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Diets and habitat selection of takhi and red deer in Hustai National Park, Mongolia

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Hustai National Park in Mongolia became a refuge for takhi *Equus ferus przewalskii*, a wild horse native to central Asia, in 1992. Wild takhi became extinct in the wild in the 1960s, although there was a small captive population in European zoos that was used to repopulate Hustai National Park. This park is also inhabited by red deer *Cervus elaphus*, which may compete with takhi for food. We analyzed the fecal composition and habitat use of takhi and red deer. Takhi mainly foraged on grasses in the steppe, while red deer foraged on grasses and dicots in the forest. The percentage similarity (PS) of foods was 65% in summer and 58% in winter. There does not appear to be competition for food or habitat between these species because both diets and the habitat selection were different. We discuss some management implications and emphasize the importance of integrated management of the refuge.

Keywords: competition, food habits, habitat use, interspecific relation, particle size, protein

Takhi, or Przewalski's horse *Equus ferus przewalskii*, is native to steppe habitats of central Asia, including Mongolia (Bouman and Bouman 1994). Takhi is widely considered to be a wild horse, but a recent study indicated that it is a feral descendent of horses domesticated in Botai 5500 years ago (Gaunitz et al. 2018). Wild takhi became extinct in Mongolia in 1968. However, 16 captive takhis from European zoos were released in Hustai National Park (HNP) in 1992 (Ryder 1993), and the takhi population in HNP subsequently increased to 335 (<www.hustai.mn/wp/language/en/>). This is one of the rare cases of successful restoration of a reserve with ungulates (van Dierendonck and de Vries 1996). The Hustai National Park (HNP) is not an ungulate-free reserve. Rather, it is inhabited by another ungulate, the red deer *Cervus elaphus*, which is native to Mongolia. It is estimated that the population of red deer in Mongolia was 130 000 in 1986, but declined to 8000–10 000 by 2004 (Clark and Javzansuren 2006, Wingard and Zahler 2006). The red deer population in HNP is estimated to comprise 500 individuals (Thapaliya 2008). No other wild ungulates live in the park.

When multiple species of large ungulates live together, they often compete for resources between or among them (de Boer and Prins 1990). In fact, some studies suggested the possibilities of competition such as those between wild gazelles *Procapra gutturosa* and domestic sheep *Ovis aries* in Qinghai-Tibetan Plateau (Li et al. 2008); Ladakh urial *Ovis vignei vignei* and blue sheep *Pseudois nayaur* in Trans-Himalaya (Namgail et al. 2010); and red deer *Cervus elaphus* and chamois *Rupicapra rupicapra* in European Alps (Ferretti et al. 2015). Previous analysis of the foods of takhi and red deer in HNP (Sietses et al. 2009) demonstrated that takhi and red deer are competitors because the similarity in their foods increased during winter. This dietary competition may have important implications for park management, and therefore should be considered carefully. However, some studies on ungulate assemblages indicate competition can be avoided through partitioning resources such as with seven wild ungulates in Tibetan Plateau (Harris and Miller 1995), muskoxen *Ovibos moschatus* and reindeer *Rangifer tarandus* in Alaska (Ihl and Klein 2001) and elk *Cervus canadensis*, bison *Bison bison*, caribou *R. tarandus*, thinhorn sheep *Ovis dalli* and moose *Alces americanus* in Canada (Jung et al. 2015). Based on these examples, it is possible that habitat use and annual diets of takhi and red deer would be different.

The objective of this study was to characterize the food habit and habitat selection and food habit patterns of takhi and red deer in HNP, and thus determine whether or not these two herbivores are in competition. To assess potential food competition and resource partitioning between these two ungulates, we compared diet composition and habitat

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use. Diet composition is important because if takhi and red deer do overlap in habitat use, competition for food would not occur if their diets do not overlap. Limited dietary competition may result from differences in adaptations to distinct ecosystems and general differences in digestive physiology between equids and cervids. Equids are adapted to grassland ecosystems and use hindgut fermentation to digest grasses high in cellulose and silica (Uden and van Soest 1982, van Soest 1982, Robbins 1983, Sneddon and Argenzio 1998, Cichorska et al. 2014). However, their digestive efficiency is low (Cymbaluk 1990, Osoro et al. 2017). Cervids are adapted to forest ecosystems (Whitehead 1972) and feed on grasses and forbs. Cervids are ruminants, and exploit microbial fermentation to digest food more efficiently than equids (Hofmann 1989).

