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MAMMALIAN SPECIES 42(849):7–18

Przewalskium albirostre (Artiodactyla: Cervidae)

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Abstract: *Przewalskium albirostre* (Przewalski, 1883) is a physically unique cervid commonly called the white-lipped deer. *Przewalskium* is monotypic. This species is a high-elevation specialist endemic to the eastern Tibetan Plateau where it inhabits relatively open hills and mountains with a mosaic of forest edges, meadows, and shrublands. Populations of *P. albirostre* are highly fragmented and vulnerable because of exploitation and competition with domestic livestock of pastoralists. There have been no systematic efforts to estimate the total number of extant *P. albirostre*, and it is considered Vulnerable by the International Union for Conservation of Nature and Natural Resources. It is farmed for its antlers in China and is represented in zoos and private collections. DOI: 10.1644/849.1.

Key words: cervid, China, ecology, Gansu, Qinghai, Sichuan, Tibet, Tibetan Plateau, ungulate, vulnerable species, white-lipped deer

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Przewalskium Flerov, 1930

Cervus: Przewalski, 1883:124. Part.

Pseudaxis: Trouessart, 1898:879. Part; used as a subgenus of *Cervus* Linnaeus, 1766; contained *Cervus albirostris*, *C. sika*, *C. hortulorum*, *C. mandarinus*, and *C. taevanus*; preoccupied by *Pseudaxis* Gray, 1872.

Przewalskium Flerov, 1930:115. Type species *Cervus albirostris* Przewalski, 1883, by monotypy.

CONTEXT AND CONTENT. Order Artiodactyla, suborder Ruminantia, family Cervidae, subfamily Cervinae, tribe Cervini. *Przewalskium* is monotypic (Grubb 2005; MacKinnon 2008).

Przewalskium albirostre (Przewalski, 1883)
White-lipped Deer

Cervus albirostris Przewalski, 1883:124. Type locality "Riv. [= river] Koko-su (3 *km* above its mouth), left tributary of riv. Dan-Kho, in western ramifications of the Humboldt Mnts, Nan-Shan, [Qinghai]" vide Flerov (1930:115).

Cervus sellatus Przewalski, 1883:125. Type locality "Tibet and Upper Yellow River" vide Allen (1940:1191).

Cervus dybowskii Sclater, 1889:186, 188. Type locality unknown but "seems probable … from Tibet;" preoccupied by *Cervus dybowskii* Taczanowski, 1876.

Cervus thoroldi Blanford, 1893:444, pl. 34. Type locality "about 200 miles N.E. of Lhassa [= Lhasa]," Tibet, China.

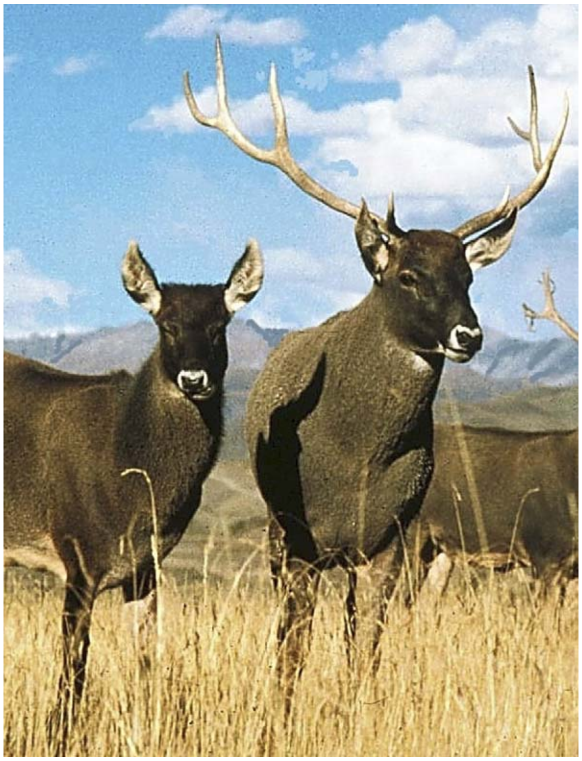

Fig. 1.—Mature female (left) and male *Przewalskium albirostre* in northeastern Tibet, China; note diagnostic features including white muzzles, inner ears, and chins; heads darker than bodies; pointed ears; and distance between the 1st and 2nd tines on the male's antlers and uniform plane of the tines. Photograph by G. B. Schaller used with permission.

[*Cervus* (*Pseudaxis*)] *albirostris*: Trouessart, 1898:879. Name combination.

Przewalskium albirostre: Flerov, 1930:115. First use of current name combination.

Cervus [(*Przewalskium*)] *albirostris*: Allen, 1940:1191. Name combination.

P[*rzewalskium*]. *albirostris*: Pocock, 1942:310. Incorrect gender agreement.

Cervus albirstru Li, Jiang, and Wang, 1999:49. Incorrect subsequent spelling of *Cervus albirostris* Przewalski, 1883.

Context and Content. Context as for genus. *P. albirostre* is monotypic (Grubb 2005; MacKinnon 2008). The origins and affinities of Old World and New World cervids are a matter of ongoing and detailed discussion among traditional taxonomists and molecular systematists (Groves 2006), resulting in frequent reconsideration of species' alignment under various genera and subgenera (Geist 1998; Groves and Grubb 1987; Meijaard and Groves 2004; Pitra et al. 2004; Polziehn and Strobeck 2002; Randi et al. 2001). Many species have been grouped variously under *Cervus* with subgeneric designations such as *Axis*, *Dama*, *Przewalskium*, *Rusa*, and *Rucervus* (e.g., Haltenorth 1963), or split into unique genera by elevation of subgeneric epithets. Groves and Grubb (1987) considered *Przewalskium* to be a sister taxon to *Rusa* (Flerov 1952) and *Rucervus* (Koizumi et al. 1993), which was disputed by Geist (1998). Although current molecular evidence closely aligns *albirostre* with other forms often grouped as species or subspecies under *Cervus* (e.g., *elaphus*, *canadensis*, *nippon*, and *wallichi*—Groves 2006), I followed Grubb (2005) and MacKinnon (2008) by using *Przewalskium* generically but reinstated the correct gender agreement of Flerov (1930; C. P. Groves, pers. comm.).

