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MAMMALIAN SPECIES 42(860):124–137

Procapra przewalskii (Artiodactyla: Bovidae)

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Abstract: *Procapra przewalskii* (Büchner, 1891), commonly called Przewalski's gazelle, is polytypic with 1 of the 2 subspecies (*P. p. diversicornis*) likely extinct. The species now occurs only in the Qinghai Lake region in northeastern Qinghai Province, western China, and predominately inhabits semiarid grassland steppe, stable sand dunes, and the desert–shrub ecotone between them. Numbers and distribution of *P. przewalskii* have decreased severely from historic levels, and up to 10 small and disjunct populations are vulnerable because of agricultural usurpation of preferred habitat, competition with livestock, and illegal hunting. Total population is perhaps as high as 1,000–1,300 individuals. It is a Class I species and listed as "Critically Endangered" in China and considered "Endangered" by the International Union for Conservation of Nature and Natural Resources. It is arguably among the most endangered large mammals on earth. DOI: 10.1644/860.1.

Key words: China, conservation, critically endangered species, Przewalski's gazelle, Qinghai, Qinghai Lake, species recovery, ungulate ecology

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Procapra przewalskii (Büchner, 1891)
Przewalski's Gazelle

Antilope Cuvieri Przewalski, 1888:110. Type locality "Ганьсу, Китай" [= "China, Qinghai, valley of Datunkhe River (Chagry-Gol)" as translated by Abramov et al. 1992:16]; based on lectotype selection by Abramov et al. (op. cit.); preoccupied by *Antilope cuvieri* Ogilby, 1841.

Gazella Przewalskii Büchner, 1891:161. Replacement name for *Antilope cuvieri* Przewalski, 1888.

[*Procapra*] *przewalskii*: Pocock, 1910:892. First use of current name combination.

Gazella (*Procapra*) *przewalskii*: Lydekker and Blaine, 1914:32. Name combination.

Procapra picticaudata przewalskii: Allen, 1940:1220. Name combination.

Gazella (*Procapra*) *przewalskii diversicornis* Stroganov, 1949:19, 25, figures 2 and 3. Type locality "Урочище Син-Жин-пу (Ганьсу, Китай)" [= "Sin-zhin-pu, Gansu (China, Ningxia Hui Autonomous Region)" as translated by Abramov et al. 1992:16].

Procapra (*Procapra*) *przewalskii*: Groves, 1967:149. Name combination.

P[*rocapra* (*Procapra*)]. *p*[*rzewalskii*]. *przewalskii*: Groves, 1967:149. Name combination.

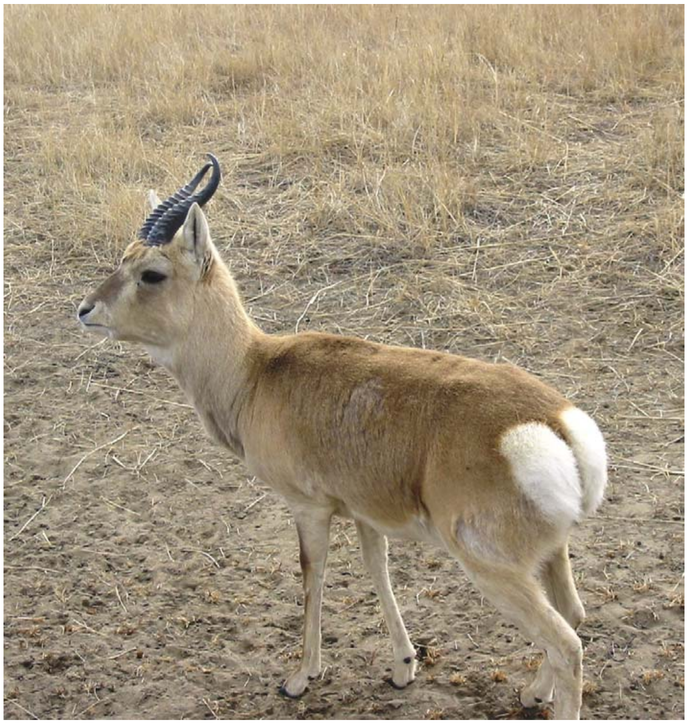

Fig. 1.—Young male *Procapra przewalskii* in northeastern Qinghai Province, China; note heart-shaped rump patch, shedding of winter pelage, and horn tips that are inturned and nearly touching each other at this age. Photograph by R. B. Harris used with permission.

P[*rocapra* (*Procapra*)]. *p*[*rzewalskii*]. *diversicornis*: Groves, 1967:149. Name combination.

Procapra prezwalskii D. Li, Jiang, and Wang, 1999a:74. Incorrect subsequent spelling of *Gazella przewalskii* Büchner, 1891.

P[*rocapra*]. *walskii* Y. Li, Gao, X. Li, Wang, and Niemelä, 2000:906, table 1. Incorrect subsequent spelling of *Gazella przewalskii* Büchner, 1891.

P[*rocapra*]. *p*[*rzewalskii*]. *przewa – lskii* Jiang, 2004:36. Incorrect subsequent spelling of *Gazella przewalskii* Büchner, 1891.

CONTEXT AND CONTENT. Order Artiodactyla, suborder Ruminantia, family Bovidae, subfamily Antilopinae, tribe Antilopini. Most morphological and phylogenetic analyses recognize the genus *Procapra* of western China, Mongolia, and southern Russia as an old, independent, gazellelike lineage (Schaller 1998) with unique characteristics: females invariably hornless; no preorbital depressions and only rudimentary face glands; nasal bones long, pointed at their ends; interdigital fossae of foot glands small; rhinarium scarcely indicated; no pronounced facial markings; and tail extremely short (Groves 1967). Groves (2000) added the following: external styles of P4 small; p3 and p4 elongated but molars shorter; lingual wall of p4 closed mesially and distally; buccal midwall complexities on lower molars very angular; lingual valleys of lower molars more developed; anterior folds of lower molars tiny or absent; distal lobe of m3 very small and simple; supraorbital foramina flush with forehead, not sunk into a pit; and no lateral prongs on nasals. The karyotype of *Procapra* appears to be primitive (Orlov et al. 1978; Sokolov and Lushchekina 1997).

Some taxonomists have included these Asian species in *Gazella* (Adlerberg 1931; Brooke 1873; Sclater and Thomas 1898; Ward et al. 1928), or at least considered them to have arisen from an old lineage of *Gazella* (Heptner et al. 1961). *Procapra* has been used generically, and sometimes subgenerically, to distinguish *przewalskii* (Fig. 1), *picticaudata*, and *gutturosa* from species of *Gazella*; some have grouped *przewalskii* and *picticaudata* as a single species (Allen 1940). Recent genetic studies of ribosomal DNA support longstanding monophyly of these species under *Procapra* (Lei et al. 2003a). The phylogenetic analyses based on the partial mitochondrial 12S rRNA and 16S rRNA gene sequences (Lei et al. 2003b) and the mitochondrial DNA D-loop region (Sorokin 2007) reveal that *P. przewalskii* is more closely related to *P. gutturosa* than to *P. picticaudata*. 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.

Morphologically, *P. przewalskii* and *P. picticaudata* form a group apart from the 3rd species in the genus, *P. gutturosa*, from which they differ by absence of preorbital glands, carpal tufts, inguinal glands, preputial glandular sac, and the specializations of the respiratory tract found in *P. gutturosa*. *P. przewalskii* differs from *P picticaudata* by its larger size, shorter facial skeleton, narrower zygomata, longer and lower braincase, cheek teeth shorter and wider, relatively shorter and more curved horns, and rump patch divided by a line of darker color (Groves 1967; Stroganov 1949). Adlerberg (1931:330) appears to be the 1st taxonomist to suggest 2 "geographical races" of *P. przewalskii*, noting "a bigger (typical?) eastern form [from Kan-su], and a smaller one westward of the upper course of the Hwang-ho [= Yellow River]" with skull lengths (mm) ranging from 185 to 220. Differences in horn spread, size, and winter pelage color led Stroganov (1949) to formally recognize 2 subspecies of *przewalskii*, which he placed in *Gazella*, unlike Pocock (1910), Groves (1967), and Grubb (2005), who used *Procapra*:

P. p. przewalskii (Büchner, 1891). See above.
P. p. diversicornis (Stroganov, 1949). See above.

Groves (1967) considered these 2 subspecies in more detail after examining additional specimens. *P. p. przewalskii*, which is restricted to the highland area of the Qinghai and Nanshan region, is relatively small in size and horns spread less, with the tips more inturned (Fig. 1), and the braincase is longer; sexes hardly differ in size. *P. p. diversicornis* is from lower elevation desert areas east of the Tibetan Plateau in upper Huang Ho region of Gansu Province and the Ordos region; males are larger than females; horns of males are longer, thinner, more divergent, and less inturned at the tips than those of male *P. p. przewalskii* (Fig. 2); the braincase is relatively shorter; and females appear smaller than males. Groves (1967) had no material to assess Stroganov's (1949) claim of color differences.

Reconsideration here by one of us (C. P. Groves) suggests that these 2 forms, *przewalskii* and *diversicornis*, actually should have been ranked as distinct species because available evidence indicates that they are absolutely different (Fig. 2). Skull measurements (mm) of 6 male *przewalskii* and 3 male *diversicornis* were: median length of nasals, 56–62 cf. 62–67; greatest skull length, 200–211 cf. 214–225; and braincase length, 120–129 cf. 120–125 (Groves 1967). A female skull of *przewalskii* was 193 mm long, only slightly less than males, whereas a female skull of *diversicornis* was 194.5 mm long, much less than the males (Groves 1967). Horn measurements (mm) of 6 *przewalskii* and 4 *diversicornis* were: horn length, 181–216 cf. 223–253; tip-to-tip, 65–116 cf. 111–189; and span 143–178 cf. 159–222. Unfortunately, perhaps because *diversicornis* was classified as "only" a subspecies, its very existence seems to have been overlooked as far as conservation is concerned, and it is likely extinct.