Habitat use is important because if takhi and red deer stay temporally separate, competition would not occur even if their diets overlap. For example, although the diet of Przewalski's gazelle *Procapra przewalskii* and Tibetan gazelle *P. picticaudata* overlap in the Qinghai-Tibet Plateau, they occupy different foraging areas, and thus are not competitive (Li et al. 2008).

Methods

Study area

Hustai National Park (HNP) comprises 50 600 ha of forest-steppe habitat, wherein steppe predominates and birch forests grow in patches on mountaintops. It is located ~100 km southwest of Ulaanbaatar (Fig. 1, 47°40′N, 105°56′E). The mean monthly temperature is −20°C in January and 20°C in July, and the mean annual precipitation is 250 mm. HNP was designated by UNESCO as a World Biosphere Network of Man and Biosphere (MAB) site in 2002, and became a member of the International Union for Conservation of Nature (IUCN) in 2007. Our study sites were in the northeastern part of the park. The vegetation of the HNP is dominated by mountain steppe and shrubland (88%, de Vries et al. 1996), and forest accounts for only 0.8% (Bayarsaikhan et al. 2009).

Food habits

To examine the food habits of takhi and red deer, we collected fecal samples in July, August and October 2010, and in February 2011. During each sampling period, we collected 10 samples each from takhi and red deer, except in October (n = 8 takhi samples) and February (n = 5 takhi samples). A sample of red deer feces was composed of 20 fecal pellets while that of takhi feces was composed of 20 of spoonful amounts. Samples were washed with tap water over a 0.5 mm aperture sieve, and the retained plant fragments were analyzed microscopically using a point-frame method (Stewart 1967). The food categories included grasses, sedges (*Carex* spp.), other monocot leaves, dicot leaves, culms and sheaths, fiber and others. We could distinguish leaves to different groups (e.g. sedges, monocots or dicots). Culms were distinguished by their parallel lines without long cells, short cells and stomata, and included all graminoids. Fiber was distinguished by less transparent parallel curves and included various browses and forbs. Other categories included ferns, mosses, fruits and unidentified materials. More than 200 points were counted for each sample. Food categories of which occupancies (i.e. counts) exceeded 10% during at least one month were regarded as the 'major foods'. The fecal compositions of takhi and red deer were compared using the Mann–Whitney test, and seasonal changes were compared using the Kruskal–Wallis test with Steel–Dwass post hoc test and Whittaker's percentage similarity, with the latter calculated as follows:

$$\mathrm{PS} = \Sigma \min\left(Pa_i, Pb_i\right)$$

where Pa_i and Pb_i are the mean percent composition of plant i in samples a and b, respectively.

The occupancies of each food category were used for detrended correspondence analysis (DCA) of Hill and Gauch (1980). The DCA is an eigenvector ordination technique by correspondence analysis which ordinates fecal samples according to the occupations of food categories (Hill and Gauch 1980) and can be used to define the fecal composition similarity among the sampling months. When fecal samples

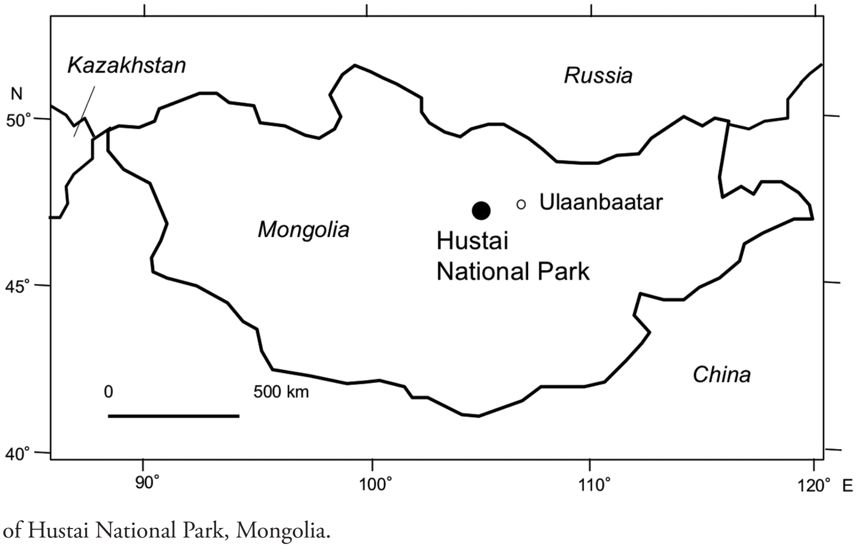

Figure 1. The location of Hustai National Park, Mongolia.

contain similar food categories of similar occupancy, the scores are calculated as similar and vice versa. By plotting the scores of the samples along the axis 1 and the axis 2, variations of the scores among different months are compared. PC-Ord ver. 4.25 (mjm co., Gleneden Beach, OR, USA) was used.

