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Dietary Overlap of Przewalski's Gazelle, Tibetan Gazelle, and Tibetan Sheep on the Qinghai-Tibet Plateau

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ABSTRACT We studied food composition and overlap among sympatric Przewalski's gazelle (*Procapra przewalskii*), Tibetan gazelle (*P. picticaudata*), and Tibetan domestic sheep (*Ovis aries*) in the Upper Buha River, Qinghai-Tibet Plateau, using microscopic fecal analysis. The 2 gazelles forage mainly on plants from Leguminosae and Compositae families and domestic sheep feed mainly on Gramineae and Cyperaceae. The dietary overlap index between the 2 gazelles and Tibetan domestic sheep increased from 0.43 to 0.58 during the plant-growing period to 0.76–0.77 during the plant-withering period, which indicated competition for foods intensified during the food-limited season. Although the 2 gazelle at e similar diets, they might avoid food competition by occupying different foraging areas. We suggest reducing numbers of overwintering Tibetan domestic sheep on pastures to lessen survival pressure on the endangered gazelles during winters. (JOURNAL OF WILDLIFE MANAGEMENT 72(4):944–948; 2008)

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As expansion of human and livestock populations continues, livestock often undergo competition with wild ungulates for food (Campos-Arceiz et al. 2004). Overgrazing by livestock can cause population declines in wild ungulates (Caughley and Sinclair 1994, Liu and Jiang 2004). Therefore it is important to determine dietary composition and overlap between wild and domestic ungulates and to maintain proper stocking levels of domestic and wild ungulates to support sustainable wildlife and ecosystem management (Schwartz and Ellis 1981, Caughley and Sinclair 1994, Harris and Miller 1995).

Przewalski's gazelle (Procapra przewalskii) and Tibetan gazelle (P. picticaudata) are 2 endemic ungulates to the Qinghai-Tibet Plateau (Yin and Liu 1993, Jiang and Wang 2001, Lei et al. 2003, Jiang 2004). Przewalski's gazelle only occurs around Qinghai Lake and has ≤300 individuals (Jiang et al. 1995, 2000). Przewalski's gazelle has been classified as Critically Endangered by the Species Survival Commission of the World Conservation Union (IUCN) since 1996 and has been a Category I (Endangered in China) National Protected Wild Animal Species in China since 1989 (Baillie and Groombridge 1996). Tibetan gazelle resides in fragmented habitat patches on the Qinghai-Tibet Plateau; however, the population is decreasing sharply and its range is rapidly shrinking (Schaller 1998, Zhang and Jiang 2006). Although it is listed as Low Risk in the IUCN Red List of Threatened Species, Tibetan gazelle is a Category II (Threatened in China) National Protected Wild Animal Species in China (Mallon and Kingswood 2003). The population declines of the 2 gazelles are caused by multiple factors, such as habitat fragmentation, pasture fencing, and over-hunting (Jiang et al. 1995, 2000; Ma and

Jiang 2006). Competition for food with Tibetan domestic sheep (*Ovis aries*) may be another important factor that limits survival of wild gazelles (Schaller 1998; Liu and Jiang 2002*a*, *b*, 2004).

Nomads still populate meadows and steppes on the Qinghai-Tibet Plateau, which shows that pastoral grassland production can be rational and efficient (Miller 1998). However, as human populations grow and living standards improve, the livestock stocking rate increases on meadows and steppes (Zhao and Zhou 1999). Because wild ungulates and domestic sheep share the same food resources, we need to know whether the 2 gazelles and domestic sheep compete for food, especially during the food-limited season. Additionally, Przewalski's gazelle and Tibetan gazelle are thought to be allopatric through most of their ranges, but Li and Jiang (2006) found that Przewalski's gazelle and Tibetan gazelle coexisted in the Upper Buha River Valley at the west end of the Qinghai Lake basin. Because the 2 gazelles are of the same genus and have similar body weight (Przewalski's gazelle, about 25 kg; Tibetan gazelle, <20 kg; Zheng 1994), it is necessary to explore how Przewalski's gazelle and Tibetan gazelle coexist in the same alpine ecosystem. Analysis of their dietary composition and food overlap will shed light on the coexistence mechanisms of the 2 species. Thus, 2 objectives of our study were 1) whether Przewalski's gazelle and Tibetan gazelle competed for food with Tibetan domestic sheep and 2) whether Przewalski's gazelle and Tibetan gazelle grazed different diets so as to avoid food competition.

