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Bos grunniens and *Bos mutus* (Artiodactyla: Bovidae)

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Abstract: *Bos grunniens* Linnaeus, 1766, and *Bos mutus* (Przewalski, 1883) are the domestic and wild forms, respectively, of the bovid commonly called the yak. *B. mutus* inhabits remote high-elevation alpine meadows and alpine steppe in rolling to mountainous terrain in the Tibetan Plateau, and *B. grunniens* is maintained widely in China and other parts of Central Asia, and uncommonly elsewhere in the world. Populations of *B. mutus* are substantially reduced and fragmented throughout its remaining range; the largest numbers occur in northern Tibet and western Qinghai. *B. mutus* is vulnerable because of poaching and competition with domestic livestock. Although no complete survey of *B. mutus* has been conducted, there are probably no more than 15,000 remaining in remote areas of the Tibetan Plateau; *B. grunniens* numbers about 14 million. DOI: 10.1644/836.1.

Key words: Chang Tang Reserve, China, domestication, nomadic pastoralist, Qinghai, Tibet, ungulate, vulnerable species, wild yak, Xinjiang

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Bos Linnaeus, 1758

Bos Linnaeus, 1758:71. Type species *Bos taurus* Linnaeus, 1758, by Linnaean tautonomy.

Taurus Rafinesque, 1814:30. Type species *Bos taurus* Linnaeus, 1758, by absolute tautonomy.

Urus Hamilton-Smith, 1827a:417. Type species *Urus scoticus* Hamilton-Smith, 1827, by monotypy; described as “the probable remains [= descendant] of the genuine *Urus*” and subsequently described as “a variety of fossil *Bos urus*” (Hamilton-Smith 1827b:376).

Bison Hamilton-Smith, 1827b:373. Type species *Bos bison* Linnaeus, 1758, by absolute tautonomy; described as a subgenus of *Bos* Linnaeus, 1758.

Bison: Jardine, 1836:259. First use as a genus.

Bibos Hodgson, 1837:499. Type species *Bos subhemachalus* Hodgson, 1837, by original designation; described as a subgenus of *Bos* Linnaeus, 1758.

Bisonus Hodgson, 1841:217. Type species *Bisonus poephagus* Hodgson, 1841, by monotypy.

Poephagus Gray, 1843:153. Type species *Bos grunniens* Linnaeus, 1766, by monotypy.

Bissonius Gray, 1843:153. Incorrect subsequent spelling of *Bisonus* Hodgson, 1841.

Gaveus Hodgson, 1847:705. Type species *Bos frontalis* (Lambert, 1804), by monotypy.

Gauribos Heude, 1901:3. No type species selected; said to include *G. laosiensis*, *G. brachyrhinus*, *G. sylvanus*, and *G. mekongensis*.

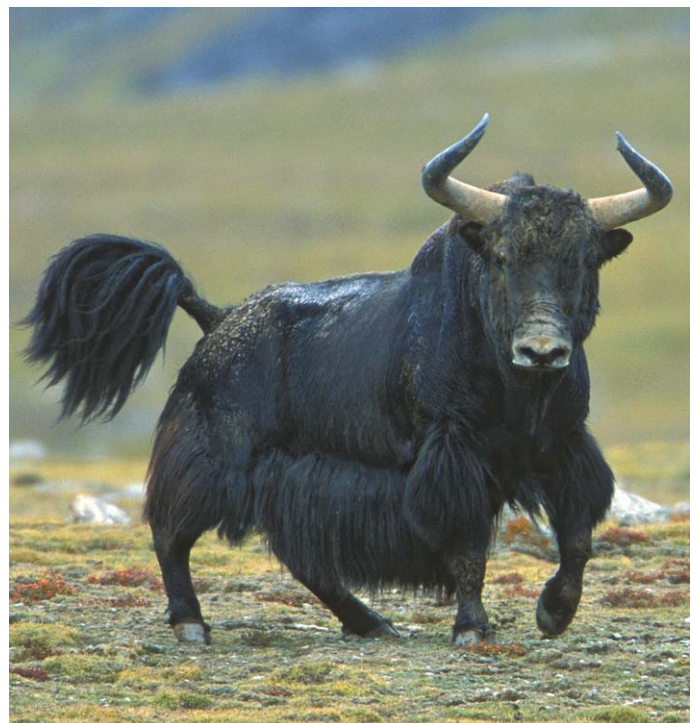


Fig. 1.—Mature male wild yak (*Bos mutus*) in Yeniugou, central Qinghai, China. Photograph courtesy of Milo Burcham (www.milophotos.com).

- Uribos* Heude, 1901:5. Type species *Uribos platyceros* Heude, 1901, by monotypy.
Bubalibos Heude, 1901:6. Type species *Bubalibos annamiticus* Heude, 1901, by monotypy.
Microbos Heude, 1901:7. No type species selected; said to include “*Bos? leptoceros*.”
Novibos Coolidge, 1940:425. Type species *Bos sauveli* Urbain, 1937, by original designation.
Poëpgahus Pilgrim, 1947:280. Incorrect subsequent spelling of *Poephagus* Gray, 1843.
Pseudonovibos Peter and Feiler, 1994:171. Nomen dubium (Grubb 2005 cf. Timm and Brandt 2001).
Peophaqus Lu, 2000:unnumbered page. Incorrect subsequent spelling of *Poephagus* Gray, 1843.

CONTEXT AND CONTENT. Order Artiodactyla, suborder Ruminantia, family Bovidae, subfamily Bovinae, tribe Bovini, genus *Bos*. There are 5 species of *Bos* (Grubb 2005). Generally, mass and body measurements (e.g., height and length) overlap among species of *Bos* and do not provide suitable characteristics for a species key (Blanford 1888); for some species, domestication and crossbreeding have altered characteristics of the wild forms (e.g., no horns in domestic females). Color, pattern, and length of pelage, horn characteristics, and morphology were used to develop the following general key.

1. White rump patch on males and females; horns of males connected by a horn-patch on the forehead ... *B. javanicus*
 No white rump patch; horns of males not connected by a horn-patch on the forehead 2
2. Long skirts of hair on chest, flanks, and rump; tail fully haired and horselike; 14 dorsal and 5 lumbar vertebrae and 14 ribs *B. grunniens* and *B. mutus*
 Pelage usually short; no skirts; tail not fully haired but tufted on the end; 13 dorsal and 6 lumbar vertebrae and 13 ribs 3
3. Concave forehead with gray mat of hair; pronounced shoulder hump in males *B. frontalis*
 Flat to slightly convex, smooth-haired forehead; generally without developed shoulder hump in males 4
4. Adult pelage color always dark brown to black with white leggings; horns in both sexes; range now limited to Cambodia, if not extinct *B. sauveli*
 Color highly variable among domestic breeds from black to white, reddish brown to brown; horns present or absent, particularly in females; under husbandry throughout the world *B. taurus*

***Bos grunniens* Linnaeus, 1766**

Domestic Yak

***Bos mutus* (Przewalski, 1883)**

Wild Yak

- [*Bos*] *grunniens* Linnaeus, 1766:99. Type locality “Asia boreali;” first use of the current name combination

and now considered the binomial for the domestic form (Gentry et al. 2004; International Commission on Zoological Nomenclature 2003).