NOMENCLATURAL NOTES. Following Corbet (1978), Abramov et al. (1992), and Grubb (2005), we did not include

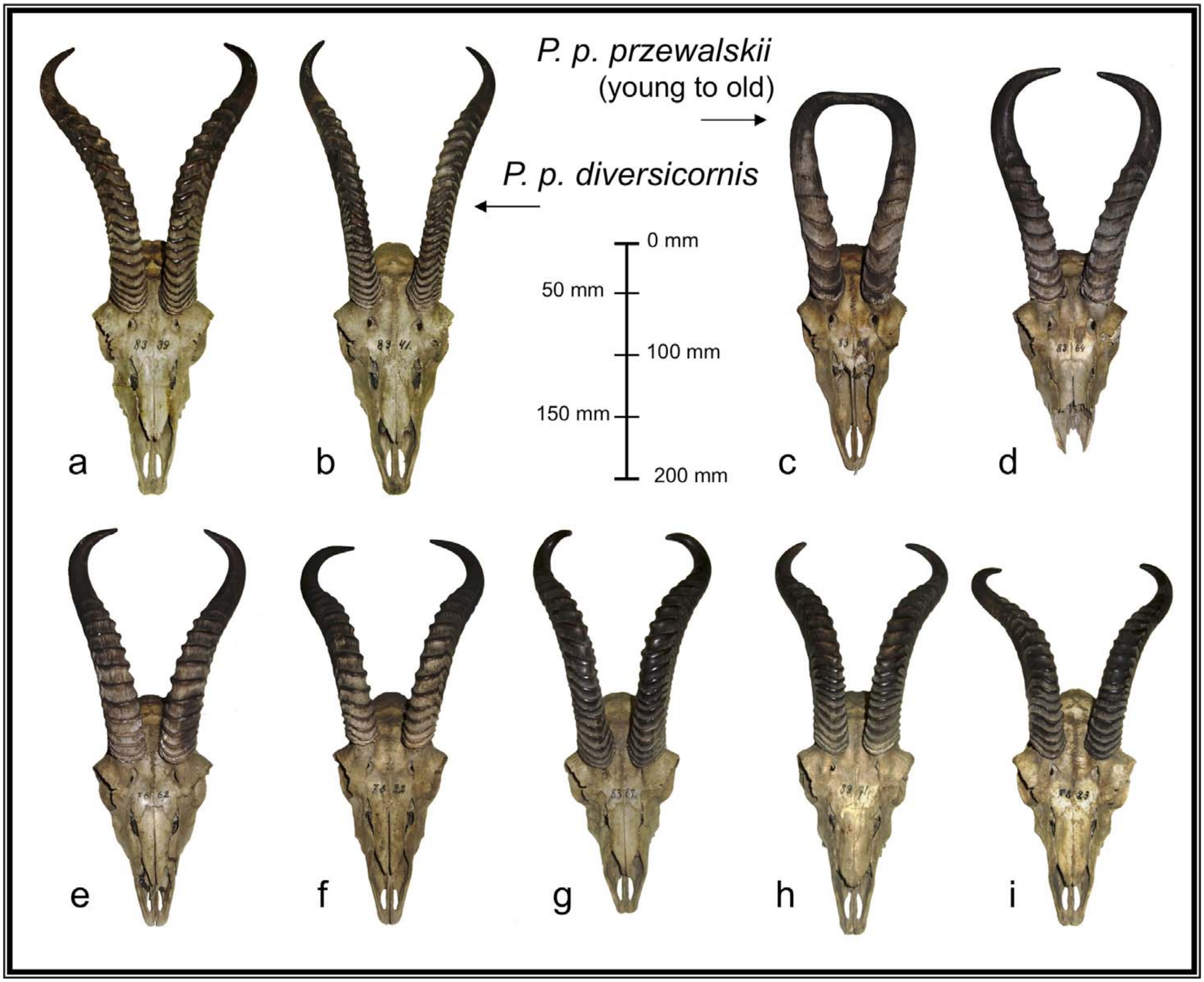

Fig. 2.—Dorsal views of skulls of male *Procapra przewalskii* from early collections in western China. a and b) *P. p. diversicornis* (Russian Academy of Sciences, Zoological Institute [ZIN] specimen numbers: O.8339 [greatest length of skull = 225.1 mm, maximum width across orbits = 102.1 mm] and O.8341 [221.2, 102.0]; both mature adults with worn teeth), collected in Gansu Province by P. K. Kozlov in 1907–1909. c–i) *P. p. przewalskii* (ZIN specimen numbers [left to right]: O.8365 [194.2, 88.9; nasals missing, often fall off in the skulls of young individuals], O.8364 [no total length available because premaxillae and nasals missing], O.7662 [201.5, 98.2], O.7822 [203.1, 94.6], O.8367 [199.0, 98.7], O.8371 [210.3, 94.8], and O.7823 [200.1, 97.0]) arranged from youngest (c and d, molars still erupting) to prime adult males (e–g, complete dentition with little wear on teeth) and oldest males (h and i, complete dentition with worn teeth), collected in Qinghai Province by V. I. Roborovskii in 1894 and P. K. Kozlov in 1899–1901. Note the greater length of skull and longer, finer, and less-robust horns of mature male *P. p. diversicornis* (a and b) and the increasing number and narrowing of ring bands and inturned horns of mature male *P. p. przewalskii* (h and i). Alderberg (1931), Stroganov (1949), and Groves (1967) also used skulls in this series. Individual skull images by A. V. Abramov.

Antilope gutturosa Pallas, 1777 (= Mongolian gazelle), as a synonym, albeit preoccupied, for *Procapra przewalskii*, despite its inclusion in synonymies by Sclater and Thomas (1898), Lydekker and Blaine (1914), Allen (1940), and Ellerman and Morrison-Scott (1966). Przewalski's (1875) original work in Russian described encounters with Mongolian gazelles known to him at the time, and Przewalski likely did not mistake *gutturosa* for what we now call *przewalskii*. Perhaps inclusion of *gutturosa* in earlier synonymies arose from reliance on E. D. Morgan's 1876 translation of Przewalski (1875) in which goat-like gazelles were referred to as *A. gutturosa*, "characteristic of the Gobi

Desert . . . and met with in Western Mongolia, and in the environs of Lake Koko-nor [= Qinghai Lake, Qinghai Province, China]" (Przewalski 1875:18). The 2 species may have been sympatric in the general area of Qinghai Lake, and Morgan's narrative may have suggested to early taxonomists that *przewalskii* was confused or combined with *gutturosa* by Przewalski (1875) in his original volume. Importantly, Abramov et al. (1992) did not include *gutturosa* as a part of the nomenclatural history of *przewalskii* after reexamination of Przewalski (1875) and the original specimens that Przewalski collected and 1st described as *A. cuvieri* (Przewalski 1888).

The generic epithet, *Procapra*, is Latin for "before goat," and the specific epithet, *przewalskii*, honors Nickolai M. Przewalski, prominent Russian explorer of central Asia in the mid-1880s. Along with Przewalski's gazelle, other common names include golmu (G. B. Schaller, pers. comm.), dzéren (general name for gazelle in Mongolian—Sclater and Thomas 1898), huangyang (= yellow sheep, used for all gazelles in Han Chinese—G. B. Schaller, pers. comm.), gazelle de Przewalski (French), and gecela de Przewalski (Spanish—International Union for Conservation of Nature and Natural Resources 2008).

DIAGNOSIS

Three species of *Procapra* and 1 species of *Gazella* that could be confused with each other occur in western China, Mongolia, and southern Russia (Grubb 2005; Jiang and Sung 2001; MacKinnon 2008; Schaller 1998): *P. przewalskii* (Sclater and Thomas 1898), Tibetan gazelle (*P. picticaudata*—Hodgson 1846; Leslie, in press), Mongolian gazelle (*P. gutturosa*—Sokolov and Lushchekina 1997), and goitered gazelle (*Gazella subgutturosa*—Kingswood and Blank 1996). Prominent generic and interspecific distinctions were described under "Context and Content," and several keys for *Procapra* are available (Lydekker and Blaine 1914; McKinnon 2008; Sokolov and Lushchekina 1997).

Only male *Procapra* have horns, but some female *G. subgutturosa marcia* have horns (Kingswood and Blank 1996). *P. przewalskii* is "rather larger" than its most similar congener, the Tibetan gazelle (Adlerberg 1931; Wallace 1913:248). *P. przewalskii* (shoulder height, 50–70 cm; mass, 17–32 kg) and the Tibetan gazelle (shoulder height, 54–65 cm; mass, 13–20 kg) are shorter and smaller than the Mongolian gazelle and the goitered gazelle (combined shoulder height, 60–84 cm; combined mass, 29–45 kg—Feng et al. 1986; D. Li et al. 1989; MacKinnon 2008). Skull characteristics and horn shapes also are distinctive among the 4 species (Groves 1967, 2000; Kingswood and Blank 1996:figure 1; MacKinnon 2008:figure 15; Schaller 1998:figure 6.2; Sokolov and Lushchekina 1997:figure 1; Stroganov 1949:figures 1–3). In general, the Tibetan gazelle has the narrowest and smallest skull and the finest and longest horns (Leslie, in press); the Mongolian gazelle has the largest and most robust skull and the smallest horns (MacKinnon 2008:figure 15). Greatest skull length, skull breadth, and horn length (mm) of the Tibetan gazelle are 182.0–187.3, 91.0–94.7, and 261.2–276.0, respectively, compared to 252.6–262.3, 101.6–110.0, and 205.5–235.2 in the Mongolian gazelle. These characteristics are intermediate in *P. przewalskii* (Groves 1967).

