual productivity of *P. picticaudata*. In the Chang Tang Nature Reserve between 1988 and 1994, ratios of yearlings (sexes combined) to adult females were 40–70 : 100 (Schaller 1998). Although it is difficult to count offspring because females are dispersed in small groups postpartum, Schaller (1998) observed an average of 47 offspring : 100 yearling + adult females and 60 offspring : 100 adult females. Considerable variation in productivity in the Chang Tang was noted depending on season: spring–summer, 4–33 offspring : 100 adult females and autumn–winter, 38–57 offspring : 100 yearling + adult females (Schaller 1998:tables 6.3 and 6.4). In southwestern Qinghai, 35–69 offspring : 100 yearling + adult females were observed in autumn–winter, 1985–1993 (Schaller 1998: table 6.4). In Shiqu County, Sichuan, Lu and Wang (2004) noted 44 juveniles : 100 adult females and 16 juveniles : 100 male + female adults.

Fig. 5.—Hiding posture of a neonatal *Procapra picticaudata* in Chang Tang Nature Reserve, Tibet. Photograph by G. B. Schaller used with permission.

ECOLOGY

Population characteristics.—Densities of *Procapra picticaudata* are difficult to estimate because of scattered small populations; small group size and cryptic coloration that reduce observability; and the large size of the Tibetan Plateau, which makes systematic counts difficult (e.g., Schaller 1998). Accounts prior to the 1950s noted that *P. picticaudata* was common but widely scattered throughout the plateau (Kozloff 1908; Teichman 1922) and even scarcer than other ungulates (Przewalski 1876). Now, *P. picticaudata* can be uncommon, or even absent, in certain areas of the Tibetan Plateau (Schaller 1998; Schaller et al. 2007).

Contemporary density estimates of *P. picticaudata*, where they occur, are generally <0.50 individuals/km^2 and often <0.10 individuals/km^2 (Schaller 1998). On the high end, Harris (1993) estimated 0.77 individuals/km^2 in Yeniugou, Qinghai, in summer 1991, and Schaller et al. (2007) estimated 2.77 individuals/km^2 along a small part of a

1,692-km transect in Qinghai in late November 2006. Disparity in density estimates reflects some combination of variation in real densities, sampling differences relative to methodology, observability of *P. picticaudata* over various distances, size of the area sampled, time of year, and human impacts (e.g., activities of pastoralists and poaching—Harris 1993, 2008; Schaller 1998).

Maximum life span of *P. picticaudata* in the wild is unknown, but 1 wild-born female *P. picticaudata* lived 5 years 7 months in the Beijing Zoo (Weigl 2005). A captive Mongolian gazelle lived 7 years (Miyashita and Nagase 1981; Nowak 1991), which may be comparable to *P. picticaudata*. Published adult sex ratios that favor males, uncommon among ungulates, may be misleading (Schaller 1998); male *P. picticaudata* are more conspicuous during the peak period of sexual segregation (May–September) when many individuals occupy lowland habitats, enhancing their observability particularly when researchers tend to be in the field. In the Chang Tang Nature Reserve, sex ratios ranged from 121 males : 100 females in late May–August to 81 males : 100 females in September–December, closer to rut in December–January (Schaller 1998). Similarly, Lu and Wang (2004) tallied 174 males : 100 females in June–August in Shiqu County, Sichuan. In Chigo Co in southwestern Tibet, the sex ratio in a sample of 238 individuals was 77 males : 100 females in October (Schaller 1998).

Extreme weather, even a single snowfall event, can result in disproportionate death of young, subadult, and female sympatric chiru (Schaller and Ren 1988), and no doubt has similar effects on densities, survival, age structures, and sex ratios of *P. picticaudata*. As many as 5,500 male and female *P. picticaudata* died in January–March 2008 after extreme cold and snowfall in Shiqu County, western Sichuan Province, China (*Tianfu Zaobao* [= *Morning Post*], www.china.org.cn/environment/news/2008-03/15/content_12678376.htm, accessed 23 December 2008).

