

Equus kiang (Perissodactyla: Equidae)

ANTOINE ST-LOUIS AND STEVE D. CÔTÉ

Département de Biologie, Université Laval, Québec, Québec G1V 0A6, Canada; antoine.st-louis.1@ulaval.ca
Centre d'Études Nordiques, Université Laval, Québec, Québec G1V 0A6, Canada

Abstract: *Equus kiang* Moorcroft, 1841, is an equid commonly called the kiang or Tibetan wild ass and is the only equid living on the Tibetan Plateau. It is the largest of the wild asses, with a distinct dark-brown coat on the back, and 1 of the 7 species of *Equus*. It is endemic to the high-elevation rangelands of China (Tibet, Xinjiang, Qinghai, and Gansu), India (Ladakh and Sikkim), Pakistan (Khunjerab National Park), and Nepal (Mustang). It inhabits open steppes and rolling hills sparsely vegetated with grasses and sedges. *E. kiang* is vulnerable to illegal poaching and competition with domestic livestock, and data are insufficient to accurately estimate its total abundance. DOI: 10.1644/835.1.

Key words: China, equid, kiang, Ladakh, Qinghai, Tibet, Tibetan wild ass, Xinjiang

Published 27 May 2009 by the American Society of Mammalogists
Synonymy completed 12 June 2008

www.mammalogy.org



Equus kiang Moorcroft, 1841 Kiang or Tibetan Wild Ass

Equus kiang Moorcroft in Moorcroft and Trebeck, 1841:312. Type locality “eastern parts of the country [= Ladakh],” state of Jammu and Kashmir, India.

Asinus equioides Hodgson, 1842:287. Nomen nudum (Grubb 2005).

Asinus polyodon Hodgson, 1847a:469. Type locality “Tibet;” restricted to the region north of Sikkim border (Groves and Mazák 1967:352).

Asinus hemionus Gray, 1852:272. Type locality “Thibet [= Tibet].”

Asinus kyang: Kinloch, 1869:13. Name combination and incorrect subsequent spelling of *Equus kiang* Moorcroft, 1841.

Equus hemionus kiang Lydekker, 1904a:432. Type locality “Tibet and Ladak [= Ladakh].”

Equus kiang holdereri Matschie, 1911:29. Type locality “[southwestern shore of] Kukunor” vide Groves and Mazák (1967:352).

Microhippus tafeli Matschie, 1924:68. Type locality “Tosson Nor, Tibet” vide Ellerman and Morrison-Scott (1966:342).

Hemionus kiang: Trumler, 1959:17. Name combination.

Hemionus nepalensis Trumler, 1959:24. Type locality “Nepal.”

CONTEXT AND CONTENT. Order Perissodactyla, suborder Hippomorpha, family Equidae, subfamily Equinae. The genus *Equus* has 7 living species: *E. asinus*, *E. burchellii*, *E. caballus*, *E. grevyi*, *E. hemionus*, *E. kiang*, and *E. zebra* (Bennett 1980; key in Grinder et al. 2006). *E. quagga* is

now extinct (Groves 1974). Three subspecies of *E. kiang* have been identified, mainly on the basis of geographical location, body size, and color differences (Groves and Mazák 1967; Neumann-Denzau and Denzau 2003; Shah 2002):

E. k. holdereri Matschie, 1911:29. See above (*tafeli* Matschie, 1924, is a synonym—Groves and Mazák 1967); vernacular name is eastern kiang.

E. k. kiang Moorcroft, 1841:312. See above (*equioides* Hodgson, 1842, *kyang* Kinloch, 1869, and *hemionus*



Fig. 1.—An adult male *Equus kiang* (subspecies *kiang*) in summer coat from eastern Ladakh, India (33°18'N, 78°00'E). Used with permission of the photographer © J. Van Gruisen.

kiang Lydekker, 1904, are synonyms); vernacular name is western kiang.

E. k. polyodon Hodgson, 1847a:469. See above (*kiang nepalensis* Trumler, 1959, is a synonym); vernacular name is southern kiang.

Current population assessments commonly recognize these 3 subspecies (Shah 2002). However, different opinions on their validity exist in the literature. Wang (2002) only recognized *E. k. kiang* and *E. k. holdereri*; Schaller (1998) questioned subspecific status because the distribution of *E. kiang* is continuous across its range and morphological differences are small, which suggests a cline rather than 3 subspecies. Little genetic information exists for extant populations of *E. kiang* (Schaller 1998).

NOMENCLATURE NOTES. Taxonomy of wild asses and hemionines, or “half-asses,” continues to generate debate. Although it is now accepted that *Equus kiang* is a distinct species, older literature often placed it as a subspecies of *E. hemionus* (Asiatic wild ass—cf. *E. h. kiang*). In this account, only information that could be specifically attributed to *E. kiang* is included. For example, information on *E. hemionus* from Tibet could be assumed to be about *E. kiang*, but information on *E. hemionus* without any geographic reference was not used.

There was historical confusion with identification of *E. kiang*. In an extensive review of early discoveries in Central Asia and Tibet, Hedin (1922) referred to the French Franciscan friar William de Rubruck as the 1st European to mention *E. kiang* from his travels in Central Asia during the 13th century. However, because William de Rubruck only traveled in Mongolia and never went to Tibet, he only could have seen *E. h. hemionus* (Mongolian kulan) or *E. h. luteus* (Gobi kulan), unless the range of *E. kiang* extended into Mongolia in the 13th century, an unlikely proposition. William Moorcroft identified *E. kiang* as a distinct species in a letter to John Fleming in 1822 but spelled it *Equus Kiang* (Moorcroft 1827). It appears that this source constitutes the 1st mention of *E. kiang* as a species. More recently, Trumler (1959) proposed the name *Hemionus kiang sinensis* for a 4th subspecies based on a fossil equid discovered by P. Teilhard de Chardin in the “Bassin du Sjara-Osso-Gol” in northern China (Trumler 1959:23). However, this name appears unavailable because it is not clear whether it is associated to *E. kiang* or another related fossil species.

In the recent literature, morphometric comparisons between *E. kiang* and *E. hemionus*, based on tooth patterns and skull measurements, revealed a close relationship between the 2 forms, which led Eisenmann (1980, 1986) to propose classifying *E. kiang* as a subspecies of *E. hemionus*. A different opinion was expressed by Groves and Mazák (1967) and Groves (1974), who argued that the allopatric separation between *E. kiang* and *E. hemionus* and their

biological and morphological differences were important enough to consider *E. kiang* as a separate species. In their view, morphological differences between the 6 recognized subspecies of *E. hemionus* are small compared with differences between *E. kiang* and the *E. hemionus* group. The name kiang is Tibetan (spelled rkyang in Tibet—Huber 2005), but its meaning remains unclear (Gotch 1979; Groves 1974; Prejevalsky 1876). *E. kiang* is named skiang in central Ladakh (Humbert-Droz and Dawa 2004; Pfister 2004) and zang yelu in China (Smith and Xie 2008).

DIAGNOSIS

Equus kiang is the largest of the wild asses (Schaller 1998; Fig. 1). The closest relative of *E. kiang* is *E. hemionus*, the Asiatic wild ass (Eisenmann 1980, 1986; Groves and Mazák 1967). *E. kiang* has a darker coat than *E. hemionus* and is stockier, with shoulder height about 5% higher and body mass about 30% greater than *E. hemionus* (Groves and Mazák 1967). The rump in *E. kiang* is narrow and descends steeply, whereas the rump in *E. hemionus* is more rounded (Groves and Mazák 1967). Hooves of *E. kiang* are broader and rounder than in other wild asses and similar to those of *E. caballus* (Lydekker 1904b). There is a distinctive white wedge behind the shoulder in *E. kiang*, which reaches high on the back. The white color on the throat is more prominent in *E. kiang* than in *E. hemionus*. Legs of *E. kiang* are never striped (Groves and Mazák 1967).