STUDY AREA

We conducted our study in the Upper Buha River Valley, Tianjun County, Qinghai Province, China (36°53'30" to approx. 48°39'12"N, 96°49'42" to approx. 99°41'48"E),

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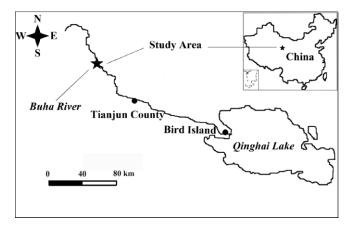


Figure 1. Location of the study area, Upper Buha River Valley, Tianjun County, Qinghai Province, China, where Przewalski's gazelle, Tibetan gazelle, and Tibetan domestic sheep coexist. Plant samples were collected from this region in 2005.

located in the northwest part of the Qinghai Lake watershed area and south of the Qilian Mountains (Fig. 1). Elevations ranged from 2,850 m to 5,826 m above sea level with an average elevation of 3,800 m. Local climate was characterized by dry, cold, and long winters, strong winds, high levels of solar radiation, and a short frost-free period. Mean annual temperature was -1.5° C; the extreme recorded low temperature was -40° C. Annual precipitation varied from 330 mm to 412 mm and most rain fell between June and September. Alpine meadow was the main vegetation in the study area. Shrubs were found along the Buha River Valley, which was the largest river flowing into Qinghai Lake. Four seasons were not clearly distinguished in the study area; however, June to September was the plant-growing period and October to the following May was the plant-withering period.

Focal populations of both Przewalski's gazelle and Tibetan gazelle, south of the Buha River, each contained about 100 individuals. The region was used as winter pastures by Tibetan pastoralists. About 10,000 Tibetan domestic sheep grazed in the area from October to May.

METHODS

We identified diets of gazelles and Tibetan domestic sheep with microscopic fecal analysis (Sparks and Malechek 1968, William 1969, Chen and Xiao 1989). We collected samples of 55 plant species from 17 families along a 5-km transect line that traversed all vegetation types of the study area in August 2005. We used these samples as references for identification of undigested plant tissue debris in the fecal samples under the microscope. We dried plant samples at 60° C to constant weights and then ground and sieved them over a 0.25-mm mesh. We made slides and photographed and identified morphological features (shape and size of stomata, cell wall structure, shape and size of cells, hairs, and trichomes) of each plant under the microscope in the laboratory.

We randomly collected fresh voided fecal samples of Przewalski's gazelle, Tibetan gazelle, and Tibetan domestic sheep after they left forage areas in June, July, and August, 2005 (plant-growing periods) and November, December 2005, and January 2006 (plant-withering periods). From each herbivore species, we collected \geq 3 samples during each week; overall we collected >30 samples during 10 weeks (3 samples/week) during each phenological period. We airdried all fecal samples and stored them in paper bags marked with species, location, vegetation type, and date. We pooled every 3 fecal samples collected during a week as one composite sample and analyzed composite samples with the microscopic techniques. We made 5 slides from each composite sample and microscopically examined 20 fields for each slide under 100× magnification.

We calculated dietary diversity on the basis of Shannon's (1948, eq 1) formula and used dietary diversity H' to indicate food niche breadth:

$$H' = -\sum (N_i/N) \times \ln(N_i/N)$$
(1)

where N is total number of identified plant fragments and N_i is number of individual fragments of plant i in all fecal samples.

We measured dietary overlap between each possible pair of the 3 herbivores with Pianka's index C (Pianka 1973):

$$C = \frac{\sum P_{ij} P_{ik}}{\sqrt{\sum P_{ij}^2 \sum P_{ik}^2}} \tag{2}$$

We calculated overlap among the 3 species:

$$C = \frac{\sum P_{ij}P_{jk}P_{il}}{\sqrt{\sum P_{ij}^2 \sum P_{ik}^2 \sum P_{il}^2}}$$
(3)

where P_{ij} , P_{ik} , and P_{il} are proportions of the *i*th partition of a given food in all fecal samples of species *j*, *k*, and *l*, respectively, and C = 0 means no overlap and C = 1 means complete overlap.