Nomenclatural Notes. The genus *Przewalskium* was named by Flerov (1930) for Colonel Nicholas M. Przewalski, who extensively explored the Tibetan Plateau and Mongolia in the 1870s and 1880s. The etymology of *albirostre* in Latin is *albus* for white and *rostrum* for snout. Along with white-lipped deer, other common names include Thorold's deer (Blanford 1893), white muzzle deer (Flerov 1930), Przewalski's deer (Flerov 1952; Pocock 1942), white faced Tibetan deer, buff-rump deer (Ohtaishi et al. 1993), and sha (Tibetan for white-lipped deer and red deer [*Cervus elaphus*]—Schaller et al. 1996).

DIAGNOSIS

Fourteen "deer" species occur near or on the Tibetan Plateau (MacKinnon 2008; Ohtaishi and Gao 1990; Schaller 1998). Ten of them are considerably smaller than *Przewalskium albirostre* (4 musk deer [*Moschus*], 4 muntjacs [*Muntiacus*] including the newly discovered leaf deer of northern Myanmar [*M. putaoensis*—Rabinowitz et al. 1999; Schaller and Rabinowitz 2004] but not yet observed in China, Siberian roe [*Capreolus pygargus*], and tufted deer [*Elaphodus cephalophus*]). Along with sika (*Cervus nippon*), those 10 species primarily inhabit low-elevation eastern to southeastern forested areas on the fringe of the Tibetan Plateau and beyond (MacKinnon 2008) and are unlikely to be seen with *P. albirostre*. Relative to size and mass, *P. albirostre* (shoulder height, 115–140 cm; mass, <180–230 kg) is larger than sika (64–110 cm; 40–150 kg) but comparable to sambar (*Rusa unicolor*—140–160 cm; 185–260 kg) and the sympatric red deer (100–150 cm; 75–240 kg—MacKinnon 2008). As an aside, the taxonomic status of "red deer" of the Tibetan Plateau is in flux. MacKinnon (2008) includes 4 of 7 Chinese subspecies of *C. elaphus* that could occur on the Plateau or at least in its eastern fringes: *kansuensis*, *macneilli*, *wallichi*, and *yarkandensis*. In contrast, Groves (2006) considered these to be "shou" and a subgroup of an eastern "wapiti" group, distinct from the "red deer" or *elaphus* group, and likely of 2 distinct species: *C. wallichi* and *C. macneilli*.

Pelage of *P. albirostre* has "exceptional harshness [= coarse]" (Pocock 1942:311). It is grayish brown in spring through autumn and paler in winter, in contrast to the reddish in spring through autumn to dark brown in winter of red deer, brownish to very dark throughout the year and sparse in sambar, and rich reddish with irregular spots, which are inconspicuous in winter, of sika. Unlike those other cervids, antlers of *P. albirostre* are "strongly flattened toward the top" (MacKinnon 2008:465), and the distinct white muzzle and large pointed ears that are ventrally fringed in white are diagnostic (Allen 1940; Flerov 1952).

GENERAL CHARACTERS

Sexes of *Przewalskium albirostre* are distinguished by larger mass of males (180–230 kg; females <180 kg; Fig. 1) and male-only antlers (MacKinnon 2008; Wu and Wang 1999). Of 12 captive adults aged 6–14 years, female mass was 125.0 kg ± 33.7 *SD*, and male mass was 204.2 ± 13.1 kg (Ohtaishi et al. 1993). Antlers of mature males are "strongly inclined backwards, as in *Rusa* generally, not superiorly, as in *Cervus*" (Flerov 1952:112) and are characterized by considerable distance between the 1st (= brow) and 2nd (= bez) tines (Engelmann 1938; Jaczewski 1986), perhaps a result of poor nutrition during early growth (Geist 1998); are believed to represent a primitive cervid character (Allen 1940; Flerov 1930); and have smooth flattened beams and tines at the tops (Flerov 1930; Schaller 1998).

Przewalskium albirostre was aptly described as a "peculiar species of the extraordinarily specialized mammalian fauna inhabiting the Tibetan Plateau" (Blanford 1893:444). Early descriptions were provided by Przewalski (1883), Blanford (1893), de Pousargues (1897, 1898), Lydekker (1915), Flerov (1930, 1952), Allen (1940), and Pocock (1942): large robust but short-legged deer; pelage stiff, thick, and coarse varying from gray-brown dorsally to yellow-pink buff ventrally, twice as thick in winter (Flerov 1930); darker ridge of hair down the back; distinct muzzle, chin, upper throat, and inside of the ears white; light-colored ring around the eyes; other parts of the head darker than body, particularly in males (Geist 1998); no neck mane; ears large, very long, pointed (about 241 mm—Blandford 1893), and fringed in white, unlike other deer (Flerov 1952); large reddish buff rump patch distinctly circumscribed about 150 mm (Allen 1940) above a very short tail one-half the length of the ears (120–130 mm—Flerov 1952); back straight; hooves bovidlike, short, broad, long, and deep with large and long 2nd and 5th phalanges (front hoof of large male 101.8 mm long and 60.2 mm wide; hind foot 97.0 mm long and 54.7 mm wide—Geist 1998), unlike other deer that have narrower and longer hooves (Allen 1940; Flerov 1930, 1952); large metatarsal glands (Lydekker 1915) surrounded by light, long, and dense hairs (Flerov 1930); and pronounced preorbital glands, larger than the eyes (Flerov 1952), and associated deep (40 mm—Flerov 1930; Pocock 1942) lachrymal fossa, twice the size of those in red deer.