There are pronounced differences in the spring molting pattern between *E. kiang* and *E. hemionus*. In *E. kiang*, hair from underneath the belly is the last to be shed, whereas in *E. hemionus* hair from the belly is shed very early during molting (Mazák 1962). The complete molt is achieved in about 80 days in *E. kiang*, whereas it is completed in 40–45 days in *E. hemionus* (Mazák 1962). The mane is longer in *E. kiang* than in *E. hemionus*, and the dorsal stripe is about 13% narrower (Groves and Mazák 1967). The tail of adult *E. kiang* has hairs starting at its base, a character only found in young individuals of other wild ass species (Groves and Mazák 1967).

The lower jaw is more massive in *E. kiang* than in *E. hemionus* with a convex lower border, and upper incisors are more vertically implanted (Groves and Mazák 1967). Although generally similar, tooth patterns differ slightly between the 2 species. The metaconid–metastylid valley of the lower teeth is more penetrating, and the hypoconulid is larger and more prominent in *E. kiang* than in *E. hemionus*, similar to horses (Groves and Mazák 1967). In early descriptions of *E. kiang*, Hodgson (1847a, 1847b) reported that dP1, often referred to as the “wolf tooth,” was an exclusive characteristic of the species. However, it appears, that this extra premolar occurs in only some *E. kiang* and also is found in adults of other equid species (Eisenmann 1980; Groves and Mazák 1967).

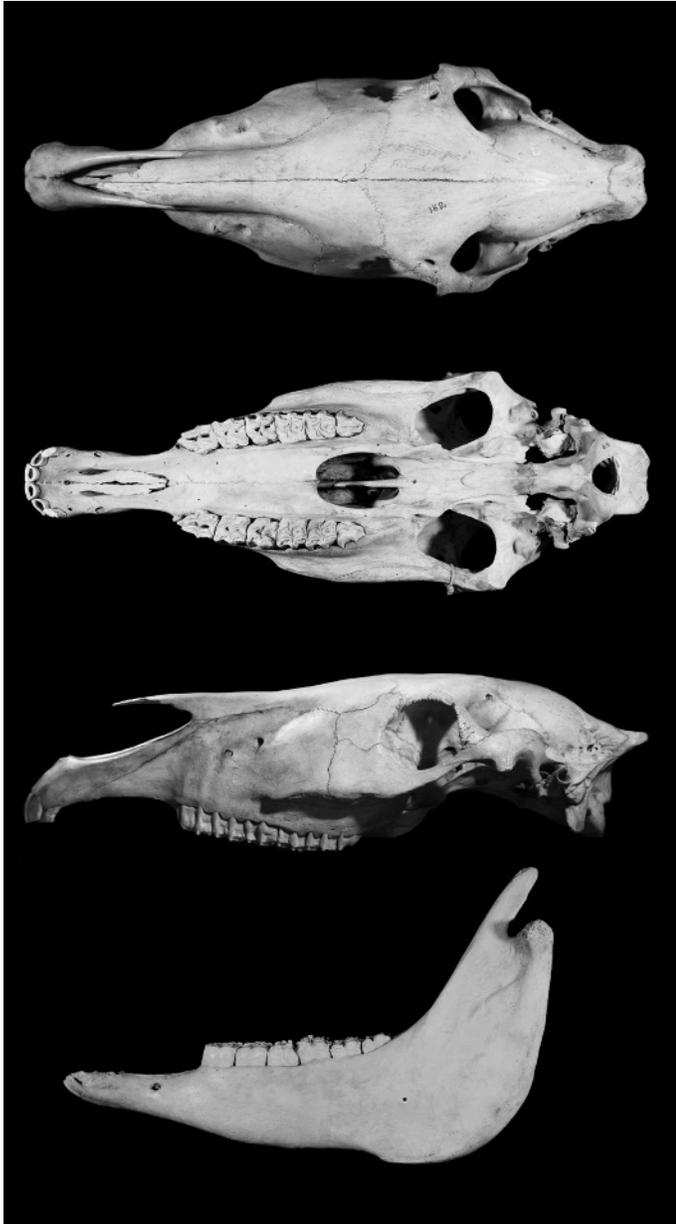


Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of a male *Equus kiang* (Field Museum of Natural History specimen 182) from Tibet. Greatest length of skull is 568 mm. Used with permission of the photographer B. D. Patterson.

GENERAL CHARACTERS

Equus kiang has a chestnut-brown coat covering the upper part of the thighs, back, upper flanks, upper part of the hind legs, dorsal part of the neck, cheeks, and forehead; undersides, throat, and insides of the ears are all white (Fig. 1). The rostrum also is white, turning gray around the mouth and nostrils. The mane and edges and tips of the ears are black. A dark brown dorsal stripe extends from the mane

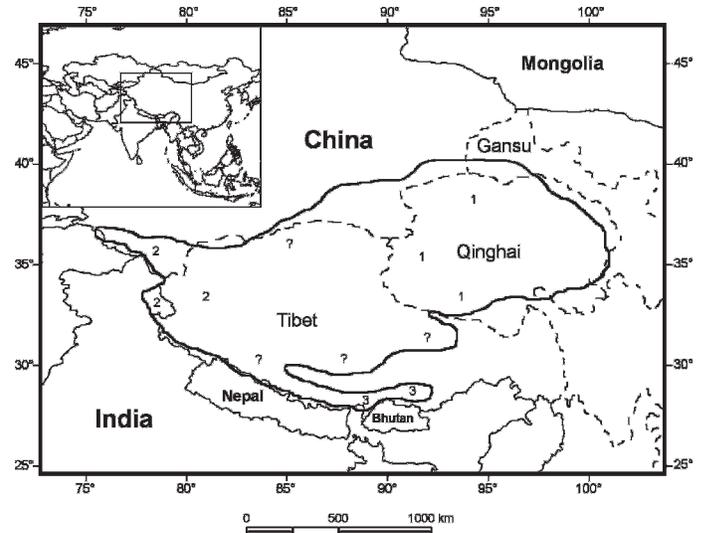


Fig. 3.—Geographic distribution of *Equus kiang*. The bold line delineates the species distribution. The distribution areas of the proposed subspecies are indicated as follows: 1, *E. k. holdereri*; 2, *E. k. kiang*; 3, *E. k. polyodon*; ? = uncertain subspecies identification (modified from Schaller 1998 and used with permission of the author).

to the tip of the tail (Schaller 1998). Legs are generally white but can be light brown on the front. A thin, dark stripe separates hooves from legs. The coat is darker in winter, and paler and more reddish in summer. The summer coat is short, with hairs 14–16 mm long. Winter hairs are thicker and longer, reaching 35–46 mm (Groves 1974; Mazák 1962).

Equus kiang has a large head, a convex nose, and a thick rostrum (Fig. 2). The snout is short (Bennett 1980). The body is relatively short, with long limbs and broad horselike hooves (Groves 1974). Chestnuts—bare skin growths located above the knees—are present on the forelegs only. Among the 3 recognized subspecies, *E. k. holdereri* is the largest, with a long nasalia, tooththrow, and diastema, and its coat has a lighter brown color than *E. k. kiang*. *E. k. kiang* has a comparatively short nasalia, tooththrow, and diastema, and its coat is dark brown, especially in winter. *E. k. polyodon* is the smallest of the 3 subspecies, with a color pattern similar to that of *E. k. holdereri* (Groves and Mazák 1967). Adult *E. kiang* have the following body measurements (cm): shoulder height, 132–142; body length, 182–214; length of tail, 32–45; length of hind foot, 41–54; and length of ear, 22 (Smith and Xie 2008).