Unlike the 3 *Procapra* species, the goitered gazelle has an externally visible goiterlike enlargement of the larynx, which is most prominent in males (Kingswood and Blank 1996:1). Color patterning of the body of some races of the goitered gazelle is pronounced and includes dark facial stripes, as occur in other *Gazella* (MacKinnon 2008). *P. przewalskii* and the Tibetan gazelle have modestly patterned pelage and are typically gray-brown to sandy-brown with white underparts; the Mongolian gazelle is intermediate but typically has a richer (= darker) coloration than the other species (Leslie, in press; MacKinnon 2008; Sokolov and Lushchekina 1997). *P. przewalskii* and the Tibetan gazelle lack infraorbital and inguinal glands; the Mongolian gazelle has both (MacKinnon 2008).

De Pousargues (1898) suggested that *P. przewalskii* was a hybrid between the goitered gazelle and the Tibetan gazelle, albeit Allen (1940:1221) noted that "characters [between the 2] do not seem intermediate." Skull and horn characteristics of *P. przewalskii* (MacKinnon 2008:figure 15) suggest that if hybridization gave rise to *P. przewalskii*, the Mongolian gazelle may have been involved. Anecdotal claims have been made that *P. przewalskii* and the Tibetan gazelle interbreed in eastern Qinghai Province (Wu 2008), but they have not been verified and disparate breeding seasons suggest that such claims are unlikely (G. B. Schaller, pers. comm.).

GENERAL CHARACTERS

Relative to mass and coloration, sexes of *Procapra przewalskii* are more dimorphic than Tibetan gazelles (Leslie, in press); males tend to be darker and are heavier than females; only males of both species have horns. Horns of male *P. przewalskii* are "much compressed laterally with the exception of terminal 2 inches, divergent and evenly curved backward, with the tips abruptly hooked inward and slightly upward" (Allen 1940:1120)—a description referring to the nominotypical *przewalskii*, not to *diversicornis* (Groves 1967). Horns arise from between the orbits (Fig. 2), which also is characteristic of other species of *Procapra* (cf. Leslie, in press:figure 2). General measurements of *P. przewalskii* for sexes combined are: body mass, 17–32 kg; shoulder height, 50–70 cm; and head and body length, 109–160 cm (MacKinnon 2008).

Early descriptions of *P. przewalskii* were provided by Przewalski (1888), Sclater and Thomas (1898), Lydekker and Blaine (1914), Ward et al. (1928), Adlerberg (1931), and Allen (1940). Using Ridgway's (1912) classic color standards, Adlerberg (1931:325) described the winter pelage of *P. przewalskii* as "grayish-sandy (between ayellaneous and light pinkish cinnamon)" and the summer pelage "of a more reddish coloring (between ochraceous buff and pinkish cinnamon)." More generally, others describe summer coloration as yellowish to deep fawn (Fig. 1) with sides of the neck and nose slate brown and nose hair covered (Pocock 1918; Sclater and Thomas 1898), giving "rather a 'puggy' expression to the face" (Wallace 1913:248–249); thick pale-fawn pelage, grizzled by light tips of hair, in winter, with adult males generally darker than females (Wallace 1913). The belly is white (Adlerberg 1931); a narrow light-brown line runs down the back to the upper surface of a short tail (7–12 cm—MacKinnon 2008), bisecting a white rump patch (Fig. 1) that runs up on the dorsal surface; tail is often hidden by fur; front of limbs are brownish with no knee-tufts (Sclater and Thomas 1898); pronounced lateral and facial markings seen in *Gazella* are lacking; ears are short and acutely pointed, which is most obvious in summer (Sclater and Thomas 1898); and eyes are large. *P. przewalskii* lacks metatarsal, inguinal, and preorbital glands but has a gland behind the horns and reduced pedal glands with a "pore-like orifice" (Pocock 1918:131).

DISTRIBUTION

Historically, *Procapra przewalskii* occurred in semiarid grassland steppe in the Chinese provinces of eastern Qinghai, Inner Mongolia (Ordos and Alashan plateaus), Gansu (Hexi Corridor), Ningxia (Helan Mountains), and Shanxi (Harris 2008:figure 7.1; Jiang et al. 1995, 2000), likely restricted to elevations of 1,000–3,000 m. Wallace (1913:248) hunted *P. przewalskii* (likely *diversicornis*) in central Gansu between "Liangchow and Kanchow" near the terminus of the Great Wall. The species is now restricted to isolated and small areas only in the vicinity of Qinghai Lake (36°32′N–37°15′N, 99°36′E–100°47′E; Fig. 3) in northeastern Qinghai Province, China (Harris 2008; International Union for Conservation of Nature and Natural Resources 2008; Jiang et al. 2003; Jiang and Sung 2001; MacKinnon 2008). No recent evidence of its occurrence east of Qinghai in Gansu or Inner Mongolia provinces has been found (Wang and Schaller 1996).

In 1986, only about 350 *P. przewalskii* were thought to occur around Qinghai Lake (Cai et al. 1991; Jiang and Sung 2001). Three populations of *P. przewalskii*, totaling only 200 individuals (Jiang et al. 1996), were reported by 1997 (Jiang et al. 2000, 2001), and 4 populations were known in 2000 (Li and Jiang 2002). By September 2003, 7 populations had been identified that were restricted to 7 disjunct locations of 32–460 km^2 at elevations of about 2,900–3,700 m (Ye et al. 2006; Fig. 3). With ongoing field research, the number of disjunct populations of *P. przewalskii* was 10 in 2006 with 471 gazelles observed in 9 of those areas and local officials estimating a total population of 685 in all 10 areas (G. B. Schaller, A. Kang, and K. Zhang, in litt. 2006). More recent estimates suggest a total population of 1,000–1,300 (G. B. Schaller, pers. comm.).

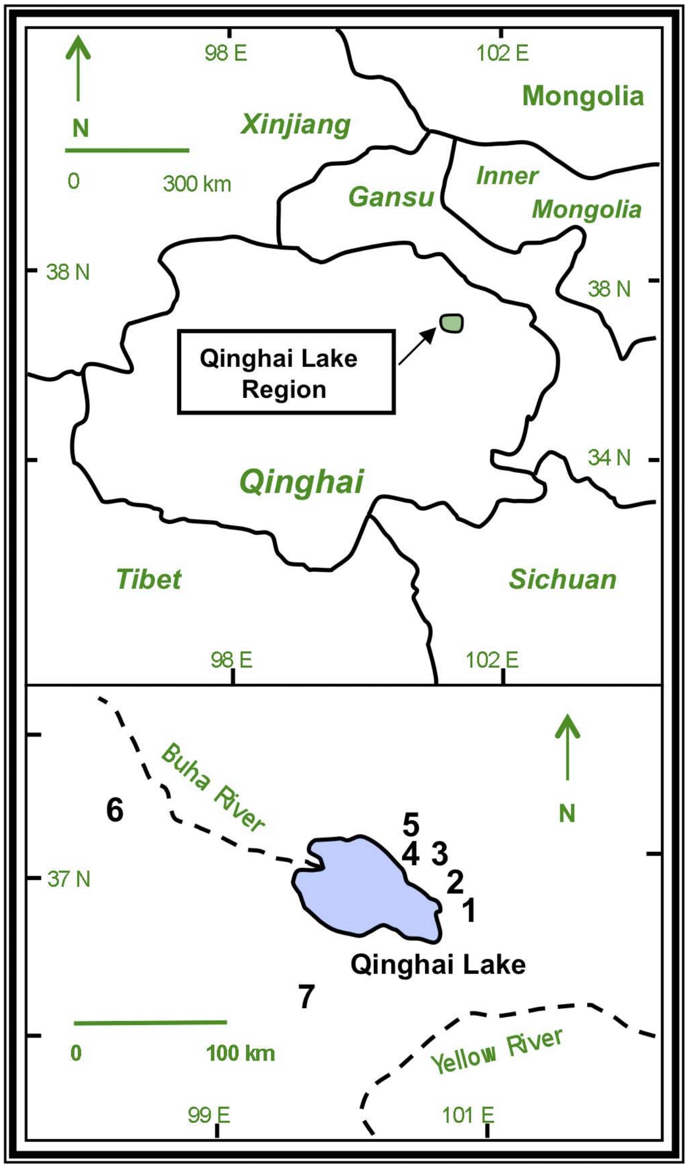

Fig. 3.—Remnant distribution of *Procapra przewalskii* near Qinghai Lake, Qinghai Province, China (top). Seven isolated populations occupying relatively small areas were known in 2006 (bottom): 1) Yuanzhe, 60 km^2; 2) Hudong-ketu, 100 km^2; 3) Haiyan-Gangcha, 460 km^2; 4) Talexuanguo, 68 km^2; 5) Niaodao, 74 km^2; 6) Shengge, 32 km^2; and 7) Qiejitan, 84 km^2 (maps adapted from Ye et al. 2006). Three additional populations in the general vicinity of Qinghai Lake have been identified (G. B. Schaller, A. Kang, and K. Zhang, in litt. 2006), but their specific locations have not been published (G. B. Schaller, pers. comm.).

FOSSIL RECORD

The fossil record of the Tibetan Plateau is limited, perhaps because geological processes there 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. 1961; Sokolov and Lushchekina 1997) or early Pleistocene (Carroll 1988; Savage and Russell 1983).

Specific fossil material of *Procapra* is limited. Isotope analyses of fossil and extant herbivores from Kunlun Basin 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 diversification of *Procapra*. The group may have arisen from an extinct species similar to *Gazella sinensis* of the late Pliocene and *G. paragutturosa* of the early Pleistocene from northern China (Sokolov 1959). Recent evidence suggests that Epipaleolithic and early Neolithic humans hunted *Procapra* species near Qinghai Lake, Qinghai, China (Rhode et al. 2007), which likely included *P. przewalskii* given its distribution in this area.

