

Sex differences in ecology of wild yaks at high elevation in the Kekexili Reserve, Tibetan Qinghai Plateau, China

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Extreme high and low altitudes and polar environments constrain the distributional limits of terrestrial mammals. In Central Asia, vegetation on the Tibetan Plateau is limited at elevations above ~5,500 m. Although aspects of the spatial ecology of ungulates are known across many ecosystems, logistical challenges slow the development of knowledge at the upper edge of life. We studied components of the distributional ecology of wild yaks (*Bos mutus*) in early winter 2012. Males and females occurred above 5,000 m, but the sexes differed socially and ecologically. On average, female groups were about 15 times larger, about 100 m higher (mean elevation 4,875 m), and in wetter or more rugged topography than males. Although females with and without young did not vary in elevation, groups with calves occurred more often in habitats with steeper slopes. An ecological surrogate and congeneric, the closely related North American bison (*Bos bison*), also exhibits social and ecological differentiation where males occurred historically at high elevation above tree-line habitats in the Rocky Mountains. What distinguishes the present ecology and conservation of wild yaks from bison is that opportunities persist for wide-ranging yak populations across unfenced landscapes in remote protected regions of the Tibetan Qinghai Plateau.

Key words: bison, *Bos mutus*, group size, high elevation, sex ratios, sex segregation, yak

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Extremes in elevation or latitude tend to limit the distribution of life (Darwin 1859; Merriam and Steineger 1890; Mathews 1915). Along the periphery of such environments, little is known about how the sexes adjust to proximate conditions despite much attention to patterns of sexual segregation (Bowyer et al. 1996; Main et al. 1996; Myserud 2000; Bowyer 2004). In Asia, the largest mammal of high elevation is wild yak (*Bos mutus*—Smith and Xie 2008), an endangered species that occurs only in the remote Tibetan Qinghai Plateau (Schaller 1998; Schaller et al. 2007; Harris and Leslie 2008). Altitudinal distributions of yaks have variously been described from 3,000 m to almost 6,000 m (Harris and Loggers 2004; Leslie and Schaller 2008), although in historic times yaks occurred at lower elevation in the less lofty Altay Range of western Mongolia (Olsen 1990). Once described as inhabiting

“the coldest, wildest, and most desolate [treeless] mountains” (Blanford 1888: 491) and “northwards to the Kuenlun, at elevations between 14,000 and 20,000 feet”; (Lydekker 1913: 32), little remains known about yak behavior or patterns of grouping at the limits of plant growth. Enhancing knowledge about ecological use of high-elevation habitats will be useful not only because physical changes induced by rapid glacial melting in the Tibetan–Himalayan system is among the fastest across terrestrial zones (IPPC 2007; Qiu 2008), but even fragmentary gains in understanding spatial uses of the 2 sexes can strengthen conservation programs.



In the tribe Bovini, yaks occur in 1 of 5 genera (*Bison*, *Bos*, *Bubalus*, *Pseudoryx*, and *Syncerus*—Grubb 2005), but only yaks and bison (*Bos bison*) are exposed to extremes in cold. As early as 1790, the 2 species were considered highly similar (Bewick 1790) and, given our contemporary knowledge, historical, ecological, and conservation parallels are now evident. For instance, close genetic affinities testify to classification at a generic level (Leslie and Schaller 2008), with reproductive compatibility demonstrable by hybridization in captivity (Archibald 1927). Yaks and bison are also the largest ruminant grazers in either Asia or North America, they seem to fulfill analogous ecological roles, and both likewise experienced excessive harvest (Berger and Cunningham 1994; Schaller 1998). Whether male and female yaks differ in habitat use in a fashion similar to that documented for bison (Post et al. 2001) is unclear but finds of contemporary bison skulls in alpine zones of the Rocky Mountains (Cannon 2007) may be reflective of congruence in the use of high-elevation environments.

Primary factors that affect how a species uses its habitat are seasonality, sex, and the presence of offspring (Clutton-Brock et al. 1982; Schaller 1998; Bowyer and Kie 2004, 2006). Among yak females, we expected calf presence to affect habitat use because, as shown for other species, vulnerability of young to predation and heightened demands of lactation intensify ecological trade-offs (Berger 1979, 1991). Differences in habitat choice by males and females also affect their enumeration because of possible variation in visibility (Bowyer 2004), an issue of evolutionary and practical relevance. For instance, in sexually dimorphic species like yak and as shown for bison, the costs of intermale competition could result in greater male mortality and hence biased adult sex ratios (ASR) that favor adult females (Darwin 1859; Berger and Gompper 1999). In addition, from a conservation perspective it is important to document ASR and then establish whether variation in ASR arises more so from immediate proximate factors such as predation or poaching, or perhaps is the simple result of sampling bias.