The literature is somewhat conflicted regarding the impact of humans on contemporary populations of *P. picticaudata* (cf. Harris 2008; Schaller 1998). Human presence affects densities of *P. picticaudata*, but perhaps less than such presence affects chiru and kiang (*Equus kiang*—Fox and Bårdsen 2005). In Chang Tang Nature Reserve in 1999–2002, encounter rates of *P. picticaudata* were similar under low (0.04–0.09 individuals/km^2 during 2 years of surveys), medium (0.05–0.12 individuals/km^2 during 3 years of surveys), and high (0.06 individuals/km^2 during 1 year of survey) human and livestock presence (Fox and Bårdsen 2005). In contrast, Schaller (1998:114) noted that densities of *P. picticaudata* were "extremely low … in the northern quarter of the [Chang Tang] reserve," which was occupied by pastoralists who "still killed [them] widely and casually for food." Such poaching has decreased since then (G. B. Schaller, pers. comm.).

Space use.—*Procapra picticaudata* inhabits "plains, hills, and even mountains … if the terrain is not precipitous" and prefers open landscapes of high-elevation alpine meadows and alpine steppe; it avoids arid desert steppe (Schaller 1998:111). Presence of herbaceous forbs is an important feature of the habitat of *P. picticaudata* (G. B. Schaller, pers. comm.). Unlike the strongly migratory chiru (Leslie and Schaller 2008; Schaller 1998), and perhaps more like the wild yak (Harris 1993; Leslie and Schaller 2009), *P. picticaudata* does not seem to move great distances between seasonal ranges (Harris 2008; Schaller 1998). Some female groups move seasonally from low-elevation breeding and winter ranges to high-alpine, mesic summer ranges to give birth; many males, and some females, stay in lowland, grass-dominated habitats; males likely establish and maintain breeding territories there (Harris 1993; Schaller 1998). Sizes of seasonal home ranges are unknown.

Diet.—Foraging preferences of *Procapra picticaudata* are understood from only a few studies that used direct observations and fecal evaluations (Harris 1993; Li et al. 2008; Lu et al. 2004; Schaller 1998). Diets of *P. picticaudata* are rather distinct from those of other Tibetan ruminants (e.g., Harris 2008; Leslie 2010; Leslie and Schaller 2008, 2009; Schaller 1998) and typically do not contain appreciable amounts of grasses or sedges, except in winter and in certain locations (Harris and Miller 1995; Yin et al. 2007). Given its small size (Jarman 1974), *P. picticaudata* is a selective feeder. Despite some sexual segregation by elevation, diets do not differ appreciably between males and females in Yeniugou, Qinghai (Harris 1993).

In the Upper Buha River, Qinghai-Tibet, diets of *P. picticaudata* determined from fecal analyses (frequency of occurrence) were 47.5% and 33.2% legumes (*Astragalus* and *Oxytropis*), 13.5% and 17.1% forbs (*Heteropappus*), 13.1% and 26.1 grasses (*Festuca* and *Stipa*), and 8.5% and 13.2% sedges (*Kobresia*) in June–September and October–May, respectively (Li et al. 2008). In Sichuan, 80% of the diet determined from direct observations in August–October consisted of *Kobresia*, *Leontopodium*, and *Oxytropis* (Lu et al. 2004). With fecal analyses, Schaller (1998) noted use of the dwarf shrubs *Ajania* (maximum 89.1%) and *Ceratoides* (2.5%) and forbs *Potentilla* (94.2%) and *Oxytropis*–*Astragalus* (39.6%) in the Chang Tang Reserve from June to December, 1991–1994; grass never exceeded 16% of the diet. Legumes and *Leontopodium* also compose a dominant part of the diet of *P. picticaudata* in Yeniugou, Qinghai (Harris and Miller 1995).

As occurs for other Tibetan ungulates (Leslie 2010; Leslie and Schaller 2008, 2009; Leslie et al. 2010), diets of *P. picticaudata* probably are deficient in protein (<6%) from October to May because of low forage quality on the Tibetan Plateau (Schaller 1998). Forage also may be deficient in minerals such as phosphorus and potassium depending on local soil fertility (Schaller 1998). Some early observers noted that *P. picticaudata* was often close to water (e.g., Przewalski 1876; Rawling 1905), but availability of free water has not been mentioned as important to *P. picticau-*

data by contemporary researchers (e.g., Harris 1993, 2008; Schaller 1998).

