Management and Conservation Article

Wolf Predation Among Reintroduced Przewalski Horses in Hustai National Park, Mongolia

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ABSTRACT Depredation by wolves (*Canis lupus*) could threaten survival of reintroduced wild Przewalski horses (*Equus ferus przewalskii*) in Hustai National Park (HNP), Mongolia. We conducted scat analysis, spatial analyses of kills, and interviews to study prey species selection and temporal and spatial factors that characterize prey choices of wolves. Diet of wolves in HNP was comprised of >50% of livestock. Diet composition varied during the year, with more livestock taken in winter. Wildlife species were selected over livestock species. From available livestock species domestic horses were predated most, whereas red deer (*Cervus elaphus*) and marmot (*Marmota sibirica*) were the preferred wildlife species. Our spatial analyses showed an unexpected significant positive relation between number of domestic horses killed and distance to the park, as well as a significant negative relation with number of gers (tents) in the area. Compared to randomly selected comparison sites ($n = 36$), we found Przewalski foal kills ($n = 36$) at sites that were closer to the forest, at higher altitudes, with lower shrub cover, higher forest cover, and higher red deer density. If the negative trend of deer numbers continues and if herdsmen protect their livestock more vigorously, depredation of wild Przewalski horses by wolves will rise. Therefore, a large red deer population could be pivotal in improving the conservation status of Przewalski horses. (JOURNAL OF WILDLIFE MANAGEMENT 73(6):836–843; 2009)

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KEY WORDS *Canis lupus*, diet, livestock depredation, Mongolia, Przewalski horses, spatial analyses, wolves.

Wolves (*Canis lupus*) are flexible and opportunistic predators. They are adapted to feeding on a wide array of prey items, but wolves' major food source is wild ungulates (Okarma 1995, Olsson et al. 1997, Gade-Jørgensen and Stagegaard 2000). Selection for wild ungulate species is affected by abundance, social behavior, and body size (Meriggi and Lovari 1996). Wolves are able to change the habitat choices of their prey species, because prey might prefer the protective cover of woody areas, and thereby sometimes even trigger important vegetation changes, such as an increase in tree seedling density due to a lower browsing pressure from herbivorous prey species in open grassland, which have a higher predation risk (Ripple and Beschta 2003, 2004; Creel et al. 2005). Wolves also prey on livestock, which in several studies has been linked to a low abundance of wildlife prey (Mech et al. 1988, Sidorovich et al. 2003, Gazzola et al. 2005).

In Hustai National Park (HNP), Mongolia, the main wildlife prey species available to wolves are red deer (*Cervus elaphus*) and marmots (*Marmota sibirica*). However, a new wildlife species, the Przewalski horse (*Equus ferus przewalskii*), has recently been reintroduced. Przewalski horses became extinct in the wild in Mongolia in the 1960s, but 84 horses have been reintroduced since a reintroduction program started in 1992. By the end of 2006, the Przewalski horse population grew to about 182 horses (P. Enkhkhuyag, Hustai National Park, personal communication). A potential conflict with wolves concerns depredation of these Przewalski horses and especially their foals. Besides diseases and accidents, HNP regards wolf predation as the main cause of death for Przewalski foals.

Wildlife populations are small in HNP relative to livestock populations, and >50% of prey items in HNP are livestock (Hovens et al. 2000). Almost all local families report livestock losses from wolf depredation each year. These livestock losses are regarded as the main conflict between HNP and the surrounding local pastoralists. A decrease in the availability of livestock could indirectly affect the predation pressure on Przewalski horses. Hustai National Park faces a difficult challenge in maintaining a natural system with a large predator population, protecting a viable population of Przewalski horses, and resolving conflicts with the surrounding herdsmen.

Our objectives were to 1) study the diet composition of wolves in HNP and investigate annual and seasonal trends in prey composition, 2) compare prey composition with prey availability and analyze prey selection, 3) study the impact of spatial factors on wolf kills, and 4) estimate the economic impact of wolf-caused livestock depredation to individual herdsmen.