Our purpose here is to describe intersexual differences in land use in yaks by concentrating on ecological and social aspects of high-elevation habitats and altitudinal ranges during winter.

Additionally, given the similarities between yak and bison we contrast the putative partitioning of space and time in yak with those of bison. Specifically, we predicted that male and female yaks would differ in use of elevation and topography, and that among female groups those with and without calves would differ ecologically.

MATERIALS AND METHODS

Study area.—We conducted our fieldwork in the 45,000-km² Kekexili National Nature Reserve on the Tibetan Qinghai Plateau (Fig. 1) from 25 November 2012 to 9 December 2012. Elevations range from ~4,300 to 6,900 m. Wildlife has rebounded as poaching has decreased during the last 2 decades

(Schaller 1998; Schaller et al. 2007); all native mammals still persist although population estimates lack for most, and the status of species like argali (*Ovis ammon*) appear precarious (Harris and Loggers 2004; Schaller 1998, 2012). Kekexili is broadly centered among other large reserves including Chang Tang (~280,000 km²), Arjinshan (~45,000 km²), West Kunlun (~30,000 km²), Mid Kunlun (~32,000 km²), and Sanjiangyuan (152,000 km²), a protected network area about the size of Kenya, or Montana and Nebraska combined. Some of this region supports nomadic herders, resident humans, and their livestock but the northern Kekexili lacks nomads and livestock. In conjunction with Arjinshan, it represents an important conservation area for wild yak (Leslie and Schaller 2008; Buzzard et al. 2010).

We covered 1,097 km on unimproved dirt roads and in cross-country travel in and to the south of the Kunlun Mountains, following routes where we had some familiarity. We had 2 groups of 3 observers driving transects and scanning for yaks, with data recorded on group size, composition, nursing activity, and distance to and direction from the vehicle. When spotting yaks in groups larger than about 7, we often approached with stealth by foot to enable complete counts and identification by sex and age and for behavioral observation (see below). Our route traversed 3 major lakes—Hoh Xil, Zhuonai (Zonag), and Kusai (Hoh Sai). Temperatures during the fieldwork were from -7°C to -32°C, and most days were windy.

Habitat classification and spatial data.—Key habitats in our study area included alpine meadows that were dominated by sedges of *Kobresia* spp., forbs, and grasses (Schaller 1998; Sheehy et al. 2006; Schaller et al. 2007). Alpine steppe (also called plains) was the most frequently encountered habitat vegetation type where *Stipa* dominated; grasses such as *Poa*, *Agropyron*, and *Festuca* also occurred. We categorized habitat operationally on the basis of topographical structure as plains, undulating hills, or slopes (Fig. 2). Although some gradation among these categories exists, areas used by yaks were clearly discernible and independently verified using measures of degree of incline (as described below). Alpine meadows appeared most abundant in undulating hills or on slopes.

All locations for yaks were initially displayed with ArcGIS Desktop version 10.0 software (Environmental Systems Research Institute [ESRI] 2011) and spatial metrics projected to WGS 1984 Universal Transverse Mercator zone 46 north so that they encompassed the study area. We mapped this region (Fig. 1) with Landsat Global Land Survey (GLS) shaded base maps (available as online coverage through the ESRI Image Service) and used natural-color, 15-m resolution pan-sharpened Landsat images, enhanced with topographic hill shading and color balancing with United States Geological Survey and the National Aeronautics and Space Administration Landsat images (<http://imagery.arcgisonline.com/arcgis/services/LandsatGLS/LandsatShadedBasemap/ImageServer>).