FORM AND FUNCTION

Reflecting its larger body size, the skull of *Procapra przewalskii* is generally more robust than that of the Tibetan gazelle (Groves 1967; Leslie, in press; Sclater and Thomas 1989; Stroganov 1949). Sclater and Thomas (1898:79) described the skull of *P. przewalskii* as "short and stoutly built [with] nasals broad and short; premaxillae not reaching up to the [nasals]," and with an "unusually large and broad" nasal opening (Fig. 4). Lengths of nasal bones are 22–32% of total skull length, and distance from front edges of an orbit to the forward ends of intermaxillaria (= premaxillae) ≤ 55% of total skull length (Adlerberg 1931).

Following Stroganov (1949), Groves (1967) provided detailed skull measurements (mm, mean ± *SD*) of 6 or 7 male and 1 female *P. p. przewalskii* from Kukunor (= Qinghai Lake region) and 3 or 4 male and 1 female *P. p. diversicornis* from Kansu (= Gansu Province), respectively: median length of nasals, 58.1 ± 1.7, 55.0, 62.4 ± 1.3, and 60.0; greatest length of skull, 202.1 ± 4.5, 194.5, 220.3 ± 4.7, and 192.5; greatest breadth of skull, 95.5 ± 2.8, 93.5, 100.7 ± 2.5, and 90.4; and braincase length, 121.3 ± 3.7, 114.0, 122.8 ± 2.8, and 108.0. Braincase length, relative to greatest length of skull, was notably disparate between the 2 subspecies and "abbreviated" in *P. p. przewalskii* (Groves 1967:147). Horn measurements (mm, mean ± *SD*) of the

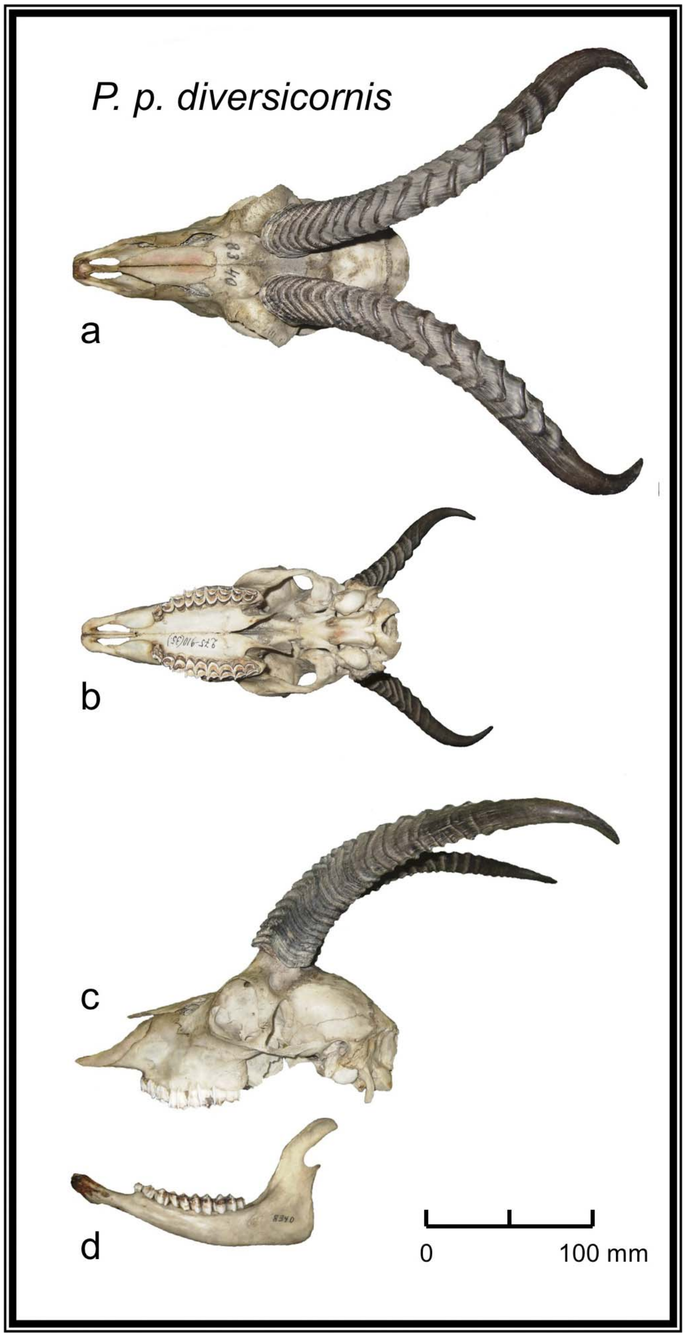

Fig. 4.—a) Dorsal, b) ventral, and c) lateral views of skull, and d) lateral view of mandible of a mature male *Procapra przewalskii diversicornis* (Russian Academy of Sciences, Zoological Institute [ZIN] specimen O.8340, collected in Sin-zhin-pu, Gansu Province, China, by P. K. Kozlov during his expedition in 1899–1901). Note the contrast in this specimen's horn configuration, particularly spread and modestly inturned points, and that of the mature male *P. p. przewalskii* in Figs. 2h and 2i. Greatest length of skull is 213.9 mm; maximum width across orbits is 95.8 mm. Individual skull images by A. V. Abramov.

same sample of male *P. p. przewalskii* and *P. p. diversicornis*, respectively, were: horn length, 193.0 ± 17.0 and 233.1 ± 14.2; tip-to-tip distance, 78.0 ± 28.8 and 134.8 ± 32.2; and greatest width across horns, 153.4 ± 17.1 and 184.1 ± 23.1.

Dental formula of *P. przewalskii* is i 0/3, c 0/1, p 3/3, m 3/3, total 32; adult dentition may be reduced by the loss of P1 (Groves 2000). Mandibular canines are incisiform. Crowns of the cheek teeth of *P. przewalskii* are wider and shorter than those of the Tibetan gazelle, and the crown of P1 is square (Groves 1967; Stroganov 1949). No specific aging techniques based on tooth eruption and wear in *P. przewalskii* have been reported. Yearling males can be distinguished from females and older males based on their small horns, and a progressive change in the horns permits general aging of males (Fig. 2). Inturned tips of the horns of young males may nearly touch each other, and the growth rings are pronounced and the distance between them wide; as males age, tips diverge and wear, and the distance between growth rings narrows (Fig. 2).

Procapra przewalskii lives in relatively high-elevation areas, but generally not >3,000 m, that experience low temperatures (average in January −12.3°C to −14.7°C—Jiang and Sung 2001), blizzard-like conditions, aridity, and intense solar radiation. Aside from the supposition that enlarged nasals enhance air flow at high elevations—a characteristic noted in other Tibetan ungulates (e.g., chiru [*Pantholops hodgsonii*]—Leslie and Schaller 2008), other adaptations to living in such extremes have not been studied in *P. przewalskii* as they have been for other species such as the Mongolian gazelle (Sokolov and Lushchekina 1997) and wild yak (*Bos mutus*—Leslie and Schaller 2009). Like Tibetan gazelle (Leslie, in press) and white-lipped deer (*Przewalskium albirostre*—Leslie 2010), *P. przewalskii* lacks an undercoat; the pelage presumably is composed of only dense guard hairs.

ONTOGENY AND REPRODUCTION

Sexual maturity of female *Procapra przewalskii* is thought to occur in the 2nd year (Li and Jiang 2002). Breeding occurs in late December and early January (You and Jiang 2005). Gestation is 5.5–6.0 months; 2 mammae are present. Parturition generally occurs from May (Przewalski 1875; Wallace 1913) to mid-June (Jiang et al. 1996; Jiang and Sung 2001), in contrast to Tibetan gazelles that give birth in mid-July to early August (Schaller 1998). Single offspring are the rule (Jiang et al. 1996). No information on the physical attributes of neonates of *P. przewalskii* is available.

In the Hudon-Ketu population near Qinghai Lake, 31 young-of-the-year : 100 females ($n = 108$; presumably including yearling females that had not been gravid yet) were observed in 1996, and 43 young : 100 females ($n = 56$) were observed in 1997; the Yuanzhe population had a higher ratio of 64 young : 100 females ($n = 51$) in 1997 (Jiang et al. 2000). Among 4 populations (Haiergai Rover, Yuanze, Hudong-Ketu, and Tainjun Shengge) with 43–105 gazelles counted, G. B. Schaller, A. Kang, and K. Zhang (in litt. 2006) noted 28–63 young : 100 females in October 2006; actual ratios were no doubt higher because samples included nonproductive yearling females.

ECOLOGY

Population characteristics.—Highlighting the need for aggressive conservation attention, population viability analysis suggested that *Procapra przewalskii* could be extinct, with a 98% probability, within 200 years; 8 years was considered the maximum life span of *P. przewalskii* in that analysis (Li and Jiang 2002), but empirical data are lacking. Longevity of other species of *Procapra* appears to be comparable: 1 wild-born female *P. picticaudata* lived 5 years 7 months in the Beijing Zoo (Weigl 2005) and a captive Mongolian gazelle lived 7 years (Miyashita and Nagase 1981; Nowak 1991). Adult sex ratios favor females: 23–68 males : 100 females; the lowest ratios may be an artifact of low observability and preferential poaching of males (Jiang et al. 2000; Lei et al. 2001a, 2001b; Li and Jiang 2002). Density of *P. przewalskii* in the Hundong-Ketu area was estimated at 0.82 individuals/km^2 ± 1.25 *SD* (Liu and Jiang 2004).

Space use.—*Procapra przewalskii* is now found in small numbers only in the vicinity of Qinghai Lake in eastern Qinghai Province, where it occupies relatively low-elevation, open valleys, grassland steppe, stable sand dunes (Fig. 5), and the desert–shrub ecotone between them (Hoffmann 1991; Jiang and Sung 2001; D. Li et al. 1999b). Unlike the related Tibetan gazelle (Leslie, in press; Schaller 1998), *P. przewalskii* appears to move little (G. B. Schaller, A. Kang, and K. Zhang, in litt. 2006). Seasonal ranges may be as close as 3–5 km, and some populations may be completely sedentary, further perpetuating isolation of extant populations and creating the possibility of the sudden extinction of a single population (G. B. Schaller, A. Kang, and K. Zhang, in litt. 2006).