Particle size distribution of plant fragments in the feces

Besides botanical compositions in the feces, particle sizes of food plants in the feces can represent differences of food plant quality and digestive physiology of takhi and red deer. To determine the size distribution of plant fragments in the fecal samples, we washed the feces over sieves differing in aperture size (0.1, 0.25, 0.5, 1.0 and 2.0 mm). The samples were as described above, but did not include winter samples collected in February 2011. The dry weight of each particle size class was determined, and the proportions of the relative weights in the feces of takhi and red deer were compared among the same size classes using the Mann–Whitney test.

Crude protein content of feces

Since ungulates can face protein deficiencies (Robbins 1983), crude protein level is important to evaluate food quality. Therefore, we determined the concentrations of crude protein in their feces using the Kjeldahl method (Conklin-Brittain et al. 1999). Fecal samples were collected in July, August and October 2010, and in February 2011. The crude protein contents were compared between species using the Mann–Whitney test, and seasonal changes were compared using the Kruskal–Wallis test with Steel–Dwass post hoc test.

Habitat use

To determine the habitat use of takhi and red deer, we adopted the fecal pellet count method (Neff 1968, Campbell et al. 2004). We counted fecal piles in 10 quadrat plots (10 × 10 m) which were randomly taken and were separated by at least 500 m in the forest, forest edge and steppe in August 2009. The densities of the fecal piles in the three habitats were compared between takhi and red deer using the Mann–Whitney test, and the densities among habitats for each species were compared using the Kruskal–Wallis test with Steel–Dwass post hoc test.

Results

Interspecific comparison of fecal compositions at each season

The results of the major foods are shown in Table 1 and Fig. 2. In July, grasses accounted for 37.7% in the takhi feces which was significantly greater than in red deer feces (8.8%, Mann–Whitney test, $U=3.78$, $df=1$, $p < 0.001$). Dicot leaves were greater in the red deer feces (15.3%) than in the takhi feces (2.6%, $U=3.62$, $df=1$, $p < 0.001$). Culms and sheaths were not significantly different between takhi and red deer ($U=0.45$, $df=1$, $p=0.050$). Fiber was greater in the red deer feces (15.7%) than in the takhi feces (3.8%, $U=3.78$, $df=1$, $p < 0.001$).

In August, grasses accounted for 39.9% in the takhi feces which was significantly greater than in red deer feces (9.5%, $U=3.97$, $df=1$, $p < 0.001$). Dicot leaves were greater in the red deer feces (28.0%) than in the takhi feces (5.7%, $U=3.97$, $df=1$, $p < 0.001$). Culms and sheaths were not significantly different between the animals ($U=0.89$, $df=1$, $p=0.375$). Fiber was greater in the red deer feces (9.4%) than in the takhi feces (3.8%, $U=3.33$, $df=1$, $p=0.001$).

In October, grasses accounted for 26.1% in the takhi feces which was significantly greater than red deer feces (10.8%, $U=3.38$, $df=1$, $p=0.001$). Dicot leaves were greater in the red deer feces (16.1%) than in the takhi feces (1.1%, $U=3.64$, $df=1$, $p < 0.001$). Culms and sheaths were greater in the takhi feces (52.6%) than in the red deer feces (35.2%, $U=3.64$, $df=1$, $p < 0.001$). Fiber was greater in the red deer feces (21.9%) than in the takhi feces (9.4%, $U=2.49$, $df=1$, $p=0.013$).

In February, grasses accounted for 24.2% in the takhi feces which was significantly greater than red deer feces (3.8%, $U=3.32$, $df=1$, $p=0.001$). Dicot leaves were greater in the red deer feces (8.9%) than in the takhi feces (2.2%, $U=3.25$, $df=1$, $p=0.001$). Culms and sheaths were greater in the takhi feces (49.7%) than in the red deer feces (29.3%, $U=2.94$, $df=1$, $p=0.003$). Fiber was greater in the red deer feces (43.6%) than in the takhi feces (15.5%, $U=2.71$, $df=1$, $p=0.007$). As a whole, takhi were more dependent on grasses while red deer foraged on mainly dicot leaves and fibrous plants.