STUDY AREA

Hustai National Park was located 100 km southwest of Ulan Bator, the capital of Mongolia, and was part of a

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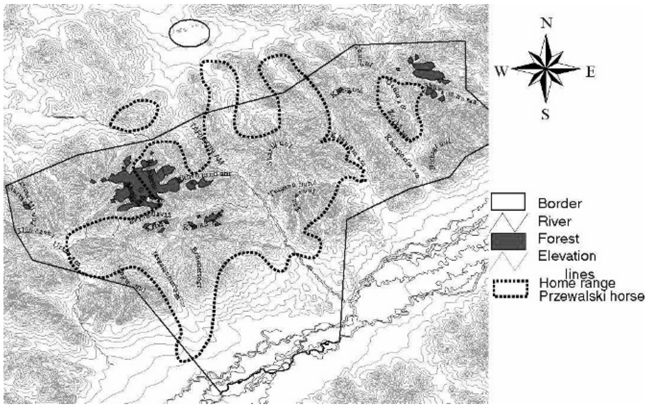

Figure 1. Map of Hustai National Park, Mongolia, showing park boundaries, forest patches, rivers, elevation lines, and the 2007 home ranges of the Przewalski horses.

mountain chain that runs northeast–southwest. Hustai National Park covered 50,600 ha, of which the largest part was steppe and only 4% was forested. The forest contained 3 birch species (*Betula fruticosa*, *B. fusca*, *B. platyphylla*) and poplar (*Populus pilosa*). The Tuul valley in the south was covered with steppe vegetation and some riverine forest. Average annual precipitation was 270 mm and mean annual temperature was 0.2° C (Wallis de Vries et al. 1996).

Hustai National Park was legally protected since 1994, and hunting, logging, and grazing of livestock in the park were prohibited. All nomadic herdsmen lived outside the park's borders, most of them in the Buffer Zone (Hustai National Park 2007). In summer, most of them moved to the valley of the Tuul River for better access to water. In winter they moved back toward HNP and lived in gers (i.e., tents) in the valleys just outside the park. Sheep and goats were herded in large groups, whereas domestic horses roamed freely. Our research area comprised HNP and its direct surroundings (Fig. 1). We conducted all research within park boundaries, except for interviews with herdsmen, which occurred at their summer or winter camps in the Buffer Zone area (Hustai National Park 2007).

Several prey species were available in HNP. In 2003 D. Usukhjargal (Hustai National Park, unpublished report) estimated the population of red deer at 355 individuals. Otgonbaatar (2004) estimated the marmot population at 8,486 individuals. Besides red deer and marmots the following prey wildlife species were present in low numbers in HNP: roe deer (*Capreolus capreolus*), Mongolian gazelle (*Procapra gutturosa*), wild boar (*Sus scrofa*), hare (*Lepus tolai*), and several species of rodents (*Ratus* spp.). Other carnivores in the park besides the wolf were lynx (*Lynx lynx*), red fox (*Vulpes vulpes*), corsac fox (*V. corsac*), badger (*Meles meles*), and several species of birds of prey such as golden eagle (*Aquila chrysaetos*). A common scavenger was the cinereous vulture (*Aegypius monachus*). Hustai National Park was not fenced, but most wildlife species only occurred in the park, whereas wolves were known to have larger home ranges and also hunted outside the park.

Wolves occupied all of Mongolia. Exact numbers are not known, but estimates exceed 10,000 (World Wolf Congress 2003). Wolf hunting was not prohibited, and populations were thought to be declining (Sillero-Zubiri et al. 2004, Wingard and Zahler 2006). Wolf density inside HNP was probably higher than outside, because wolves could find shelter, food, and protection more easily inside the park. The HNP staff and the herdsmen around the park claim that there are about 50 wolves living in the park (P. Enkhkhuyag, personal communication). We estimated the population at 20–50 individuals (C. van Duyne and E. Ras, Wageningen University, unpublished data), based on calculations that included wolf energy requirements (Nagy 1987), interview data, and scat analysis.

METHODS

Prey-Species Population Estimates

We estimated populations of potential prey species using transects and total counts. We conducted surveys each year along transects on foot or on horseback once per month in winter and twice per month in summer. We recorded all mammals sighted and their sighting location. We used transect counts to estimate population size of red deer in HNP following the outer bound method proposed by Robson and Whitlock (1964). We estimated hare numbers according to Rühe and Hohmann (2004).