- [*Bos?*] *corriculus* von Schreber, 1789:?. Vide Grubb (2005); see “Nomenclatural Notes.”
Bos gruniens Ghainouk Kerr, 1792:338. Type locality not mentioned and incorrect subsequent spelling of *Bos grunniens* Linnaeus, 1766.
Bos gruniens Sarlyk Kerr, 1792:338. Nomen nudum and incorrect subsequent spelling of *Bos grunniens* Linnaeus, 1766.
Bos gruniens ecornis Kerr, 1792:338. No type locality mentioned and incorrect subsequent spelling of *Bos grunniens* Linnaeus, 1766.
Bos Poephagus Pallas, 1811:248, table xxii. Replacement name for *Bos grunniens* Linnaeus, 1766.
B[os (Bison)]. poephagus: Hamilton-Smith, 1827b:374. Name combination.
Bison poephagus: Jardine, 1836:259. Name combination.
[*Bisonus*] *Poephagus*: Hodgson, 1841:217. Name combination; said to occur as “tame and wild samples.”
Poephagus gruniens: Gray, 1843:153. Name combination and incorrect subsequent spelling of *Bos grunniens* Linnaeus, 1766.
B[ison]. grunniens: Turner, 1850:177. Name combination.
Poëphagus grunniens domesticus Fitzinger, 1860:294. No type locality mentioned; described generally as the domestic form in Tibet and Mongolia.
Poëphagus grunniens, ferus Przewalski, 1879:85. Type locality “Altyn-tagh [Mountains],” Xinjiang Province, China.
Poëphagus mutus Przewalski, 1883:191, unnumbered plate. Type locality “Alpine region of the western part of the Nan Shan (approximately lat. 39°20’N., 95°E.), between the Anembar-Ula in the west and the Humboldt Range on the east; cf. Harper, 1940, pp. 325–326” vide Harper (1945:528).
Bos (Poëphagus) grunniens: Huet, 1891:334. Name combination vide Allen (1940:1259).
Bos [(Bison)] grunniens: Lydekker, 1898:51. Name combination.
Bos grunniens mutus Lydekker, 1913:33. Type locality “eastern part of Ladak [=Ladakh, India], in the neighbourhood of Chang-Chenmo (where they now appear to be exterminated) as far east as Kan-su and northwards to the Kuen-lun, at elevations between 14,000 and 20,000 feet;” described as “the wild race” (Lydekker 1913:32).
Poëphagus grunniens mutus: Harper, 1945:528. Name combination.
Bos (Poëphagus) mutus grunniens: Bohlken, 1958:168. Name combination.
Bos mutus: Bohlken, 1964:325. First use of the current name combination; current binomial for the wild form of *Bos*

grunniens Linnaeus, 1766 (Gentry et al. 2004; International Commission on Zoological Nomenclature 2003). *Poephagus muths* Li, Jiang, and Wang, 1999:49. Incorrect subsequent spelling of *Poephagus mutus* Przewalski, 1883. *B[os]. runniens* Wang et al., 2008:76. Incorrect subsequent spelling of *Bos grunniens* Linnaeus, 1766.

CONTEXT AND CONTENT. Context as for genus. No subspecies are recognized (Grubb 2005).

NOMENCLATURE NOTES. We were unable to verify Grubb's (2005) assertion that *corriculus* von Schreber, 1789, was a synonym of *grunniens* Linnaeus, 1766. All plates (A. L. Gardner, pers. comm.) and text (D. Wingreen-Mason, pers. comm.) associated with J. C. D. von Schreber's *Die Säugthiere in Abbildungen der Natur mit Beschreibungen* in the Smithsonian Institution's Cullman Library were reviewed, and no mention of *corriculus* was found. Review of all 30 volumes of *Die Naturforscher (Halle, Germany)* edited by J. E. I. Walch (1774–1779) and von Schreber (1780–1804) also failed to identify any use of *corriculus*. No other literature by von Schreber was located that revealed use of *corriculus* in the nomenclatural history of *Bos grunniens*. Nevertheless, we retain *corriculus* von Schreber, 1789, in our synonymy, affiliate it with [*Bos?*], but question its validity.

The nomenclatural history of Linnaeus's *grunniens* has involved placements under the genera *Bos*, *Poephagus*, and *Bison* (Gray 1846; Groves 1981; Olsen 1990; Pal 1996; Turner 1850). Harper (1945) and Ellerman and Morrison-Scott (1966) incorrectly attributed *Poephagus grunniens mutus*, the wild yak, to Przewalski (1883), who named the wild yak, *Poephagus mutus*, in his original Russian publication. Lydekker (1913) appears to be the 1st to use *Poephagus grunniens mutus*. Nomenclatural distinction between the wild and domestic forms has been attempted frequently in the literature. The recent Opinion 2027 of the International Commission on Zoological Nomenclature (2003) retained Linnaeus's *grunniens* and Przewalski's *mutus* to distinguish between the domestic and wild forms of the yak, respectively (Gentry et al. 2004).

The etymology of *Bos* in Latin is ox, *grunniens* is grunting, and *mutus* is mute (a poor description because wild yaks are quite noisy). Along with yak (як in Russian), other common names include drong, brong-dong (wild), ya (domestic male), dri (domestic female), pegu (tame), ban-chour, kuch-gau, boku (old male), and kotass. Various metaphorical expressions for the domestic yak emphasize its importance for transportation of goods and services throughout western Asia: “ship of the cold region” (Prasad 1997:517), “biological snow plough” (Wiener et al. 2003:81), and “boat of the plateau” (Wiener et al. 2003:165).

DIAGNOSIS

The subfamily Bovinae has 9 genera (Grubb 2005) with species of large size, stout bodies, hollow horns, relatively

short legs, long tails with at least a terminal tuft of hair (*Bos grunniens* and *B. mutus* fully haired), broad muzzles, and no facial, pedal, or inguinal glands (Blanford 1888; Lydekker 1913). Five of the 9 genera in Bovinae (Grubb 2005) are currently considered in the tribe Bovini: *Bison*, *Bos*, *Bubalus*, *Pseudoryx*, and *Syncerus*. Both sexes of extant species of Bovini have typically smooth horns (often relatively large in females), arising far apart and generally outward and then turning inward; upper molars are strongly hypsodont with “broad prismatic crowns and an accessory column between the two main columns on the inner side” (Lydekker 1913:11).

Bos mutus, *B. grunniens*, *Bison bison* (American bison—Meagher 1986), and *Bison bonasus* (European wisent) have 14 dorsal and 5 lumbar vertebrae, unlike other Bovini that have 13 dorsal and 6 lumbar vertebrae (Groves 1981; Vasey 1857). *B. mutus* and *B. grunniens* can be distinguished from *B. bison* and *B. bonasus* by long draping hair on the former's chest, flanks and thighs, described as “splendid tresses like a ‘skirt,’ which imparts ... an entirely distinctive appearance” (Heptner et al. 1989:550; Lydekker 1898, 1913). Olsen (1990:78) noted that an “extension of the dorsal margin of the maxilla prevent[ed] the nasal from reaching the premaxillae” in *B. grunniens* and *B. mutus* but not in *Bison*. Mass varies widely among *Bos*, but *B. mutus* is generally considered the largest in the genus and the 3rd largest extant mammal in Asia (Harris 2008) after the Asian elephant (*Elephas maximus*—Shoshani and Eisenberg 1982) and Indian rhinoceros (*Rhinoceros unicornis*—Laurie et al. 1983).

GENERAL CHARACTERS

We focused this monograph on the wild yak, unless particular information was considered comparable between the 2 forms (e.g., physiology, anatomy, and morphology). Specific aspects related to domestication of the yak (e.g., reproductive performance, rangeland management, and meat quality) are confined to the “Husbandry” section.

Female domestic yaks are about 35% lighter than males, which is probably similar for wild yaks (Buchholtz and Sambras 1990; Przewalski 1876; Schaller 1998). Both sexes have nearly smooth, cylindrical, gray-to-black horns, but those of males are larger and longer and sweep outward and forward more than the upright smaller horns of females (Allen 1940; Blanford 1888; Fitzinger 1860; Harper 1945; Heptner et al. 1989; Lydekker 1898; Schaller 1998); the forehead is “short, wide, and slightly convex” (Lydekker 1913:30).