We used multivariate analysis of variance and *t*-test to test whether proportions of the main plant families (Leguminosae, Gramineae, Compositae, Cyperaceae) and species were similar in the diets of 3 herbivores (Campos-Arceiz et al. 2004). We used P = 0.05 to accept significant differences.

RESULTS

Over the whole year, Przewalski's gazelle ate 40 plant species from 14 families and Tibetan gazelle fed on 43 plant species from 16 families, whereas Tibetan domestic sheep ate 39 plant species from 15 families. Przewalski's gazelle had the most diverse diet (H' = 3.04-3.18), Tibetan domestic sheep had the least diverse diet (H' = 2.80-2.95), and Tibetan gazelle were intermediate (H' = 2.87-3.01) among the 3 species.

Proportions of the main plant families eaten differed during both periods among the 3 ungulates (plant-growing period: $F_{2,27} = 12.531$, P < 0.001; plant-withering period: $F_{2,27} = 12.771$, P < 0.001; Table 1). During the plant-growing period, Przewalski's gazelle grazed more on Leguminosae ($t_{18} = 13.412$, P < 0.001) and Compositae ($t_{18} = 5.703$, P < 0.001), and less on Gramineae ($t_{18} = 12.5703$).

Table 1. Dietary composition ($\dot{x} \pm SD$, %) of Przewalski's gazelle, Tibetan gazelle, and Tibetan domestic sheep in Upper Buha River, Qinghai-Tibet Plateau, using microscopic fecal analysis in 2005 and 2006. We divided seasons into 2 periods: June to September was the plant-growing period and October to next May was the plant-withering period. Multivariate analysis of variance was used to test differences between each species–period category.^a