Fencing for agriculture and livestock now largely restricts movement of most populations of *P. przewalskii* to the ecotone between grassland steppe and desert shrublands (Li et al. 1999b). Fencing and human disturbance have the greatest impact on habitat selection, followed by food abundance, distance from the "sandbank" (= sand dunes), and distance from agriculture (Liu and Jiang 2002a). Although as many as 9 plant communities occur within the remaining range of *P. przewalskii* (D. Li et al. 1999b), vegetation type and distance to roads appear to have little influence on habitat selection (Liu and Jiang 2002a).

Diet.—Foraging preferences of *Procapra przewalskii* have been assessed with direct observations and fecal evaluations (Jiang 2004; D. Li et al. 1999a). Given the small

Fig. 5.—*Procapra przewalskii* grazing in the foreground; the species uses a variety of habitats including grassland steppe, sand dunes, and the desert–shrub ecotone between them, in the Qinghai Lake region, western China. Photograph by G. B. Schaller used with permission.

size of *P. przewalskii*, some degree of selective feeding would be expected (Jarman 1974), but desert-like characteristics in much of its range, loss of prime habitat to agriculture, and competition with livestock may now limit availability of preferred forages and our ability to understand presettlement or natural conditions. For example, plant cover and amount of edible herbage in pastures where livestock was excluded were higher than in areas where livestock grazed (Liu and Jiang 2002c).

Unlike the congeneric Tibetan gazelle that does not eat appreciable amounts of grasses or sedges, except in winter in some locations (Leslie, in press), growing-season diets of *P. przewalskii* can be high in grasses and sedges (D. Li et al. 1999a, 1999b, 1999c, Z. Li et al. 2008; Liu and Jiang 2003). Important grasses and sedges in diets of *P. przewalskii* include *Agropyron cristatum*, *Carex stenophylla*, *C. scabrirosfris*, *Koeleria cristafa*, *Orinus kokonorica*, *Poa pratensis*, and *Stipa purpursa* (D. Li et al. 1999a, 1999b, 1999c). Herbaceous and shrubby vegetation such as *Achuatherum splendens*, *Artemisia frigida*, and *Astragalus* can account for 12–34% of the growing-season diet (D. Li et al. 1999a, 1999b).

When forage availability during the growing season decreases to <155.3 g/m^2, *P. przewalskii* begins to eat less palatable plants, which are otherwise seldom selected (Liu and Jiang 2002b); some are considered poisonous to livestock (e.g., *Astragalus*—Jiang and Sung 2001). As occurs for other Tibetan ungulates (Leslie 2010; Leslie and Schaller 2008, 2009), diets of *P. przewalskii* 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). Although no specific information was found on water requirements of *P. przewalskii*, D. Li et al. (1999b) considered distance to water to be an important component of habitat suitability.

Diseases and parasites.—Diseases and parasites of *Procapra przewalskii* are unknown, but disease transmission likely occurs among domestic and wild species. Related Mongolian gazelles are known to carry foot-and-mouth viruses east of the range of *P. przewalskii*; 67% of 33 gazelles had positive antibody tests to 7 subtypes of foot-and-mouth disease (Nyamsuren et al. 2006). Such exposure has caused significant mortality of Mongolian gazelles in the past (Sokolov and Lushchekina 1997) and theoretically poses a threat to *P. przewalskii*.

Interspecific interactions.—The wild ungulate fauna of the Tibetan Plateau is diverse (Harris 2008; Hoffmann 1991; Schaller 1998), but given the highly restricted current range of *Procapra przewalskii* and its use of relatively low-elevation and relatively flat terrain, interspecific interactions with other wild Tibetan ungulates are limited. Littledale (1894) mentioned only kiang (*Equus kiang*—St-Louis and Côté 2009) grazing in the company of *P. przewalskii* near Qinghai Lake. Distributions and habitat preferences vary among *Procapra* species. Generally, *P. przewalskii* occurs in more arid habitats and uses a narrower elevational band (several hundred meters—G. B. Schaller, pers. comm.) than the Tibetan gazelle; the Mongolian gazelle "belong[s] exclusively to the plains, and carefully avoid[s] the hilly country" (Jiang and Sung 2001; Przewalski 1875:18; Schaller 1998). Sympatry could occur among them (Li and Jiang 2006; Z. Li et al. 2008; Liu and Jiang 2004) but is now uncommon because of the rarity of *P. przewalskii* and disparate habitat preferences (Schaller 1998). Nevertheless, *P. przewalskii* and the Tibetan gazelle can still occur in the same general area with some dietary overlap (Z. Li et al. 2008; Liu and Jiang 2004).

Competition for food between *P. przewalskii* and domestic sheep is problematic with dietary overlap of 61% during the growing season (June–mid-September) and 81% when plants have senesced (late September–May—Liu and Jiang 2004). In the Hudong-Ketu area near Qinghai Lake, density of sheep is as high as 66.7 individuals/km^2 and numerically about 100 times greater than that of *P. przewalskii*; Liu and Jiang (2002a, 2004) noted that mortality of both species was highest after winter (May–June) when forage availability and likely quality were lowest and grassland degradation was the highest (X. Li et al. 2009). Hao (2008:634) noted that recent assessments suggest that rangelands around Qinghai Lake can support a "maximum

Fig. 6.—Male *Procapra przewalskii* spend most of year in small bachelor groups or alone, Qinghai Lake region, western China. Photograph by G. B. Schaller used with permission.

livestock equivalent" of 3.65 million domestic sheep but that about 6 million sheep currently use the area.

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; Leslie and Schaller 2008, 2009; Schaller 1998; Schaller et al. 1988). The wolf (*Canis lupus*) occurs throughout the range of *P. przewalskii*, but little information exists to evaluate its importance as predator of this species (Jiang et al. 2000; Liu and Jiang 2003). Fencing may trap *P. przewalskii* making it easier for wolves to catch it (G. B. Schaller, A. Kang, and K. Zhang, in litt. 2006). In western China and Mongolia, wolves are known to regularly prey on goitered gazelle (Hovens et al. 2000).

BEHAVIOR

Grouping behavior.—*Procapra przewalskii* does not now occur in large gregarious herds, as do some other ungulates in western Asia such as the related Mongolian gazelle (Sokolov and Lushchekina 1997) and the chiru (Leslie and Schaller 2008; Schaller 1998). Similar to Tibetan gazelle (Leslie, in press; Schaller 1998), *P. przewalskii* occurs in 5 types of small groups: male-only groups outside the breeding season (Fig. 6); female groups, with and without offspring, outside the breeding season; mixed groups, particularly during rut in late December through early February; and solitary individuals (Jiang 2004; Li and Jiang 2006; Lei et al. 2001a, 2001b).

Przewalski (1875) noted that typical groups of *P. przewalskii* were 15–40 individuals and occasionally several hundred to even thousands—a thing of the past. Group sizes of *P. przewalskii* from contemporary observations near Qinghai Lake were 22% solitary, 63% 2–8 individuals, and 16% ≥9 individuals (Li and Jiang 2006). Throughout the year, mixed-sex groups are the largest (range of monthly mean number of individuals: 15 in March to 27 in December), followed by female groups with and without young (range: 4 in November to 13 in August) and male groups (range: 2 in November and December to 3 in September and October—Jiang 2004: extrapolated from figure 10.3A). Male groups are consistently small, 2 or 3 individuals, throughout the year, and size of mixed groups change the most from March to December (6–17 individuals, highest in November–December—Lei et al. 2001a, 2001b). Female groups are smallest after lambing (Li and Jiang 2006). Group sizes of sympatric male and female *P. przewalskii* and Tibetan gazelles do not differ during the plant-growing season in Upper Buha River, Qinghai (Li and Jiang 2006).

Reproductive behavior.—*Procapra przewalskii* does not move elevationally to breeding or calving ranges. During the nonbreeding season, *P. przewalskii* is "male spaced–female sociable," largely co-occurring in the same areas (Lei et al. 2001a:123, 2001b). Group dynamics during rut have been described as "temporary mobile harems when males disperse to court females" (Lei et al. 2001a:123).

You and Jiang (2005:figure 2) observed horn-to-horn combat among male *P. przewalskii* involving face offs, horn clashes, and fighting with locked horns similar to that described for Tibetan gazelles (Schaller 1998). Wear patterns of horns as males age, resulting in a shortening of horns as they inturn (Fig. 2), suggest considerable horn-to-horn interactions among males and horn rubbing on vegetation and other objects. Male *P. przewalskii* establish breeding "leks" in late autumn (Jiang and Sung 2001) to display to females and regularly scent mark them by urinating in a deep crouch of their hindquarters (You and Jiang 2005:figure 3). Females have been observed fighting and chasing with an apparent dominate female driving a subordinate female from a group (Lei et al. 2001a).

You and Jiang (2005) described the courtship display and mating by male *P. przewalskii* as unique. Courtship involves a male standing erect on his hind legs while prancing toward a female; if the female is receptive, she stands with tail raised, and the male's display is followed by a brief, no-leg-lock copulation with a single 1- to 2-s intromission; the pair barely touches each other while the male holds his front legs curled near his chest (You and Jiang 2005:figure 4B). Following a successful mating, a male will often tend his mate for about 30 min. Copulation is rare; only 85 of 1,009 attempts were successful (You and Jiang

Fig. 7.—Young *Procapra przewalskii* bedded in high-quality grassland habitat in the Qinghai Lake region, western China. Photograph by G. B. Schaller used with permission.

2005). You and Jiang (2005) noted that courtship and mating of *P. przewalskii* are often interrupted by livestock and pastoralists and that the majority of copulations occurred before livestock reached, or after they left, breeding areas.

