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SHORT COMMUNICATION

Feeding ecology of the wolf (*Canis lupus*) in a near-natural ecosystem in Mongolia

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Abstract

The increasing animosity towards wolves (*Canis lupus*) by livestock-keeping nomads in Mongolia and the accompanying conflicts highlight the urgent need for knowledge about the feeding behavior of wolves, since information on the feeding ecology of wolves in Mongolia is rare, especially in the mountain taiga and mountain forest steppe regions of Northern Mongolia. Those regions are characterized by a relatively high wildlife diversity and are sparsely populated by humans. To face this problem, 137 wolf scats were collected in the Khentii Mountain range in Northern Mongolia between 2008 and 2012. Almost all wolf faeces contained remnants of wild ungulates, which made up 89% of the consumed biomass. Siberian roe deer (*Capreolus pygargus*) was the most important and positively selected prey species. It was followed by red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*), which was negatively selected by wolves. Wolves also fed on buffer prey species such as lagomorphs and small mammals. No evidence of domestic ungulates was found in the wolf diet. Thus, near-natural habitats with a diverse fauna of wild animals are important to limit livestock depredation.

Keywords Diet composition · Scat analysis · Prey selection · Wild ungulates · Livestock · Forest steppe

Throughout its range in Northern America and Europe, the wolf (*Canis lupus*) mainly feeds on wild ungulate species (Okarma 1995; Jędrzejewska and Jędrzejewski 1998; Peterson and Ciucci 2003; Mattioli et al. 2011; Lanszki et al. 2012; Wagner et al. 2012; Barber-Meyer and Mech 2016; Goldthorpe 2016; Newsome et al. 2016; Bassi et al. 2020; Figueiredo et al. 2020; Trbojević et al. 2020). In times of primary prey shortage, wolves switch to secondary "buffer" prey (Forbes and Theberge 1996; Sidorovich et al. 2003; Barber-Meyer and Mech 2016). Since the domestication of livestock came along with an impoverishment of wild ungulate species, wolves are more and more forced to change their feeding habits towards prevalently available domestic prey (Boitani 1995; Vos 2000; Peterson and Ciucci 2003; Capitani et al. 2004; Ciucci et al. 2018). This is particularly true in most parts of Southern Europe and Asia, where the availability of natural prey is low and poor husbandry techniques with weak prevention measures are prevailing (Janeiro-Otero et al. 2020; Lyngdoh et al. 2020). The consumption of livestock has been confirmed in several study areas in Southern Europe, where it constitutes the bulk of wolf diet (Torres et al. 2015; Petridou et al. 2019; Ciucci et al. 2020) or the second most consumed food category (Meriggi et al. 2015; Imbert et al. 2016; Ciucci et al. 2018; Trbojević et al. 2020). However, the studies by Meriggi et al. 2015 and Imbert et al. 2016 indicate a decreasing livestock predation with simultaneously increasing wildlife consumption by wolves, once wild ungulate restoration programs got established, that came along with an increase in forested areas and the implementation of depredation prevention techniques. Moreover, a high occurrence of livestock in wolf diet was reported for all over Asia, especially in Mongolia, China, Pakistan, and Iran (Goldthorpe 2016; Newsome et al. 2016; Janeiro-Otero et al. 2020; Lyngdoh et al. 2020). On the other hand, livestock consumption lies below two percent in several parts of Central Europe, where wildlife density is

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high and livestock is mostly kept protected (Ansorge et al. 2006; Nowak et al. 2011; Wagner et al. 2012).

In Mongolia, an ongoing decline of wildlife populations has been recorded during the last decades. It is caused by unsustainable hunting due to an increasing wildlife trade as a consequence of Mongolia's transition to a free market economy (Zahler et al. 2004; Wingard and Zahler 2006; Chimed-Ochir et al. 2010). At the same time, the amount of livestock increased from about 25 million to more than 40 million animals with a total population of only 2.8 million inhabitants (Erdenesan 2016). This led to a transformation of natural habitats into pasturelands, which cover more than one-third of the Mongolian territory. Livestock depredation plays a significant role in Mongolia, since livestock serves both as a food source and as source of income for more than 50% of the Mongolian population (Mijiddorj et al. 2018). Up-to-date information on livestock depredation rates in Mongolia is missing, since consistent recordings stopped after the Soviet Union collapse, but it is believed that rates are increasing (Eregdenedagva et al. 2016).