Slope usage for each yak group location was estimated from digital elevation models (DEMs) and consisted of Shuttle Radar Topography Mission (<https://lta.cr.usgs.gov/SRTM2>)

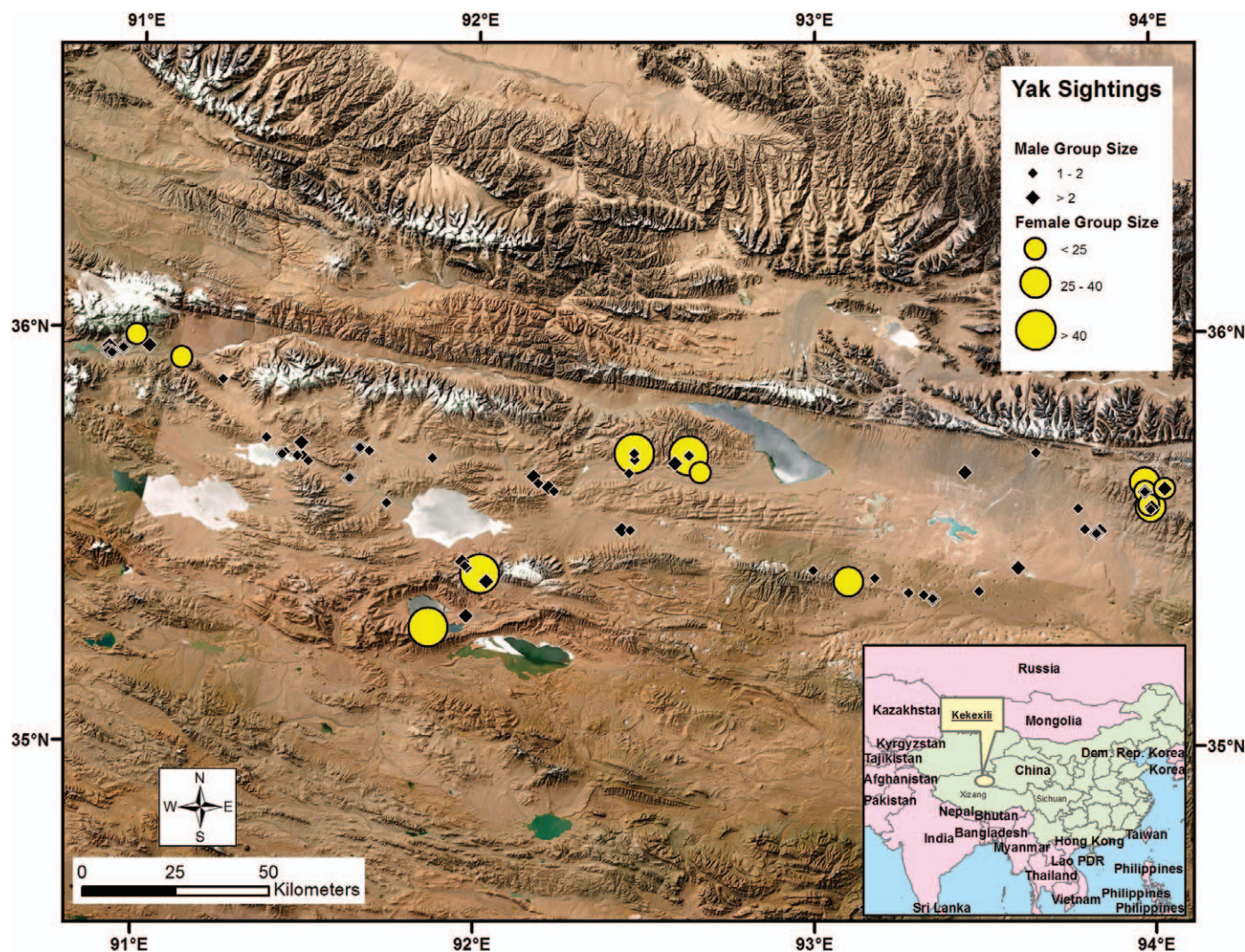


FIG. 1.—Overview of wild yak (*Bos mutus*) study area in northeastern Kekexili Nature Reserve in the western edge of the Qinghai Province, generalized transect routes, and sex-specific locations by group size in early winter 2012.

images that are 3 arc-second in resolution (approximately 90 m), collected in 2000 and available in 1°-tile formats. Metrics of the inclines were then derived from elevation data using the slope function in ArcGIS Spatial Analyst, and steepness expressed in degrees from horizontal (0–90). Bilinear interpolation was used to reproject and resample the raster to provide more reliable estimates of individual incline values (Burrough and McDonnell 1998; ESRI 2011) with output cell sizes for slope surfaces at approximately 100 m.