Some early descriptions of specimens of *P. albirostre* noted a "saddle … along the spine, where the nap of the hairs goes in reversed direction … 30–40 cm [from] directly behind the shoulders" toward the rump (Flerov 1930:119, 1952). Lydekker (1915) considered this character uniquely diagnostic, but others noted that not all specimens had this characteristic and opined that "the reversal [of hairs] is characteristic of old hair, and not a valid specific character, or it may occur only in old males" (Allen 1940:1192). Koizumi et al. (1993:310) reported that <50% of individuals at a deer farm in China had a "remarkable white marking on the face between the muzzle and the forehead."

DISTRIBUTION

Przewalskium albirostre is endemic to the eastern Tibetan Plateau (Fig. 2) at elevations of 3,500–5,100 m (MacKinnon 2008) from 29.5°N to 38.7°N and 92.5°E to 102.0°E (Koizumi et al. 1993). It currently exists in highly fragmented and frequently small populations in the Chinese provinces of Tibet, Qinghai, Gansu, and Sichuan, and 1 county in extreme northwestern Yunnan (Harris 2008; Kaji et al. 1993; Ohtaishi and Gao 1990; Schaller 1998; Schaller et al. 1988; Wu and Wang 1999), representing only one-tenth of its historic contiguous distribution (Koizumi et al. 1993; Fig. 2).

Although thorough systematic surveys are lacking, numbers of *P. albirostre* appear to be highest, and interconnected suitable habitat most abundant, in remote areas of northwestern Sichuan (Kaji et al. 1993; Koizumi et al. 1993), and they may be increasing elsewhere (Harris 2000; Harris and Loggers 2004). Residents of southern Qinghai consistently reported seeing more *P. albirostre* in 2004 than in previous years (R. B. Harris, pers. comm.). Some populations occur in religious areas and around monasteries where they receive refuge from pernicious human activities, including illegal harvest (Allen 1938; Harris 1991; Kaji et al. 1993; Koizumi et al. 1993; Schaller 1998). Wu and Wang (1999) roughly estimated the total number of wild *P. albirostre* at 15,800, likely a conservative number.

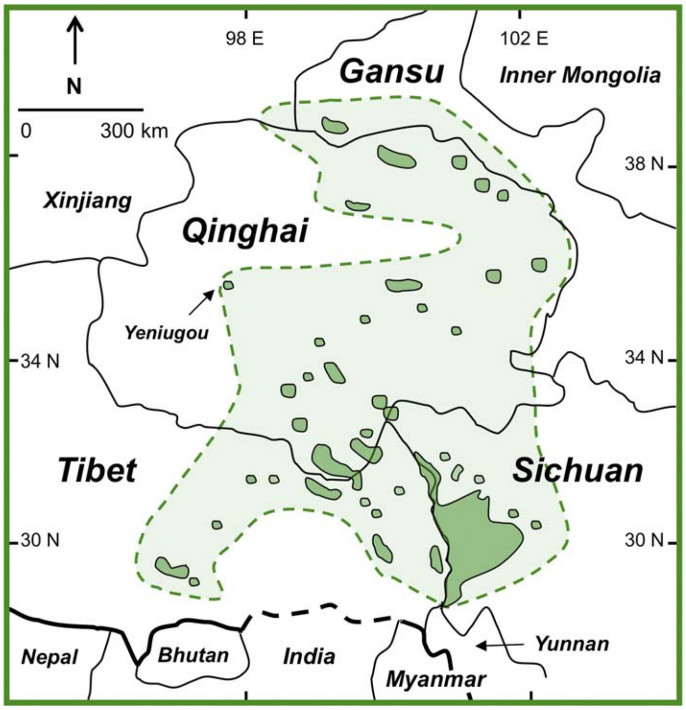

Fig. 2.—Current fragmented distribution of *Przewalskium albirostre* in the eastern Tibetan Plateau including Chinese provinces of Gansu, Qinghai, Sichuan, and Tibet (dark green) modified from Schaller (1998) and Harris et al. (1999), and historical distribution (dashed line, light green) proposed by Kaji et al. (1993). Dashed line of the darker southern international boundary is disputed between China and India.

FOSSIL RECORD

Cervidae is a rich family of Eurasian origin with as many as 26 fossil genera and 80–84 fossil species (Dong 1993; Wu and Wang 1999). Paleomerycines (e.g., *Amphitragulus*) and cervulines (e.g., *Eusylocerus*) of the Miocene were likely precursors of species now included in the family Cervidae (Flerov 1952). The fossil deer *Archeaomerys optatus* found in Inner Mongolia, China, may have been a key step in the evolution of modern cervids (Wu and Wang 1999). Despite a relatively recent radiation into South America during the Pliocene (Eisenberg 1987), Cervidae is mainly a family of the Northern Hemisphere (Geist 1998;

Gentry 2000; Scott and Janis 1987; Webb 2000); the only cervid in Africa, *Cervus elaphus barbarus* (Barbary red deer), may have been introduced by humans from Europe along the southern Mediterranean coast as long as 8,000 years ago (V. Geist, in litt.).

Although *Przewalskium albirostre* is believed to be a singularly evolved high-elevation specialist (Geist 1998), particular insight on its origin from the fossil record is speculative. *P. albirostre* no doubt evolved in temperate northern Eurasia perhaps from the extinct Pleistocene forms such as *Epirusa hilzheimeri* (Di Stefano and Petronio 2002; Flerov 1952; Zhdanski 1925) or *Eucladocerus* (Geist 1998; Grubb 1990; Koizumi et al. 1993). Nakaya (1993) proposed 3 hypotheses that involved shared lineage with sika through extinct relatives including *Axis shansius* of the late Pliocene, *Cervus grayi* of the early Pleistocene, and *Cervus elegans* of the late Pleistocene (Dong 1993). *P. albirostre* may have differentiated from extant and related sika (Nakaya 1993; Polziehn and Strobeck 2002) and converged, relative to physical characteristics, with extant but distantly related *C. elaphus* (Geist 1987, 1998; see "Genetics" section). Di Stefano and Petronio (2002) proposed that *Rusa* (= *Cervus*) *elegans* branched in the mid-Villafranchian, 2.0–2.5 million years ago, giving rise to the extinct *R. hilzheimeri*, the species proposed to have evolved into *P. albirostre*, and *R. unicolor*, the extant sambar of India and southeastern Asia.