DISTRIBUTION

Equus kiang is endemic to the Tibetan Plateau of Central Asia at elevations of 2,700–5,300 m (Schaller 1998; Shah 2002; Fig. 3). The western limit of its distribution lies on the border of Khunjerab National Park in Pakistan (75°19'E), and its eastern limit occurs in Qinghai, China (102°54'E). To

the south, *E. kiang* is limited mainly by the Himalayas (27°53'N) and to the north by the Kunlun-Arjin Shan Mountains in Xinjiang, Qinghai, and Gansu, along the northern edge of the Tibetan Plateau (40°20'N). Approximately 95% of the population of *E. kiang* occurs in China, mainly in Tibet but also in Xinjiang, Qinghai, and Gansu (Schaller 1998). Outside of China, *E. kiang* occurs mainly in the Ladakh region of India, and small numbers are found in Sikkim (Fox et al. 1991; Shah 2002). *E. kiang* is reported in the Dolpo and Mustang regions of Nepal in small numbers (Paklina and van Orden 2003; Schaller 1998; Shah 2002). In Pakistan, the species probably occurs only sporadically, coming from Xinjiang (G. B. Schaller, pers. comm.).

Because of the geographical extent and remoteness of the Tibetan Plateau, wildlife surveys are difficult to conduct, and no intensive survey of *E. kiang* has been undertaken over its entire range. Numbers of *E. kiang* were estimated in several regions of its range, but most of those censuses were carried out >15 years ago and used different methods, thus making any estimation of actual population sizes difficult. Available rough estimates are: Tibet: 37,000–48,000 individuals; Xinjiang: 4,500–5,500 individuals; Qinghai and Gansu: 15,000 individuals (Schaller 1998); Ladakh: 1,500–2,000 individuals (Fox et al. 1991); Sikkim: 74–120 individuals (Shah 2002); and Pakistan: 15–25 individuals (Rasool 1992; Shafiq and Ali 1998). Available numbers for Nepal range from 37 to 500 individuals (Shah 2002; Sharma et al. 2004). Total abundance of *E. kiang* was estimated at 60,000–70,000 individuals by Schaller (1998) and 200,000 individuals by Gao and Gu (1989). It is difficult to know which estimate is more reliable because of the lack of statistical testing in both attempts. Gao and Gu (1989) may have overestimated numbers of *E. kiang* in the Arjin Mountain Reserve of Xinjiang (Schaller 1998), so their rangewide evaluation also appears doubtful (Schaller 1998; Shah 2002).

Wildlife surveys conducted on the Tibetan Plateau after 1999 have not resulted in a new population estimate for *E. kiang*, but they illustrate local trends in population changes (e.g., Bhatnagar et al. 2006; Fox and Bårdsen 2005; Schaller et al. 2005, 2007). For example, Schaller et al. (2005) documented an increase of *E. kiang* in Tibet since their surveys in the early 1990s (see “Conservation” section). Intensive survey efforts are still required to achieve a more accurate evaluation of numbers of *E. kiang* in the wild.

FOSSIL RECORD

Despite extensive literature on fossil horses, little paleontological information is available for *Equus kiang*. *E. kiang* and the extinct Pleistocene species *E. conversidens* share common features that distinguish them from *E. hemionus* and the extinct Pleistocene stilt-legged horse, *E. calobatus* (Bennett 1980). Similarities in bone size and proportions of limbs and dental morphology exist between

E. kiang and the extinct Plio-Pleistocene *E. sivalensis* from India and Pakistan (Forstén 1986). A fossilized right metatarsal attributed to *Equus* cf. *E. kiang* was found in Pleistocene deposits at Gold Run Creek, Yukon Territory, Canada (Harington and Clulow 1973). A left metatarsal assigned to *Equus* cf. *E. kiang* also was found at Lost Chicken Creek, Alaska (Harington 1980). Environmental conditions similar to those prevailing on the Central Asian steppes and the Bering land bridge may have allowed *E. kiang* to colonize North America (Harington and Clulow 1973). This hypothesis has been questioned by other authors because no such bones have been found in northeastern Siberia; the North American fossils may have belonged to the strictly New World “stilt-legged” *Equus* (V. Eisenmann, in litt.).

FORM AND FUNCTION

Equus kiang is slightly sexually dimorphic. Female body mass is 250–300 kg, whereas males may weigh 350–400 kg (Schäfer 1937). The skull of *E. kiang* is characterized by a large and short muzzle, high facial height, and narrow occipital breadth (Eisenmann 1980; Fig. 2). Skull measurements (mm \pm SD) of adult specimens are: greatest length, 506.7 \pm 19.0 ($n = 43$); basilar length, 449.2 \pm 21.6 (43); diastema length, 82.6 \pm 8.3 (41); maximal palatal length, 229.2 \pm 10.9 (46); muzzle length, 111.0 \pm 7.5 (50); skull height, 94.2 \pm 5.4 (46); facial width, 144.3 \pm 8.4 (47); minimal muzzle width, 42.8 \pm 3.7 (49); frontal width, 203.9 \pm 11.0 (49); length of upper toothrow, 161.0 \pm 6.1 (36); orbital height, 57.1 \pm 2.6 (47); and orbital length, 61.6 \pm 3.0 (47—Eisenmann 1980). Additional skull measurements can be found in Groves and Mazák (1967), Eisenmann (1980), Groves and Willoughby (1981), and Feng et al. (1986). Postcranial measurements are available in Groves and Mazák (1967) and Groves and Willoughby (1981).

Dental formula of *E. kiang* is $i\ 3/3, c\ 0-1/0-1, p\ 3-4/3, m\ 3/3$, total 36–42 (Hodgson 1847a). Canine and 4th premolars may be present or absent. Like other equids, *E. kiang* has long molar and premolar teeth showing complex enamel patterns on the grinding surface. Three subgroups of *Equus* can be discriminated based on lower cheek-tooth patterns: zebrines, caballines, and asinines and hemionines (Eisenmann 1986). *E. kiang* belongs to the latter group, characterized by shallow ectoflexids and shallow V- or U-shaped linguaflexids (Eisenmann 1986; McFadden 1992), but these characters can vary geographically (McFadden 1992). In northern populations of *E. kiang*, the linguaflexids tend to be U-shaped, but they tend to be more V-shaped in southern populations (McFadden 1992). Eisenmann (1980, 1986) noted various characteristics of upper cheek teeth: caballine fold in 36% of premolars and 4% on M1 and M2 and absent on M3; 3 or 4 folds on P3 and P4; 47% of M3 with isolated hypoglyphs; 27% of M3 with open postfos-



Fig. 4.—A group of female *Equus kiang* with 1 foal in summer from eastern Ladakh, India. Used with permission of the photographer © J. Van Gruisen.

settes; and the wolf tooth (dP1) in 30% of the specimens. On P3 and P4, the protocone has a slight fold at its roots (Groves and Mazák 1967).

ONTOGENY AND REPRODUCTION

Mating season in *Equus kiang* occurs from late July to the end of August (Schaller 1998). Various lengths of gestation have been reported: 11 months (Schaller 1998), 7–10 months (Hayssen et al. 1993), 355 days (Shah 2002), and 365 days (Groves and Willoughby 1981). Females give birth to 1 offspring in summer between mid-July and mid-August every 2 years, although no data on marked animals exist (Schaller 1998; Fig. 4). Newborns are ≤ 90 cm at the shoulder and weigh ≤ 36 kg (Pohle 1991); they can walk a few hours after birth (Denzau and Denzau 1999). Little is known about age of sexual maturity or 1st reproduction. In the Gobi Desert of Mongolia, female *E. hemionus* breed for the 1st time at 3 or 4 years (Feh et al. 2001; Schaller 1998). *E. kiang* may be comparable (Schaller 1998). A captive male did not show any sign of sexual maturity at 3.5 years of age (Groves 1974). It is likely that females can come into estrus shortly after giving birth because mating of females accompanied by newborns has been observed (Pfister 2004). This is the case in other arid-adapted species, such as Grévy's zebra (*E. grevyi*)—Rubenstein 1994).

Infanticide occurs in captive *E. kiang* (Berger 1986). In the wild, a male attempting to mate with a female also inflicted severe injuries to her newborn foal (B. Humbert-Droz, pers. comm.). Infanticide has often been observed in other equid species (Cameron et al. 2003; Duncan 1982; Linklater et al. 1999). Induced abortion has been observed in wild horses (Berger 1983), but whether it occurs in *E. kiang* is unknown.