Hustai National Park biologists kept a detailed record of births and deaths of Przewalski horses and foals each year, and each year an internal report detailed these data. All individual Przewalski horses in each harem and bachelor group were known and were monitored daily by HNP biologists, rangers, or in summer by volunteers. When a horse or foal went missing a search was launched. Usually the missing horse or its remains (often indicated by vultures) were quickly found. When a horse could not be found it was regarded as killed by wolves unless it was known that the horse was sick or injured. As a consequence it is possible that some horses that actually died because of accidents or disease were falsely attributed to wolf depredation.

We calculated livestock numbers from interviews with herdsmen that lived around HNP. We developed a questionnaire (available upon request) and interviewed most herdsmen living in the surroundings of HNP in 2003, 2004 and 2005 (2003: 53 interviews; 2004: 30; 2005: 38). The interview was comprised of questions on wolf attacks (no. of attacks, approx. dates, and livestock prey species), circumstances of the attack (no. of domestic animals, grazing location, methods of protecting livestock), and herding methods.

Scat Collection and Laboratory Procedure

We collected wolf scats from June 2003 through October 2005. Collections were made by different people (e.g., rangers, eco-volunteers, students) throughout the park and throughout the year. However, weather conditions made it more difficult to collect scats in winter, and fewer people were available then.

To avoid a strong bias in scat composition we avoided collecting scats near wolf kills, wolf dens, or livestock areas. We collected scats incidentally from all over the park, but because some parts of the park were more used (i.e., more accessible) by people than other parts, the distribution of samples over the park was not entirely even. We only used nonweathered scats and scats that we considered collectable for analysis (Floyd et al. 1978, Ciucci et al. 1996). We stored scats in bags, labeled them with date and location, and froze them prior to analysis.

Domestic dog scats could easily be mistaken for wolf scats. All herdsmen had dogs that normally stayed close to the ger. Because herdsmen lived outside the park the chance that collected scats were from domestic dogs was minimal. However, some rangers lived with their dogs inside the park so we made sure we did not collect scats in the immediate surroundings of their gers.

After thawing a scat, we extracted ≥ 20 hairs (Jethva and Jhala 2003) from different places on the scat, especially when we could see that a scat consisted of multiple prey species (i.e., hairs of different structure or color). With an identification key made during earlier research in HNP and Teerink's (1991) reference manual we microscopically identified each hair to species level.

Wolf Diet Composition Analysis

To estimate consumption of prey from scats we used the regression method of Floyd et al. (1978), as refined by Weaver (1993). Scat analysis leads to an overestimation of the contribution of smaller prey species in the diet because smaller prey species have more hair and other indigestible matter per unit body mass, which produces more scats per unit prey mass consumed (Mech 1970, Floyd et al. 1978, Weaver 1993). The equation from Weaver (1993) describes the relationship between prey body mass (kg) and prey mass consumed (kg) per collectable scat:

$$y = 0.439 + 0.008x \tag{1}$$

where y is the prey mass consumed per collectible scat and x is the average body mass of an individual of a certain prey species. By multiplying y by the number of scats found containing each prey species, we estimated the mass of each of the prey species in the scats and derived proportional representation. We estimated body masses of the following prey species based on the literature and estimates by herdsman and HNP biologists: red deer (112 kg), marmot (6 kg), hare (2 kg), Przewalski horse (257 kg, foals 38 kg), cow (400 kg), domestic horse (226 kg), goat (30 kg), and sheep (40 kg).

Hairs of domestic horses and Przewalski horses were not distinguishable, so we had to indirectly estimate the contribution of these 2 species in the diet. We obtained the number of Przewalski horse kills from the annual HNP reports and from Wit and Bouman (2007) and the number of domestic horse kills from interviews. We multiplied the numbers by the mean body mass of the animals to calculate the total biomass of each species killed by wolves (ratio Przewalski:domestic horses was 1:102). However, in HNP carcasses of domestic animals were normally not completely eaten by wolves. Herdsmen set traps around carcasses and wolves, therefore, rarely return. Cinereous vultures quickly consume the remains. We based percentages of livestock kills consumed by wolves on interviews with herdsmen and the HNP biologist, and we then used these percentages to estimate actual biomass consumed of each species (ratio 1:78). Domestic horses are heavier than Przewalski horses and more Przewalski foals are predated than foals of domestic horses, which therefore yields fewer scats for domestic horses. The amount of consumed biomass per collectable scat (y in eq 1) is, therefore, a factor 2.3 higher for domestic horses than for Przewalski horse. We divided total biomass consumed per species, corrected for incomplete consumption, by the amount of consumed biomass per collectable scat (y) to find the number of scats produced per species. Hence, the ratio of number of scats with remains of domestic and Przewalski horses is about 1:34. We used this ratio to divide the scats labeled horse into scats from Przewalski horses and domestic horses.