	Przewalski's gazelle				Tibetan gazelle				Tibetan domestic sheep			
	Plant-growing		Plant-withering		Plant-growing		Plant-withering		Plant-growing		Plant-withering	
Food species	\bar{x}	SD	x	SD	\bar{x}	SD	x	SD	\bar{x}	SD	x	SD
Leguminosae	36.5A	4.2	27.6B	3.3	47.5C	8.2	33.2AB	3.5	7.1D	5.5	13.2D	5.1
Floriated astragalus, Astragalus floridus	9.4A	2.9	5.3CD	1.4	14.4B	4.1	8.7AC	2.1	1.7E	1.2	3.4DE	1.6
Poly-branched astragals, A. polycladus	7.2A	3.0	7.5A	1.1	7.2A	1.9	6.4A	1.4	1.1B	1.2	2.3B	3.0
Falcate whin, Oxytropis falcate	6.3A	2.8	3.2B	1.5	6.9A	1.6	5.7A	2.1	0.9B	1.1	1.9B	1.1
Golden whin, O. ochrocephala	6.8A	3.0	7.0A	2.1	11.8B	2.6	7.2A	1.6	1.3C	1.8	3.2C	2.4
Golden banner, Thermopsis lanceolata	6.8A	2.5	4.6AB	1.5	7.2A	3.8	5.3AC	1.0	2.1BC	2.7	2.4A	1.6
Gramineae	22.0A	3.1	29.2B	4.8	13.1C	4.5	26.1AB	4.6	62.1D	9.5	53.1D	7.0
Papery spikelets quitch, Littledalea spp.	1.1AB	1.0	1.5AB	1.2	0.8A	1.6	0.6A	1.1	5.8C	2.9	3.4B	1.4
Ewenki automomous banner, Elymus nutans	1.2A	1.2	1.8A	1.4	0.5A	0.8	1.7A	1.0	2.8AB	2.3	4.6B	2.0
Common leymus, Leymus secalinus	1.9A	1.5	2.3AB	1.4	1.1A	1.2	2.1AB	1.4	4.6BC	3.0	2.5AC	1.8
June grass, Koeleria cristata	1.8AB	1.8	1.0A	1.7	0.6A	0.9	1.9AB	1.8	6.1B	3.7	3.3AB	2.6
Fescue, <i>Festuca</i> spp.	4.2A	2.4	5.9A	2.6	3.8A	1.5	6.9A	2.9	11.5B	4.0	12.0B	3.5
Oat grass, Helictotrichon schellianum	3.1AB	1.1	2.6AB	1.4	1.5B	1.3	3.0AB	1.3	5.5A	2.4	4.9AB	3.1
Bluegrass, Poa pratensis	3.8B	1.4	5.2BD	1.3	1.5A	1.5	3.3AB	1.4	10.6CD	4.8	10.1C	2.7
Purple needlegrass, Stipa purpurea	4.9AD	2.0	8.9BC	2.2	3.2D	1.8	6.6AB	2.1	15.2C	6.6	12.4C	3.3
Compositae	16.9AB	2.8	19.8A	3.1	13.5B	3.1	17.1AB	1.7	5.5C	5.7	3.5C	2.6
Altai bule chrysanthemum,												
Heteropappus altaicus	5.6B	1.0	9.7A	1.5	6.5AB	3.5	8.6A	2.1	1.9C	1.8	0.6C	1.1
Short snow lotus, Saussurea eopygmaea	4.3AC	1.6	4.6A	2.0	2.2B	1.8	3.6AB	0.9	1.7B	2.0	2.0BC	1.9
Edelweiss, Leontopodium spp.	4.0A	2.0	3.1AB	1.5	2.6AB	1.8	1.4BC	1.1	1.0BC	1.6	0.3C	0.7
Sub-others	1.9AB	2.3	2.4A	1.8	2.2AB	1.4	3.5A	2.1	0.8B	1.1	0.5B	0.9
Cyperaceae	7.1A	2.0	10.6AB	2.1	8.5A	2.4	13.2B	3.6	17.8C	3.5	21.7C	4.1
Short kobresia, Kobresia humilis	4.8A	1.2	7.6AB	2.1	5.5AB	1.9	8.6B	2.7	13.0C	3.1	16.2C	3.9
Little kobresia, K. pygmaea	2.3A	1.3	3.0AB	1.8	2.9AB	1.3	4.6AB	1.6	4.8AB	2.4	5.5B	4.2
Others	17.5A	3.9	12.9AB	2.0	17.4A	4.4	10.4B	3.0	7.5B	5.9	8.4B	4.1
Gentian, Gentiana spp.	5.7A	1.3	1.3B	1.0	5.4A	2.6	1.6B	1.4	1.4B	2.4	0C	
Bifurcated potentilla, Potentilla bifurca	3.4AB	1.7	2.0BC	1.4	3.9A	1.2	0.8C	0.9	1.2C	2.3	1.4C	1.2
Bush cinquefoil, P. fruticosa	1.1A	1.0	1.7A	1.5	2.2A	1.5	2.9A	1.7	0.9A	1.6	2.4A	1.9
Tansy potentilla, <i>P. tanacetifolia</i>	2.4A	1.3	1.0AB	1.0	1.0AB	1.2	0.1B	0.4	0.3B	0.7	0C	
Chinese iris, Iris lacteal	1.1AC	0.9	4.6B	1.4	0.6C	0.7	2.5AB	1.5	1.3AC	1.5	3.4AB	3.2
Sub-others	4.9A	2.5	2.2AB	1.8	4.6A	2.3	2.6A	2.1	2.5AB	2.7	1.3B	1.3

^a The data in the same line with the same letters denote no difference at P < 0.05.