General descriptions of the wild yak have been consistent through time (Blanford 1888; de Pousargues 1898; Lydekker 1898; Przewalski 1876; Schaller 1998; Wiener et al. 2003): massive body on sturdy short legs but compact (Fig. 1); small ears; no dewlap; large and rounded hooves (Wiener et al. 2003); conspicuous hump, more

pronounced in males, arising abruptly behind the short neck as a result of elongated neural spines of cervical and dorsal vertebrae tapering level at the mid-back (Lydekker 1913) and “not falling away above the hips” (Blanford 1888:490); black pelage with rust-brown hues and sometimes “a sprinkling of gray on the head and neck” (Blanford 1888; Lydekker 1898:53) of older adults (except for a rare light golden-brown mutation in about 2% of animals around the Aru Basin, Tibet—Deasy 1901; Schaller 1998:128); tip of muzzle grayish; young dark brown; pelage dense with an undercoat of wool and long coarse guard hairs (Wiener et al. 2003); long draping hair on chest, flanks and thighs, which is longer and almost to the ground in mature males (≤ 70 cm long—Schaller 1998); tail long and bushy on the lower one-half, often described as horselike (Heptner et al. 1989); few functional sweat glands (Wiener et al. 2003); and no preorbital glands or associated lachrymal fossa. Generally, *Bos grunniens* shares similar physical characteristics, but it is smaller, and coloration ranges from black to brown, white, and pied (Blanford 1888; Vasey 1857; Wiener et al. 2003).

DISTRIBUTION

The wild yak occurs on the Tibetan Plateau at elevations of 3,000–5,500 m, where it “inhabits the coldest, wildest, and most desolate [treeless] mountains” (Blanford 1888:491). It is currently restricted to a small part of Indian Ladak (Fox et al. 1991; Ul-Haq 2002) and Chinese provinces of Tibet, Qinghai, and Xinjiang, with 1 isolated population on the border of Qinghai and Gansu and another near the northern boarder of Tibet and Nepal (Achuff and Petocz 1988; R. B. Harris, pers. comm.; Miller et al. 1994; Schaller 1998; Fig. 2). The core range of the wild yak has shrunk northward, and only isolated and fragmented populations occur south and east of that core area in northern Tibet and northwestern Qinghai (Fig. 2). Recent protection from illegal hunting may be permitting wild yaks to recolonize former habitat and increase in numbers (Harris et al. 2005; Harris and Loggers 2004; Schaller et al. 2005). About 14 million domestic yaks occur from Afghanistan east through China (about 90%) and northward in Mongolia and Russia, with more elsewhere in the world where ambient conditions permit (Harris 2008; Wiener et al. 2003; Zhang et al. 1994). There are probably no more than 15,000 wild yaks in remote high-elevation areas of the Tibetan Plateau (Harris 2008; Miller et al. 1994; Schaller 1998; Schaller and Liu 1996).

The 300,000-km² Chang Tang Reserve (hereafter, Chang Tang), located in north-central Tibet (Fig. 2), was established as a nature reserve in 1993 and upgraded to a national reserve in 1999. Important contiguous reserves to the north in Xinjiang include West Kunlun Reserve (30,000 km²), Mid-Kunlun Reserve (32,000 km²), and Arjin Shan Reserve (45,000 km²). Kekexili Reserve (45,000 km²)

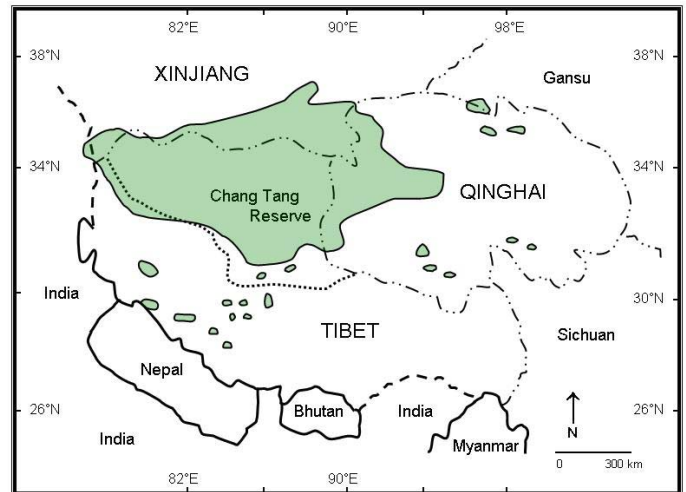


Fig. 2.—Distribution of the wild yak (*Bos mutus*) is restricted to the Tibetan Plateau of western China and includes at least 20 fragmented populations; map adapted from Schaller (1998:131) with updates from R. B. Harris (pers. comm.).

and Sanjiangyuan Reserve (150,000 km²) are east of Chang Tang in Qinghai. Despite this impressive reserve network, extant populations of *Bos mutus* and other Tibetan Plateau fauna are still threatened by human activities, including illegal harvest, mining activities and associated roads, and competition with domestic livestock (see “Conservation” section—Harris 2008; Leslie and Schaller 2008; Schaller 1998).

FOSSIL RECORD

The fossil record for bovids from the Tibetan Plateau is fragmentary (Olsen 1990), but areas to the south in India may have been the “developmental centre,” or close to it, of Bovinae because from the Miocene “onward the number and variety of Bovine [fossil] genera found in India is out of all proportion to what is the case in other parts of the world” (Pilgrim 1939:27). Bovinae differentiated considerably during the late Miocene (McKenna and Bell 1997:445), giving rise to the early forms such as *Proleptobos*, *Proamphibos*, and *Parabos* (Pilgrim 1939).

Pilgrim (1939:253) considered the yak to be a species of *Poephagus* and, based on the fossil record, placed it in his Taurina group that included *Bos*, *Bibos*, and *Bison*. The Taurina group was thought to have arisen from a common ancestor, *Proleptobos*, at the beginning of the late Miocene (Groves 1981; Pilgrim 1939). Pilgrim (1939:327) concluded that *Poephagus* shared characters most associated with *Bibos* and *Bison*, but their common “hypothetical” ancestor that lived before the late Pliocene has not been identified. 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 greater in the Pliocene 2–3 million years ago than they are now (Wang et

al. 2008); such conditions could have led to greater diversification of *Bos*.

Particular alignment of the yak with fossil species such as *Bison sivalensis* is debated because of incomplete and lost fossil material (Groves 1981; Olsen 1990; Pilgrim 1939). Nevertheless, *Bos mutus* likely shares a common ancestry with the North American *Bison bison* at some point in the past (Lydekker 1898; Olsen 1990). Most agree that both evolved in central Asia from a common ancestor (Groves 1981). The yak remained in western Asia, but *Bison* lineages spread north and eventually crossed the Bering Land Bridge into North America sometime in the middle to late Pleistocene (McDonald 1981; Meagher 1986). Late Pleistocene fossils of extinct yaks have been found in eastern Russia (e.g., *Poephagus baikalensis*—Verestchagin 1954 not seen, cited in Abramov et al. 1992), Tibet, and Nepal (Olsen 1990). A skull and mandible from a single wild yak have been described from Quaternary deposits in the Pakistani Himalayas (Thewissen et al. 1997).

FORM AND FUNCTION

Form.—Most of the published research that relates to form and function has been conducted on the domestic yak, but results likely parallel, or even understate, characteristics and adaptations of the wild yak under wild conditions (Jianlin et al. 2002; Wiener et al. 2003). Both forms are highly adapted for existence under extreme conditions of low temperature, high elevation and associated low oxygen availability, extreme solar radiation at southern latitudes, and relatively arid conditions (e.g., Jianlin et al. 2002; Wiener et al. 2003). Even under husbandry, domestic yaks do not do well when ambient conditions depart from their ancestral condition (Wiener et al. 2003).