We compared changes in diet composition from 1994 to 1997 (Hovens et al. 2000) to present. The study by Hovens et al. (2000) did not differentiate between domestic horses and Przewalski horses or between cows and goats. Therefore, we reclassified these prey species into categories horse and cow–goat, respectively. To minimize errors in scat age estimation we excluded scats older than 3 months and divided scats into winter (Sep–Apr) and summer (May–Aug). We tested for differences in diet composition between seasons using a chi-square test.

We calculated selection of prey species by wolves with Ivlev's selectivity index (Jacobs 1974, Johnson 1980, Jędrzejewski et al. 2000). Ivlev's selectivity index is based on biomass of prey species in the study area and biomass of each of the prey species observed in the diet. We calculated an index for the total diet, as well as for winter and summer separately. We used annual estimates of available prey; we excluded marmots from analysis of winter diet because they hibernate and are, thus, unavailable as prey for wolves. We used a chi-square test to evaluate potential seasonal differences between food supply and prey selection.

Because some livestock owners suffer more losses than others, we conducted a spatial risk analysis to determine which environmental factors influenced wolf predation of domestic horses. We used the travel distance from a herdsman's residence to the herds, determined in interviews, to estimate location and size of grazing areas. Grazing areas differed in summer and winter. Within each area we measured number of rock formations, number of gers, surface (%) containing shrub vegetation, surface (%) belonging in the park, radius and area of the grazing area, herd size, and number of grazing herbivores that could have been present from the gers within the area and from gers with overlapping grazing areas (i.e., more livestock can be present in a grazing area if the grazing areas of other gers overlap), distance of the ger to the park, and distance to the forest. We determined the location of each ger with Global Positioning Systems. We recorded all variables in Arcview for the analysis. We recorded summer and winter values of these variables separately in the database for each species. We analyzed the influence of these independent variables on differences in the arcsin-transformed percentages killed per

Table 1. Wolf diet prey-species composition in 2003, 2004, and 2005 in Hustai National Park, Mongolia, calculated from scat analysis using the equation of Weaver (1993).

Food category	2003 (%, $n = 80$)	2004 (%, $n = 60$)	2005 (%, $n = 96$)	Average (%, $n = 236$)
Cow	18	9	10	13
Domestic horse	40	31	26	32
Goat	10	5	5	7
Sheep	11	13	10	11
Deer	17	29	37	28
Hare	1	3	2	2
Marmot	3	10	10	7
Przewalski horse	1	<1	<1	<1
Rodent	1	1	1	<1
Livestock	79	57	51	63
Wildlife	21	43	49	37

owner with a Generalized Linear Model (GLM), using a backward-selection procedure.

To evaluate factors influencing depredation of Przewalski horses, we used 36 locations where Przewalski foals were killed by wolves recorded by HNP staff. For comparison, we selected 36 unpaired random locations from a 500 × 500-m raster, covering the area where wolf attacks could occur and the home ranges of Przewalski horses (Wit and Bouman 2007). To quantify landscape characteristics associated with each predation location and random point, we created 500-m buffers around the points in Arcview (we also applied other buffer radii that yielded similar results). Within each buffer, we measured percentage forest cover, percentage shrub cover, percentage herb cover, distance (km) to forest, distance (km) to nearest water source, distance (km) to closest ger, elevation (m), distance (km) to park boundary, average home range overlap of Przewalski harems (see below), mean red deer density, and distance (km) to nearest road (calculated from deer survey data and density estimates).

Przewalski horses have been followed and studied by students, eco-volunteers, and rangers of HNP for many years (Wit and Bouman 2007). The data are stored in Arcview, and the home range of each herd is, therefore, well known. Home ranges of harems sometimes overlap, ranging from zero (no overlap with other home ranges) to 10 (overlap with 10 other harems). We calculated average home range overlap by multiplying overlap values of the different areas within the buffer and dividing the sum of those values by the total area of the buffer.

We compared differences in environmental factors of kill sites and random points. We used a Kolmogorov–Smirnov test to check data for normality and compared variables that followed normal distributions using a one-way analysis of variance. We analyzed with a Mann–Whitney *U*-test variables that did not follow a normal distribution and that we could not transform successfully. We applied a multiple backward logistic regression to determine which variables best explained the difference between kill sites and random sites.