FORM AND FUNCTION

Form.—Pelage of *Przewalskium albirostre* consists mainly of needle-shaped guard hairs (Chen and Wang 1991) that are brownish at the base and have an off-white ring before a black tip (Flerov 1930). Rigidity and thickness of the pelage of *P. albirostre* exceeds all other species of deer, and hairs are "hollow, very brittle, slightly wavy and abruptly narrowed towards the base" (Flerov 1930:118). Guard hairs vary in length (mean in mm ± *SD*): 152.0 ± 22.6 on the back, 4.52 ± 0.54 dorsally, and 3.07 ± 0.65 on the legs; depth of the pelage is 33.5 ± 7.5 in winter (Sheng et al. 1993). Winter pelage is twice as thick as summer pelage and longer than that of other Cervidae, even moose (*Alces alces*—Geist 1998; Sheng et al. 1993). As in other Cervidae, the central medulla of guard hairs of *P. albirostre* has a lattice arrangement of cells: medulla width, 635 µm (range: 341–659 µm) and cortex width, 12.0 µm (Sheng et al. 1993). Conflicting accounts exist on the extent of an undercoat in *P. albirostre*; fine undercoat hairs were noted by Sheng et al. (1993), but others did not note a developed undercoat (Chen and Wang 1991; Flerov 1930, 1952; Jaczewski 1986).

The skull of *P. albirostre* is "large, massive, shortened, very long and relatively flattened [with] a maximum length of about 400 mm" (Flerov 1952:109; Fig. 3). It is differentiated from other cervids by wide posterior nasals, convex upper profile of the braincase, large lachrymal fossa, broad, flat palate, and short incisive foramina (Allen 1940; Flerov 1952; Geist 1998). Early descriptions include various skull measurements of individual specimens (Allen 1940; Blanford 1893; Flerov 1930, 1952; Sclater 1889), but Ohtaishi et al. (1993) provide the most thorough measurements (mean in mm ± *SD*) of 2–6 males and 24–27 females, all ≥5 years old: total length, 397 ± 9.7 and 364 ± 11.4; condylobasal length,

Fig. 3.—Ventral, dorsal, and lateral views of skull and lateral view of mandible of an adult male *Przewalskium albirostre* (Bristish Museum [Natural History], specimen 1892.16.11.1). This is the type specimen of *Cervus thoroldi* collected by Dr. G. W. Thorold and described by W. T. Blanford (1893:plate 34), now considered a synonym of *P. albirostre*. The annotation of "Pr. albirostris" on the top of the skull no doubt postdated C. Flerov's (1930) naming of the genus *Przewalskium*. Greatest length of skull is 373.1 mm.

374 ± 8.8 and 335 ± 9.2; nasal length, 131 ± 8.1 and 115 ± 7.0; median palatal length, 214 ± 2.5 and 200 ± 6.5; maximum width of lachrymal fossa, 52.8 ± 2.2 and 45.8 ± 2.7; length of upper cheek toothrow, 107 ± 5.5 and 102 ± 3.6; length of lower cheek toothrow, 120 ± 8.6 and 112 ± 3.6; length of diastema, 91 ± 6.9 and 83 ± 4.7; and length of mandible, 299 ± 10.1 and 280 ± 6.4.

During growth, antlers are covered in modified skin, or velvet, that nourishes the growing bone (Bubenik 1993); velvet is particularly prized in Chinese medicine (Koizumi et al. 1993). Antlers of male *P. albirostre* are whitish (Flerov 1952), yellowish, or brownish, likely dependent on the vegetation used to rub off the velvet. Antlers are grown annually, are shed early in March, begin to grow almost immediately, and attain full growth in late August and September (Geist 1998; Schaller 1998). Characteristically, all antler tines lay on the same plane, unlike antlers of male red deer whose 4th tines branch inward (Ohtaishi et al. 1993). Length and mass of antlers and the number of tines (maximum = 7) increase with age; maximum circumference of beam is reached at about 4 years of age (Ohtaishi et al. 1993). Total antler length along the beam (mean in mm ± *SD*) relative to the number of tines is: 3 tines, 48 ± 5.4; 4 tines, 66 ± 7.8; 5 tines, 92 ± 8.2; and 6 tines, 93.8 ± 18.5 (Ohtaishi et al. 1993). Total antler mass (mean in kg ± *SD*) is: 3 tines, 0.45 ± 0.13; 4 tines, 0.85 ± 0.21; 5 tines, 2.9 ± 1.5; and 6 tines, 3.0 ± 0.86 (Ohtaishi et al. 1993). Males can be grouped in 4 general age classes (I–IV) based on their antler characteristics: I, yearlings with spike antlers; II, juveniles with 2 or 3 antler tines; III, subadults with 3 or 4 tines; and IV, adults with 4–7 tines (Miura et al. 1993).

Dentition of adult *P. albirostre* is typical of cervids: i 0/3, c 1/1, p 3/3, m 3/3, total 34 (Flerov 1952; Fig. 2). Teeth are small compared with species of *Cervus* and *Rusa*, dental row is "short and flat," cheek teeth are subhypsodont, roots of P2 are fused, lower canines are incisoriform, and upper canines in males and females are rudimentary (Brokx 1972; Flerov 1930:118; Flerov 1952). *P. albirostre* can be aged by patterns of replacement of deciduous teeth and eruption of permanent teeth in ≤2.5-year-old individuals; for example, m1 and M1 erupt at about 3 months old; i1, m2, and M2 erupt at about 1.5 years old; and m3 and M3 erupt at about 2.5 years old (Ohtaishi et al. 1993). Other methods for aging *P. albirostre* include the appearance of lingual and buccal cervical lines in permanent molars of 2.5–8.5 year olds, assessment of wear patterns as individuals age (particularly useful for >8.5 year olds), and counts of cementum annuli of incisors and molars (Ohtaishi et al. 1990).