Female *P. przewalskii* may select "thickets and high grass" for parturition (Przewalski 1875)—habitats otherwise avoided. Unlike Tibetan gazelles that hide their neonates for 2 weeks postpartum (Leslie, in press; Schaller 1998), newborns of *P. przewalskii* (Fig. 7) can follow their mothers within a "few minutes" postpartum (Jiang et al. 1996:60) but might "spend a few days mostly hiding" (G. B. Schaller, pers. comm.).

Miscellaneous behavior.—*Procapra przewalskii* is active 10 h/day in March–April, 13–15 h/day in June–July during the peak of the growing season, and 12 h/day in August (Chen et al. 1997). During spring green-up, 66% of daily activity is spent foraging during 3 peak periods evenly spaced throughout the day; foraging time decreases in summer (46% versus 45% bedding) and autumn (40% versus 37% bedding—Chen et al. 1997). D. Li et al. (1999d) reported only 2 feeding bouts in summer: early morning and late afternoon, often synchronized to avoid livestock.

Przewalski (1875:18), and reiterated by Sclater and Thomas (1898), noted that *P. przewalskii* was seldom vocal but occasionally gave "a short loud bleat." Males are said to "roar" during rut (Jiang and Sung 2001). Przewalski (1875) further noted that this species was "marvelously" swift. *P. przewalskii* is capable of jumping fences of 90–100 cm high but hesitates to jump fences 120–140 cm (G. B. Schaller, A. Kang, and K. Zhang, in litt. 2006). Fences are a greater impediment to "young and pregnant animals" (Hao 2008:634). During the early western explorations, *P. przewalskii* was easy to hunt, and its meat was considered excellent (Przewalskii 1875; Sclater and Thomas 1898; Wallace 1913).

GENETICS

Chromosomal characteristics of *Procapra przewalskii* have not been reported. In congeneric *P. gutturosa*, 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). To Effron et al. (1976), Orlov et al. (1978), and Groves (2000), these characteristics suggested a primitive karyotype.

Haplotypic diversity (0.67–0.95), nucleotide diversity ($\pi = 0.0032–0.0044$), and population structuring ($\Phi = 0.793$) from assessment of the mitochondrial DNA D-loop region were determined in 4 disjunct populations of *P. przewalskii* in the Qinghai Lake area (Lei et al. 2003a). Despite the close proximity of the 4 populations (as close as 7 km), none of the 15 unique haplotypes was shared among the populations, and gene flow among the populations was low ($Nm = 0.3$ migrants/generation—Lei et al. 2003a). The degree to which reproductive behavior, dispersal patterns or sedentary habits, and human impacts (e.g., habitat loss from agriculture and fencing) affect the pronounced genetic isolation of these 4 populations on a very small spatial scale, as well as the other populations that have been identified since, requires additional research (Lei et al. 2003a).

CONSERVATION

Early accounts suggested that *Procapra przewalskii* was abundant in the area of Qinghai Lake (Littledale 1894; Przewalskii 1875) and was commonly encountered further east in Gansu in the late 1880s and early 1900s (Wallace 1913). The species now is arguably among the most endangered large mammals on earth (Harris 2008; Jiang 2004; Jiang et al. 2000). It has been protected as a Class I species and listed as "Critically Endangered" in China since 1984 (Jiang et al. 1996; Jiang and Sung 2001) and is classified as "Endangered" by the International Union for Conservation of Nature and Natural Resources (2008) because of extreme rarity, declining populations, and habitat loss. Nevertheless, *P. przewalskii* is not listed under the Appendices of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (2008).

Harris (2008) provided a cogent summary of the decline of populations of *P. przewalskii* throughout the historic range. In that summary, he acknowledged that our understanding of the species' requirements is imperfect because we know it only from what might be the less than optimum habitats that it has been relegated to in the western reaches of its former distribution. If C. P. Groves's contention that *diversicornis* and *przewalskii* are distinct species is correct (see "Context and Content"), how their unknown respective distributions contracted is even more obscure. Nevertheless, the westward range contraction of the single species, or perhaps dual species complex, has been caused by the synergistic effect of various anthropogenic impacts that spread from east to west as human settlement and densities increased (Harris 2008). Now, illegal hunting, agriculture, overgrazing by livestock and associated fencing, and wolf predation are considered critical impediments to recovery of *P. przewalskii* (Harris 2008; D. Li et al. 1999b; Jiang et al. 1996, 2000; G. B. Schaller, A. Kang, and K. Zhang, in litt. 2006).

Extensive fencing in the Qinghai Lake region, predominantly for sheep but also for domestic yak and horses, is particularly counterproductive to successful conservation and recovery of *P. przewalskii* (Jiang and Sung 2001; G. B. Schaller, A. Kang, and K. Zhang, in litt. 2006). Despite the jumping abilities of *P. przewalskii* (males likely more adept than females and no doubt young—Hao 2008), individuals occasionally get caught in fences and die (Jiang 2004). At least 4 types of fences are used in the Qinghai Lake region, and those with barbed wire on the top, rectangular mesh panels, and >100 cm high (Fig. 8) represent serious constraints to movement and likely increase mortality of *P. przewalskii* (G. B. Schaller, A. Kang, and K. Zhang, in litt. 2006). Unfortunately, mesh fencing of 130–140 cm high and with 1 or 2 strands of barbed wire on the top is becoming widespread (G. B. Schaller, A. Kang, and K. Zhang, in litt. 2006). Notably, *P. przewalskii* is most abundant in areas with minimal fencing (Tianjun, Shengge, Haergai River, and Hudong-Ketu populations) and least abundant in areas with a high density of small fenced pastures (Jiang and Sung 2001; G. B. Schaller, A. Kang, and K. Zhang, in litt. 2006).

Although other large ungulates of the Tibetan Plateau have experienced declines and similar impacts (Leslie 2010, in press; Leslie and Schaller 2008, 2009; Mallon and Jiang 2009; St-Louis and Côté 2009), none have been as seriously affected as *P. przewalskii*. Li and Jiang (2002) highlighted the need for the establishment of a reserve network in the remaining range of *P. przewalskii*, encouraging lower heights of fences to permit freedom of movement, and even feeding programs during catastrophic weather events. A reserve network has been established for *P. przewalskii* (Jiang and Sung 2001; D. Li et al. 1999a, 1999b; http://eng.tibet.cn/news/phn/ptn/t20071231_293325.htm, accessed 29 March 2009). Provincial officials in Qinghai recently began a 10-year plan to convert wheat farms back to rangelands, restore wetlands, decrease or eliminate livestock grazing, and relocate pastoralists to enhance conservation of Qinghai Lake and other important ecological areas in Qinghai Province (Hao 2008). Such activities, generally favorable to *P. przewalskii*, could inevitably increase tourism and its associated negative impacts; 800,000 visitors/year now visit the Qinghai Lake region (X. Li et al. 2009).

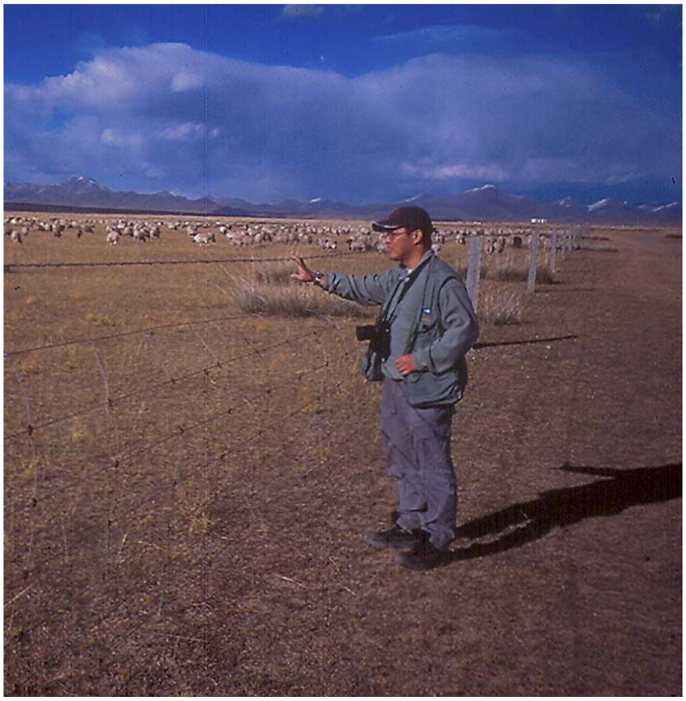

Fig. 8.—Extensive fencing to contain livestock in the Qinghai Lake region, western China, is a serious impediment to conservation of *Procapra przewalskii*. Photograph by G. B. Schaller used with permission.

Threats to all Tibetan fauna 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 2000, 2008; Jenkins 2009; Leslie and Schaller 2008, 2009; Mallon and Jiang 2009; Schaller 1998). Human activities that result in habitat loss and fragmentation because of fencing and displacement by encroaching pastoralists and competition with their livestock continue to be the major threats to continued existence of *P. przewalskii* (Harris 2008; Laidler and Laidler 1996; Y. Li et al. 2000; Schaller 1998; Yan et al. 2005). Illegal hunting of *P. przewalskii* has been reduced through education and enforcement, but it still occurs (G. B. Schaller, A. Kang, and K. Zhang, in litt. 2006). Climate change appears to be involved in decreasing water levels of Qinghai Lake and may further enhance pernicious anthropogenic impacts (X. Li et al. 2009). Additional basic ecological and behavioral research is needed on *P. przewalskii* and other fauna and flora of the Tibetan Plateau to affect lasting conservation strategies.

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LITERATURE CITED

Abramov, A. V., G. F. Baryshnikov, and A. N. Tikhonov. 1992. Catalogue of the type specimens in the collection of the Zoological Russian Academy of Sciences. Mammals. Vol. 3: Marsupialia, Pinnipedia, Perissodactyla, Artiodactyla. Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.