RESULTS

We collected 236 scats, showing that wolf diet was ≥51% livestock (Table 1). On average domestic horses were the most important livestock species (32%), whereas red deer were the most important wildlife species (27%). Przewalski horses composed <1% of wolf diets. Wolf diet varied by year (Fig. 2), and there appeared to be a negative relationship between percentage of horses in the diet and percentages of deer and marmot. When percentage of horses (either domestic or Przewalski horse) in the diet was great, percentage of deer declined, and vice versa (Fig. 3; $n = 6$, $r = -0.76$, $t = 2.34$, $P = 0.07$).

Using 155 scats, we found that livestock formed a greater proportion of winter than summer diet (Table 2; $\chi^2_1 = 11.85$, $P < 0.001$). Wolves ate more of all livestock species in winter, except for sheep, which were taken more in summer. We found the opposite trend for wildlife species, with a greater percentage occurring in wolf diets during summer (44% of all prey items) than in winter (27%). An analysis at species level showed that more deer were taken in summer (31% of prey items, against 21% in winter), and more cows, domestic horses, and goats in winter (Table 2; $\chi^2_8 = 28.92$, $P < 0.001$).

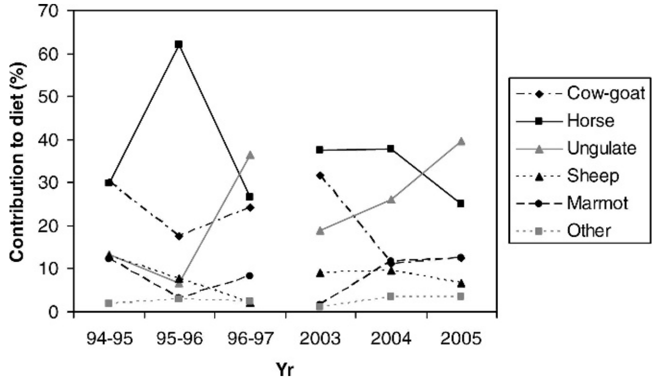

Figure 2. Changes in diet composition (cow–goats, horse, other ungulates, sheep, marmot, and other prey species) of wolves in Hustai National Park, Mongolia, from 1994 to 2005. The diet composition over the years 1994–1997 is obtained from Hovens et al. (2000).

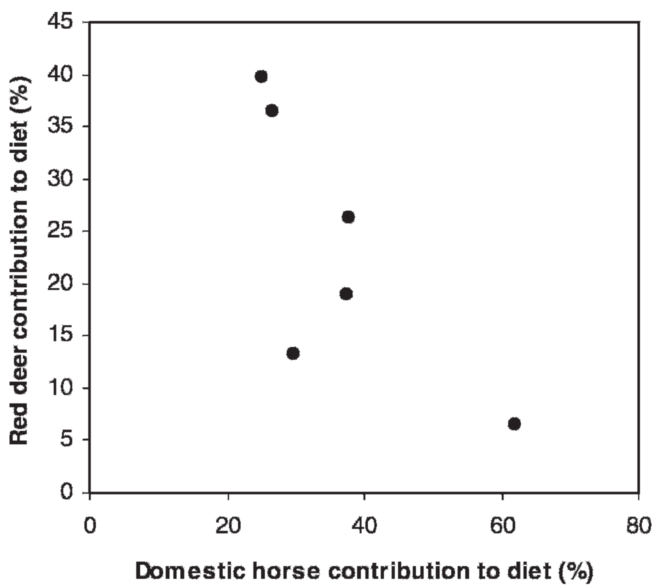

Figure 3. Correlation between the percentage of horses and the percentage of deer in the diet of the wolves in Hustai National Park from 1994 to 2005.

Table 2. Diet composition of wolves for winter and summer in Hustai National Park, Mongolia, calculated from an analysis of scats from 2003 to 2005, using the equation of Weaver (1993). To minimize errors in scat age estimation we excluded scats older than 3 months; therefore, $n = 155$.

Food category	Winter (%, $n = 35$)[a]	Summer (%, $n = 120$)[a]
Cow	22	11
Domestic horse	35	30
Goat	11	5
Sheep	5	10
Deer	21	31
Hare	1	2
Marmot	4	9
Przewalski horse	<1	1
Rodent	1	<1
Livestock	73	56
Wildlife	27	44

[a] Winter: Sep–Apr; summer: May–Aug.