-12.645, P < 0.001) and Cyperaceae ($t_{18} = -8.364, P < 0.001$) 0.001) than did Tibetan domestic sheep. Tibetan gazelle also grazed more on Leguminosae ($t_{18} = 13.005, P < 0.001$) and Compositae ($t_{18} = 3.923$, P < 0.001), and less on Gramineae ($t_{18} = -14.692$, P < 0.001) and Cyperaceae (t_{18} = -6.903, P < 0.001) than did Tibetan domestic sheep. There were no differences in proportions of Compositae (t_{18} = 2.003, P = 0.112) and Cyperaceae ($t_{18} = -1.422, P =$ 0.172) between Przewalski's gazelle and Tibetan gazelle, although percentages of Leguminosae ($t_{18} = -3.796$, P =0.001) and Gramineae ($t_{18} = 5.139$, P < 0.001) differed. During the plant-withering period, we noted the same result between Tibetan domestic sheep and the 2 gazelles. Przewalski's gazelle grazed more on Leguminosae ($t_{18} =$ 7.399, P < 0.001) and Compositae ($t_{18} = 12.711$, P < 0.001) 0.001), and less on Gramineae $(t_{18} = -8.919, P < 0.001)$ and Cyperaceae ($t_{18} = -7.618$, P < 0.001) than did Tibetan domestic sheep. Similarly, Tibetan gazelle grazed more on Leguminosae ($t_{18} = 10.197$, P < 0.001) and Compositae (t_{18} = 13.765, P < 0.001), and less on Gramineae ($t_{18} =$ -10.216, P < 0.001) and Cyperaceae ($t_{18} = -4.946, P < 0.001$) 0.001) than did Tibetan domestic sheep. However, we found no differences in proportions of Leguminosae ($t_{18} =$

osae (t_{18} = Analysis of fecal samples of the sympatric Przewalski's gazelle, Tibetan gazelle, and Tibetan domestic sheep revealed food preferences and diet overlaps among the three

Tibetan gazelle.

DISCUSSION

changed between the 2 gazelles.

gazelle, Tibetan gazelle, and Tibetan domestic sheep revealed food preferences and diet overlaps among the three ungulates. Our conclusions are 1) diets of Tibetan domestic sheep and the two gazelles were highly overlapped during the plant-withering period, indicating a competition for food resources during food-limited period; 2) Przewalski's gazelle and Tibetan gazelle foraged similar diets.

-2.197, P = 0.058), Compositae ($t_{18} = 1.753$, P = 0.101), Gramineae ($t_{18} = 1.467$, P = 0.160), and Cyperaceae (

-2.005, P = 0.060) between Przewalski's gazelle and

Dietary overlaps were relatively high among all species

during the plant-withering period with values ranging from

0.76 to 0.95 (Table 2). All Pianka's indexes, regardless of whether measured between each gazelle and sheep or among

the 3 species, increased from the plant-growing period to

the plant-withering period. Pianka's index remained un-

For wild ungulates, exploitative competition with livestock is usually unavoidable (Putman 1996, Mishra et al. 2004).

Table 2. Pianka's index *C* on the dietary overlap among Przewalski's gazelle, Tibetan gazelle, and Tibetan domestic sheep in Upper Buha River, Qinghai-Tibet Plateau, using microscopic fecal analysis in 2005 and 2006. We divided seasons into 2 periods: June to September was the plant-growing period and October to next May was the plant-withering period. C = 0 means no overlap and C = 1 means complete overlap.

1 1	1	
Ungulate pair	Periods	С
Przewalski's gazelle vs. Tibetan	Plant-growing	0.58
domestic sheep	Plant-withering	0.77
Tibetan gazelle vs. Tibetan domestic sheep	Plant-growing	0.43
	Plant-withering	0.76
Przewalski's gazelle vs. Tibetan gazelle	Plant-growing	0.95
	Plant-withering	0.95
Przewalski's gazelle vs. Tibetan gazelle vs.	Plant-growing	0.09
Tibetan domestic sheep	Plant-withering	0.20