The pelage consists of 3 types of hairs: long, coarse guard hairs 52 μm in diameter, intermediate down fibers 25–52 μm in diameter, and dense, fine down fibers <25 μm in diameter (Wiener et al. 2003). Down fibers grow dense in winter, particularly on the neck, shoulders, and back increasing to 17–30% of the pelage by weight in winter (Xi et al. 1983). Density of down fiber can be as high as about 3,000/cm² (Wiener et al. 2003). Pelage of domestic yak calves <6 months of age is almost entirely down fiber with few guard hairs; the proportion by weight declines to 62% of the pelage at 1 year of age, 52% at 2 years of age, 44% at 3 years of age, and 43% at 4–5 years of age (Wiener et al. 2003; Zhang et al. 1982).

Relative to mass, a small female wild yak may be only one-third the size of a large male; in contrast, female domestic yaks are 25–50% smaller (Harris 2008; Miller et al. 1994; Wiener et al. 2003). Body mass (kg) of adult male wild yaks has been estimated at >800 kg (Engelmann 1938) and as high as 1,000 kg (Schäfer 1937; Wiener et al. 2003:43) and 1,200 kg (Lu 2000; Lu and Li 1994); females are about



Fig. 3.—Skulls of male (left) and female (right) wild yaks (*Bos mutus*) from Yeniugou, central Qinghai, China, highlighting relative mass and sexual dimorphism in skull size and horn shape. Photograph courtesy of Daniel J. Miller.

350 kg (Schaller 1998). Wild yak calves at 3 months of age (62.5 kg, $n = 5$) are nearly twice as large as domestic yak calves (33.6 kg, $n = 19$), but in captivity, calves grow slower relative to their weight such that at 16 months old, the wild yak is 63% heavier than the domestic yak (Wiener et al. 2003). Shoulder heights (cm) of wild yak are 175–203 for adult males and 137–156 for adult females (Schaller 1998); 1 newborn was 67 cm at the shoulder (Zhang et al. 1994). Although not completely disjunct geographically, 2 “ecological types” of wild yaks have been described based on body characteristics, temperament, and geographical location: the smaller, more docile Qilian Mountain type and the massive, aggressive Kunlun Mountain type (Lu 2000; Lu and Li 1994; Lu et al. 1993).

Horns of male and female wild yaks vary in size and shape and are far more massive in males (Fig. 3). Generally, they have a “wide lateral sweep, turning then forward and finally upward and slightly bent inward,” are smooth except for a “few low transverse ridges at the base,” and vary among individuals (Allen 1940:1260). Early descriptions provide fragmentary summaries of various horn measurements (Allen 1940; Blanford 1888; Lydekker 1898, 1913; Przewalski 1876, 1883). A recent sample of 53 adult male and 12 adult female wild yaks from the Chang Tang provides a contemporary reference (cm): length of outside curve, male 47.5–99.0, female 37.0–64.5; basal circumference, male 26.0–42.0, female 17.5–23.0; and tip-to-tip, male 26–83, female 18–67 (Schaller 1998). In Yeniugou (“Wild Yak Valley”), Qinghai, a particularly large male had a basal circumference of 45 cm (Miller et al. 1994). Such wild yak horns are used as milk pails by nomadic peoples (Ekvall 1968).

Although there are few published cranial measurements (Olsen 1990), Allen (1940) provided a general description

(Fig. 4): heavy; broad nasals with tapering ends; narrow lachrymal; upper edge of maxillary in contact with middle of nasals; and outer sides of premaxillaries nearly parallel, not tapering. Cranial measurements (mm) from 2 large male wild yaks from eastern Tibet were: tip of premaxillaries to vertex of skull, 576–610; basal length, 506–528; condylobasal length, 540–555; nasal length, 230–255; combined nasal width, 81–97.5; and width of occipital shield, 250–252 (Allen 1940). Numbers of vertebrae are 7 C, 14 T, 5 L, 5 S, 14 Ca, total 45 (Vasey 1857).

Dental formula of adult yaks is: $i\ 0/4, c\ 0/0, p\ 3/3, m\ 3/3$, total 32. No information exists on replacement and wear of teeth in wild yaks, but they have been evaluated in domestic yaks (Pal et al. 2002). Unlike domestic cattle, domestic yak neonates are not born with their deciduous incisors; the 1st pair erupts after about 1 week, with successive pairs erupting weekly thereafter ending at 4 weeks of age; fully erupted deciduous incisors are 1.2–1.6 cm in length and 0.6–1.1 cm in width (Pal et al. 2002). At about 2 years of age, the 1st pair of deciduous incisors is replaced by permanent incisors, and that process continues until about 5 years of age; fully erupted permanent incisors are 0.8–2.0 cm in length and 0.8–1.4 cm in width (Pal et al. 2002). Wear of permanent incisors is purported to be useful in aging after 5 years, albeit specific standards were not provided by Pal et al. (2002).

Morphology of the penis of the yak is characterized by “a urethral canal [that] is produced into a short tube free from the terminal cushion-like thickening of the glans” (Pocock 1918:454–455). These characteristics parallel the penial morphology in the genus *Bibos* and in *Bos frontalis* and *B. javanicus* but are disparate from *B. taurus* (Allen 1940). The scrotum of the yak is relatively small and hairy, an adaptation to the cold (Wiener et al. 2003). Semen of the wild yak has 2.13×10^{10} spermatozoa/ml with motility of 63% (about twice that in domestic yaks), defective rate of 6.3%, pH of 6.6, specific gravity of 1.055, and osmotic pressure of 0.65 (Lu 2000).

Female reproductive organs of domestic yaks differ by breed and from those of domestic cattle; cervix averages 5.0 cm long and 3.2 cm in diameter with 3 or 4 transverse circles each with small tight folds; corpus uteri are short, averaging 2.1 cm; and ovarian weight is only 2 g (Cui and Yu 1999a; Li 1980 not seen, cited in Wiener et al. 2003). Four mammae are present, and the udder is small and haired. Morphology and anatomy of the ovary (Cui and Yu 1999b), tongue (Sarma et al. 2005), nasal cavity (Kalita and Kalita 2005), bronchioles (Kalita and Bordolop 2005), spinal nerves (Kulbhushan et al. 1999), sternum (Sarma et al. 1997), and thyroid gland (Baishya et al. 1998) also have been described for *B. grunniens*.

The alimentary organs of the yak have evolved to deal with the limited forage availability and quality in its native range (Wiener et al. 2003). The mouth is broad, muzzle small, and lips flexible. Incisors have flat grinding surfaces,



Fig. 4.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult male domestic yak (*Bos grunniens*); zoo specimen of unknown origin (National Museum of Natural History, specimen 174734). Greatest length of skull 525 mm.

and the tongue is broad and blunt with highly cutinized and developed papillae. Such adaptations allow yaks to forage like cattle on long grasses or like sheep on grasses as short as 2–3 cm. In winter when sedges such as *Kobresia* are short and brittle, yaks simply “lick” them up with their rough tongue. Relative percentages of the rumen and omasum of the domestic yak are about 50% larger and 200% smaller, respectively, than in some domestic cattle breeds—the former maximizes intake and microbial fermentation of low-quality forages (Wiener et al. 2003).