Diseases and parasites.—Diseases and parasites of *Procapra picticaudata* are unknown, but disease transmission likely occurs among domestic and wild species. Mongolian gazelles are known to carry foot-and-mouth viruses east of the range of *P. picticaudata*; 67% of 33 gazelles had positive antibody tests to 7 subtypes of foot-and-mouth disease (Nyamsuren et al. 2006). In the past, such exposure has caused significant mortality of Mongolian gazelles that form herds in the thousands (Sokolov and Lushchekina 1997), but similar events have not been reported for *P. picticaudata*, which does not aggregate into large herds (D. Mallon, pers. comm.).

Interspecific interactions.—The wild ungulate fauna of the Tibetan Plateau is diverse (Harris 2008; Harris and Loggers 2004; Hoffmann 1991; Jiang and Wung 2001; Schaller 1998; Xiang et al. 2004). *Procapra picticaudata* generally prefers nondesert steppe and plains and avoids precipitous terrain (Schaller 1998). It is most likely to be found with kiang (St.-Louis and Côté 2009; Zheng et al. 1989), chiru (Harris and Miller 1995; Schaller 1998; Yin et al. 2007), and wild yak (Leslie and Schaller 2009; Schaller and Liu 1996) and least likely to be found with argali (*Ovis ammon*—Fedosenko and Blank 2005) and, in most areas, bharal (*Pseudois nayaur*—Wang and Hoffmann 1987).

Because of the rarity of many of these species throughout the Tibetan Plateau, competitive interactions among them are now reduced (Harris 1993, 2008; Schaller 1998), but competition may occur among *P. picticaudata*, chiru, and kiang in particular locations (Yin et al. 2007). As in mixed ungulate assemblages elsewhere, Tibetan herbivores likely partition food and space, relative to size and digestive capabilities, to minimize competition (Harris 1993; Harris and Miller 1995; Schaller 1998; Schaller et al. 1991). Preferences of *P. picticaudata* for nongrass forage may minimize competition between most wild and domestic herbivores (Harris 1993, 2008), but competition and habitat displacement caused by the livestock of pastoralists remains a common threat to all wild species. *P. picticaudata* prefers grasslands with abundant forbs, the same areas selected by pastoralists for their livestock (G. B. Schaller, pers. comm.); localized displacement of *P. picticaudata* by livestock may be temporary when the livestock are removed (R. Harris, pers. comm.).

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 (Harris 2008; Schaller 1998; Schaller et al. 1988). Predators within the range of *P. picticaudata* include the wolf (*Canis lupus*), Tibetan brown bear (*Ursus arctos pruinosus*), snow leopard (*Uncia uncia*), and Eurasian lynx (*Lynx lynx*—Schaller 1998). *P. picticaudata* occurred in only 4.6–5.2% and 9.5% of the feces of wolves in Aru Basin of the Chang Tang Nature Reserve and Qinghai, respectively (Schaller 1998). Elsewhere, wolves are known to prey on related Przewalski's gazelles in western China (Liu and Jiang 2003) and Mongolian gazelles in Mongolia (Hovens et al. 2000). Xu et al. (2008) stated that *P. picticaudata* was important prey for snow leopards in some locations, but no quantitative data were provided; this proposition seems quite unlikely given the disparity of habitat preferences between the 2 species (R. Harris, pers. comm.; D. Mallon, pers. comm.).

BEHAVIOR

Grouping behavior.—*Procapra picticaudata* does not occur in large gregarious herds, as does the sympatric chiru (Leslie and Schaller 2008; Schaller 1998). When initially described, and paralleling Przewalski's (1876) later observations, Hodgson (1846:335) noted that *P. picticaudata* "dwells, either solitarily or in pairs, or at most small families, never in large flocks." Therefore, MacKinnon's (2008:471) notation that "huge herds [of *P. picticaudata*] used to migrate with the seasons" and Grzimek's (2003) summary that during "migration in spring … herds of 6,000–8,000 individuals form" are in direct odds to what early naturalists and contemporary biologists have observed (Hodgson 1846; Przewalski 1876; Schaller 1998); they are no doubt misstatements and perhaps confusion with goitered gazelles, which do form large herds (Kingswood and Blank 1996). *P. picticaudata* occurs in several types of small groups: male-only groups outside the breeding season; female groups, with and without offspring (Fig. 6), outside the breeding season; mixed groups, particularly during rut in late December through early February; and solitary individuals, most commonly males (Li and Jiang 2006, 2007; Lian et al. 2004; Lu and Wang 2004; Schaller 1998).