Conflicts might not be severe during the plant-growing season due to abundant food resources, but competition intensifies during the plant-withering season because of reduction of aboveground biomass (Litvaits and Harrison 1989, Caughley and Sinclair 1994, Ego et al. 2003). Pianka's index between Tibetan domestic sheep and the 2 gazelles increased from ≤ 0.58 during the plant-growing period to nearly 0.8 during the plant-withering period, showing that their diets were highly overlapped in winter. High overlap in dietary composition indicated a high possibility of food competition, particularly when available aboveground biomass is low in winter on the Qinghai-Tibet Plateau (Lawlor 1980, Schoener 1983, Liu and Jiang 2002a, Li et al. 2006). Studies on plant communities of the nearby areas (Haibei, Qinghai Province) showed that aboveground biomass dropped from >250 g/m² in the plant-growing season to $<100 \text{ g/m}^2$ in the plant-withering season (Zhao and Zhou 1999). Furthermore, nutrient contents in aboveground plants also decreased from the plant-growing season to the plant-withering season; for example, crude protein content in Leguminosae decreased from 13% to <5% (Zhao and Zhou 1999). When food resources became limited and nutrient contents decreased, food competition between gazelles and domestic sheep became more intense; gazelles had to shift their diets to less preferred plants to fulfill their food requirements. Liu and Jiang (2004) reported that Chinese iris (Iris lacteal), Chinese stellera (Stellera chamaejasme), and dilled wormwood (Artemisia anethifolia) were the 3 most important substituted food species for Przewalski's gazelle. These plants did not appear in the diet of Przewalski's gazelle during the plant-growing period but contributed to >30% of the diet of the gazelle in November. We also found some substituted food species, for example, Chinese iris, contributed only 0.6-1.1% to diets of the 2 gazelles during the plant-growing period, whereas proportions increased to 2.5-4.6% during the plant-withering period.

Przewalski's gazelle and Tibetan gazelle had highly overlapped diets, indicating that there might be no niche separation on the food compositions. Recent studies on these species living separately in other areas showed they had similar diets as well (Li and Jiang 1999; Liu and Jiang 2002*a*, 2004; Lu et al. 2004); both foraged mainly on plant families Leguminosae, Compositae, and Gramineae. Competitive exclusion principle predicts that if different species have the same diets, then they compete for food resources when coexisting in the same ecosystem (Hardin 1960). Consequently, competitive displacement should have taken place or the species may separate their niches along other niche dimensions to avoid competition (Pianka 1969, Gordon and Illius 1989, Prins and Olff 1998, Bagchi et al. 2003, Prins et al. 2006). Ungulates might select different foraging areas or utilize different microhabitat to avoid interspecific competition, as observed between roe deer (Capreolus capreolus) and muntjac (Muntiacus reevesi; Hemami et al. 2004). Alternatively, one species might shift its foraging time to avoid the overlap, such as Przewalski's gazelle grazing longer in the morning and dusk to avoid the feeding peaks of sympatric Tibetan domestic sheep during daylight (Liu and Jiang 2004). Thirdly, gazelles might show some differences on bite depth into the swards, which is also an important dimension of food niches for grazers on grassland. Of these 3 possible factors, we considered that the foraging area partition might be the main reason for avoiding food competition. From a 3year field observation, Li and Jiang (2006) found that Przewalski's gazelle generally occupied the southern portion of the study area, whereas Tibetan gazelle resided more in the northern portion. Sometimes, one species ran into the range of the other species, and even formed mixed-species groups, but usually the species would go back to their own range as soon as possible. Li and Jiang (2006) also observed the feeding rhythm of the 2 gazelles but found no significant differences between them. Both species showed feeding peaks at morning and dusk. Similar results were also found in these species living separately in other areas (Chen et al. 1997, Li et al. 1999, Lu and Wang 2004, Lu et al. 2004). The overlap of feeding rhythm indicated they might compete for food with each other in this niche dimension. More studies on bite depth of the 2 gazelles should be done in the future to check whether there is a difference in bite depth and whether bite depth differences could decrease food competition.

Management Implications

Aboveground biomass on Qinghai-Tibet Plateau pasture is highest in late August. Tibetan domestic sheep gain body weight as grasses green up and until grasses wither, after which sheep start losing body weight (Zhao and Zhou, 1999). From the viewpoint of range management and conservation of the endangered gazelles, Tibetan domestic sheep should be removed (i.e., sent to market) in autumn to reduce populations in winter, which is essential to lessen food competition in the alpine meadows on the plateau and to guarantee adequate food resources for the 2 gazelles to survive harsh winters.

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