Function.—Unlike some other species of *Bos*, yaks possess physiological adaptations to the extreme conditions of high elevation, high solar radiation, low temperature, and aridity under which they live (Christopherson et al. 1978; Prasad 1997; Wiener et al. 2003). Adaptations to maximize oxygen exchange at high elevations include an expanded thoracic capacity with 14 widely spaced and relatively thin ribs and large “trachea supported by annular cartilages at considerable distances” (Prasad 1997:518); attenuation of the hypoxic pulmonary vasoconstrictor response (Anand et al. 1986; Heath et al. 1984), nitric oxide-regulated pulmonary circulation (Ishizaki et al. 2005), and associated genetic adaptations to hypoxia (Wang et al. 2006); small pulmonary arteries of 75–250 μm of smooth muscle with long, wide, and rounded endothelial cells (Durmowicz et al. 1993; Heath et al. 1984); transitional pulmonary arteries of 228–760 μm in diameter (Heath et al. 1984); hemoglobin with a high affinity for oxygen (Lalthantluanga et al. 1985; Prasad 1997); and persistent fetal hemoglobin with its high affinity for oxygen through life, unlike most other mammals (Sarkar et al. 1999b). The ratio of right-to-left ventricular weight of the heart is 0.37, lower than would be expected if a species experienced chronic hypertension due to high elevation, as is seen in domestic cattle (Heath et al. 1984).

Consistently low temperatures and low primary productivity in the range of the wild yak, and most domestic yaks, result in a strategy of heat conservation rather than heat production (Sarkar et al. 1999a; Wiener et al. 2003), although digestive efficiency of low-quality forage may be enhanced (Richmond et al. 1977; Schaefer et al. 1978). In Tibet, average annual temperatures are only -4°C and winter temperatures as low as -40°C are common; most areas have no frost-free days. Adaptations for heat conservation include a compact body, despite a large mass, with relatively short legs, neck, and ears and a low surface-to-volume ratio; thick pelage particularly on neck, back, and rump; pelage and skin pigmentation always dark in the wild yak to minimize effects of intense solar radiation but maximize heat absorption; thick unwrinkled skin with nonfunctional apocrine sweat glands, except on the muzzle, but with highly developed piloerection muscles; and a thick, but seasonal, subcutaneous fat layer (Wiener et al. 2003). Adaptations to the cold are so developed that even the domestic yak shows signs of heat exhaustion when ambient temperatures exceed 13°C ; heart rate and respiration

increase and most activity ceases when ambient temperatures approach 20°C (Li et al. 1981 not seen, cited in Wiener et al. 2003). Early accounts note the propensity of wild yaks to maximize heat dissipation and minimize heat production by seeking the coldest spots and shade, bedding in snow, and standing in icy water even during inclement weather (Przewalski 1876).

Sense of smell is keen; eye sight and hearing less so (Blanford 1888; Bower 1894). Przewalski (1876) and others described the ease with which wild yaks could be stalked, particularly upwind, yet other early accounts and present day researchers often remark on the species’ wariness; when startled, they often flee many kilometers (Rockhill 1895; Schaller 1998).

ONTOGENY AND REPRODUCTION

Estrus has been described in detail in the domestic yak (Wiener et al. 2003); we presume it to be comparable in the wild yak. Both wild and domestic yaks are seasonal breeders (Zi 2003). Generally, 1–4 estrous cycles of about 20 days each occur during summer, and up to 75% of female domestic yaks conceive during their 1st estrus of the year. Estrus generally lasts <1 day (Sarkar and Prakash 2005). Physical changes of female domestic yaks in estrus include swollen vulva, vaginal redness, mucus discharge, raised tail, and frequent urination (Sarkar and Prakash 2005; Wiener et al. 2003).

The majority of females breed for the 1st time at 3–4 years of age, but this, and annual timing of estrus, varies depending on climate, latitude, elevation, and availability of nutritious forage (Wiener et al. 2003; Yu and Li 2001; Zi 2003). Gestation is 258–270 days, and premature termination of pregnancies from unknown causes can be 5–10% in domestic yaks (Wiener et al. 2003). Postpartum anestrus is about 125 days. Peak productivity of female domestic yaks occurs at 5–6 years old and declines after 9 years of age. Domestic yaks generally produce a calf every other year, or longer (Buchholtz and Sambras 1990; Wiener et al. 2003), which parallels observation of wild yaks (Miller et al. 1994; Schaller 1998). Most calves in Chang Tang are born from mid-May through June (Schaller 1998).

Parturition of the domestic yak occurs during the day, rarely at night, in a sheltered location away from the herd (Wiener et al. 2003). Birth is often from a standing position although the female may spend considerable time lying on her side. Females may be very aggressive during parturition. Twinning is rare, $<0.5\%$ of births of domestic yaks. Offspring are precocial and attempt to stand within about 10 min postpartum; 1st nursing occurs 11–30 min postpartum and may last 3–5 min (Wiener et al. 2003). Females and their offspring rejoin the herd shortly thereafter (Fig. 5). Similar to muskoxen (*Ovibos moschatus*—Lent 1988), groups of wild yaks will protect offspring from threats by forming a “phalanx, calves in the centre [and] some of the full-grown



Fig. 5.—Wild yak (*Bos mutus*) adult females and calves in Yeniugou, central Qinghai, China. Photograph courtesy of Milo Burcham (www.milophotos.com).

males advancing to reconnoiter” (Przewalski 1876:190; Rawling 1905; Schaller 1998).

Ratios of young of the year to adult + juvenile (2–3 year olds) females in Yeniugou, Qinghai, were 20 calves:100 females and ranged from 9.7 to 49.0 in various herds (Miller et al. 1994). To the west in Chang Tang, percentages of calves to females were considerably lower and ranged from 1.0% to 12.7% in the early 1990s, with 2 years of apparent reproductive failure or loss of all offspring to predators (Schaller 1998). Given the vulnerable status of the wild yak, recent interspecific cloning experiments (Li et al. 2007) with other bovine species may be applied in the future.

ECOLOGY

Population characteristics.—Accurate densities of wild yaks are difficult to estimate because of the large size of the Tibetan Plateau, seasonal movements, and greatly reduced numbers from past and present illegal hunting (Clark 1954; Harris 2008; Harris et al. 2005; Schaller 1998). These factors and demarcation and size of survey areas result in widely disparate density estimates that may do little more than reflect a highly clumped and seasonally dynamic distribution of extant wild yaks. For example, in Yeniugou, Qinghai, Harris (2008) estimated that 1,200–1,700 wild yaks occupied 1,100 km² from the early 1990s through 2002, or 1.1–1.5 individuals/km². In sharp contrast, only 9 male wild yaks were counted along a transect that covered 20,000 km² in western Qinghai just south of Yeniugou (Schaller 1998; Schaller et al. 1991). Regardless, overall densities of wild yaks are clearly much lower now than they were historically (Bower 1894; Harris 2008; Przewalski 1876; Schaller 1998).

Maximum life span of the yak in captivity is generally about 20 years (Wiener et al. 2003). One wild yak lived 22 years and 9 months in the Beijing Zoo, China (Weigl 2005). Longevity probably is comparable in the wild (Schaller 1998). Miller et al. (1994) found that the oldest of 6 reliably aged wild yaks died at 16 years, based on cementum annuli. Sex ratios are difficult to estimate because many males occur singly or in small groups and are widely spaced. Of 507 wild male yaks observed in the Aru Basin, 36% were alone, 43% in groups of 2–5, 13% in groups of 6–10, and the rest in groups up to 19. Observations from Chang Tang suggest a sex ratio of 67–75 males:100 females (Schaller 1998).

Space use.—The wild yak is now restricted to very high-elevation and remote uplands, usually free of human harassment. It is not daunted by mountainous terrain (Schaller 1998) because of its “strong limbs and small hooves of compact texture, with a narrow and sharp hoof tip, hard hoof edges and a close hoof fork” (Wiener et al. 2003:81). The Tibetan Plateau contains as many as 17 vegetation types, but alpine meadows (45%), alpine steppe (29%), and desert-type grasslands and steppe (14%) comprise 88% of the land cover (Sheehy et al. 2006). The wild yak occurs in greatest abundance on alpine meadows, less so in alpine steppe, and is scarce in desert steppe (Schaller and Liu 1996). Preferred habitats in Chang Tang include partially glaciated mountains with slopes of alpine meadows, seasonally lush alpine steppe that may green up 2–3 weeks before the plains, and edges of streams (Schaller 1998). Male wild yaks occur often on gentle slopes, and female herds occur more often on high hills and upper slopes (Harris 1993; Miller et al. 1994; Schaller 1998).