Groups of yaks were assigned to 1 of the previously described 3 topographies and, from Global Positioning System coordinates, elevation and incline estimated. We subsequently checked the extent to which our assessment of slopes, undulating hills, and plains reflected differences in steepness (i.e., incline). Our output values of incline were conservative and underestimated steepness because data were from sites where we drove and hiked (e.g., not randomly selected points because we avoided displacing yaks from the precise locations where they fed), and then projected to yak locations.

Field observations.—Our observational methods were in accordance with American Society of Mammalogists guidelines for research (Sikes et al. 2011) and approved by the University of Montana institutional animal care committee (#036-11). We defined a group as one or more animals within ~50 m of another and moving with cohesiveness (Bowler et al. 2007).

Because distances of observation could be as great as 5 km, we were not always certain of group composition, although groups with females tend to be significantly larger than those with males (Miller et al. 1994; Leslie and Schaller 2008). We tallied a total of 108 groups, 15 of which contained identifiable females, 51 of which contained identifiable males, and 42 of which sex was not confirmed. We assumed groups of 7 or less were males, and checked this assumption by contrasting group sizes between those we documented with known males and those with presumptive males. All female groups were > 7. Had differences between our putative male groups existed, then our assumption would of course be violated. Means and 95%

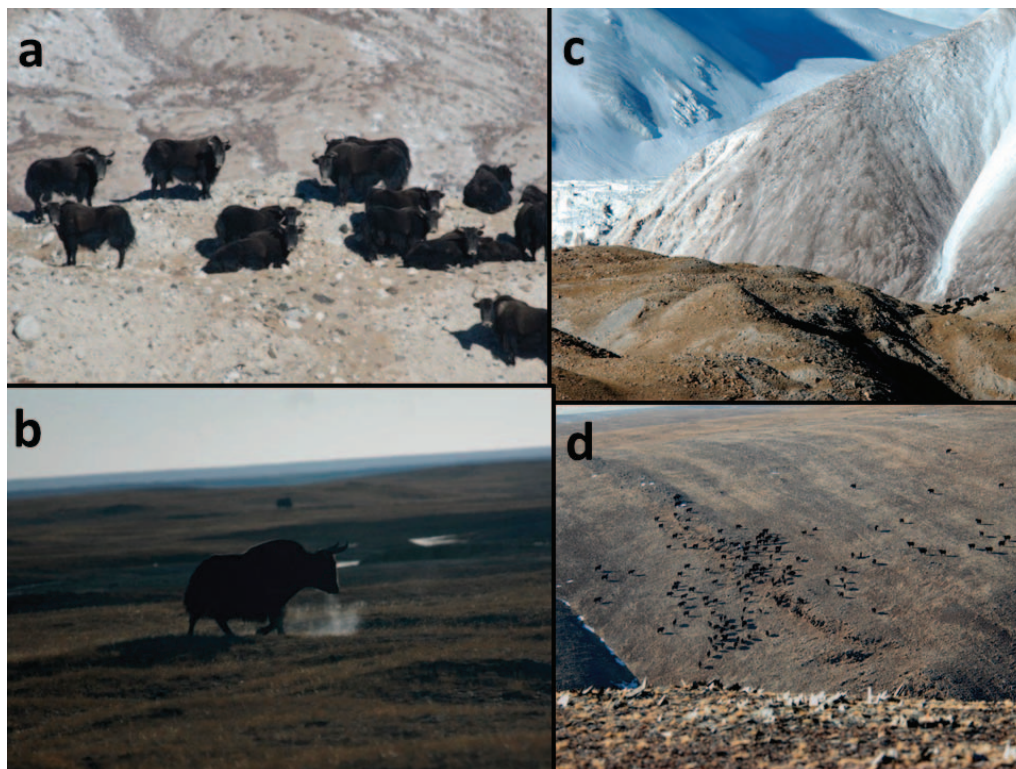


FIG. 2.—a) Female yak (*Bos mutus*) group. b) Two solitary males on plains (alpine steppe). c) Females and young at juncture of crest on slopes above moraine (lower right) at base of $\sim 422 \text{ km}^2$ Bukubada Glacier. d) Large mixed group (mostly females and juveniles) on undulating hills.

confidence intervals (*CI*) of known and putative male groups were 2.56 (1.97 to 3.21) and 2.59 (1.95 to 3.17); these did not differ when compared by *t*-test ($P = 0.947$; $t_{1,93} = 0.066$).