ECOLOGY

Population characteristics.—Although population estimates of *Equus kiang* are difficult to obtain, density estimates conducted in specific locations and repeated in time are more reliable, and thus can help understand population trends at a regional scale. Densities of *E. kiang* in the southeastern part of the Chang Tang Nature Reserve were 0.07 individuals/km² in 1991 and 0.19 individuals/km² in 2003, indicating a recent population increase (Schaller et al. 2005). Surveys conducted between 1999 and 2002 along a different route across the Chang Tang Nature Reserve gave densities of 0.48–0.82 individuals/km² (Fox and Bårdsen 2005). In Ladakh, densities were estimated at 0.25 individuals/km² (Fox et al. 1991). A survey in Ladakh in 2000 gave comparable figures, with densities of 0.03–0.86 individuals/km² (\bar{X} = 0.24 individuals/km²—Bhatnagar et al. 2006). Surveys in the Hanle Valley of eastern Ladakh between 2001 and 2004 yielded densities of 0.56 individuals/km² (Bhatnagar et al. 2006). Other available estimates are: Lhasa–Golmud road (Qinghai), 0.1 individuals/km² (Schaller et al. 1991); Yeniugou (Qinghai), 0.8 individuals/km² (Harris and Miller 1995); and Xinjiang, 0.3 individuals/km² (Schaller 1998). Human presence appears to negatively impact densities of *E. kiang*. In the Chang Tang Nature Reserve, densities were 1.06–1.53 individuals/km² under low human influence and 0.88 individuals/km² under medium human influence (Fox and Bårdsen 2005).

Adult *E. kiang* have been reported to live up to 20 years in the wild, based on comparative tooth wear with zebras (Schaller 1998). Young of the year comprised 11% of the individuals censused in Chang Tang Nature Reserve in 1985–1993, and survival of offspring seemed low in some years (Schaller 1998). Mortality rates are poorly known. Illegal hunting may be an important cause of mortality because nomadic communities often hunt for subsistence (Huber 2005; Schaller 1998). Blizzards also may cause mortality in some occasions due to starvation (Schaller 1998).

Space use.—Three major vegetation formations cover the distributional range of *Equus kiang*: alpine meadow, alpine steppe, and desert steppe (Miller and Schaller 1996; Schaller 1998). Alpine meadows are generally found at elevations $< 4,500$ m in regions where precipitation exceeds 400 mm/year (Schaller 1998); alpine meadows occur mostly in the eastern part of the Chang Tang Nature Reserve and Qinghai. To the west, alpine meadows are associated with riparian habitat along streams and lakes. Vegetation in meadows is dominated by short sedges (e.g., *Kobresia*) and various forbs and covers about 25–30% of the ground (Miller and Schaller 1996; Schaller 1998). The growing season starts earlier in riparian areas than in other habitats because water is usually present for a longer period. Alpine steppe is the most widely found vegetation formation in western Tibet and occupies most of the southern one-half of the Chang Tang Nature Reserve (Schaller 1998). Alpine

steppe occurs at elevations of 4,000–5,000 m in regions with low precipitation and is generally devoid of any sod layer (Schaller 1998). Vegetation is scarce with a cover of about 15%, and is mostly represented by *Stipa*, other grasses such as *Festuca* and *Poa*, and sedges such as *Carex moorcroftii* (Miller and Schaller 1996; Schaller 1998). Desert steppe occurs at elevations >5,000 m and is mostly found in the northern one-half of the Chang Tang Nature Reserve and in Xinjiang. Plant composition is similar to the that of alpine steppe along with cushion plants and dwarf shrubs such as *Ceratoides compacta*, but vegetation cover is much lower, averaging only 5% (Miller and Schaller 1996; Schaller 1998).

Equus kiang mostly inhabits alpine steppes and alpine meadows and rarely occurs in desert steppes (Schaller 1998). The species typically occurs in plains and hills in generally broad and open valleys and basins (Harris and Miller 1995; Schaller 1998). Harris and Miller (1995) found *E. kiang* mostly in xeric south-facing basins. In eastern Ladakh, most groups were found in wide valleys (79%), and a lesser proportion was observed in hills (19%—Bhatnagar et al. 2006). *E. kiang* may use flat and open areas as escape terrain where it can flee easily, a common antipredator strategy among wild equids (Harris and Miller 1995; Schaller 1998). In the Hanle Valley of eastern Ladakh, most groups (74%) were observed on alpine meadows (Bhatnagar et al. 2006). Schaller (1998) and Bhatnagar et al. (2006) suggested that these meadows represented critical habitats for *E. kiang* in summer and winter.

No regular migration patterns among populations of *E. kiang* have been observed (Schaller 1998). However, *E. kiang* makes seasonal movements between different habitat types, often dispersing in small groups into hilly terrain in summer and concentrating in basins and flat terrain during winter (Schaller 1998). It has been suggested that these movements are linked to availability of relatively high-quality forage such as *Stipa* (Schaller 1998). In summer, groups have often been observed making daily movements, shifting from meadows and flat basins in early morning to higher-elevation terrain later in the day and returning to lower terrain after sunset (Denzau and Denzau 1999). This movement pattern also occurs in other wild equids such as feral horses in the Great Plains, United States, probably as a strategy to avoid heat (Berger 1986).

Diet.—Equids are hind-gut fermenters, and the majority of microbial digestion occurs in the cecum (Janis 1976). This allows equids to feed on coarse and fibrous forage with a high stem-to-leaf ratio (Duncan 1992; Janis 1976; McNaughton 1985). *Equus kiang* mostly feeds on graminoids (Harris and Miller 1995; Schaller 1998; Fig. 5). On the Chang Tang Plateau, the summer diet of *E. kiang* was approximately 65% *Stipa*, followed by *Kobresia*, *Carex*, *Poa*, *Elymus*, and small amounts of a few forbs and shrubs (Schaller 1998). In the same area, the proportion of *Stipa* in winter diets increased to >90% (Schaller 1998). In Qinghai, the diet of *E. kiang* was 95% *Stipa* (Harris and Miller 1995). Forbs were rarely eaten,



Fig. 5.—A group of *Equus kiang* feeding in a mixed vegetation patch of grasses and sedges in the alpine steppe of eastern Ladakh, India. Photograph by S. D. Côté.

so legumes were usually consumed in lower proportion than their relative availability (Harris and Miller 1995). Occasionally, *E. kiang* has been observed digging *Oxytropis* roots, mostly in fall and winter when little dry grass is available (Schaller 1998). In desert steppe, shrubs such as *Ceratoides* may be important in the diet (Schaller 1998). Hay (1859:356) reported seeing *E. kiang* “feeding almost entirely on the roots of a species of *Artemisia*, or Worm-wood.”

Water requirements of *E. kiang* are poorly documented. Ungulates living in arid environments are often dependent on water sources, and this may restrict their movements and habitat use (Berger 1986; Duncan 1992). On the Tibetan Plateau, however, water sources are generally scarce and mostly frozen in winter (Schaller 1998). Occasionally, *E. kiang* drinks from waterholes, lakes, and streams, but this behavior is not common (Denzau and Denzau 1999; Schaller 1998). It seems that most of the ungulate species, including *E. kiang*, of the Tibetan Plateau fulfill their water requirements from vegetation and snow (Schaller 1998).

Diseases and parasites.—Little information is available on diseases of *Equus kiang*. A neonate in captivity died from omphalitis (Benirschke 2008), and hemorrhages have been found in the digestive tract of a dead foal in the wild (Schaller 1998). The following parasites are known to occur in *E. kiang*: *Strongylus*, *Trichonema*, *Ascaris*, *Skrjabinema*, *Anoplocephala perfoliata*, and *Paranoplocephala mamillana* (Feng et al. 1986). Oestrid fly (*Gasterophilus*) infestations also are reported in *E. kiang* (Feng et al. 1986; Schaller 1998).