Seasonal changes of fecal compositions for each animal

The primary food categories for takhi were grasses and culms (Table 1, Fig. 2). The proportion of grasses was not signifi-

Table 1. Fecal compositions (%) of takhi and red deer in Hustai National Park, Monglia.

	Takhi				Red deer			
	Jul	Aug	Oct	Feb	Jul	Aug	Oct	Feb
Grass	37.7	39.9	26.1	24.2	8.8	9.5	10.8	3.8
Sedge	7.7	5.3	2.6	2.4	4.0	4.4	1.9	0.6
Monocot	1.4	3.8	2.6	2.7	0.9	1.5	9.2	9.8
Culm, sheath	42.1	39.2	52.6	49.7	41.2	42.1	35.2	29.3
Dicot	2.6	5.7	1.1	2.2	15.3	28.0	16.1	8.9
Fiber	3.8	3.8	9.4	15.5	15.7	9.4	21.9	43.6
Others	4.7	2.3	5.6	3.4	14.2	5.2	5.0	4.0
Total	100	100	100	100	100	100	100	100

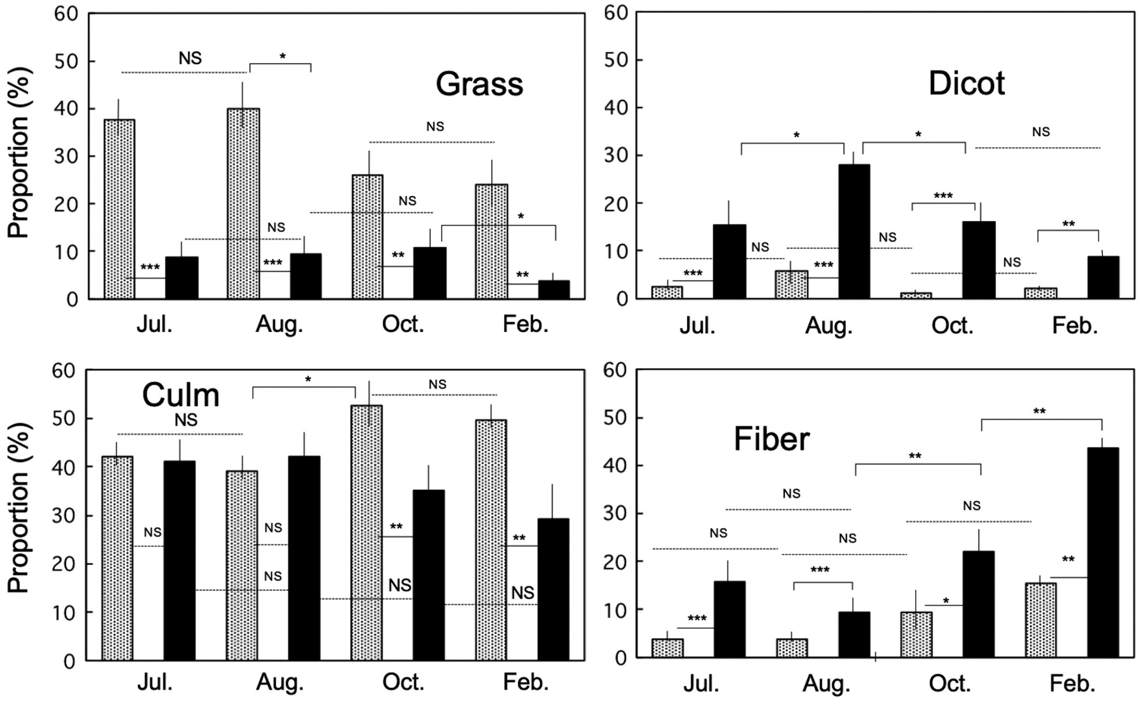

Figure 2. Seasonal changes in the fecal compositions of takhi (dotted bar) and red deer (black bar) at Hustai National Park, Mongolia. Vertical bars show SD (standard deviation). *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, NS: non-significant.

cantly different between the adjacent seasons (July–August: Kruskal–Wallis test, $\chi^2 = -0.83$, df = 3, p = 0.84; October–February: $\chi^2 = 0.71$, df = 3, p = 0.89), except between August and October when the proportion of grasses in August was higher than in October ($\chi^2 = 2.86$, df = 3, p = 0.02). The proportion of culms and sheaths increased from August (39.2%) to October (52.6%), but was not different between July and August ($\chi^2 = -1.13$, df = 3, p = 0.67) or October and February ($\chi^2 = 0.87$, df = 3, p = 0.82). The proportion of fiber did not differ by season (July–August: $\chi^2 = -1.82$, df = 3, p = 0.27; August–October: $\chi^2 = -2.13$, df = 3, p = 0.14; October–February: $\chi^2 = 2.22$, df = 3, p = 0.12).