Group sizes of *P. picticaudata* from contemporary observations in Tibet, Qinghai, and Sichuan vary from 1 to 46 individuals (Harris 1993; Lian et al. 2004; Lu and Wang 2004; Schaller 1998; Xu et al. 2008). Schaller (1998) concluded that female–offspring pairs, and sometimes related yearling females, represented the only stable association and that larger groups were temporary aggregations. In the Chang Tang Nature Reserve, average group sizes were: mixed groups, 6.1 individuals; female groups, 3.4 individuals in late spring–summer and 4.9 in winter; and male groups, excluding solitary males, 3.6 in summer and 3.4 in winter (Schaller 1998). The largest aggregations in the Chang Tang were 25–46 individuals (Schaller 1998). Lian et al. (2004) observed 1–17 individuals in 924 groups in Hoh Xil (= Kekexili), Qinghai, with 70% of the groups having 2–10 individuals; more males than females were solitary. In Yeniugou, Qinghai, mean group size was 4.1 individuals in summer 1991 (Harris 1993). In Shiqu County, Sichuan, 70% of the groups had 2–8 individuals (Lu and Wang 2004).

Group sizes of male and female *P. picticaudata* and Przewalski's gazelle did not differ during the plant growing

Fig. 6.—Female *Procapra picticaudata* foraging in Chang Tang Nature Reserve, Tibet; note the characteristic heart-shaped white rump patch. Photograph by G. B. Schaller used with permission.

season in Upper Buha River, Qinghai (Lu and Wang 2004). Group size of *P. picticaudata* was related to vigilance: the larger the group, the less time individual *P. picticaudata* spent scanning, likely to detect predators, and the more time individuals spent feeding and engaging in other behaviors (Li and Jiang 2008).

Reproductive behavior.—Sexes of *Procapra picticaudata* are spatially segregated outside rut (May–December—Schaller 1998), often elevationally (Harris 1993), but they may occur in close proximity to one another (G. B. Schaller, pers. comm.). Male *P. picticaudata* establish breeding territories in lower-elevation valleys and plains, and some individual males may remain in their general vicinity throughout the year (Harris 1993). In these territories, male *P. picticaudata* paw the ground creating shallow pits, likely imparting additional scent from interdigital glands (Pocock 1910, 1918). Such areas are visited repeatedly by male and subadult males throughout summer and are marked by frequent urination followed by defecation in and around the pits, thereby establishing latrines (Harris 1993; Schaller 1998, G. B. Schaller, pers. comm.).

Females that ascend to high elevations in summer descend in September. Male groups dissolve as rut approaches in late December, and mature males begin to chase each other from breeding territories. Przewalski (1876) did not observe horn-to-horn combat, but Schaller (1998) described aggressive interactions between rutting males involving face-offs, horn clashes, and pushing and twisting with locked horns. Mature males, which become predominantly solitary at this time of year (Schaller 1998), apparently wait for receptive females. Specific courtship and copulatory behaviors have not been described for *P. picticaudata*. These behaviors may be similar to those of Przewalski's gazelles, which are unique among ungulates and include a "courtship performance" where males dance on their hind legs and a brief intromission with no "locking" of the front legs by males (You and Jiang 2005:187).

Miscellaneous behavior.—A few vocalizations of *Procapra picticaudata* have been noted. Przewalski (1876:209) heard "a snort on seeing a man; and the does when startled give a short cry very similar to that of the young pygarg [= Biblical reference to goat-like animal, or perhaps a harrier]." Rawling (1905:314) noted a "sharp, penetrating shoo" to alert the herd and the erect white hairs on the rump that form a conspicuous "perfect ruff" when alarmed.

Procapra picticaudata was described as tame, particularly around religious areas where hunting was forbidden (Teichman 1922), to very wary (Przewalski 1876) and difficult to approach (Rawling 1905), apparently in response to exploitation. G. B. Schaller (in litt.) noted that *P. picticaudata* "adapt to people and houses better than any other species" of large Tibetan mammals, and they are common "feeding near roads and houses, and when not hunted, they become very tolerant." *P. picticaudata* is uncommon in zoos and private collections.