Interspecific interactions.—Distribution of *Equus kiang* overlaps with the range of 6 other wild ungulate species: Tibetan gazelle (*Procapra picticaudata*), chiru or Tibetan antelope (*Pantholops hodgsonii*—Leslie and Schaller 2008), blue sheep (*Pseudois nayaur*—Wang and Hoffmann 1987),

wild yak (*Bos mutus*), Tibetan argali (*Ovis ammon hodgsoni*—Fedosenko and Blank 2005), and white-lipped deer (*Prezawlaskium albirostris*—Harris and Miller 1995; Schaller 1998). In Chang Tang, open basins are used by *P. hodgsonii* and *P. picticaudata* alongside *E. kiang* (Schaller 1998). *E. kiang* has a high degree of spatial co-occurrence with *P. picticaudata*, and to a lesser extent with domestic yaks (*Bos grunniens*) in eastern Ladakh close to the Tibet border (Namgail et al. 2008). In the Rupshu area of Ladakh, *E. kiang* and *O. ammon* are often seen in the same habitats but rarely interact (Fox et al. 1991; Hay 1859).

The predominantly grass-based diet of *E. kiang* overlaps little with diets of sympatric wild ungulates on the Tibetan Plateau (Harris and Miller 1995; Schaller 1998). Domestic sheep, goats, yaks, and horses are kept by pastoral herders in most of the range of *E. kiang* (Goldstein and Beall 1989; Miller and Schaller 1996). In Yeniugou, Qinghai, *E. kiang* has a high degree of dietary overlap with domestic sheep (Harris and Miller 1995). Wild ungulates of the Tibetan Plateau likely coevolved over a long period and may thus partition their ecological niche, whereas domestic livestock, because they were introduced only recently, may have a greater potential of interspecific competition with wild ungulates (Namgail et al. 2008; Schaller 1998).

Among potential predators, Tibetan wolf (*Canis lupus chanco*) and snow leopard (*Uncia uncia*) may occasionally prey on young and old individuals, but overall predation is unlikely to be an important limiting factor in populations of *E. kiang* (J. Van Gruisen, pers. comm.; Schaller 1998). Remains of *E. kiang* were absent in scats of *C. lupus* ($n = 384$), *U. uncia* ($n = 193$), and *Ursus arctos* (Tibetan brown bear— $n = 48$) from Qinghai and Tibet (Schaller 1998). Observations from Mongolia report *E. hemionus* in scats of *C. lupus* (Feh et al. 2001).

Miscellaneous.—According to the International Species Information System, there were 114 individuals of *Equus kiang* in captivity in May 2008, all *E. k. holdereri* (International Species Information System 2008). Although attempts to domesticate *E. kiang* have occurred (Hay 1859), they have never been successful (Groves 1974; Tegetmeier and Sutherland 1895).

BEHAVIOR

Grouping behavior.—*Equus kiang* is often found alone or in small groups but also may form herds of several hundred individuals (Foggin 2000; Paklina and van Orden 2003; Schäfer 1937; Schaller 1998). Herds of 500–1,000 animals were reported in the 1800s (Rockhill 1895), and large aggregations still occur today. Schaller (1998) observed aggregations of up to 261 individuals in the Chang Tang Nature Reserve. More than 500 *E. kiang* were observed in 4 or 5 herds on the edge of the Kekexili range in Qinghai (Foggin 2000). In Ladakh, groups ranged from 1 to 74

individuals ($\bar{X} = 2.8$, $n = 365$ —Bhatnagar et al. 2006). Group size appears to vary seasonally. Individuals of *E. kiang* are dispersed in summer and tend to congregate in fall and winter after rut. Average group size was 6.8 individuals in summer and 10.9 in winter in the Chang Tang Nature Reserve (Schaller 1998). In Qinghai and Tibet, 13.6% of the animals observed were alone in summer, but it dropped to 2.5% in September–December (Schaller 1998). In November–December 2006, 2.2% of the animals observed in the Chang Tang Nature Reserve were solitary, and 73% were in groups of 2–10 individuals ($n = 48$ —Schaller et al. 2007). During surveys conducted in September and October 1998 in southwestern Tibet, 1.1% of *E. kiang* were solitary, 1.6% were in pairs, and 97.3% were in groups of 3–160 individuals (Paklina and van Orden 2003).

Two distinct types of social organizations have been described in wild equids (Klingel 1975, 1977). In the 1st type, permanent groups contain a few males and several females and young, and males are not territorial. This type of social organization occurs in equids from temperate ecosystems such as *E. burchellii* (Burchell's zebra), *E. zebra* (mountain zebra), and *E. caballus przewalskii* (Przewalski's horse—Moehlman 1998). In the 2nd type, the only permanent associations occur between mother and foal. Only temporary groups are formed, comprising several females and their young or only males (bachelor groups); adult males are often territorial. This type of social organization has been documented in equids adapted to arid environments, such as *E. grevyi*, *E. asinus africanus* (African wild ass—Grinder et al. 2006), and *E. hemionus* (Klingel 1977; Moehlman 1988; Rubenstein 1989). In those environments where food is often scarce, resource needs between males and females may be too different to maintain a tight social structure (Rubenstein 1989, 1994).

Equus kiang seems to display the 2nd type of social organization (Groves and Willoughby 1981; Schaller 1998). Groups of *E. kiang* are not permanent but seem to be formed of temporary aggregations; only female and foal remain together at all times (Fig. 4). Young adult males typically form bachelor groups, and older males are often solitary and show territorial behavior (Denzau and Denzau 1999; Schaller 1998). Solitary males often herd female or family groups that pass within their territory (Schaller 1998). Defecating at dung piles is common in territorial equids (Klingel 1977; Moehlman 1998) and occurs in *E. kiang* (Denzau and Denzau 1999). In Ladakh, territory size varies from 0.5 to 5.0 km² (Denzau and Denzau 1999). Territorial defense by males involves aggressive chases toward intruding males (Denzau and Denzau 1999; Schaller 1998). These chases are often preceded by threatening behavior when a defending male approaches an intruder with its head up, ears laid back, and tail horizontal, often grunting or making a “wheezing bray” at the same time (Schaller 1998:272). One of us (AS-L) observed chases that lasted >20 min. Aggressive fighting between adult males also occurs, involving

kicking and biting the neck, mane, and tail; such males often have scars and wounds resulting from aggressive interactions (Denzau and Denzau 1999).

Reproductive behavior.—Male *Equus kiang* tend females by trotting around them and chasing those that wander from the group, often with their head down and their ears laid back (Schaller 1998). Such chases typically precede mating, and copulation is often followed by the male trotting away with its head held high and obliquely (Pfister 2004).

Communication.—The vocalization of *Equus kiang* has been described as a “shrieking bray” (Lydekker 1904b:584). Hay (1859) noted that it was distinct from neighing of the horse and braying of the ass. *E. kiang* makes a snort puff when alarmed (Pfister 2004).

GENETICS

Two diploid numbers (2n) are exhibited by members of *Equus kiang*. Karyotypes exhibit either 52 or 51 chromosomes and each karyotype possesses 92 chromosomal arms (Ryder and Chemnick 1990). This polymorphism of diploid number occurs in both male and female *E. kiang* and is attributed to a Roberstonian translocation (Ryder and Chemnick 1990). The X chromosome is submetacentric; the Y chromosome is acrocentric (Ryder and Chemnick 1990).

Equus kiang is often considered a subspecies of *E. hemionus* (Groves 1974; Groves and Mazák 1967; Pohle 1991). Nevertheless, genetic analyses demonstrate that *E. kiang* is a distinct species and that divergence from *E. hemionus* occurred approximately 500,000 years ago (Ryder and Chemnick 1990). Genetic variation among the 3 subspecies of *E. kiang* has not been investigated.