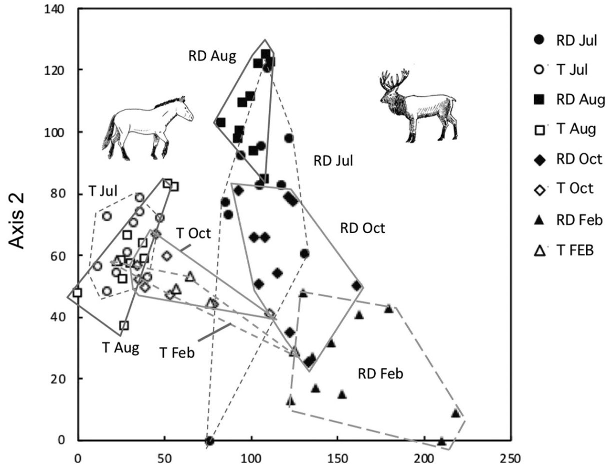

Figure 3. Detrended correspondence analysis plot of takhi (T, open symbols) and red deer (RD, solid symbols) fecal samples collected across four seasons in Hustai National Park, Mongolia.

These results indicate that takhi feed on grasses throughout the year, except in autumn and winter when they feed primarily on culms or the woody parts of dicots.

The diet of red deer was primarily composed of dicot leaves, culms and sheaths, and fibers (Table 1, Fig. 2). The proportion of grasses was not significantly different between the adjacent seasons (July–August: $\chi^2 = -1.36$, df = 3, p = 0.52; August–October: $\chi^2 = 2.42$, df = 3, p = 0.07), except for October–February when the proportion of grasses in October was higher than in February ($\chi^2 = 3.33$, df = 3, p = 0.005). The proportion of dicot leaves increased from July to August ($\chi^2 = -3.02$, df = 3, p = 0.01) and decreased from August to October ($\chi^2 = 3.01$, df = 3, p = 0.01), but did not differ between October and February ($\chi^2 = 2.34$, df = 3, p = 0.09). The proportion of culms did not differ between seasons (July–August: $\chi^2 = -0.23$, df = 3, p = 1.00; August–October: $\chi^2 = 1.89$; df = 3, p = 0.23; October–February: $\chi^2 = 0.53$, df = 3, p = 0.95). The proportion of fiber did not differ between July and August ($\chi^2 = -0.19$, df = 3, p = 0.99), but increased from August to October ($\chi^2 = -2.13$, df = 3, p = 0.14) and from October to February ($\chi^2 = 0.95$, df = 3, p = 0.78). Dependence on dicot leaves in summer and fiber in winter suggest that red deer feed on browse species: they consume browse leaves in the summer and twigs in the winter once the leaves have dropped in autumn.

Detrended correspondence analysis

Fecal samples of takhi and red deer in all four seasons were subjected to detrended correspondence analysis (DCA; Fig. 3). The plot distributions indicate that fecal samples containing more dicot leaves fall on the right side of the x-axis, while those fecal samples containing more grass fall on the left side of the x-axis. Red deer fecal samples with high dicot leaf content are situated along the upper y-axis, while samples with more fiber are situated lower on the y-axis. Takhi, but not red deer, samples containing more culms were positioned on the right side.

The takhi samples for July were plotted on the left side of the plot, while those for red deer were plotted in the upper-central section. The samples in both species showed minimal variation and did not overlap with each other in July. In August, the takhi samples were all similar, while those for red deer were more variable and the samples of the two species showed no overlap. In October, the takhi samples were more variable, those for the red deer samples were positioned in the central part of the plot and the samples of the two species were in closer proximity. In February, takhi samples showed similar plot positions to the autumn samples, the red deer samples extended into the right-lower part and the samples of the two species did not overlap.

Percentage similarity of fecal compositions

Whittaker's percentage similarities (PS) for the fecal sample compositions between takhi and red deer were around 66%, except in February when it was 57.5% (Table 2).