The wild yak is capable of long-distance and unpredictable movements (Harris 1993, 2008), some of which may be associated with avoidance of human activities. The wild yak is not migratory, typically moves up and down slopes seasonally to take advantage of the best forage availability, and may shift ranges seasonally or if harassed (Schaller 1998). Most of the Tibetan Plateau has sparse vegetative cover (e.g., only about 10–15% in alpine steppe of the Chang Tang—Schaller and Ren 1988) with low primary productivity (80–160 kg/ha dry matter—Schaller 1998; Schaller et al. 2005), but alpine meadows, preferred by wild yaks, can be up to 9 times as productive as alpine steppe and alpine desert-type habitats (Long 2003a; Sheehy et al. 2006). Such meadows are frequently covered with a heavily grazed turf of the sedge *Kobresia* about 5 cm above the ground (Koizumi et al. 1993; Rockhill 1895).

Diet.—The yak is a herbivorous ruminant. Foraging preferences of the wild yak are understood mainly from limited microhistological analyses of feces (Harris and Miller 1995; Miller et al. 1994; Schaller and Liu 1996). The yak is a grazer (*Poepagus* = grass eater), seasonally eating grasses, sedges, and forbs. Hedin (1934:29) noted that wild yaks “find nourishment in the mosses and lichens on mountain slopes and among old and new moraines.”

For all ungulates of the Tibetan Plateau (Harris 2008; Schaller 1998), dietary diversity is constrained substantially by seasonally limited forage availability and diversity, but sedges and grasses, followed by forbs, dominate diets during the short summer growing season (Harris and Miller 1995; Miller et al. 1994). In Chang Tang, analyses of wild yak feces show a preference for grasses and sedges (*Stipa*, 52%; *Kobresia*, 4%; *Carex moorcroftii*, 14%; and other grasses, 4%), followed by herbaceous plants (12%) and the dwarf shrub *Ceratoides compacta* (10%—Schaller and Liu 1996). In Yeniugou, Qinghai, wild yak feces in summer contain 85.5% sedges and grass (sedges: 67.1% *Kobresia* and 5.3% *Carex*; and grasses: 13.1%) and almost 4% mosses (Harris and Miller 1995). In autumn, grasses dominate (68.8%) the diet of wild yaks in Yeniugou, and sedges become less important (25.3%—Miller et al. 1994).

Generally, ungulates of the Tibetan Plateau must contend with nutritionally deficient diets from winter and early spring (Long 2003a; Schaller 1998; Wiener et al. 2003). Diets of wild and domestic yaks are low in protein (about 6%) from October to May (Long 2003b; Ping et al. 2002; Schaller 1998). Deficiencies of sodium (Ping et al. 2002), copper (Clauss and Dierenfeld 1999; Shen et al. 2006), and molybdenum (Long 2003b) and plant-induced pyrrolizidine alkaloid poisoning in India (Mondal et al. 1999) and Bhutan (Winter et al. 1993) have been noted in domestic yaks. Little is known about the specific water requirements of wild yaks, but early chroniclers noted frequent visits to mineral-rich warm springs (Przewalski 1876) and rivers (Rockhill 1894) and consumption of snow. Herders drive domestic yaks to water sources as often as twice a day, particularly under twice-a-day milking regimes (Wiener et al. 2003).

Diseases and parasites.—Rockhill (1894:118) mentioned a type of “cattle plague” in eastern Tibet that killed pastoralists’ livestock and was particularly hard on wild yaks in the late 1800s. Przewalski (1876) described “mange” (“homun” in Mongolian) on wild yaks and considerable loss of hair on some individuals that he shot. Currently, no known pathogen or disease singularly affects extant populations of wild yaks, but they are at serious risk of disease transmission from association with domestic yaks, which frequently associate with domestic cattle, particularly on winter range (Dorji et al. 2003).

Many of the serious disease- and mortality-causing pathogens of domestic cattle can be transmitted to, and many of them have been found in, domestic yaks (Dorji et al. 2003; Pal and Kar 1999), including bacterial (anthrax, brucellosis, bovine pleuropneumonia, *Chlamydia*, and *Salmonella* [Sharma et al. 1996]) and viral (foot-and-mouth disease [Barman et al. 1999] and infectious bovine rhinotracheitis) diseases. Although impractical for wild yaks, domestic yaks can be effectively vaccinated against many of these. Various ecto- and endoparasites, such as warble fly larvae (Li et al. 2004), ticks (*Haemaphysalis*—Yin et al.

2002), and the bladder larval tapeworm *Coenurus cerebralis* (Sharma and Chauhan 2006), among others (Dorji et al. 2003; Heath et al. 1984), infect domestic yaks and probably wild yaks.

Interspecific interactions.—The Tibetan Plateau has a rich wild ungulate fauna, although it has been diminished greatly by human activities (Harris 2008; Schaller 1998). Wild yaks can be sympatric with chiru or Tibetan antelope (*Pantholops hodgsonii*—Leslie and Schaller 2008), Tibetan gazelle (*Procapra picticaudata*—Schaller 1998), kiang or Tibetan wild ass (*Equus kiang*—St-Louis and Côté 2009), bharal or blue sheep (*Pseudois nayaur*—Wang and Hoffmann 1987), Tibetan argali (*Ovis ammon hodgsoni*—Fedosenko and Blank 2005), and occasionally others, such as white-lipped deer (*Przewalskium albirostris*—Harris and Miller 1995; Schaller 1998). As in mixed ungulate assemblages elsewhere, Tibetan species likely partition food and space, relative to size and digestive capabilities, to minimize competition (Harris and Miller 1995; Schaller 1998; Schaller et al. 1991). For example, wild yaks and argalis tend to use hilly to mountainous areas, chirus share flatlands with Tibetan gazelles, and the kiang uses both (Schaller et al. 1991). Nikol’skii and Ulak (2006) concluded that habitats of Himalayan marmots (*Marmota himalayana*) benefitted from heavy use in the past by wild yaks and currently by domestic yaks.

Scant information exists on the predator–prey dynamics on the Tibetan Plateau, and current dynamics are a product of greatly reduced populations of both due to various human activities. The degree to which ungulates are preyed on or scavenged is largely unknown, and separating wild and domestic yaks in predators’ feces, for example, is difficult in places where they both occur. In Kekexili Nature Reserve, Qinghai, contents of feces from Tibetan brown bear (*Ursus arctos pruinosus*; predator and scavenger) suggested a summer diet of 31% wild yak (dry weight in feces—Xu et al. 2006), but Schaller (1998) noted only 0.4% in bear feces from Chang Tang. Feces of wolves (*Canis lupus*) contain 0–10.4% yak in various parts of Tibet, Qinghai, and Xinjiang (Schaller 1998), but depredation of domestic yaks can represent 60% of the total livestock losses in India (Namgail et al. 2007). The snow leopard (*Uncia uncia*) preys on domestic yaks in limited areas, notably Mongolia and Nepal (Ikeda 2004; Namgail et al. 2007; Oli 1994; Oli et al. 1993; Schaller 1998). The lynx (*Lynx lynx*) is an uncommon predator of yaks (Namigail et al. 2007).

HUSBANDRY

Humans apparently have occupied the low-elevation periphery of the Tibetan Plateau for 30,000 years, making only seasonal forays into high-elevation areas; archeological evidence suggests that permanent occupation of the Plateau occurred 6,000–8,200 years ago (Brantingham et al. 2007).