However, only few studies on the feeding ecology of wolves were performed in Mongolia and all of them state a high consumption of livestock by wolves. Those studies were carried out in protected areas of Central Mongolia: Khustai National Park (Hovens and Tungalaktuja 2005; Van Duyne et al. 2009), Ikh Nart Nature Reserve (Davie et al. 2014) and Bogdkhan Mountain Strictly Protected Area (Nakazawa et al. 2008). Nevertheless, the diversity and density of large wild ungulates in all study areas were comparatively low, regarding the high amount of free-ranging livestock grazing in and around the protected areas. The studies were conducted mainly in steppe habitats of Central Mongolia, which commonly suffer from overgrazing, except for the protected areas itself.

There is no information on the feeding habits of wolves in mountain taiga and mountain forest steppe regions of Northern Mongolia, where a relatively high wildlife diversity and sparse human presence is prevailing. Therefore, this study aims to investigate the diet composition and prey selection of wolves in a near-natural ecosystem and to contribute to a better description and understanding of wolf predation in Mongolia.

Wolf scats were collected in an area of about 450 km^2 within the valley of Khonin Nuga (49°05′ N, 107°17′ E, elevation 900–1600 m), Selenge Aimag, which is located in the West Khentii Mountain range approximately 130 km north of the capital Ulaanbaatar. Khonin Nuga is situated in the buffer zone of the 'Strictly Protected Area of Khan Khentii' (KKSPA), where the Siberian mountain taiga borders the Mongolian-Daurian mountain forest steppe (Dulamsuren et al. 2005). This transition zone harbors a rich diversity of plant and animal species. Overall, more than 50 species of mammals, 200 bird species, and several reptile, amphibian, and fish species (Mühlenberg 2012) offer a broad prey spectrum for predators. Accordingly, Khonin Nuga can be considered as a biodiversity hotspot (Townsend et al. 2010; Mühlenberg 2012). The study site is an almost untouched and nearly unsettled area, where only few families are present with their free-ranging livestock (mainly horses and cattle), sporadically scattered along the rivers.

Information on wildlife populations in Khonin Nuga, especially data on population size and density, is rare. A camera trapping study carried out in summer 2010 reports average rates of detection per 100 trap nights of 15.8 for wild ungulates, 3.2 for livestock and 0.1 for wolves (Townsend et al. 2010, 2014). The wolf density and home range size in Khonin Nuga is unknown. Rangers claimed the presence of one wolf pack in the Khonin Nuga area. Based on distance sampling surveys conducted by the Mammal Ecology Laboratory of the Mongolian Academy of Sciences (MAS), the population densities of forest ungulates in the KKSPA are defined as 7.6/10 km^2 for wild boar (*Sus scrofa*), 5.7/10 km^2 for Siberian roe deer (*Capreolus pygargus*), 2.8/10 km^2 for red deer (*Cervus elaphus*), 1.0/10 km^2 for Siberian musk deer (*Moschus moschiferus*), and 0.5/10 km^2 for moose (*Alces alces*). Density estimates were calculated using the formula by Buckland et al. (2001) (MAS 2011).