Particle size distribution of the plant fragments in the feces

The plant particles in takhi feces were larger than those in red deer feces across all seasons (Fig. 4). The proportion of particles larger than 0.5 mm was higher in takhi samples than in red deer. The proportion of particles smaller than 0.5 mm was higher in red deer samples than in takhi. The differences were significant in almost all particle size classes, except for 0.5–1.0 mm in October (Supplementary information).

Crude protein contents in the feces

The content of crude protein in takhi feces was lower than in red deer feces (Fig. 6) in August (U = 4.49, df = 26, $p < 0.001$) October (U = 3.55, df = 16, $p < 0.001$) and February (U = 3.06, df = 13, p = 0.002). In red deer, the fecal crude protein content was significantly higher in August (16.1%) than in October (9.5%, U = 4.16, df = 2, $p < 0.001$) which did not differ from February (U = 0.529, df = 2, p = 0.857). In takhi, crude protein content did not differ between seasons (August–October: U = 0.941, df = 2, p = 0.614, October–February: U = 0.439, df = 2, p = 0.899).

Habitat use

The density of dung piles differed between species across habitat types and among habitat types within a species (Fig. 6). Density of dung piles were significantly lower for takhi than for red deer, both in the forest (4.0/100 m^2 for takhi, 31.7/100 m^2 for red deer, Mann–Whitney test, U = 3.78, df = 18, $p < 0.001$) and at the forest edge (9.6/100 m^2 for takhi, 26.0/100 m^2 for red deer, U = 2.92, df = 18, p = 0.004). In contrast, density of dung piles was significantly higher for takhi than for red deer in the grassland (25.1/100 m^2 for takhi, 4.6/100 m^2 for red deer; U = 3.33, df = 18, p = 0.001). The density of takhi dung was significantly higher in the grassland than at the forest edge (Kruskal–Wallis test, $\chi^2 = -2.54$, df = 2, p = 0.030), but did not differ between the forest and the forest edge ($\chi^2 = -1.72$, df = 2, p = 0.202). The density of red deer feces was significantly lower in the grassland than at the forest edge ($\chi^2 = 3.52$, df = 2, p = 0.001), but did not differ between the forest and the forest edge ($\chi^2 = 1.06$, df = 2, p = 0.538).

Discussion

We compared habitat selection and food habits of takhi which were introduced into Hustai National Park (HNP) in 1992 from zoos in Europe and native red deer. From previous studies, we had the following predictions. Predic-

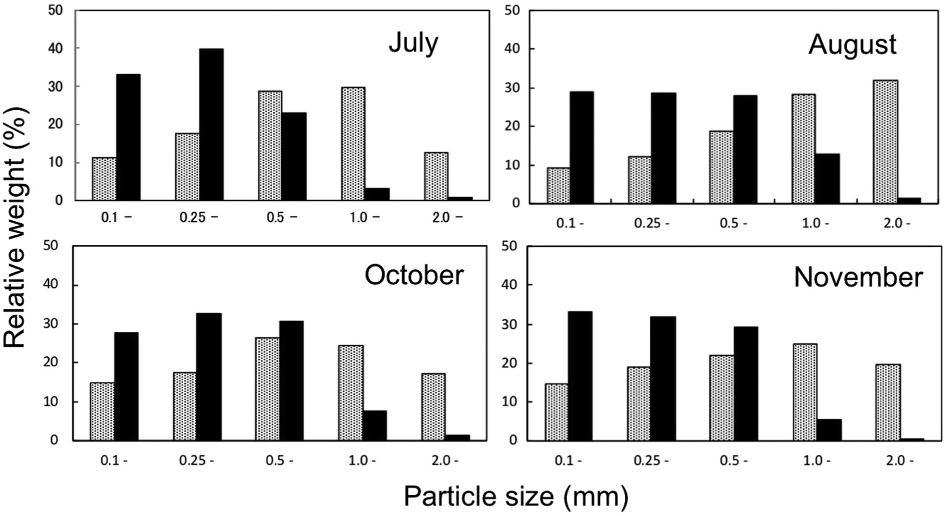

Figure 4. Weight (%) distribution of plant particles in the feces of takhi (dotted bar) and red deer (black bar) in Hustai National Park, Mongolia.

Table 2. Whittaker's PS (percentage similarity, %) for the takhi and red deer fecal sample compositions across four seasons.