Function.—In captive herds at elevations of 2,300–4,200 m in Qinghai, China, basic hematology of *Przewalskium albirostre* is: hemoglobin, 126.0–145.6 g/l; packed red blood cell volume, 42.13–46.75%; and mean corpuscular hemoglobin concentration, 28.39–36.60% (Li et al. 1993). Representative serum constituents of *P. albirostre* in captivity in Germany are: protein, 61.9–68.1 g/l; alkaline phosphatase, 189.6–428.9 IU/l; creatinine, 181–190 mmol/l; sodium, 148–165 mmol/l; potassium, 5.1–7.5 mmol/l; calcium, 2.2–2.4 mmol/l; and phosphorus, 2.1–3.4 mmol/l (Seidel 1993). Additional measurements of blood and serum chemistry were provided (in Chinese) by Wu and Wang (1999).

Similar to the wild yak (*Bos mutus*—Leslie and Schaller 2009) and other Tibetan species, *P. albirostre* is adapted to living in high-elevation areas with associated low temperatures, intense solar radiation, and limited oxygen availability. Vascular adaptations of *P. albirostre* include a high number of relatively small red blood cells (mean diameter, 4.37 µm ± 0.13 *SD* compared to 5.6 µm in cattle), low red blood cell packed volume, and low mean corpuscular volume, resulting in greater surface area of red blood cell membranes to enhance oxygen transport; plasma viscosity is low, which also speeds oxygen transport (Li et al. 1993). Hypertrophy of the right ventricle of the heart—an expectation if hypoxia from elevated pulmonary arterial blood pressure at high elevations occurs (cf. Heath et al. 1984)—has not been observed in *P. albirostre* (Li et al. 1993).

The modulus of fineness (MOF—Poppi et al. 1980) of fecal particle size from digesta residue suggests that *P. albirostre* (MOF = 2.12) is an intermediate feeder (Clauss et al. 2002). Percentage of fecal particles passing through various sieve sizes are: 4-mm sieve, 1.17%; 2-mm sieve, 1.72%; 1-mm sieve, 4.47%; 0.25-mm sieve, 15.06%; and <0.125-mm sieve, 45.69% (Clauss et al. 2002).

As occurs in other large Tibetan mammals (Leslie and Schaller 2008, 2009), enlarged nasals and associated cranial features of *P. albirostre* permit greater passage of rarified air in its high-elevations habitats (Wu and Wang 1999). Its dense pelage dominated by long, air-filled guard hairs protects it from the extreme low temperatures of the Tibetan Plateau.

ONTOGENY AND REPRODUCTION

Age of sexual maturity of *Przewalskium albirostre* is 1.5–2.5 years (Sheng and Ohtaishi 1993), likely closer to the older age in the wild depending on nutrition. Gestation is reported as 220–250 days (Sheng and Ohtaishi 1993; Wu and Wang 1999; Yu et al. 1993). Parturition generally occurs in May–June (Sheng and Ohtaishi 1993), but dates vary depending on location and elevation, particularly at captive facilities: late April to mid-May, Tibet (3,650 m); mid-June to early July, northern Sichuan (4,200 m); and late June to late July, Qinghai (3,850–4,300 m—Yu et al. 1993). Productivity varies considerably; in Qinghai and Sichuan, it ranged from 16 to 80 calves : 100 females, averaging 36 calves : 100 females and being lowest at elevations >4,500 m (Koizumi et al. 1993). Average ratios were 32 calves : 100 females in Qinghai and 33 calves : 100 females in Sichuan in June–December 1985–1990 and January 1991; the highest ratios of

72 calves : 100 females occurred in areas free from livestock and human disturbance in Penda, Sichuan (Kaji et al. 1989, 1993).

Twinning in *P. albirostre* appears to be very rare (Koizumi et al. 1993); no multiple births were noted among 21 wild females in Sichuan, but 1 other female was observed with 2 neonates, presumably twins (Yu et al. 1993). Five wild neonates from 2 h to 3 days old in Sichuan had an average body mass of 8.9 kg (range: 8.6–9.2 kg), body length of 79 cm (71–83 cm), shoulder height of 53.7 cm (51.0–54.5 cm), hind leg length of 29.9 cm (28.0–31.0 cm), and body temperature of 38.8°C (38.3–39.4°C—Yu et al. 1993). Neonates are precocial and born with spots that begin to fade quickly at 1.5 months (Koizumi et al. 1993); adult color is attained by 2.5 months, and the muzzle is white by 1 year (Ohtasishi et al. 1993).

ECOLOGY

Population characteristics.—Densities of *Przewalskium albirostre* are difficult to estimate because of fragmented small populations and the expansive nature of the Tibetan Plateau. Density estimates of *P. albirostre* in Qinghai and Sichuan vary greatly from 0.01 individuals/km^2 to 4.41 individuals/km^2 (Koizumi et al. 1993:table 1; Schaller et al. 1988; Yu et al. 1993; Zheng et al. 1989). Disparity in density estimates reflects some combination of real densities, sampling differences relative to methodology, size of the area sampled, time of year, and human impacts (e.g., protection, livestock grazing, and poaching—Harris 2008; Schaller 1998).

In a sample of 45 *P. albirostre* collected in Qinghai and Sichuan in 1986–1988, maximum age of females was 12 years in the wild and 19 years in captivity; maximum age of males was 9 years in the wild and 12 years in captivity (Koizumi et al. 1993). Two females lived 21 years and 2 months and 21 years and 3 months in captivity at the San Diego Wild Animal Park (Weigl 2005). From observations during a variety of months in 1985–1988 and 1990, sex ratios of *P. albirostre* ranged from 26 males : 100 females in Qinghai to 42 males : 100 females in Sichuan (Kaji et al. 1993). During rut in Zhenda, Sichuan, when males and females occurred together, Miura et al. (1993) noted 59 males : 100 females, as calculated by Schaller (1998). Low ratios of males in some areas are thought to reflect selective poaching for antlers, particularly in velvet, although population statistics from areas around monasteries and in heavy hunted areas are lacking (Schaller 1998).