Because of an interest in females, we approached such groups on foot, and classified membership as adult, young-of-the-year (i.e., calves), or juvenile (yearling or 2-year-old) to the extent possible. Larger groups typically contained young 2–3-year-old males that were difficult to recognize, especially at a distance, and such uncertainty affects estimates of ASR. Calves, on the other hand, were always distinguishable. Similar approaches for group classification have been applied to other ungulates (Schroeder et al. 2010) including bison, which were more approachable than yaks and enabled distinction between immature males and females (Berger and Cunningham 1994; Bowyer et al. 2007). We also used scan sampling to record behavioral events including nursing, which we corrected for observation time/calving/group.

Analyses.—We calculated measures of central tendency and variance for group size and inclines (using degree slope), and used analysis of variance to compare association with habitat types. Treatments were sex or habitat as appropriate with degree of slope as the response variable. Differences in elevation use or group size were examined by *t*-test or, when the assumption of homogeneity of variance violated, a Mann–Whitney *U*-test. Groups, rather than individuals, were treated as independent sampling units. To check whether our assignment of groups to habitats would have produced results similar to those had individuals been considered

instead of groups, we checked for an association between measures with groups and with individuals. We modeled x versus y using linear regression, and weighted group size by percent number of individuals (x) against the percentage of group sizes by habitat (y). We avoided the possibility of pseudoreplication in our counts because our drive transects were unidirectional and therefore circumvented recounting of the same animals. If we were uncertain that a group had been censused previously or perhaps moved to within our census zone within 24 h, it was censored from analyses.

We explored the extent to which females with and without young varied in mean elevation with a *t*-test. We followed up on this to examine the exact probability that nursing events would occur at progressively higher elevations—an expectation only if elevation is related in a positive way with relatively moister conditions and if mothers were associated with these resources for milk production in early winter. The probability (P) that nursing would occur at only the lowest elevation (when standardized for observation time/calving/group) was estimated as:

$$P = \frac{N!}{k!(N-k)!} (p^k)(q^{N-k})$$

where N is the total number of groups with calves observed, k is frequency that nursing occurred at an elevation greater than the minimum, p is the probability that nursing could occur at any given elevation, and q the probability that nursing did not occur at a predicted location.

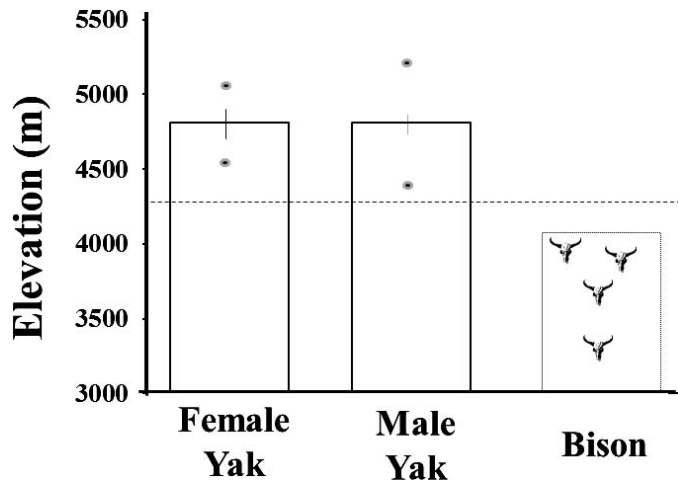


FIG. 3.—Mean (and 95% CI) elevation (m) of use by female ($n = 15$) and male ($n = 93$) yak (*Bos mutus*) groups in Kekexili Nature Reserve. Dotted line is approximate lowest elevation in the reserve. Black circles are maximum and minimal elevations used by yaks. Skulls depict extreme high-elevation sites used by male bison (*B. bison*) in 4 states of the Rocky Mountains as described in text.

RESULTS

The sexes differed ecologically and socially. Female groups occurred at only slightly greater mean elevation (4,874.80 m, 95% CI = 4,794.62 to 4,954.98 m, $n = 15$) than male groups (4,781.32 m, 95% CI = 4,746.01 to 4,816.64 m, $n = 93$; $t = 1.997$, $P < 0.048$; Fig. 3). Variance in elevation use was less in males, although males were found at an absolute greater range and at higher elevation than females (5,194 versus 5,107 m; Fig. 3).

The sexes used habitats differently; male groups were 3 times more frequent on lower-elevation plains, whereas female groups were primarily on slopes and undulating hills (Fig. 4). Group size and the number of groups were highly associated with habitat: ($y = 0.609x + 13.25$; $r^2 = 0.884$, $P < 0.01$), suggesting that our conclusions about sex differences are unaffected whether assessed by groups or number of individuals.