	Jul	Aug	Oct	Feb
PS	65.9	66.4	66.0	57.5

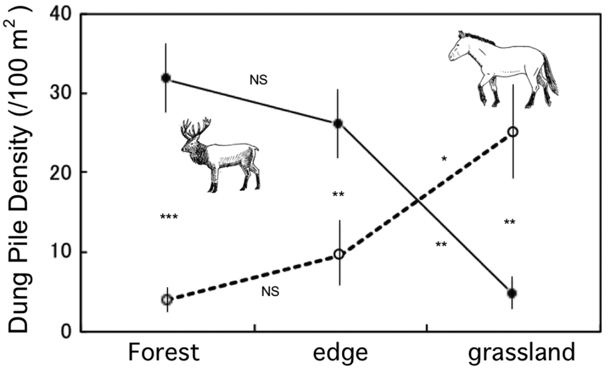

Figure 6. Densities of dung piles of takhi (closed circle and solid line) and red deer (open circle and dotted line) in the forest, forest edge and steppe at Hustai National Park. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, NS: non-significant.

tion 1: takhi, an equid, would stay in grassland (King 2002) while red deer, a cervid, would stay in forests (Mitchell et al. 1977). Prediction 2: takhi would mainly eat grasses (Sietses et al. 2009) while red deer would eat both dicots and grasses (Sietses et al. 2009). Prediction 3: foods would be more similar during winter because animals would have to feed on a limited number of plants available (Mishra et al. 2004, Kobayashi and Takatsuki 2012). Prediction 4: the feces of takhi, a hid-gut fermenter (Osoro et al. 2017), would contain larger plant fragments while feces of red deer, a ruminant (Hofmann 1989). Prediction 5: the feces of red deer would have higher crude protein during summer when they feed more on dicots.

Prediction 1 was supported by the greater number of fecal piles of takhi in grasslands while those of red deer were found more in forests (Fig. 6). This is a general characteristic of equids and is reflected in their excellent running ability (Janis and Bernor 2019), well-developed molars that allow them to masticate fibrous grasses (Strömberg 2006, Evans and Janis 2014), and well-developed caecum for fermentation (Santos et al. 2011).

Prediction 2 was also supported by fecal analysis which showed that takhi feces were predominated by grasses while deer feces contained both dicots and grasses (Table 1).

Prediction 3 was not supported as the percentage similarities of fecal compositions were similar regardless seasons, and even slightly smaller in winter (Table 2). DCA presentation also showed that although intra-specific seasonal variations were great, inter-specific differences were not affected by seasons (Fig. 3). This suggests that food compositions of the two ungulates were strongly affected by seasons, but each ungulate fed on different foods according to their differences in habitat use (King 2002), tooth morphology (Schrock et al. 2013) and digestive physiology (Sneddon and Argenzio 1998, Osoro et al. 2017). Our results were different from those of Sietses et al. (2009) who found that fecal composition was more similar between takhi and red deer in winter than in summer. However, Kulcynski's similarity index in winter was 54.9%, which is not markedly different from the summer value (50.6%). When the data were reanalyzed using Whittaker's PS, the PS values in summer and winter were 61% and 60%, respectively. Although previous work did not indicate the presence of culms, it is unrealistic that neither ungulate fed on culms. The authors emphasized that diets of takhi and red deer overlapped more in winter than in summer, and suggested that forage quality can trigger competition between them. However, our data showed that food similarity was greater (PS = 65.9%) in summer, when plants are more abundant, than in winter (57.5%, Table 2). The greater similarity in summer may be attributed to the fact that both takhi and red deer could feed on highly abundant plants in summer. Furthermore, habitat use differed between takhi and red deer (Fig. 6). Takhi and red deer differ in their digestion (hindgut fermentation versus, rumination), foraging style (grazer versus intermediate feeder), body size (300 kg versus 100 kg) and habitat (grassland versus forest). Our results are consistent with differences in the diets between equids and cervids reported between wild horse and elk or mule deer *Odocoileus hemionus* (Hubbard and Hansen 1976, Hansen et al. 1977, Salter and Hudson 1980, Hanley and Hanley 1982, Scasta et al. 2016) and between wild ass *Equus kiang* and white-lipped deer *Cervus albirostris* in Tibet (Harris and Miller 1995).