Ivlev's selectivity index indicated that wolves in HNP preferred wildlife and domestic horses as prey (selectivity index D varies between from 0.12 and 0.81) over remaining livestock species and Przewalski horses (D = −0.33 to −0.61; Fig. 4). Over the entire year, red deer (D = 0.81) were selected most, followed by hare (D = 0.67), marmot (D = 0.18), and domestic horses (D = 0.12). Cow, goat, and sheep (D = −0.33 to −0.46) were selected more as prey than Przewalski horses (D = −0.61). The relative preference for certain species was evident in the summer and winter diet and, hence, independent of season (Fig. 4). Wolves selected cows, goats, and domestic horses more in winter (D respectively −0.06, 0.16, and −0.14) than in summer (D = −0.44, 0.05, and −0.44), although cows and goats were still selected against, illustrated by the negative indices. Selection for red deer decreased in winter ($D_{winter} = 0.73$, $D_{summer} = 0.83$). These Ivlev's selectivity indices for the different species are calculated from the observed number of prey items in the scats and the expected number of prey items, which is based on prey availability. The differences between observed and expected number of prey items was highly significant over the year ($\chi^2_7 = 169.33$, $P < 0.001$), as well as in summer ($\chi^2_7 = 215.70$, $P < 0.001$) and in winter ($\chi^2_6 = 95.95$, $P < 0.001$), with a larger than expected number of prey items in the diet for deer, marmot, and hare.

The GLM retained 2 variables that explained differences in the percentage of domestic horses killed: the squared distance to the park ($\beta = 0.02$, $P < 0.01$) and the number of gers per grazing area ($\beta = -4.62$, $P < 0.04$). Hence, the further from HNP, the higher the percentage of horse kills; the lower the densities of gers in the area, the higher the percentage of domestic horses lost by wolf predation. No other variables yielded significant correlations.

Przewalski foal kills were recorded more often at sites at a higher altitude (about 100 m higher than at random sites; $F_{1,70} = 11.289$, $P < 0.001$) and closer to forest (average distance to forest = 1.9 km for random sites vs. 0.6 km for foal kill sites; $F_{1,70} = 20.618$, $P < 0.001$). Compared to random sites, sites with Przewalski foal kills had lower shrub cover (medians respectively 0.15% and 0.00%; Mann–Whitney $U = 453$, $P < 0.01$), higher forest cover (0.00% and 0.06%, respectively; $U = 468$, $P < 0.01$), and higher red

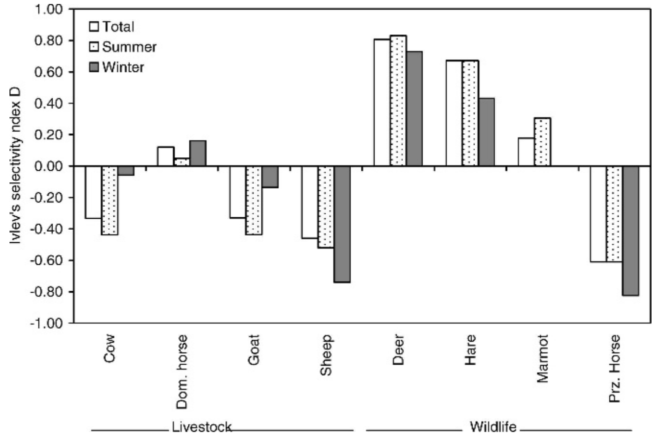

Figure 4. Prey selectivity (Ivlev's D) for prey species (cow, domestic horses, goat, sheep, deer, hare, marmot, and Przewalski horse) by the wolves of Hustai National Park, Mongolia, between 2003 and 2005 for the entire year and for summer and winter separately.

deer density (3.19 deer/km^2 and 11.71 deer/km^2, respectively; $U = 278$, $P < 0.01$). The multiple logistic regression retained 2 variables and indicated that distance to forest was smaller at kill locations compared to random locations (Wald = 11.582, $P < 0.001$) and that the shrub cover was lower (Wald = 4.718, $P < 0.05$, Nagelkerke $R^2 = 0.39$).