Space use.—*Przewalskium albirostre* occupies the highest elevation (up to 5,100 m) and most open habitats of any deer species on the Tibetan Plateau. Among other deer species of the world, only the Peruvian huemel (*Hippocamelus antisensis*) occurs at such high elevations, rarely below 3,960 m and up to 5,000 m in South American Andes (Putz 2003). *P. albirostre* generally prefers mosaics of grassland, shrubland, and forest, often above timberline, and alpine meadows and even arid, treeless areas (Schaller 1998; Wu and Wang 1999). Unlike other deer species, its "short-legged body form, large haunches, and large, blunt hooves" allow it to use steep mountainous terrain to escape danger (Geist 1998:97). *P. albirostre* often is found in the same areas as other mountain specialists such as the Tibetan argali (*Ovis ammon hodgsonii*—Fedosenko and Blank 2005) and blue sheep (*Pseudois nayaur*—Wang and Hoffmann 1987), which have similar habitat preferences (Cai 1988; Zheng et al. 1989). In summer, high-elevation sedge meadows may be preferred by *P. albirostre* (Harris and Miller 1995).

Unlike the strongly migratory ungulates of the Tibetan Plateau such as the Tibetan antelope or chiru (*Pantholops hodgsonii*—Leslie and Schaller 2008; Schaller 1998) but similar to the wild yak (Leslie and Schaller 2009), *P. albirostre* moves seasonally from high-alpine summer ranges to low-elevation winter range and has been described as nomadic (Kaji et al. 1989). Miura et al. (1989) observed a herd of 25 *P. albirostre* that moved across a relatively large area of 35 km^2 in only 9 days in August. Harris and Loggers (2004) suggested that *P. albirostre* moved among the large drainages in Yeniugou, Qinghai, unlike wild yak (Leslie and Shaller 2009), and although not confirmed definitively, they believed that 1 herd (based on comparable group composition) moved 21.5 km in 9 days. Like other cervids, *P. albirostre* is adept at swimming. Miura et al. (1989) and Koizumi et al. (1993) noted summer use of islands in Gyaring Lake, Qinghai, which required up to a 25-min swim.

Diet.—*Przewalskium albirostre* is an herbivorous ruminant and is foremost a grazer that is not particularly selective of species or plant parts (Takatsuki et al. 1988). As many as 95 species of plants have been noted in the diets of *P. albirostre*, of which 35 species are regularly eaten (Wu and Wang 1999). Foraging preferences are understood only from limited direct observations and evaluation of stomach contents and feces (Cai 1988; Harris 1993; Harris and Miller 1995; Takatsuki et al. 1988). Overall, grasses (*Stipa* and *Poa*) and sedges (*Kobresia* and *Carex*) dominate the summer diet of *P. albirostre*, not unlike other ungulates of the Tibetan Plateau (Leslie and Schaller 2008, 2009); 1 composite fecal sample from mesic sedge meadows in Yeniugou, Qinghai, suggested a summer diet of <90% *Kobresia* (Harris and Miller 1995). Woody plants (*Rhododendron*, *Salix*, and *Potentilla*) also are eaten depending on availability (Cai 1988). *P. albirostre* drinks water (Cai 1988), but specific requirements are unknown.

As occurs for other Tibetan ungulates (Leslie and Schaller 2008, 2009), diets of *P. albirostre* 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).

Interspecific interactions.—The Tibetan Plateau has a rich ungulate fauna (Hoffmann 1991), although many species have declined numerically because of human activities (Harris 2008; Schaller 1998). *P. albirostre* occurs at higher elevations than other deer species of the Tibetan Plateau (MacKinnon 2008) but is most likely to be sympatric with red deer (Schaller et al. 1996) and alpine musk deer (*Moschus chrysogaster*), albeit the 3 species are rarely observed together (Kaji et al. 1993). *P. albirostre* can occur generally in the same areas as Tibetan argali, blue sheep, wild yak (Leslie and Schaller 2009; Schaller and Liu 1996), and Tibetan gazelle (*Procapra picticaudata*), and less so with Tibetan wild ass or kiang (*Equus kiang*—St.-Louis and Côté 2009) and chiru (Cai 1988; Harris and Miller 1995; Kaji et al. 1993; Schaller 1998). Because of the rarity of many of these species in the eastern Tibetan Plateau, direct interactions among them are now reduced. 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), but competition with livestock remains the most common threat.

Scant information exists on the 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). Predators within the range of *P. albirostre* include the wolf (*Canis lupus*), snow leopard (*Uncia uncia*), lynx (*Lynx lynx*), and Tibetan brown bear (*Ursus arctos pruinosus*), but only wolves and snow leopards have been documented to consume *P. albirostre*, albeit infrequently. Schaller (1998) found *P. albirostre* in only 1 of 46 fecal samples of snow leopards and 1 of 29 fecal samples of wolves in Qinghai. No information on diseases and parasites of *P. albirostre* is available.

HUSBANDRY

The 1st record of captive rearing of *Przewalskium albirostre* was in 1958 in Qilian County, Qinghai (Wu and Wang 1999). Because of the perceived medicinal value of velvet during antler growth, farms of *P. albirostre* and other species such as red deer were established in western China in the 1970s and 1980s. By 1983, 60 farms housing about 7,000 *P. albirostre* occurred throughout Qinghai and Gansu (Wu and Wang 1999), but they fell on economic hard times in the late 1980s (Koizumi et al. 1993). *P. albirostre* and red deer hybridize in captivity, and hybrid escapees could compromise the genetic integrity of wild populations (Schaller 1998).