Fig. 6.—Nomadic pastoralists were dependent on domestic yaks (*Bos grunniens*) to move supplies throughout the Tibetan Plateau; trucks now deliver most supplies. Photograph by G. B. Schaller.

Because of the harsh environmental conditions in the Tibetan Plateau, the genesis and persistence of nomadic pastoralism likely involved an early domesticated form of the wild yak (Buchholtz and Sambraus 1990; Goldstein and Beall 1990). Although the specifics of the domestication of the yak are obscure (Rhode et al. 2007), it is thought to have occurred during at least 2 separate events (Bailey et al. 2002) in the northern part of Tibet (Flad et al. 2007). The 2,500-year-old Ordos Bronzes of the horned heads and bodies of domestic yaks that form buckles and plaques from Tibet through southern Russia attest to the species' cultural importance after domestication (Olsen 1986).

For centuries to the present day, nomadic pastoralists have depended on domestic yaks for transportation and sustenance (Fig. 6), consuming milk, butter, and meat, and using by-products of culling for clothing, tents, leather goods, and medicinal (= blood) purposes (Anderson 1912; Ekvall 1968; Goldstein and Beall 1990; Jiang 2002; Kala 2005; Wu 2003; Zhang et al. 1994). Feces of domestic yaks and other livestock are a primary source of fuel on the Tibetan Plateau (Goldstein and Beall 1990; Hedin 1934); yak dung is purported to make a greater total energetic contribution to the nomadic way of life than all other yak by-products combined (Rhode et al. 2007). Yak dung contains about 900 kcal/l and if converted completely efficiently into electricity, 1.0 kg could operate a personal computer for 9.6 h (Rhode et al. 2007).

Accounts from the late 1800s described regular caravans (Fig. 6) of ≥ 200 domestic yaks, and exceptionally 1,500

domestic yaks and 300 ponies (Wellby 1898), moving salt, hides, and other provisions along regular trade routes of the Tibetan Plateau. At the same time, herds of 200–300 wild yaks were observed, and expeditions depended on them regularly for fresh meat (Bower 1894; Hedin 1934; Rockhill 1894). Pastoral herds are still dominated by domestic yaks in alpine meadow areas, but sheep and goats can be more important to local economies in alpine steppe areas (Goldstein and Beall 1990; Miller 2005; Yan et al. 2005).

Considerable literature exists on domestic yaks, particularly in the areas of adaptations to ambient conditions (see “Form and Function”), milk and meat quality, reproductive performance, hybridization, and genetics (e.g., Jianlin et al. 2002; Wiener et al. 2003). Milk from the domestic yak is high in fat (5.4–7.2%), protein (4.9–5.3%), lactose (4.5–5.0%), and milk solids (16.9–17.7%), with average daily yields of 0.8–3.0 kg, depending on breed, food availability, and weather; colostrum is 2–3 times richer than milk (Wiener et al. 2003). Most of the milk and by-products such as butter are used locally and, if transportation is available, sold in towns (Zhang et al. 1994). Meat of the domestic yak from the harvest of surplus males and unproductive females is critical to sustenance and can provide some income from its sale (Wiener et al. 2003; Zhang et al. 1994). It is lean, beef-like in flavor, and rich in myoglobins (Wiener et al. 2003), but there is no evidence that introducing blood lines of wild yaks into domesticated breeds improves nutrient levels (Luo et al. 2006).

Wild and domestic yaks interbreed when wild males enter domestic herds and commonly abscond with females, generally not considered desirable by pastoralists (Harris 2008). Hybrids can be shyer and difficult to domesticate. Nevertheless, some pastoralists consider the introduction of wild yak blood lines into their domestic herd desirable (Wiener et al. 2003). Records of the 1st hybridization of domestic yaks with other *Bos* types date back to the Han Dynasty (206–220 BC), but serious crossbreeding was initiated in the mid-1900s (Zhang et al. 1994). Although outcomes vary, the domestic yak has been crossed with *Bison bison* (American bison), *Bos frontalis* (gaur), *B. taurus* (domestic cattle, including zebu cattle), and *Bos javanicus* (banteng—Bonnemaire and Teissier 1976; Gray 1953; Wiener et al. 2003). Such crosses often result in hybrids with variable fertility by sex; for example, crossing domestic yaks with bison, zebu cattle, and other breeds of domestic cattle results in females of low fertility and sterile males (Wishart et al. 1988), and crossing *B. grunniens* with banteng results in viable female hybrids with unspecified fertility rates (Gray 1953; Wiener et al. 2003).

BEHAVIOR

Grouping behavior.—Yaks are herding ungulates. Groups of wild yaks vary from single males to aggregations

of >200 (Schaller et al. 2007) and even 400 (Miller 1992) individuals. Aggregations of 1,000 individuals were reported by Przewalski (1876). Groups are not stable through time (Schaller 1998). Grouping behavior depends on sex, time of year, and location. Group types included solitary adult males, mixed-aged males, females and offspring (Fig. 5), and mixed sexes; females rarely occur alone or in groups of <5–10 individuals (Miller et al. 1994; Schaller 1998).

In the northern Chang Tang, Tibet, in November 2006, groups of male wild yaks averaged 1.7 individuals (range: 1–7, $n = 93$ groups); 7 female herds averaged 17.0 individuals (range: 8–24; an 8th female group had 60 individuals—Schaller et al. 2007). In the Aru Basin in the Chang Tang in July–August, about 40% of female–young and mixed male–female groups had 81–110 individuals ($n = 1,610$ groups—Schaller 1998; Schaller and Liu 1996). In Yeniugou, Qinghai, groups of 10–245 female wild yaks with their young of the year and yearling offspring, juveniles, barren females, and adult males (about 4% of the herd) were observed in summer; male-only groups averaged 6.2 (Harris 1993; Miller et al. 1994).

Reproductive behavior.—Few published accounts on the reproductive behavior of wild yaks exist, but observations from domestic yaks likely are comparable, although intensity, duration, and timing probably vary between the 2 forms. Some males stay with female herds throughout the year (Schaller 1998), but others live alone or in bachelor groups until rut in summer—as late as July for domestic yaks at high elevations in Tibet (Wiener et al. 2003; Zi 2003) and perhaps even mid-August through September for wild yaks (Przewalski 1876; Schaller 1998). At some point, older males may become less competitive in obtaining mates than prime males and may live alone or in small groups apart from other groups (Harris 2008; Miller et al. 1994; Schaller 1998; Schaller and Liu 1996). During rut, males do not establish a territory or harem apart from a herd or each other, but rather they “wander day and night” (Przewalski 1876:192) and attempt to tend and breed receptive females within existing herds (Schaller 1998; Wiener et al. 2003). Estrous females stop eating, become excited, and occasionally attempt to mount other females (Prasad 1997; Sarkar and Prakash 2005).

As rut commences, males maintain a dominance hierarchy by fighting each other and attain maximum breeding performance at 5–10 years, at least among domestic breeds (Wiener et al. 2003). Aggressive behavior among males in rut is intense and comparable between wild and domestic yaks (Schaller 1977). Przewalski (1876) noted considerable scarring, wounds, and horn damage on male wild yaks incurred during rut-induced fights. Indirect threats involve lateral displays that emphasize the shoulder hump and mantle of hair by standing head to head or head to tail 3–6 m apart for ≥ 5 min; direct threats include charges with lowered heads and head-to-head sparring that can last 15 min (Schaller 1998). Rutting male wild yaks frequently

wallow on dry ground, sometimes while defecating and urinating, which distinguishes them from other *Bos* but parallels behavior of *Bison*. Other rutting behaviors include grunting, bellowing, horning the ground and vegetation, rubbing the face and neck on the ground, and teeth grinding (Schaller 1998). Copulation is abrupt and of short duration.