GENETICS

Published descriptions of chromosomes of *Procapra picticaudata* could not be found. In congeneric Mongolian gazelle, diploid number (2n) is 58 chromosomes and fundamental number (FN) is 60; somatic and sex chromosomes are acrocentric (Orlov et al. 1978; Sokolov and Lushchekina 1997). The Y chromosome in 1 male Mongolian gazelle was "smaller acrocentric without fuzzy arms" (Soma et al. 1979:7). In contrast, the goitered gazelle has a reduced fundamental number of 31, suggesting to Effron et al. (1976) and Groves (2000) that Mongolian gazelle (and other *Procapra* species) represents the primitive karyotype.

Haplotypic diversity (1.00) and nucleotide diversity (0.0296) were high in a single population of *P. picticaudata* in Kekexili National Nature Reserve, Qinghai (Zhou et al. 2006). Similarly, high genetic diversities in the mitochondrial control region and cytochrome-*b* gene (haplotypic diversity = 0.98; nucleotide diversity = 0.08) of *P. picticaudata* were noted in a broader geographic study of 12 localities in Tibet, Qinghai, Xinjiang, Gansu, and Sichuan (Zhang and Jiang 2006).

CONSERVATION

Published literature provides a somewhat mixed message on the conservation status of *Procapra picticaudata*.

Harris (2008) contended that its small size and dispersed nature protects it from poaching; its forage preferences minimizes competition with domestic livestock; it often occupies habitats where human presence is low; and it has no unique uses in Asian medicine. Nevertheless, *P. picticaudata* is protected as a Class II species in China (Harris 2008; Jiang and Wung 2001; Li and Jiang 2007) and was reclassified from "Vulnerable" to "Near Threatened" by the International Union for Conservation of Nature and Natural Resources (Mallon and Bhatnagar 2008) because the population has seemingly declined about 20% over 3 generations. *P. picticaudata* is not protected under the appendices of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (2008).

Harris (2000, 2008) noted that international interest in trophy hunting could be used effectively in wildlife conservation on the Tibetan Plateau, although Schaller et al. (2005) were not convinced. Chinese international hunting areas were established in the 1980s and provide limited trophy hunting for *P. picticaudata* and other ungulates in Subei, Gansu, and Dulan, Qinghai; hunters pay $1,500 (U.S.) per sportsperson to harvest *P. picticaudata*, the lowest fee of any trophy hunt (Harris 2008:table 8.1). During 1985–2001, 238 *P. picticaudata* were harvested under the trophy hunting provisions of the Chinese Wildlife Protection Law of 1988 (Harris 2008).

The Tibetan Plateau is unique zoogeographically (Xiang et al. 2004) and, in particular, has high ungulate endemism: 8 of 9 species are endemic according to Hoffmann (1991). Comparable to other ungulates of the Tibetan Plateau (Harris 2008; Leslie 2010; Leslie and Schaller 2008, 2009; Leslie et al. 2010; Schaller 1997, 1998; St.-Louis and Côté 2009), extant populations of *P. picticaudata* are threatened by human activities, including poaching, now mostly restricted to remote areas (G. B. Schaller, pers. comm.), and habitat displacement by encroaching pastoralists and their livestock (Harris 2008; Harris et al. 1999; Jiang and Wung 2001; Li et al. 2000; Qiu and Feng 2004; Schaller 1997, 1998; Yan et al. 2005). Grassland degradation on the Tibetan steppe—considered moderate to severe in one-third of the grasslands—may be a complicated synergism of overgrazing, persistent drought, and climate change (Miller 2005). Such threats have changed in recent decades as more and more of western China has been developed for agriculture, industry, and tourism (Banks 2003; Banks et al. 2003; Harris 2008; Hoffmann 1991; Jenkins 2009; Jiang and Wung 2001; Miller 2005; Schaller 1998). Considerable basic ecological and behavioral research is needed on *P. picticaudata* and other fauna and flora of the Tibetan Plateau to establish effective and lasting conservation strategies.

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