Hybrids between *E. kiang* and *E. caballus*, *E. asinus*, *E. hemionus*, and *E. burchellii* have been reported in captivity (Gray 1972; Hay 1859; Kinloch 1869). A female hybrid between *E. kiang* and *E. caballus*, born in the Jardin des Plantes, Paris, France, lived for >36 years (Gray 1972). Another female hybrid between *E. kiang* and *E. burchellii* lived there for >32 years (Gray 1972). Hybrids between captive *E. kiang* and captive *E. hemionus* are reported for both *E. h. hemionus* and *E. h. khur* (Gray 1972). In the wild, geographical barriers likely prevented hybridization of *E. kiang* with adjacent populations of *E. h. hemionus* and *E. h. khur* (Groves and Mazák 1967). No evidence exists that hybrids of *E. kiang* can reproduce. Genetic analyses have established that *E. a. asinus* (domestic donkey) did not originate from *E. kiang* or *E. hemionus*, but from *E. a. africanus* (Beja-Pereira et al. 2004).

CONSERVATION

Equus kiang is fully protected in China and India (China Class I; Indian Wildlife Protection Act 1972 Schedule I—Shah 2002). In Pakistan, *E. kiang* is listed on the national red

list as Critically Endangered (Shafiq and Ali 1998). *E. kiang* is listed on the World Conservation Union (IUCN) *Red List* as Lower Risk/Least Concern (LR/LC—Baillie and Groombridge 1996). Each subspecies is designated separately by World Conservation Union: Lower Risk/Least Concern for *E. k. holdereri* and Data Deficient for *E. k. kiang* and *E. k. polyodon* (Baillie and Groombridge 1996). *E. kiang* is in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (Shah 2002).

Historically, *E. kiang* and other wildlife species were hunted by nomads on the Tibetan Plateau for their subsistence (Huber 2005). However, religious beliefs prohibited killing equids in ancient civilizations of Tibet, and although it could have occasionally been a necessity, *E. kiang* was not traditionally hunted on a wide scale (Bellezza 2008; Harris 2008; Huber 2005). Hunting of *E. kiang* drastically increased around the mid-20th century due to easier access to remote locations with roads and availability of the modern rifle (Leslie and Schaller 2008; Schaller et al. 2005). *E. kiang* was heavily hunted in China during the socioeconomic changes and the great famine of 1958–1961 (Harris 2008; Schaller 1998; Schaller et al. 2005). In southeastern Qinghai, for example, populations of *E. kiang* have been diminished, and they are now absent or scattered (Schaller 1998). In Ladakh, populations of *E. kiang* were greatly reduced during the 1962 war with China (Bhatnagar et al. 2006).

During the last decade, the Chinese government took successful wildlife protection measures. Illegal hunting has been strictly controlled, and a 600,000-km² reserve network was established in the Chang Tang region (Harris 2008; Leslie and Schaller 2008; Schaller et al. 2005). *E. kiang* is now abundant enough that there is no immediate threat to its persistence, and populations are reported to be increasing (Schaller et al. 2005). In the southeastern part of the Chang Tang Nature Reserve, populations of *E. kiang* have increased since the early 1990s to the extent that they are now perceived by pastoralists as serious competitors with livestock (Fox et al. 2004; Schaller et al. 2005; Tsering et al. 2006). In Nyima County, Tibet, for example, *E. kiang* was reported to damage pastures in early spring when they dig for grass roots (Tsering et al. 2006). Although harvesting of *E. kiang* does not occur at a wide scale, they are often chased from pastures on motorbikes (Tsering et al. 2006). Herders and local authorities have requested permission to cull *E. kiang* to reduce their potential negative impact on pastures, but culling was denied by the Chinese government because of the national protection status of *E. kiang* (Tsering et al. 2006).

In remote regions of Chang Tang, changes in rangeland use policy are increasing human densities and movements in key wildlife areas, along with increasing livestock numbers (Fox and Tsering 2005; Schaller et al. 2005). Rangelands in some locations are turned into private ranches owned by

several families (G. B. Schaller, pers. comm.), likely causing an intensification of pasture use and deteriorating wildlife habitats (Fox and Tsering 2005). Rangelands are often fenced from wildlife, which not only prevents *E. kiang* access to key resources but also may cause injuries and mortalities (Bhatnagar et al. 2006; Schaller et al. 2005). Conflicts with domestic livestock may be the biggest challenge for the long-term conservation of *E. kiang* (Fox et al. 2004; Fox and Tsering 2005; Schaller et al. 2005; Tsering et al. 2006). Whether these conflicts are real or perceived depends on the location (Bhatnagar et al. 2006; Tsering et al. 2006). Large numbers of *E. kiang* may compete with livestock, but this situation probably occurs mainly at a local scale. For example, Bhatnagar et al. (2006) estimated that throughout Ladakh, populations of *E. kiang* use only 10–11% of the total forage consumed, whereas the other 89–90% is used by livestock.

Increased human densities in remote areas of the Tibetan Plateau augment the threats to *E. kiang* and other wildlife species. Mining activities occur in parts of Qinghai and Xinjiang, and the easier access to remote regions by road facilitates illegal hunting (Fox and Tsering 2005; Schaller et al. 2005; Tsering et al. 2006). In some places of Qinghai, poaching continues and is accepted by the nomads, who see *E. kiang* as a nuisance to their livestock (G. B. Schaller, pers. comm.). Since early 2006, male *E. kiang* have been poached for their penis, which is reputed to enhance men's virility when eaten (Tsering et al. 2006).

Long-term conservation of *E. kiang* lies mainly in the resolution of potential conflicts with domestic livestock, minimizing habitat degradation from pastoralists and human development (e.g., fences, road, and mining), and control of poaching. Because conflicts mostly occur at local scales, solutions also must be implemented at that scale. For example, different management and conservation strategies could be considered inside and outside wildlife reserves. Pilot projects could be initiated in specific places to reduce the number and impact of *E. kiang*, but these changes would first need to be accompanied with policy changes and ecological studies (Harris 2008; G. B. Schaller, pers. comm.). Data are needed on the dynamics of populations of *E. kiang* and resource use to identify at which scale and to what extent competition with livestock occurs, during which season, and for what resource components. Moreover, genetic analyses are needed to ascertain the status of the 3 named subspecies of *E. kiang*. If recognized as such, *E. k. polyodon* may require specific conservation measures because of its low abundance and restricted distribution (Neumann-Denzau and Denzau 2003).

ACKNOWLEDGMENTS

We thank C. Barrette, J. Mainguy, G. B. Schaller, and an anonymous reviewer for their constructive comments on earlier versions of the manuscript; V. Eisenmann for helping

with the osteology section and fossil records; A. D. Jungblut for translating German texts; and Xiao-Mian Xie for translating Chinese texts. We are indebted to J. Van Gruisen for providing photographs of *E. kiang* in the wild (copyright J. Van Gruisen), B. Patterson of the Field Museum of Chicago for providing skull photographs of *E. kiang*, and G. B. Schaller for permission to reproduce the distribution map. This manuscript benefited from fruitful communications with J. V. Bellezza, G. Denzau, B. Humbert-Droz, O. Pfister, A. Shrieber, and J. Van Gruisen. Finally, the staff of the scientific library of Université Laval provided invaluable help to find rare literature. Funding to A. St-Louis during writing was granted through a doctoral scholarship from the Natural Sciences and Engineering Research Council of Canada and the Natural Sciences and Engineering Research Council of Canada Discovery Grant to SDC.