With respect to habitat, the 3 structurally classified topographies differed in slope, as calculated from DEM. Mean angle of inclination varied: plains (2.89, standard error of the mean [SEM] = 0.69), undulating hills (3.55, SEM = 0.48), and slopes (6.17, SEM = 0.43; $F_{2,106} = 16.86$; $P < 0.0001$). Sex also was associated with steepness ($F_{1,106} = 31.13$; $P < 0.001$), and females consistently occurred on more precipitous terrain than males (Fig. 4b). An interaction between habitat and sex was not evident ($F_{1,2} = 0.395$; $P = 0.249$).

Mean group size for females (34.27, 95% CI = 7.60 to 60.94) was about 15× larger than that for males (2.41, 95% CI = 1.27 to 3.26; $z = -5.83$; $P < 0.001$). The largest female group contained ~210, and for males it was 11. Median group size for females was 23 and for males 1. Two-thirds of the 93 male groups consisted of 1–2 individuals. Despite differences in grouping and spatial distribution, the adult sex ratio approached parity (0.95:1.0, adult males : adult female; $n = 472$).

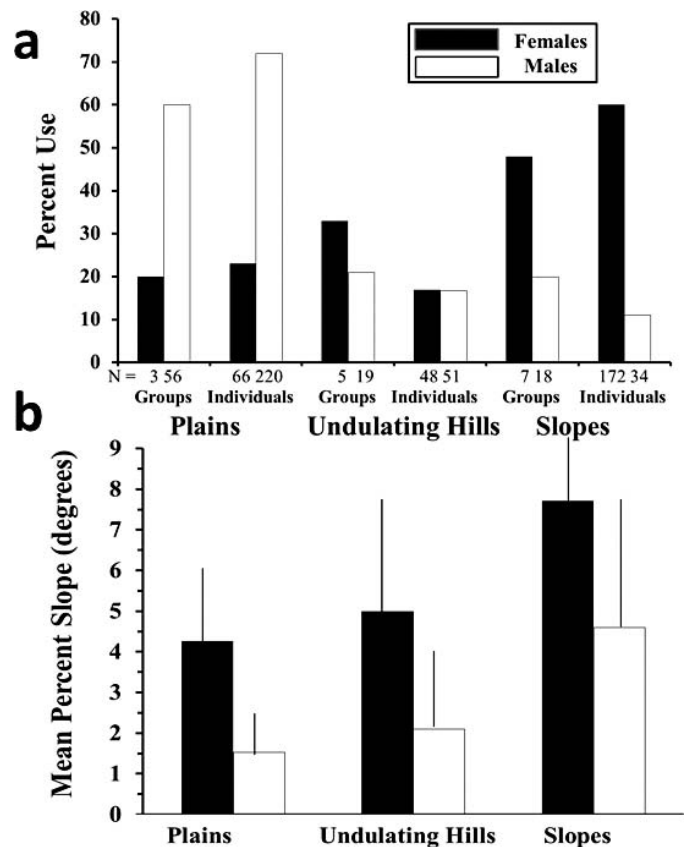


FIG. 4.—a) Relative percent use of 3 structurally classified topographies by independent groups and by cumulative total of individual yak females and males as defined in text. b) Mean slope as determined by DEM groups of female and male groups by topography. Bars are SEM.

Mean elevation for groups of females with calves (4,888.11 m, SEM = 48.77 m, $n = 9$) and without (4,824.5 m, SEM = 51.18 m, $n = 6$) failed to differ ($t = 0.871$, $P = 0.40$; Fig. 5). In contrast, female groups with calves were in undulating hills or on steeper slopes more frequently than those lacking calves ($P = 0.011$), and among the 4 groups on steppes none had calves (Fig. 5). Although we noted 9 total groups with calves (Fig. 5), observations for nursing behavior occurred only among 8. Suckling bouts occurred at greater mean elevation (4,877.4 m, SEM = 52.44, $n = 7$) than the single group with calves in which suckling was not observed (4,587 m). The binomial probability that suckling events would occur at elevations higher than nonsuckling was 0.03; all such behavior was in alpine meadows or on high ridges.