On average, a ranching family owned between 250 and 500 animals, mainly goats and sheep (about 85%), and 9–15 animals per family were lost to wolves each year. Horses and sheep were killed most often with an annual depredation rate of respectively 4.9% and 0.5%, whereas cows were killed least (0.2%). On average, the livestock a family owned was valued between US$14,000–23,000, and losses due to wolf predation were US$600–1900/year (or 5–11%). Domestic horses were the most valuable (US$200), and the largest economic damage to the herdsmen (70–95% of the yearly losses in US$/yr) was, therefore, caused by loss of horses.

DISCUSSION

Results of the diet composition indicated that wolves mainly killed livestock, but that wildlife species were positively selected, especially in winter. The predation of domestic horses comprised the largest economic loss to herdsmen. Factors like a high forest cover, a low shrub cover, a high altitude, a high red deer density, a low density of gers, and a large distance from the park had increased the predation risk of wolves.

Livestock was an important food source, contributing >50% to the diet (Table 1). Hovens et al. (2000) found similar values. As Bibikov (1982) and Okarma (1995) found in their studies on wolf predation in Eurasia, we suggest 3 factors were correlated with an increase of livestock kills in HNP. The first factor was scarcity of wild ungulates. The main wild ungulate species in HNP was red deer, although their population was low (estimated at 195–355 individuals from 2000 to 2003). No other large wildlife species is present in high numbers in HNP. The second factor was the disruption of pack social structure due to intensive hunting. Hunting was prohibited in the park but wolves that ventured outside the park were often killed. This hunting pressure, and also the former tradition of killing wolf pups, could have contributed to disruption of the pack's social structure and pack size, changed the prey preference, and thereby have increased the livestock kills, as has been reported in other studies (Bibikov 1982, Okarma 1995). The final factor was husbandry practices. Livestock was available around the park in large numbers, an attractive but probably risky alternative prey to wildlife when times were harsh for wolves.

The large proportion of livestock in the diet of wolves was also caused by the larger availability of livestock, because the Ivlev's selectivity index (Fig. 4) only showed a positive selection for domestic horses, whereas other livestock species were selected against. The 3 wildlife species (red deer, hare, and marmot) had the highest selectivity indices. Thus, wolves positively selected for wildlife and negatively selected livestock, with domestic horses as the one exception. Wolves are opportunistic predators and switch prey easily. Wolves can, therefore, survive in an array of habitats with large differences in food availability. When there is a high abundance, richness, and diversity of wild ungulates species, use of livestock species is low (Meriggi and Lovari 1996). We also found a negative relationship between ungulates and livestock; a high percentage of deer in the diet reduced the contribution of domestic horses in the diet (Fig. 3). Our results indicated that deer and marmot were probably key wildlife prey species in the wolf's diet. In some years, marmots are available in large numbers, such as in 1998 when the total population size was estimated at about 24,000 individuals. In such a year marmots contribute the most to the total biomass, making them good prey for wolves in summer. However, marmots hibernate from September until March and their absence might be compensated by increased predation on livestock. A year with exceptionally low marmot densities, such as in 2003, appeared to increase the contribution of livestock in the diet (Table 1). The low 2003 marmot density was probably caused by reduced forage availability in the summer of 2002, forcing marmots to start hibernating with poor body conditions. The percentage of deer in the diet was highest from all wildlife species, although the deer population size is low. This switch between wildlife (deer) and livestock has also been recorded in other study areas, and generally livestock losses only decrease when availability and diversity of potential wildlife prey is increased (Bibikov 1982, Mech et al. 1988, Meriggi and Lovari 1996, Jedrzejewski et al. 2000, Sidorovich et al. 2003).

Przewalski horses are only a minor part of the diet of the wolves in HNP, with approximately 5–15 foals (of the 30–40 born) killed each year. The population is still growing although not at its maximum rate. We reassert that although it is exactly known how many Przewalski horses die each year, it can be difficult to determine whether wolf predation was the primary cause of death or whether wolves only scavenged on the carcass. Even if all dead Przewalski horses for which cause of death was unknown were attributed to wolves, contribution to the wolf diet would still be $<1\%$. However, the effect of wolf predation on Przewalski horses could still be large, and a detailed population fluctuation analysis should be carried out of the Przewalski population to quantify the effect of wolf depredation on Przewalski population growth.