Adlerberg, G. 1931. Les antilopes du Tibéte septentrional et des regions limitrophes. Doklady Akademii nauk Soiuza Sovetskikh Sotsialisticheskikh Respublik 1931A:321–330.

Allen, G. M. 1940. The mammals of China and Mongolia. Natural history of central Asia. Vol. XI. Part 2. American Museum of Natural History, New York.

Banks, T. 2003. Property rights reform in rangeland China: dilemmas on the road to the household ranch. World Development 31: 2129–2142.

Banks, T., C. Richard, P. Li, and Z. Yan. 2003. Community-based grassland management in western China. Mountain Research and Development 23:132–140.

Brooke, V. 1873. On the antelopes of the genus *Gazella*, and their distribution. Proceedings of Zoological Society of London 41: 535–554.

Büchner, E. 1891. Die Säugethiere der Ganssu-Expedition (1884–87). Mélanges Biologiques Tirés du Bulletin de l'Académie Imperiale des Sciences de St.-Pétersbourg, Tome XIII, Livraison 1: 143–164.

Cai, G., Y. Kiu, Z. Feng, Y. Lin, X. Gao, and J. Zhao. 1992. Report on investigation of mammals in the typical habitats in Qinghai Province. Acta Biologica Plateau Sinica 11:63–90 (not seen, cited in Jiang et al. 1996).

Carroll, R. L. 1988. Vertebrate paleontology and evolution. W. H. Freeman and Company, New York.

Chen, L., et al. 1997. Studies on the diurnal activities and time budgets of Przewalski's gazelle. Acta Theriologica Sinica 17:172–183.

Convention on International Trade in Endangered Species of Wild Fauna and Flora. 2008. Appendices I, II, and III. www.cites.org/eng/app/appendices.shtml, accessed 4 November 2008.

Corbet, G. B. 1978. The mammals of the Palaearctic region: a taxonomic review. British Museum (Natural History) and Cornell University Press, London, United Kingdom.

de Pousargues, E. 1898. Etude sur les ruminants de l'Asie centrale. Memories de la Société Zoologique de France 11:126–224.

Duncan, F. M. 1937. On the dates of publications of the Society's 'Proceedings,' 1859–1926. With an appendix containing the dates of publication of 'Proceedings,' 1830–1858, complied by the late F. H. Waterhouse, and of the 'Transactions,' by the late Henry Peavot, originally published in P.Z.S. 1893, 1913. Proceedings of the Zoological Society of London 107A:71–84.

Effron, M., M. H. Bogart, A. T. Kumamoto, and K. Benirschke. 1976. Chromosome studies in the mammalian subfamily Antilopinae. Genetica 46:419–444.

Ellerman, J. R., and T. C. S. Morrison-Scott. 1966. Checklist of Palaearctic and Indian mammals 1758 to 1956. 2nd ed. Trustees of the British Museum (Natural History), London, United Kingdom.

Feng, Z., G. Cai, and C. Zheng. 1986. Mammals of Tibet (Xizang burulei). Science Press, Beijing, China.

Groves, C. P. 1967. On the gazelles of the genus *Procapra* Hodgson, 1846. Zeitschrift für Säugetierkunde 32:144–149.

Groves, C. P. 2000. Phylogenetic relationships within recent Antilopini (Bovidae). Pp. 223–233 in Antelopes, deer, and relatives: fossil record, behavioral ecology, systematics, and conservation (E. S. Vrba and G. B. Schaller.). Yale University Press, New Haven, Connecticut.

Grubb, P. 2005. Artiodactyla. Pp. 637–722 in Mammal species of the world: a taxonomic and geographic reference (D. E. Wilson and D. M. Reeder.). 3rd ed. Johns Hopkins University Press, Baltimore, Maryland.

Hao, X. 2008. China's environmental challenges: a green fervors sweeps the Qinghai–Tibetan Plateau. Science 321(5889):633–635.

Harris, R. B. 2000. Conservation of large mammals in non-protected areas in Qinghai and Gansu. Pp. 29–39 in Tibet's biodiversity: conservation and management (N. Wu, D. Miller, L. Zhi, and J. Springer.). China Forestry Press Publishing House, Beijing, China.

Harris, R. B. 2008. Wildlife conservation in China: preserving the habitat of China's Wild West. M. E. Sharpe, Armonk, New York.

Heptner, V. G., A. A. Nasimovich, and A. G. Bannikov. 1961. Mlekopytayushchie Sovetskogo Soyuza. Tom 1, Parnokopytnye i neparnokopytnye. Vysshaya Shkola, Moscow, Russia. [Translated as Heptner, V. G., A. A. Nasimovich, and A. G. Bannikov. 1989. Mammals of the Soviet Union. Vol. I. Ungulates. E. J. Brill, Leiden, The Netherlands.]

Hodgson, B. H. 1846. Description of a new species of Tibetan antelope, with plates. Journal of the Asiatic Society of Bengal 15:334–338.

Hoffmann, R. S. 1991. The Tibetan Plateau fauna, a high altitude desert associated with the Sahara-Gobi. Pp. 285–297 in Mammals in the Palaearctic desert: status and trends in the Sahara-Gobian region. Russian Academy of Sciences, Moscow, Russia.

Hovens, J. P. M., K. H. Tungalaktuja, T. Todgeril, and D. Batdorj. 2000. The impact of wolves *Canis lupus* (L., 1758) on wild ungulates and nomadic livestock in and around the Hustain Nuruu Steppe Reserve (Mongolia). Lutra 43:39–50.

International Union for Conservation of Nature and Natural Resources. 2008. The IUCN Red list of threatened species. www.iucnredlist.org, accessed 23 November 2008.

Jarman, P. J. 1974. The social organization of antelopes in relation to their ecology. Behaviour 48:215–267.

Jenkins, M. 2009. Searching for Shangri-La: two visions of the future compete for the soul of China's western frontier. National Geographic 215(5):56–83.

Jiang, Z. 2004. Przewalski's gazelle. China Forestry Publishing House, Beijing, China.

Jiang, Z., Z. Feng, Z. Wang, L. Chen, P. Cai, and Y. Li. 1995. Historical and current distributions of Przewalski's gazelles. Acta Theriologica Sinica 15:241–245.

Jiang, Z., Z. Gao, and Y. Sun. 1996. Current status of antelopes in China. Journal of the Northeast Forestry University 7:58–62.

Jiang, Z., R.-H. Lei, B.-W. Liu, and C.-W. Li. 2003. A review on the researches of Przewalski's gazelle. Chinese Journal of Zoology 38: 129–132.

Jiang, Z., D. Li, and Z. Wang. 2000. Population decline of Przewalski's gazelle around Qinghai Lake, China. Oryx 34: 129–135.

Jiang, Z., D.-Q. Li, Z.-W. Wang, S.-W. Zhu, and W.-H. Wei. 2001. Population structure of the Przewalski's gazelle around the Qinghai Lake, China. Acta Zoologica Sinica 47:158–162.

Jiang, Z., and W. Sung. 2001. China. Pp. 168–177 in Antelopes. Part 4: North Africa, the Middle East, and Asia (D. P. Mallon and S. C. Kingswood, comps.). Global Survey and Regional Action Plans, International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.

Kingswood, S. C., and D. A. Blank. 1996. *Gazella subgutturosa*. Mammalian Species 518:1–10.

Korotkevich, E. L. 1968. On the problem of taxonomic position of Miocene gazelles in the south of the USSR. Vestnik Zoologii 1968: 42–50.

Laidler, L., and K. Laidler. 1996. China's threatened wildlife. Blandford, London, United Kingdom.

Lei, R., Z. Hu, Z. Jiang, and W. Yang. 2003a. Phylogeography and genetic diversity of the critically endangered Przewalski's gazelle. Animal Conservation 6:361–367.

Lei, R., Z. Jiang, Z. Hu, and W. Yang. 2003b. Phylogenetic relationships of Chinese antelopes (subfamily Antilopinae) based on mitochondrial ribosomal RNA gene sequences. Journal of Zoology (London) 261:227–237.

Lei, R., Z. Jiang, and B. Liu. 2001a. Group size and group composition in Przewalski's gazelle. Folia Zoologica 50:117–126.

Lei, R., Z. Jiang, and B. Liu. 2001b. Group pattern and social segregation in Przewalski's gazelle (*Procapra przewalskii*) around Qinghai Lake, China. Journal of Zoology (London) 255:175–180.

Leslie, D. M., Jr. 2010. *Przewalskium albirostre* (Artiodactyla: Cervidae). Mammalian Species 42(849):7–18.

Leslie, D. M., Jr. In press. *Procapra picticaudata* (Artiodactyla: Bovidae). Mammalian Species 42(861).

Leslie, D. M., Jr., and G. B. Schaller. 2008. *Pantholops hodgsonii* (Artiodactyla: Bovidae). Mammalian Species 817:1–13.

Leslie, D. M., Jr., and G. B. Schaller. 2009. *Bos grunniens* and *Bos mutus* (Artiodactyla: Bovidae). Mammalian Species 836:1–17.

Li, D., and Z. Jiang. 2002. Population viability analysis for the Przewalski's gazelle. Russian Journal of Ecology 33:115–120.

Li, D., Z. Jiang, and Z. Wang. 1999a. Diet analysis of *Procapra przewalskii*. Zoological Research 20:74–77.

Li, D., Z. Jiang, and Z. Wang. 1999b. Impacts of human activities on the distribution of the critically endangered Przewalski's gazelle. Acta Ecologica Sinica 19:890–895.

Li, D., Z. Jiang, and Z. Wang. 1999c. Activity patterns and habitat selection of the Przewalski's gazelle (*Procapra przewalskii*) in the Qinghai Lake region. Acta Theriologica Sinica 19:17–24.

Li, D., et al. 1989. Economic animals of Qinghai (Qinghai jingji dongwu zhi). Qinghai People's Publishing House, Xining, Qinghai, China.