DISCUSSION

Our finding of parity in the adult sex ratio of wild yaks was unanticipated given expectations from evolutionary theory. Whether it stemmed from survey methods, sampling bias, or something else is unclear. Yaks, like other large Artiodactyls, are sexually dimorphic with males about one-third larger than females (Leslie and Schaller 2008). Among dimorphic

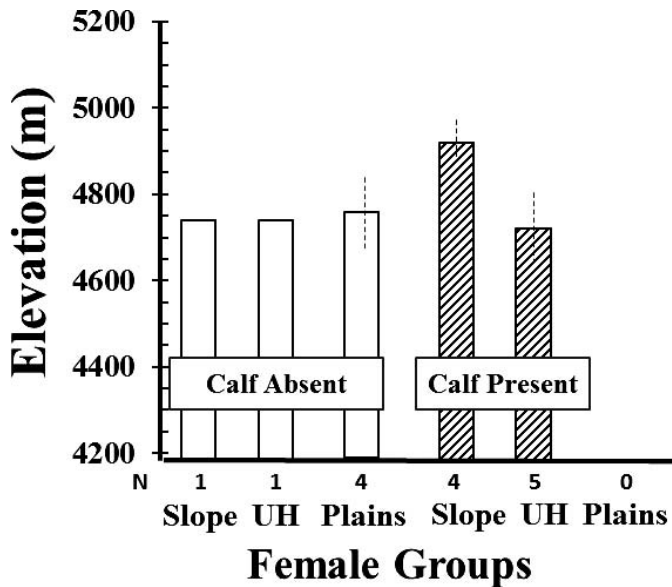


FIG. 5.—Relationships among wild yak (*Bos mutus*) female groups, habitat (UH, undulating hills), and elevation (m). Columns reflect elevation of groups with and without calves.

ungulates males typically incur greater mortality than females (Clutton-Brock et al. 1982; Berger and Gompper 1999) and the sexes tend to segregate throughout much of the year (Bowyer 2004; Bowyer and Kie 2004). On the Tibetan Plateau, for example, chiru (*Pantholops hodgsonii*) fit both patterns (Schaller and Ren 1988), as also noted elsewhere for North American bison (Berger and Cunningham 1994). For Kekexili yaks, however, as suggested by our results, there was concordance in ASR.

Such observed parity in ASR could arise if the assumption of intrasexual mating costs is wrong (which seems unlikely) or mitigated by abundant food, mild winter conditions, or differences in dispersal. Our sampling, which represented a single season, might have unwittingly resulted in greater detection of males because bulls appeared less skittish than females. It is also possible that we inadvertently sampled areas of relatively large male wintering concentrations, or missed females because of occurrences in topographically rugged areas. Other limitations of our sampling may have affected our interpretation of sex ratio dynamics. As mentioned, 2–3-year-old males are often difficult to ascertain, a problem that will affect the enumeration of young-to-female ratios to an unknown extent. Finally, like bison, yaks were strongly persecuted from relatively lower elevation and more accessible areas (Schaller 1998). Consequently, it is unclear whether our results reflect yaks of remote areas using habitats in ways they did historically or if Kekexili animals modified their current habitat use due to poaching pressures during the latter 20th century.

The sexes of wild yaks showed great differences in sociality. Mean group size of Kekexili males was 2.4, a value identical to the 2.4 reported for another large bovid, wood bison (*B. b. athabasca*)—Melton et al. 1989), and similar to that for plain's

bison (< 3) at Badlands National Park; median group size for bison males (Berger and Cunningham 1994) and yak bulls was 1 each. Small group sizes and sexual segregation were noted historically among these putative ecological analogues more than 125 years ago: “The old bulls (*bison*) . . . and this habitual separation of the large (*female*) herd into numerous small herds seems to be an instinctive act” (Allen 1875:463), and “the cows (*yak*) are generally to be found in herds varying in numbers from ten to one hundred, while the old bulls are for the most part solitary or in small parties of three or four” (Kinloch 1892:118).

Our findings of variation in yak group size parallel other reports of larger groups among females than males (Kinloch 1892; Schaller and Gu 1994; Harris and Loggers 2004; Schaller et al. 2007). What differs, however, is our provision of data on the extent to which usage of elevation and varied topography by female groups distinguishes them from male groups. Males were found at absolute higher altitudes than females but males were also less variable in use of elevation (Fig. 3). Whether the slight overall differences in mean elevation use by males and females are ecologically important is doubtful.