Tibetan species such as the yak suffer under husbandry at lower elevations and in warmer climates (Leslie and Schaller 2009). However, *P. albirostre* appears to adapt successfully to captivity under those conditions, as confinement in zoos in the southern United States, Germany, Japan, and Nepal attests (Seidel 1993; Weigl 2005; Wu and Wang 1999). Captive *P. albirostre* can develop toxemia, dysentery, and pneumonia (Wu and Wang 1999). *P. albirostre* can be immobilized, depending on weight, with a mixture of xylazine at 2.5–3.8 mg/kg and ketamine at 2.5–3.8 mg/kg (Seidel 1993). Neonatal levels of gamma-glutamyltransferase can be used clinically to assess the immune function in captivity: normal levels, 224 IU/l ± 115 *SD* ($n = 19$) and abnormal level, 43 IU/l ($n = 1$—Howard et al. 2005).

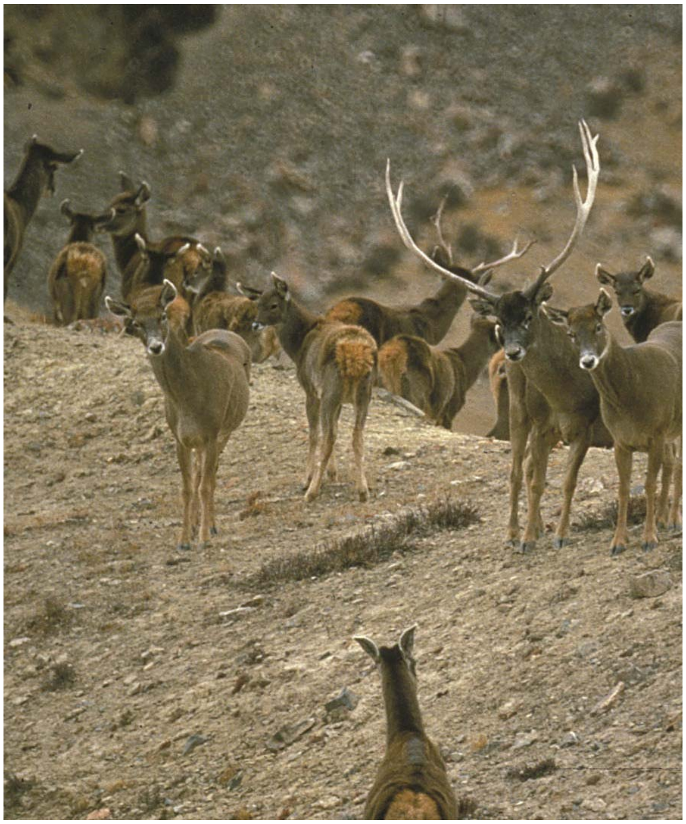

Fig. 4.—Mature male *Przewalskium albirostre* guarding an estrous female by standing up against her in a typically mixed group during rut in September–November, Qilian Mountains, northeastern Qinghai; note the diagnostic reddish buff rump patch that circumscribes the short, similarly colored tail. Photograph by G. B. Schaller used with permission.

BEHAVIOR

Grouping behavior.—*Przewalskium albirostre* is a gregarious herding ungulate that typically occurs in 3 types of groups: male groups outside the breeding season, female groups outside the breeding season, and mixed groups throughout the year (Fig. 4), particularly during rut in September–November, depending on location (Miura et al. 1993; Schaller 1998). Group sizes in Qinghai and Sichuan varied from 1 to 169 individuals; 97% of groups contained

≥10 individuals and tended to be the largest during rut; and group cohesion appears to be high (Miura et al. 1993). Groups observed by Schaller (1998) in eastern Tibet and Qinghai ranged from 8 to 92 individuals. *P. albirostre* rarely occurs alone; Miura et al. (1993) observed only 2 males alone out of 48 observations. Historically, group sizes were larger; for example, groups of up to 800 individuals (200 males) were observed in Zhidoi, Qinghai, in the late 1960s, but by the mid-1980s, few *P. albirostre* were encountered (Kaji et al. 1989). *P. albirostre* is crepuscular in its daily activity patterns (Cai 1988; Miura et al. 1989).

Reproductive behavior.—*Przewalskium albirostre* displays sexual segregation outside of rut (Miura et al. 1993; Schaller 1998). The breeding system of *P. albirostre* is "micro-scale" harem-based, wherein multiple mature males (class IV, 4–7 tines) often occur in mixed groups and either maintain small harems within the group or tend individual females when they are receptive to breeding (Miura et al. 1993:227). In Zhenda, Sichuan, the number of mature males per mating aggregation was 1–8, and females were divided into as many as 8 harems depending on the size of the group (Miura et al. 1993). Such mating aggregations often have peripheral groups of subordinate males (Miura et al. 1993). In captivity, male *P. albirostre* >5 years old breed, but 7-year-old males display the most rutting behavior (Koizumi et al. 1993). During rut, adult males display to each other with behaviors typical of cervids (Geist 1998): regular vocalizations, marking by antler thrashing with open preorbital glands, urine spraying, pawing, and aggressive interactions (e.g., head-down postures, rushing, chasing, parallel-walking displays, and clashing with joined antlers, but not a head-up threat—Koizumi et al. 1993; Miura et al. 1988, 1993). Biting and kicking also occur among males (Wu and Wang 1999). Males wallow in dry and wet spots; muddy wallows are conspicuous and sought out in particular by mature males (Fig. 5; G. B. Schaller, pers. comm.).

In Qinghai and Sichuan, courtship behavior among wild *P. albirostre* was always the purview of mature males with fully developed antlers (Miura et al. 1993). Courtship behaviors, typical of cervids (Geist 1998), include lip-curling, licking, low-neck stretch with rapid tongue flicking, and herding or tending with head-down postures and rushing (Miura et al. 1993). When receptive, males rest their chin on the female's back prior to mounting; copulation is accomplished with a "single violent thrust," but only after an average of 6.7 unsuccessful mountings based on 23 breeding events observed in Qinghai and Sichuan (Miura et al. 1993:227). Males guard females (Fig. 4), even from their offspring from the year before, for ≥3 h postcopulation (Miura et al. 1993).