Li, X., Y.-J. Ma, H.-Y. Xu, J.-H. Wang, and D.-S. Zhang. 2009. Impact on land use and land cover change on environmental degradation in Lake Qinghai watershed, northeast Qinghai–Tibet Plateau. Land Degradation & Development 20:69–83.

Li, Y., Z. Gao, X. Li, S. Wang, and J. Niemelä. 2000. Illegal wildlife trade in the Himalayan region of China. Biodiversity and Conservation 9:901–918.

Li, Z., and Z. Jiang. 2006. Group patterns of sympatric Przewalski's gazelle and the Tibetan gazelle during the green grass period in Upper Buha River, Tianjun County, Qinghai Province. Zoological Research 27:396–402.

Li, Z., Z. Jiang, and C. Li. 2008. Dietary overlap of Przewalski's gazelle, Tibetan gazelle, and Tibetan sheep on the Qinghai–Tibet plateau. Journal of Wildlife Management 72:944–948.

Littledale, G. R. 1894. A journey across central Asia. Geographical Journal 3:445–472.

Liu, B., and Z. Jiang. 2002a. Quantitative analysis of the habitat selection by *Procapra przewalskii*. Acta Theriologica Sinica 22: 15–21.

Liu, B., and Z. Jiang. 2002b. Foraging strategy of Przewalski's gazelle. Acta Zoologica Sinica 48:309–316.

Liu, B., and Z. Jiang. 2002c. Impacts of grassland fencing on plant communities and conservation of a rare gazelle, the Przewalski's gazelle. Biodiversity Science 10:326–331.

Liu, B., and Z. Jiang. 2003. Diet composition of wolves *Canis lupus* in the northwestern Qinghai–Tibet Plateau. Acta Theriologica 48: 255–263.

Liu, B., and Z. Jiang. 2004. Dietary overlap between Przewalski's gazelle and domestic sheep in the Qinghai Lake region and implications for rangeland management. Journal of Wildlife Management 68:241–246.

Liu, B., Z. Jiang, and Z. Wang. 1999. Biodiversity spatial characteristics and Gap Analysis in Qinghai Lake region. Journal of Natural Resources 14:47–54.

Lydekker, R., and G. Blaine. 1914. Catalogue of the ungulate mammals in the British Museum (Natural History). Vol. III. Trustees of the British Museum, London, United Kingdom.

MacKinnon, J. 2008. Order Artiodactyla. Pp. 451–480 in A guide to the mammals of China (A. T. Smith and Y. Xie, eds.). Princeton University Press, Princeton, New Jersey.

Mallon, D. P., and Z. Jiang. 2009. Grazers on the plains: challenges and prospects for large herbivores in central Asia. Journal of Applied Ecology 46:516–519.

Mayashita, M., and K. Nagase. 1981. Breeding of the Mongolian gazelle *Procapra gutturosa* at Osaka Zoo. International Zoo Yearbook 21:158–162.

Nowak, R. M. 1991. Walker's mammals of the world. 5th ed., Vol. II. Johns Hopkins University Press, Baltimore, Maryland.

Nyamsuren, D., et al. 2006. Exposure of Mongolian gazelles (*Procapra gutturosa*) to foot and mouth disease virus. Journal of Wildlife Diseases 42:154–158.

Ogilby, W. 1841. On a new species of antelope (*Antilope Cuvieri*). Proceedings of the Zoological Society of London 8:34–35. [Dated 1840, but published January 1841; see Duncan 1937 for dates of publication for the Proceedings.]

Orlov, V. N., et al. 1978. Kariotipy mlekopitayushchikh Mongolii. [Karyotypes of mammals of Mongolia.] Pp. 149–164 in Geografiya i dinamika rastitel'nogo i zhivotnogo mira Mongol's-koi Narodnoi Respubliki [Geography and dynamics of the fauna and flora in the Mongolian People's Republic] (I. A. Bannikova, et al., eds.). Nauka, Moscow, Russia.

Pallas, P. S. 1777. Spicilegia zoologica quibus novae imprimis et obscurae animalium species iconibus, descriptionibus atque commentariis illustrantur cura P.S. Pallas. Berloni, prostant apud Christianum Fridericum Voss, Langed, Sweden.

Pilgrim, G. E. 1939. The fossil Bovidae of India. Memoirs of the Geological Survey of India, New Series 26:1–356 + plates I–VIII.

Pocock, R. I. 1910. On the specialised cutaneous glands of ruminants. Proceedings of the Zoological Society of London 78:840–986.

Pocock, R. I. 1918. On some external characters of ruminant Artiodactyla. Part II. The Antilopinae, Rupicaprinae, and Caprinae, with a note on the penis of the Cephalophinae and Neotraginae. Annals and Magazine of Natural History, Serie 9, 8: 125–144.

Przewalski, N. M. 1875. Mongoliya i strana tangutov. Trekhletnee puteshestvie v vostochnoi nagornoi Azii. Vol. I. Imperatorskoe Russkoe Geograficheskoe Obshchestvo, St. Petersburg, Russia. [Translated by E. D. Morgan from original notes as Prejevalsky, N. 1876. Mongolia, the Tangut country, and the solitudes of northern Tibet, being a narrative of three years' travel in eastern high Asia. Vol. I. Sampson Low, Marston, Searle, & Rivington, London, United Kingdom.]

Przewalski, N. M. 1888. Chetvertoe puteshestvie v Tsentral'noi Azii. Ot Kyakhty na istoki Zheltoi reki, issledovanie severnoi okrainy Tibeta i put' cherez Lob-nor po basseiny Tarima. [Fourth journey in central Asia. From Kyakhta to the source of the Yellow River, exploration of the northern border of Tibet and route via Lob-Nor along the basin of the Tarim.] Imperatorskoe Russkoe Geograficheskoe Obshchestvo, St. Petersburg, Russia.

Rhode, D., et al. 2007. Epipaleolithic/early Neolithic settlements at Qinghai Lake, western China. Journal of Archaeological Science 34:600–612.

Ridgway, M. S. 1912. Color standards and color nomenclature. Published by the author, Washington, D.C.

Savage, D. E., and D. E. Russell. 1983. Mammalian paleofaunas of the world. Addison-Wesley Publishing Company, Inc., Reading, Massachusetts.

Schaller, G. B. 1998. Wildlife of the Tibetan steppe. University of Chicago Press, Chicago, Illinois.

Schaller, G. B., J. Ren, and M. Qiu. 1988. Status of the snow leopard (*Panthera uncia*) in Qinghai and Gansu provinces, China. Biological Conservation 45:179–194.

Sclater, W. L., and O. Thomas. 1898. The book of antelopes. Vol. III. R. H. Porter, London, United Kingdom.

Sokolov, I. I. 1959. Kopytnye zveri (otryady Perissodactyla i Artiodactyla). Fauna SSSR, Mlekopitayushchie. Tom 1, vypusk 3. [Ungulates of Perissodactyla and Artiodactyla orders. Fauna of USSR, Mammals. Vol. 1, issue 3.] Nauka, Moscow-Leningrad, Russia.

Sokolov, V. E., and A. A. Lushchekina. 1997. *Procapra gutturosa*. Mammalian Species 571:1–5.

Sorokin, P. A. 2007. Filogeneticheskie svyazi vnutri roda *Procapra*, problema proiskhozhdeniya dzerena Przheval'skogo (*Procapra przewalskii*). [Phylogenetic relations within genus *Procapra* and the origin of Przewalski's gazelle (*Procapra przewalskii*).] Pp. 250–257 in Molekulyarno-geneticheskie osnovy sokhraneniya bioraznoobraziya mlekopitayushchikh Golarktiki [Genetic foundations for the conservation of Holarctic mammal biodiversity] (V. V. Rozhnov, et al., eds.). KMK Scientific Press, Moscow, Russia.

St-Louis, A., and S. D. Côté. 2009. *Equus kiang* (Perissodactyla: Equidae). Mammalian Species 835:1–11.

Stroganov, S. U. 1949. K sistematike i geograficheskomu rasprostraneniyu nekotorykh antilop Tsentral'noi Azii. [Systematics and distribution of some antelopes of central Asia.] Bulleten Moskovskogo Obshchestva Ispytatelei Prirody. Otdel Biologicheskii 54:15–26.

Wallace, H. F. 1913. The big game of central and western China being an account of a journey from Shanghai to London overland across the Gobi Desert. Duffield and Company, New York.

Wang, Y., et al. 2008. Stable isotopes in fossil mammals, fish and shells from Kunlun Pass Basin, Tibetan Plateau: paleo-climatic and paleo-elevation implications. Earth and Planetary Science Letters 270:73–85.

Wang, X., and G. B. Schaller. 1996. Status of large mammals in western Inner Mongolia, China. Journal of East China Normal University, Natural Science, Special Issue of Zoology 12: 93–104.

Ward, R., R. Lydekker, and J. B. Burlace. 1928. Rowland Ward's records of big game. 9th ed. Rowland Ward, Limited, London, United Kingdom.

Weigl, R. 2005. Longevity of mammals in captivity; from the living collections of the world. Kleine Senckenberg-Reihe 48:1–214.

Wu, M. 2008. Approaching world's endangered animal—Przewalski's gazelle. China Tibet Information Center. http://eng.tobet.cn/news/today/200809/t20080926_429307.htm, accessed 21 March 2009.

Yan, Z., N. Wu, D. Yeshi, and J. Ru. 2005. A review of rangeland privatisation and it implications in the Tibetan Plateau, China. Nomadic Peoples 9:31–51.

Ye, R., P. Cai, M. Peng, X. Lu, and S. Ma. 2006. The investigation about distribution and population size of Przewalski's gazelle (*Procapra przewalskii*) in Qinghai Province, China. Acta Theriologica Sinica 26:373–379.

You, Z., and Z. Jiang. 2005. Courtship and mating behaviors in Przewalski's gazelle *Procapra przewalskii*. Acta Zoologica Sinica 51:187–194.

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