LITERATURE CITED

- BAILLIE, J., AND B. GROOMBRIDGE (EDS.). 1996. 1996 IUCN Red list of threatened animals. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.
- BEJA-PEREIRA, A., ET AL. 2004. African origins of the domestic donkey. *Science* 304:1781.
- BELLEZZA, J. V. 2008. Zhang Zhung: the foundations of civilization in Tibet. Austrian Academy of Sciences Press, Vienna, Austria.
- BENIRSCHKE, K. 2008. Comparative placentalion: eastern kiang. University of California San Diego, La Jolla, California. www.placentalion.ucsd.edu/kiang.html, accessed 29 May 2008.
- BENNETT, D. K. 1980. Stripes do not a zebra make, part I: a cladistic analysis of *Equus*. *Systematic Zoology* 29:272–287.
- BERGER, J. 1983. Induced abortion and social factors in wild horses. *Nature* 303:59–61.
- BERGER, J. 1986. Wild horses of the Great Basin: social competition and population size. University of Chicago Press, Chicago, Illinois.
- BHATNAGAR, Y. V., R. WANGCHUK, H. H. T. PRINS, S. E. VAN WIEREN, AND C. MISHRA. 2006. Perceived conflicts between pastoralism and conservation of the kiang *E. kiang* in the Ladakh Trans-Himalaya, India. *Environmental Management* 38:934–941.
- CAMERON, E. Z., W. L. LINKLATER, K. J. STAFFORD, AND E. O. MINOT. 2003. Social grouping and maternal behaviour in feral horses (*Equus caballus*): the influence of males on maternal protectiveness. *Behavioral Ecology and Sociobiology* 53:92–101.
- DENZAU, G., AND H. DENZAU. 1999. Wildesel. Thorbecke, Stuttgart, Germany.
- DUNCAN, P. 1982. Foal killing by stallions. *Applied Animal Ethology* 8: 567–570.
- DUNCAN, P. 1992. Horses and grasses: the nutritional ecology of equids and their impact on the Camargue. Springer-Verlag, New York.
- EISENMANN, V. 1980. Les chevaux (*Equus sensu lato*) fossiles et actuels: crânes et dents jugales supérieures. Centre National de la Recherche Scientifique, Paris, France. www.vera-eisenmann.com, accessed 20 May 2008.
- EISENMANN, V. 1986. Comparative osteology of modern and fossil horses, half-asses, and asses. Pp. 67–116 in *Equids in the ancient world* (R. H. Meadow and H.-P. Uerpmann, eds.). Reichert, Wiesbaden, Germany.
- ELLERMAN, J. R., AND T. C. S. MORRISON-SCOTT. 1966. Checklist of Palaearctic and Indian mammals: 1758 to 1946. 2nd ed. Trustees of the British Museum of Natural History, London, United Kingdom.
- FEDOSENKO, A. K., AND D. A. BLANK. 2005. *Ovis ammon*. *Mammalian Species* 773:1–15.
- FEH, C., B. MUNKHTUYA, S. ENKHBOL, AND T. SUKHAATAR. 2001. Ecology and social structure of the Gobi khulan *Equus hemionus* subsp. in the Gobi B National Park, Mongolia. *Biological Conservation* 101:51–61.

- FENG, Z., G. CAI, AND C. ZHENG. 1986. The mammals of Xizang. Science Press, Beijing, China.
- FOGGIN, J. M. 2000. Biodiversity protection and the search for sustainability in Tibetan Plateau grasslands (Qinghai, China). Ph.D. dissertation, Arizona State University, Tempe.
- FORSTÉN, A. 1986. Chinese fossil horses of the genus *Equus*. *Acta Zoologica Fennica* 181:1–40.
- FOX, J. L., AND B.-J. BÄRDSÉN. 2005. Density of Tibetan antelope, Tibetan wild ass and Tibetan gazelle in relation to human presence across the Chang Tang Nature Reserve of Tibet, China. *Acta Zoologica Sinica* 51:586–597.
- FOX, J. L., P. MATHIESEN, D. YANGZOM, M. W. NAESS, AND X. BINRONG. 2004. Modern wildlife conservation initiatives and the pastoralist/hunter nomads of northwestern Tibet. *Rangifer* (Special Issue) 15: 17–27.
- FOX, J. L., C. NURBU, AND R. S. CHUNDAWAT. 1991. The mountain ungulates of Ladakh, India. *Biological Conservation* 58:167–190.
- FOX, J. L., AND D. TSERING. 2005. Biodiversity conservation and natural resource exploitation on Tibet's northwest Chang Tang highlands. *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* 33:49–57.
- GAO, X., AND J. GU. 1989. The distribution and status of the Equidae in China. *Acta Theriologica Sinica* 9:269–274.
- GOLDSTEIN, M. C., AND C. M. BEALL. 1989. Nomads of western Tibet: the survival of a way of life. Serindia Publications, London, United Kingdom.
- GOTCH, A. F. 1979. Mammals, their Latin names explained: a guide to animal classification. Blandford Press, Poole, United Kingdom.
- GRAY, A. P. 1972. Mammalian hybrids. 2nd ed. Commonwealth Agricultural Bureaux, Farnham Royal, Slough, United Kingdom.
- GRAY, J. E. 1852. Catalogue of the specimens of Mammalia in the collection of the British Museum. Part III: ungulata furcipedata. Trustees of the British Museum, London, United Kingdom.
- GRINDER, M., P. R. KRAUSMAN, AND R. S. HOFFMANN. 2006. *Equus asinus*. *Mammalian Species* 794:1–9.
- GROVES, C. P. 1974. Horses, asses and zebras in the wild. David and Charles, London, United Kingdom.
- GROVES, C. P., AND V. MAZÁK. 1967. On some taxonomic problems of Asiatic wild asses; with the description of a new subspecies (*Perissodactyla*; Equidae). *Zeitschrift für Säugetierkunde* 32: 321–355.
- GROVES, C. P., AND D. P. WILLOUGHBY. 1981. Studies on the taxonomy and phylogeny of the genus *Equus*. 1: subgeneric classification of the recent species. *Mammalia* 45:321–354.
- GRUBB, P. 2005. Order Perissodactyla. Pp. 629–636 in *Mammal species of the world: a taxonomic and geographic reference* (D. E. Wilson and D. M. Reeder, eds.). 3rd ed. Johns Hopkins University Press, Baltimore, Maryland.
- HARINGTON, C. R. 1980. Pleistocene mammals from Lost Chicken Creek, Alaska. *Canadian Journal of Earth Sciences* 17:168–198.
- HARINGTON, C. R., AND F. V. CLULOW. 1973. Pleistocene mammals from Gold Run Creek, Yukon Territory. *Canadian Journal of Earth Sciences* 10:697–749.
- HARRIS, R. B. 2008. Wildlife Conservation in China: preserving the habitat of China's Wild West. M. E. Sharpe Inc., Armonk, New York.
- HARRIS, R. B., AND D. J. MILLER. 1995. Overlap in summer habitats and diets of Tibetan Plateau ungulates. *Mammalia* 59:197–212.
- HAY, W. E. 1859. Notes on the kiang of Thibet (*E. kiang*). *Proceedings of the Zoological Society of London* 27:353–357.
- HAYSEN, V., A. VAN TIENHOVEN, AND A. VAN TIENHOVEN. 1993. Asdell's patterns of mammalian reproduction: a compendium of species-specific data. Cornell University Press, Ithaca, New York.
- HEDIN, S. A. 1922. Southern Tibet: discoveries in former times compared with my own researches in 1906–1908. Lithographic Institute of the General Staff of the Swedish Army, Stockholm, Sweden.
- HODGSON, B. H. 1842. Notice of the mammals of Tibet, with descriptions and plates of some new species. *Journal of the Asiatic Society of Bengal* 11:275–289.
- HODGSON, B. H. 1847a. Description of the wild ass and wolf of Tibet, with illustrations. *Calcutta Journal of Natural History* 7:469–477.
- HODGSON, B. H. 1847b. Note on the kiang. *Calcutta Journal of Natural History* 8:98–100.
- HUBER, T. 2005. Antelope hunting in northern Tibet: cultural adaptations to wildlife behaviour. *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* 33:5–17.
- HUMBERT-DROZ, B., AND S. DAWA (EDS.). 2004. Biodiversity of Ladakh: strategy and action plan. Sampark, New Delhi, India.
- INTERNATIONAL SPECIES INFORMATION SYSTEM. 2008. Zoological information management system. International Species Information System, Eagan, Minnesota. www.isis.org, accessed 28 May 2008.
- JANIS, C. 1976. The evolutionary strategy of the Equidae and the origins of rumen and caecal digestion. *Evolution* 30:757–774.
- KINLOCH, A. 1869. Large game shooting in Thibet and the north west. Harrison and Sons, London, United Kingdom.
- KLINGEL, H. 1975. Social organization and reproduction in equids. *Journal of Reproduction and Fertility, Supplement* 23:7–11.
- KLINGEL, H. 1977. Observations on social organization and behaviour of African and Asiatic wild asses (*Equus africanus* and *Equus hemionus*). *Zeitschrift für Tierpsychologie* 44:323–331.
- LESLIE, D. M., JR., AND G. B. SCHALLER. 2008. *Pantholops hodgsonii*. *Mammalian Species* 817:1–13.
- LINKLATER, W. L., E. Z. CAMERON, E. O. MINOT, AND K. J. STAFFORD. 1999. Stallion harassment and the mating system of horses. *Animal Behaviour* 58:295–306.
- LYDEKKER, R. 1904a. Note on the wild ass of Mongolia. *Proceedings of the Zoological Society of London* 1:431–432.
- LYDEKKER, R. 1904b. Notes on the specimens of wild asses in English collections. *Novitates Zoologicae* 11:583–596.
- MAZÁK, V. 1962. Spring moult in *Equus hemionus kiang* Moorcroft (1841) and a contribution to the phylogenesis of moulting in the subfamily Equinae (*Perissodactyla*, Mammalia). *Zoologischer Anzeiger* 168:164–170.
- McFADDEN, B. J. 1992. Fossil horses: systematics, paleobiology, and evolution of the family Equidae. Cambridge University Press, Cambridge, United Kingdom.
- MCNAUGHTON, S. J. 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs* 55:259–294.
- MILLER, D. J., AND G. B. SCHALLER. 1996. Rangelands of the Chang Tang Wildlife Reserve in Tibet. *Rangelands* 18:91–96.
- MOEHLMAN, P. D. 1998. Feral asses (*Equus africanus*): intraspecific variation in social organization in arid and mesic habitats. *Applied Animal Behaviour Science* 60:171–195.
- MOORCROFT, W. 1827. On the Purik sheep of Ladakh; and some other animals, principally of the goat kind: with general observations on the country of Ladakh, etc. *Transactions of the Royal Asiatic Society of Great Britain and Ireland* 1:49–55.
- MOORCROFT, W., AND G. TREBECK. 1841. Travels in the provinces of Hindustan and the Panjab; in Ladakh and Kashmir; in Peshawar, Kabul, Kunduz, and Bokhara; from 1819 to 1825. John Murray, London, United Kingdom.
- NAMGAIL, T., S. BAGCHI, C. MISHRA, AND Y. V. BHATNAGAR. 2008. Distributional correlates of the Tibetan gazelle *Procapra picticaudata* in Ladakh, northern India: towards a recovery program. *Oryx* 42:107–112.
- NEUMANN-DENZAU, G., AND H. DENZAU. 2003. The southern kiang *E. kiang polyodon*. *Journal of the Bombay Natural History Society* 100:322–340.
- PAKLINA, N. V., AND C. VAN ORDEN. 2003. The current state of kiang (*Equus kiang*) population in the southwestern part of its range. *Zoologicheskyy Zhurnal* 82:413–416.
- PFISTER, O. 2004. Birds and mammals of Ladakh. Oxford University Press, Oxford, United Kingdom.
- POHLE, C. P. 1991. Zur neueren Geschichte der Kiang-Haltung in Tiergärten außerhalb Chinas. *Der Zoologische Garten* 61: 263–266.
- PREJEVALSKY [PRZEWAŁSKI], N. 1876. Mongolia, the Tangut country, and the solitudes of northern Tibet: being a narrative of three years' travel in eastern high Asia. Sampson, Low, Marston, Searle and Rivington, London, United Kingdom (translated by E. D. Morgan from original notes).
- RASOOL, G. 1992. Tibetan wild ass—verging on extinction. *Tiger Paper* 19:16–17.