North American bison, which are typically considered a species of the Great Plains, may parallel yaks ecologically in areas where they use high-elevation sites (Fig. 3). Male skulls have been recovered from ~3,550 to 3,900 m in Colorado (Beidelman 1955; Lee and Benedict 2012), 2,897 to 3,659 m in Wyoming (Fryxell 1928), 3,200 m in Montana (Pattie and Verbeek 1967), and 3,840 m in Utah (Cannon 2007). Other than a group of 15 late Pleistocene bison (*B. antiquus*) at 2,548 m in Colorado that lacked evidence of calves (Kornfeld et al. 1999), females occur far lower in elevation than males (Cannon 2008). In grassland habitats far from mountainous terrain and where bison densities were historically the greatest, variation in elevation by the sexes was probably slight, as noted for yaks. Nevertheless, at a prairie site in Montana, male bison used elevations ~50 m higher than females (Mooring et al. 2005), although the fencing of pastures obviously constrained movements.

Sex differences in habitat use clearly result from trade-offs involving predation, nutrition, parental investment, and gastrointestinal capacity (Bowyer 2004; Main et al. 1996). That male and female bison use topographic features differently is partially explained by choices of food (Post et al. 2001) but not exclusively. In Badlands National Park (South Dakota), for instance, lactating female bison were more frequently in open areas where visibility was better, in contrast to nonlactating females that used ravines and rolling hills (Berger and Cunningham 1994). If predation by wolves (*Canis lupus*) focused more on juveniles than other age classes, then maternal groups would likely be less vulnerable in open areas with associated better visibility.

Unlike bison, female yaks used rugged terrain more frequently than males (Figs. 2 and 4), perhaps as an antipredator tactic, a suggestion that gains some traction given the differences between lactating yak females and nonlactating ones (the latter being on steppes). We witnessed only 3

interactions between wolves and yaks, all on steppes. One was a close approach to a solitary bull that grew vigilant in Kekexili; another was in Chang Tang and involved an unsuccessful predation attempt by 5 wolves on a group with calves that fled to adjacent mountains (Schaller 1998). Finally, a group with a yearling was killed by 4 wolves on a frozen lake in steppes (Zhao Xin Lu, pers. comm.).

Predation alone cannot account for distributional patterns because female wild yaks certainly derive nutritional benefits by their primary choices of habitat with streams, snowmelt, and slope. In domestic yaks, lactating females preferentially consume sedges (Cincotta et al. 1991), where crude protein follows a high-elevation gradient (Ding et al. 2006). Because alpine meadows have higher standing plant biomass and, with their underlying moisture, hold nitrogen longer than regions lacking in water or snow (Schaller 1998), these habitats may be differentially attractive to lactating wild yaks, a hypothesis that we did not test.

Despite general ecological similarities between yaks and bison, striking differences also exist. Bison were more catholic in modern distribution, having experienced ambient temperatures and habitats from the Chihuahu Desert in northern Mexico to the boreal of northern Canada (Soper 1941; Sanderson et al. 2007), whereas wild yaks were restricted to cold climes of the Tibetan Plateau, Mongolia, and perhaps the Altay-Sayan region toward Baikal in Russia (Olsen 1990; Schaller 1998). Given the dramatic variation in plant productivity and biomass between high-elevation deserts and mountains of the Tibetan Plateau and temperate North American grasslands, it is unclear whether the ecological partitioning of space and time in yak males and females would parallel that for bison.

Understanding the extent to which, and why, intra- and intersexual variation in the distribution of wild yaks exists in the absence of spatial restrictions has relevance from 2 angles. First, the Tibetan Plateau is a relatively simple system that can enable insights about altitudinal limits of life for a large-bodied species. Because neither habitat destruction nor fragmentation is a major issue here, opportunities to learn about proximate causes of segregation from abiotic and biotic perspectives exist. Second, of fundamental importance is that conservation requires knowledge of species distribution and abundance. Although poaching has been reduced (Schaller 2012), conservation of wild yaks will require vigilance about effects of incursions into their remote habitats. Threats might stem from food competition or from hybridization with domestic yaks (Schaller and Gu 1994; Harris and Leslie 2008). Poaching might increase. Increased climate warming will certainly alter habitats. Initially, perhaps, this will be in positive directions through increased glacial melt to supply or create alpine meadows or in less favorable ways by degrading lower-elevation sites through desiccation and the loss of permafrost. With continued deglaciation, however, preferred habitats will be diminished or lost. But, to know the extent to which any impacts force change will require knowing something about how the two genders use space.

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