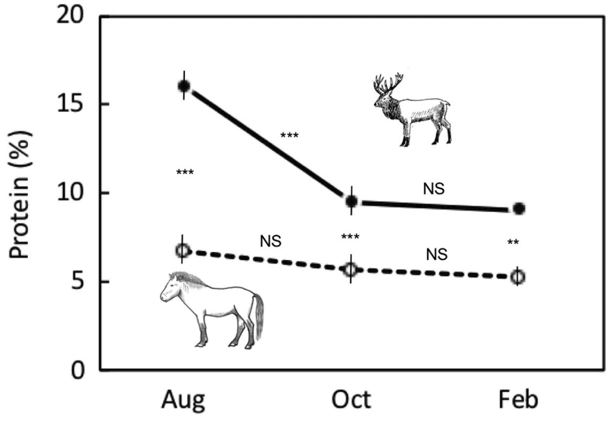

Figure 5. Seasonal changes in fecal crude protein contents in takhi (closed circle and solid line) and red deer (open circle and dotted line) in Hustai National Park, Mongolia. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, NS: non-significant.

Prediction 4 was supported by larger fragments in takhi feces compared to deer feces (Fig. 4) which may reflect differences in digestive physiology between equids and ruminants and are consistent with comparisons reported by Uden and van Soest (1982), Grenet et al. (1984), Okamoto (1997), Clauss et al. (2002) and Marcus et al. (2002). The smaller fragments in red deer feces could be attributed to more efficient digestion in this species (Cichorska et al. 2014) and their tendency to consume forbs which are more digestible than grasses.

Prediction 5 was well supported by higher protein levels in deer feces than in takhi, particularly during summer (Fig. 5). For red deer, a diet with a crude protein level of 13–20% is optimal for growth, while 6–7% is necessary for maintenance (Mitchell et al. 1977). The crude protein level of elk feces in North America, the same species as red deer, reached at least 14% in April–June, declined to 10% in August, and then dropped to 5% in winter (Swift 1983). Crude protein levels below 5% can be dangerous for elk. Red deer feces in HNP was higher than in North American elk and may suggest that it is likely that the park seems suitable for red deer as far as forests exist since food quality is good and competition with takhi is avoided by differences in habitat use and food habits.

Although results are generally consistent with previous work, the methods we adopted, particularly fecal analysis, has limitation (Gill et al. 1985, Bartolome et al. 1995). More digestible foods are underestimated and vice versa. However, since this study was done within a single site using the same methods, comparisons show relative similarities and differences between the species and among the seasons. Although our sample size was limited compared to other studies (Suter et al. 2004, Zweifel-Schielly et al. 2012), it is similar to others (Marin et al. 2020) and showed significant differences in the main food plants like grasses, dicots and fiber (Fig. 2). For food plant categorization, we went beyond proportions of leaves common in other studies (Sietses et al. 2009, Zweifel-Schielly et al. 2012, Jung et al. 2015) and included non-leaf parts which allowed us to compare ingestion of culms when animals feed on grass and fiber when animals feed on shrubs or the branches and bark of plants. The inclusion of culms and fiber, coupled with particle size and fecal protein, represent qualitative traits of plants that may offer more functional insight into nutritional consequences of habitat use and diet composition.

After the reintroduction of takhi in 1992, the population steadily increased to 124 in 2008. Thereafter, the population declined to 50 in 2009, but increased again to 335 in 2016 (<www.hustai.mn/wp/language/en/>). Thus, the population recovery effort has been successful. However, there seem to be some problems with ecosystem management, the first of which concerns resource sharing between takhi and red deer. Our data showed that red deer inhabited forests and foraged therein. If the takhi population increases and begins to consume forest plants, they may compete with red deer. Additionally, some tree species, such as birch *Betula platyphylla*, are declining in HNP (Verhoeven et al. 2018). Verhoeven et al. (2018) suggested that the birch forest of HNP was converting into a steppe ecosystem. If the forests decline, habitat for red deer may become limited. Our research provides baseline data that could help evaluate whether future decreases in red deer populations are due to habitat loss or competition with takhi relative to predation by wolves (Hovens and Khuukheduu 2005).

Objectives of a national park should not only include recovery of reintroduced animals, but also management of the ecosystems. In HNP, where both large herbivores and predators reside, wolf predation should be regarded as a healthy ecosystem process. From this perspective, if predation becomes a significant concern with respect to the takhi population, transporting takhi to other reserves should be considered (van Dierendonck and de Vries 1996). It is important to monitor the population dynamics and food habits of takhi, red deer and wolves, as well as vegetation. Van Dierendonck and de Vries (1996) emphasized that for ungulate reintroduction, it is necessary to implement a program that monitors the development of the reintroduced species and its interaction with other wildlife and vegetation. In the case of HNP, monitoring the population dynamics and food habits of takhi, red deer, wolves and forest changes is important.

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Supplementary information (available online as Appendix wlb-00749 at <www.wildlifebiology.org/appendix/wlb-00749>).