- ROCKHILL, W. W. 1895. Big game of Mongolia and Tibet. Pp. 255–277 in *Hunting in many lands. The book of the Boone and Crockett club* (T. Roosevelt and G. B. Grinnell, eds.). Harper & Brothers, Publishers, New York.
- RUBENSTEIN, D. I. 1989. Life history and social organization in arid adapted ungulates. *Journal of Arid Environment* 17:145–156.
- RUBENSTEIN, D. I. 1994. The ecology of female social behaviour in horses, zebras, and asses. Pp. 13–28 in *Animal societies: individuals, interactions, and organization* (P. Jarman and A. Rossiter, eds.). Kyoto University Press, Kyoto, Japan.
- RYDER, O. A., AND L. G. CHEMNICK. 1990. Chromosomal and molecular evolution in Asiatic wild asses. *Genetica* 83:67–72.
- SCHÄFER, E. 1937. Zur kenntnis des kiang (*Equus kiang* Moorcroft). *Der Zoologische Garten* 9:122–139.
- SCHALLER, G. B. 1998. *Wildlife of the Tibetan steppe*. University of Chicago Press, Chicago, Illinois.
- SCHALLER, G. B., A. KANG, T. D. HASHI, AND P. CAI. 2007. A winter wildlife survey in the northern Qiangtang of Tibet Autonomous Region and Qinghai Province, China. *Acta Theriologica Sinica* 27: 309–316.
- SCHALLER, G. B., Z. LU, H. WANG, AND T. SU. 2005. Wildlife and nomads in the eastern Chang Tang Reserve, Tibet. *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* 33:59–67.
- SCHALLER, G. B., J. REN, AND M. QIU. 1991. Observations on the Tibetan antelope (*Pantholops hodgsoni*). *Applied Animal Behaviour Science* 29:361–378.
- SHAFIQ, M. M., AND A. ALI. 1998. Status of large mammal species in Khunjerab National Park. *Pakistan Journal of Forestry* 48: 91–96.
- SHAH, N. 2002. Status and action plan for the kiang (*Equus kiang*). Pp. 72–81 in *Equids: zebras, asses and horses. Status survey and conservation action plan* (P. D. Moehlman, ed.). International Union for Conservation of Nature and Natural Resources/Species Survival Commission, Equid Specialist Group, Gland, Switzerland.
- SHARMA, B. D., J. CLEVERS, R. DE GRAAF, AND N. R. CHAPAGALN. 2004. Mapping *Equus kiang* (Tibetan wild ass) habitat in Surkhang, Upper Mustang, Nepal. *Mountain Research and Development* 24: 149–156.
- SMITH, A. T., AND Y. XIE. 2008. *A guide to the mammals of China*. Princeton University Press, Princeton, New Jersey.
- TEGETMEIER, W. B., AND C. L. SUTHERLAND. 1895. *Horses, asses, zebras, mules, and mule breeding*. Horace Cox, London, United Kingdom.
- TRUMLER, E. 1959. Die unterarten des kiangs, *Hemionus kiang* (Moorcroft, 1841). *Säugetierkundliche Mitteilungen* 7:17–24.
- TSERING, D., J. FARRINGTON, AND K. NORBU. 2006. Human–wildlife conflict in the Chang Tang region of Tibet. *World Wide Fund for Nature (WWF) China–Tibet Program*, Lhasa, Tibet, China.
- WANG, X., AND R. S. HOFFMANN. 1987. *Pseudois nayaur* and *Pseudois schaeferi*. *Mammalian Species* 278:1–6.
- WANG, Y. X. 2002. *A complete check-list of mammal species and subspecies in China: a taxonomic and geographic reference*. China Forestry Publishing House, Beijing, China.

Associate editors of this account were DAVID M. LESLIE, JR. and PAMELA R. OWEN. COLIN GROVES and IGOR PAVLINOV reviewed the synonymy. Editor was MEREDITH J. HAMILTON.