Because vulnerability and availability of prey species change seasonally, diet composition of wolves also changes (Mech and Boitani 2003). Our results indicated that livestock was more important to wolves in winter than in summer (Table 2 and Fig. 4), although this result could be biased because we found few scats in winter. However, our results concur with findings of Hovens and Tungalaktuja (2005) and with information provided by herdsmen. A reason for a high livestock:wildlife ratio in winter could be the unavailability of marmots due to hibernation. Also, vulnerable deer calves are born in summer, which are suitable prey items for wolves, thereby decreasing the need for preying on livestock in summer. Another reason for diet composition changes could be that herding families live closer to the park in winter and are more dispersed, improving accessibility of wolves to livestock. Another factor that could explain the larger livestock losses in winter is that mares are milked in summer. Kept closer to the gers, mares are better protected. Hovens and Tungalaktuja (2005) found that fewer domestic horses were killed in summer and attributed this to the effect of milking on spatial distribution of the mares.

We expected that predation risk on livestock would increase when livestock owners were living closer to the park because we assumed wolves would take refuge in the park. However, results of the spatial analyses showed that more domestic horses were killed further from the park. It might be that in the park more wildlife is present and wolves prefer wildlife above livestock. Livestock near the park would, therefore, be safer. Also, wolves might have larger home ranges than the park area alone. Wildlife density decreases drastically further away from the park and the only potential prey is livestock. Thus, it is therefore best for nomads to live closer to the park with several gers together to reduce the predation risk on domestic horses.

Domestic horses roamed freely and were not herded or looked after, making them easy prey for wolves. Horses are the most valuable livestock species, and herdsmen might prevent domestic horse predation by keeping horses closer to the ger or by herding them. Killing of sheep and goats could be reduced by use of livestock-guarding dogs, which in the French Alps has proven to reduce livestock losses considerably (Espuno et al. 2004).

Przewalski foals were killed at higher altitudes, in areas with less shrub cover, closer to forest, and where red deer densities were higher. However, locations where dead Przewalski foals were found may not necessarily correspond with actual kill locations. Foals could have been dragged away from actual kill locations. It is not a surprise that Przewalski foals were killed at places with higher red deer density, because wolves follow prey. The preferred habitat of red deer are small grassland patches, situated near or within closed forest (i.e., ridges, natural openings, or margins between forest and unplanted hill grounds; Welch et al. 1990). When wolves are present red deer might move into the protective cover of wooded areas, reducing their use of the preferred grassland that has higher predation risk (Creel et al. 2005).

Similar to findings by Oakleaf et al. (2003) we expect that vulnerability to wolf predation is related to proximity of horses to wolf home ranges. Our results concur with those of Jedrzejewski et al. (2005) who revealed that places where wolves were spotted were closer to forests and on higher altitudes than places without wolves. In forests wolves find suitable den sites and food resources. Sites at higher elevation and closer to forests are also preferred resting sites for Przewalski horses, increasing their chances of encountering a wolf pack.

Lower shrub cover at foal predation sites might be related to larger forest cover in these areas. Shrubs might offer suitable hiding places for wolves but might also hinder wolves chasing prey. In contrast to solitary living felids who ambush prey, canids chase their prey and exhaust it (Biknevicius and Van Valkenburgh 1996). Less shrub cover might, therefore, also increase predation success of wolves.

MANAGEMENT IMPLICATIONS

Wolves at HNP mainly depredated livestock species that were widely available in the area. Red deer was their preferred wildlife prey species. Przewalski horses (mostly foals) were only a minor part of wolves' diet. However, as herdsmen increase protection of their livestock (e.g., through increased surveillance or by using livestock-guarding dogs) livestock will become less accessible to wolves. We expect this reduced livestock availability to increase wolf hunting pressure on wildlife species, including Przewalski horses, especially in winter. Red deer are an important prey species, and improving conservation of the deer population could, therefore, be pivotal in management of HNP, because red deer can constitute a buffer species that will prevent wolves from taking livestock and Przewalski horses. Thus, we recommend more efforts be put into preventing poaching of red deer and into activities that might stimulate red deer population growth, such as banning capture of red deer juveniles in HNP for reintroduction elsewhere. Livestock-guarding dogs might decrease number of sheep and goats killed by wolves and decrease economic damage to herdsmen. However, the potential of compensation schemes for livestock losses (Treves et al. 2002) should be evaluated, because this might lower pressure on Przewalski horses.

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