Miscellaneous behavior.—The ill-temper and ferocity of wild yaks have been mentioned repeatedly since the early descriptions (Hedin 1934; Przewalski 1876), but most accounts, outside the breeding and calving seasons, involve wounded and threatened individuals and particularly, solitary males (Rockhill 1895). Przewalski (1876:196) remarked that “the nearer they are to the sportsman the more cowardly and undecided they become” and that few individuals advanced closer than “40 paces of us.” Harris (2008:151, 154) referred to the wild yak as a “ferocious coward” and opined that its “bellicose nature has been exaggerated.” Perhaps years of armed persecution, including that by Mongol and Tibetan yak hunters over centuries (Hedin 1934), has led to the now common response of fleeing “until visual contact is no longer possible” (Harris 2008:154). Schaller (1998:126) noted that wild yaks “fled fast and far” after detection of humans or cars and recalled a group fleeing 20 km after spotting him. Nevertheless, almost every village close to areas frequented by wild yaks in the Chang Tang has experienced attacks, injuries, and even deaths caused by wild male yaks, particularly during rut. Achuff and Petocz (1988:45) recounted an incidence where 3 wild yaks “charged at full speed” and chased their jeep for 3 km.

GENETICS

Similar to congeners, the yak has a diploid chromosome number ($2n$) of 60 and fundamental number (FN) of 62 with 58 acrocentric and subacrocentric autosomes and no metacentric or submetacentric autosomes (Das et al. 2004; Gupta et al. 1996; Prasad 1997; Tu et al. 2000; Wurster and Benirschke 1968). The X chromosome has been reported as a large metacentric (Wurster and Benirschke 1968) to submetacentric with no differences in autosomal chromosome length between sexes (Das et al. 2004; Gupta et al. 1996). The Y chromosome is submetacentric (Das et al. 2004; Gupta et al. 1996; Prasad 1997; Wurster and Benirschke 1968). Chromosomally, the domestic yak is most similar to *Bos taurus*, including zebu cattle (Gupta et al. 1996).

Analyses of 12S and 16S rRNA and 22 tRNA mitochondrial genes suggest that the wild yak diverged from *B. taurus* about 5 million years ago, from *Bubalus bubalis* (water buffalo) about 12 million years ago, and *Ovis* (sheep) and *Capra* (goats) about 13–28 million years ago (Gu et al. 2007). In contrast, mitochondrial DNA analyses suggest that the yak diverged from *B. taurus* about 1–2 million years ago (Tu et al. 2002). D-loop sequences from

mitochondrial DNA suggest that the yak is more closely related to *Bison bison* (Guo et al. 2006a; Miyamoto et al. 1989) than *Bison bonasus* (Buryńska et al. 1999); the 3 species cluster together, but apart from other Bovini, in recent DNA fingerprinting analyses (Buntjer et al. 2002).

Genetic evaluation suggests that the domestic yak was derived from at least 2 matrilineal sources (Bailey et al. 2002; Guo et al. 2006b; Lai et al. 2007) in the Tibet–Qinghai region of China. Genetic diversity among most domestic yak populations is high (Xuebin et al. 2005) and comparable to that of European cattle breeds (Bailey et al. 2002; Wang et al. 2003). In contrast, genetic diversity of domestic yaks was very low among 6 Chinese populations in Qinghai, Gansu, and Sichuan, suggesting prior bottlenecks (Tu et al. 1997). Samples from 2 geographically isolated populations had identical haplotypes (Schaller and Amato 1998). No information exists on genetic diversity of extant populations of wild yaks.

CONSERVATION

The great herds of wild yaks (Schaller and Liu 1996), and other Tibetan ungulates, are a distant memory, and substantial conservation challenges have been incurred by changing governmental policies and their impact on culture and ecology (Harris 2008; Schaller 1998). Hunting is, and has been, part of the traditional lifestyle of nomadic pastoralists in western Asia for millennia (Huber 2005). In the late 1800s, the wild yak was abundant enough in parts of the Tibet Plateau to provide regular meat to nomadic peoples and western expeditions (Bower 1894; Hedin 1934; Przewalski 1876; Rockhill 1894, 1895; Schäfer 1937; Wellby 1898). During more recent times, with the construction of roads allowing penetration into remote areas and availability of more sophisticated firearms and motorized vehicles, examples of excessive harvest, even for markets beyond the Tibetan Plateau, were common (Harris 2008; Harris et al. 1999; Schaller 1998). In the late 1940s in Qinghai, Clark (1954:266) observed “hundreds if not thousands of the enormous white skulls of wild yaks, the fate of the herds written in bone and horn, as was that of the American bison a century ago.”

The wild yak is now one of the most endangered species of the Tibetan Plateau and has been persecuted to the point that it only finds refuge in the most remote, relatively human-free areas (Buchholtz and Samba 1990; Harris 2008; Lu 2000; Schaller 1998). It is a Class I protected species in China, and hunting has been prohibited since the early 1990s (Schaller 1998). The wild yak is perhaps underclassified as Vulnerable by the International Union for Conservation of Nature and Natural Resources (2008) and has been protected under Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (2007) since 1962.

Most pastoralists reside in alpine steppe and alpine meadows at >4,200 m in elevation, preferred habitats of wild yaks (Bedunah and Harris 2002; Miller and Bedunah 1994; Ryavec 1998). The human population of the Tibetan Plateau has increased greatly in the past 50 years to such an extent that all good grazing lands are now occupied and remnant populations of wild yaks are seriously affected. Competition between wild and domestic yaks, and possible disease transmission, are problems (Banks et al. 2003; Fox et al. 2002; Mishra et al. 2001), and the large numerical dominance of the domestic yak excludes wild yaks from former habitat (Harris 2008; Mishra et al. 2002). Furthermore, introduction of the “anthropogenic architecture” of the domestic yak “genome” into extant populations of wild yaks is a serious conservation challenge (Harris 2008:155). Some hybrids with white spots have been noted among herds of wild yaks (Harris 2008), but the extent of this genetic mixing throughout the remaining range of the wild yak is unknown (Harris 2008). One isolated group of feral domestic yaks is suspected in Helan Mountains of Inner Mongolia (Wiener et al. 2003)—fortunately disjunct from the remaining range of the wild yak.

The yak, perhaps more than any other species, symbolizes the “conservation leaks” in the “roof of the world” that clearly need repair. Leslie and Schaller (2008) recently summarized conservation challenges faced by the chiru, relative to policy and sociological changes in western China; Schaller (1998) and Harris (2008) provided considerably more detail for Tibetan fauna in general. Among the many “conservation leaks,” roads encroach into heretofore remote areas, which can lead to increased poaching, and invariably increase densities of humans and domestic livestock—often on the most productive rangeland (Harris 2008; Schaller et al. 2005). Roads can cause unintentional habitat degradation (Banks 2003; Banks et al. 2003) and reduced carrying capacity for wildlife (Schaller 1998). Changes in land-use policy that fence and divide previously open rangeland into private parcels affect movements of wild yaks and other wildlife (Leslie and Schaller 2008).

The Chinese government has made significant progress in establishing and expanding a reserve network to protect all wild fauna of the Tibetan Plateau (Schaller 1998). As Harris (2008) pointed out, wildlife management in China currently involves little more than protection, which is often constrained by limited manpower, and regulations inside and outside reserves are basically the same. Appropriate and sustainable management strategies should be focused on species-specific conservation needs, as exemplified by the wild yak. Critically, more basic ecological insights on the wild yak and associated fauna and flora of the Tibetan Plateau are needed to establish the most effective and lasting conservation strategies (Harris 1995, 2008; Heinen and Srikosamatara 1996; Schaller 1998).

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