Yu et al. (1993) provided the following details on behavior of female *P. albirostre* during parturition. Females separate themselves from other females and seek secluded places to give birth and hide their neonates. Among 37 birthing sites in Sichuan, 46% occurred in *Rhododendron* shrub habitats, 32% occurred at the ecotone of grassland–shrub habitats, and 22% occurred in forested, but not dense, areas; east-facing slopes at elevations of 3,850–4,450 m were preferred. One wild female was observed giving birth in a standing position, and she consumed the afterbirth and licked the amniotic fluid on the ground. Females vigorously lick, muzzle, and push the anogential region of their neonates, encouraging them to stand soon after birth; 2 wild neonates stood 30–38 min postpartum (Yu et al. 1993). Neonates begin to move away from the birth site within a couple of hours; during their 1st day of life, neonates may move 40–80 m from the birth site, and during the next 4 days, they may use several hiding sites per day and move 80–200 m between them (Yu et al. 1993). Females visit their offspring to nurse in the morning and evening; otherwise, they remain apart. After about 2 weeks, neonates follow their mothers and begin associating with other conspecifics (Yu et al. 1993).

Fig. 5.—Male *Przewalskium albirostre* standing near a muddy wallow in Qilian Mountains, northeastern Qinghai; mature males seek out such wet wallows, a behavior that departs from some other large deer species. Photograph by G. B. Schaller used with permission.

Communication.—Vocalizations of *Przewalskium albirostre* include alarm barks by both sexes; "gurgling roars" and "short, whiny bugles" (Schaller 1998:149) and "low quavering" growls of males in rut; and grunts, bleats, and "soft, mew-like" sounds of females and their offspring (Miura et al. 1988:107, 1993:225). Roars of males consist of 3–5 syllables, last for about 5 s with a frequency range of 1.2–1.8 kHz and 4–6 harmonic bands, and can be heard >500 m away (Miura et al. 1988, 1993). Grunts of females when approaching their offspring last about 5 s with a frequency range of 0.4–2.2 kHz (Miura et al. 1988). Although nonvocal, both sexes and all ages older than calves emit "resonant snapping sounds" from their carpal joints that can be heard ≤30 m away (Miura et al. 1988:107; Schaller 1998). The function of this sound is unknown; it is absent in most deer but present in caribou (*Rangifer tarandus*) and Père David's deer (*Elaphurus davidianus*—Schaller 1998; Schaller and Hamer 1978).

GENETICS

Przewalskium albirostre has a diploid number (2n) of 66 (Bonnet-Garnier et al. 2003; Wang and Du 1983; Wang et al. 1982) with a fundamental number (FN) of 70 (consistent in Cervinae); 2 metacentric, 2 submetacentric, and 60 acrocentric autosomes (Wang et al. 1982); and 68 autosomal arms (Groves and Grubb 1987). Relative to other cervids, submetacentric chromosome 2 represents a Robertsonian translocation unique to *P. albirostre* (Bonnet-Garnier et al. 2003). The Y chromosome is a small metacentric; the X chromosome is a large acrocentric (Bonnet-Garnier et al. 2003; Wang et al. 1982). G-banding patterns are similar to those in red deer and sika (Wang et al. 1982) and suggest that *Przewalskium* is a sister group of *Rusa* and *Rucervus* (Groves and Grubb 1987).

Ongoing interest in the molecular systematics of Cervidae (e.g., Liu et al. 2003; Pitra et al. 2004; Randi et al. 2001) led Groves (2006:21) to note that the conspicuous external features that led to particular taxonomic affiliations in the past are likely more involved with convergence caused by "climatic-related lifestyle factors" than shared phylogeny. Genetically, various species of *Cervus* appear to form 2 distinct groups with *P. albirostre* and sika more closely linked to an eastern clade (= *C. canadensis*) than to a western clade (= *C. elaphus*—Groves 2006; Pitra et al. 2004). Evaluations of mitochondrial DNA and cytochrome-*b* gene (and changes in the number of antler tines) indicate that *P. albirostre* and sika diverged 0.2–0.9 million years ago during the Villafranchian (Polziehn and Strobeck 2002).

CONSERVATION

Concern over the status of *Przewalskium albirostre* (Cai 1988; McTaggart-Cowan and Holloway 1978) led to its protection as a Class I species in China under the 1988 Wildlife Protection Law, and hunting has been prohibited, except under special permit, since 1989 (Harris 2008; Koizumi et al. 1993). Such protection, including a decrease in poaching (R. B. Harris, pers. comm.), may have allowed some populations of *P. albirostre* to increase (e.g., Yeniugou, Qinghai—Harris and Loggers 2004; Harris et al. 1999). *P. albirostre* is classified as Vulnerable by the International Union for Conservation of Nature and Natural Resources (2008), but it is not protected under Appendix I 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 for wildlife conservation on the Tibetan Plateau. Chinese international hunting areas were established in the 1980s, but they are not yet providing effective habitat security (Harris 2008). Limited trophy hunts of *P. albirostre* and other ungulates occur in Subei, Gansu, and Dulan, Qinghai; hunters pay $14,400 (US) to harvest a trophy *P. albirostre* ($13,400/animal if 2 individuals hunt together)—the 2nd highest fee following argali ($19,500–$29,000—Harris 2008). In 1985–2001, only 18 *P. albirostre* were harvested under such trophy-hunting provisions (Harris 2008).

Comparable to other large mammals of the Tibetan Plateau (Leslie and Schaller 2008, 2009; St.-Louis and Côté 2009), extant populations of *P. albirostre* are threatened by human activities, including some illegal harvest and competition with domestic yak, sheep, and goats (e.g., Harris 2008; Harris et al. 1999; Koizumi et al. 1993; Li et al. 2000; Miura et al. 1993; Qiu and Feng 2004; Schaller 1998). These threats have changed in recent decades as more of western China has been developed for agricultural and industrial purposes (Banks 2003; Banks et al. 2003; Schaller 1998; Yan et al. 2005), but considerable conservation efforts are needed (Harris 2008). Basic ecological insight, including a comprehensive population census, would enhance conservation of *P. albirostre*.

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