The scat collection was performed during both summer (2008, 2011, 2012) and winter (2009, 2010) season. In total, 137 useful wolf scats were collected for the diet analysis. The scats were identified as wolf scats due to their high amount of good visible hairs and bone fragments and a diameter of at least 25 mm (Ciucci et al. 1996). Confusion with dog faeces is unlikely since feral dogs do not exist at the collection site, except for two watchdogs of a ranger family, which stay with the yurts and are hand fed. Scat collection was carried out by horse or by foot at preferred wolf locations, which included den sites, rendezvous sites, kill sites, forest roads and trails, mountain ridges, natural corridors as well as along creeks and rivers (Lucchini et al. 2002; Kunkel et al. 2005; Kaczensky et al. 2008). In addition, locals were consulted for sites of recent wolf records. During winter, wolf scats were also collected by backtracking in snow. Study locations were resampled in biweekly time intervals.

Following Jędrzejewska and Jędrzejewski (1998), scats were prepared for the determination of food remains as described by Wagner et al. (2012). Hair identification was based on keys and hair atlases of Teerink (1991) and Meyer et al. (2002) as well as a reference hair collection of local species. Data analysis includes the frequency of occurrence (Ansorge et al. 2006) and the biomass consumed following the method suggested by Goszczyński (1974) using coefficients of digestibility (Wagner et al. 2012). Furthermore, Ivlev's Electivity Index (Ivlev 1961) modified by Jacobs (1974) was used to describe the predator preference for the three most important ungulate species (Mattioli et al. 2004).

Data about ungulate abundance were taken from the survey by MAS 2011 as stated above.

In total, 28 different food items, classified into 8 food categories, were detected in the scats of the Khonin Nuga area (Table 1). Wild ungulates constituted the most consumed food category (frequency of occurrence 95.6%, biomass 86.8%). The most consumed prey species was the Siberian roe deer (frequency of occurrence 43.8%, biomass 46.2%), followed by wild boar and red deer. They were detected half as often as the Siberian roe deer. The Siberian musk deer and moose composed less than 3.0% of the totally consumed biomass. Unexpectedly, with a frequency of occurrence of 36.5% and a biomass of 5.4%, small mammals of the family of voles were the second most important food category. Lagomorphs had approximately the same amount as voles regarding the consumed biomass. Other medium-sized mammals, like the Daurian hedgehog *(Mesechinus dauricus)*, were of less importance. While birds occurred quite frequently (13.1%), they represented only 0.4% of the consumed biomass. Although insects, particularly grasshoppers (Ortopthera indet.), occurred in 10.2% of all scats, their proportion of biomass was very low. Similar results were obtained for plant remnants, which were mostly fruits of the bird cherry *(Prunus*

Table 1 Composition of wolf diet in the Khentii Mountains, Mongolia ($n = 137$)

Food item	Total ($n = 137$)		Summer ($n = 106$)		Winter ($n = 31$)	
	FO%	BM%	FO%	BM%	FO%	BM%
Wild ungulates	95.6	86.8	94.3	84.0	100.0	93.1
Alces alces	7	0.8	0.9	1.1	0.0	0.0
Capreolus pygargus	43.8	46.2	42.5	42.7	48.4	54.0
Cervus elaphus	18.2	14.7	22.6	20.7	3.2	1.2
Moschus moschiferus	4.4	2.4	3.8	2.5	6.5	2.3
Sus scrofa	22.6	17.8	21.7	14.9	25.8	24.5
Cervidae indeterminable	3.6	0.6	1.9	< 0.1	9.7	2.0
Artiodactyla indeterminable	2.2	4.2	0.9	2.0	6.5	9.2
Medium-sized mammals	14.6	5.9	15.1	6.7	12.9	4.0
Lepus timidus	3.7	3.3	4.7	4.7	0.0	0.0
Mesechinus dauricus	2.2	1.1	0.9	0.2	6.5	3.2
Ondatra zibethicus	0.7	0.1	0.9	0.1	0.0	0.0
Sciurus vulgaris	0.7	< 0.1	0.9	0.2	0.0	0.0
Leporidae indeterminable	5.1	1.1	5.7	1.4	3.2	0.4
Mammalia indeterminable	2.2	0.2	1.9	0.1	3.2	0.4
Small mammals	36.5	5.4	44.3	7.4	9.7	0.8
Microtus fortis	9.5	2.9	12.3	4.1	0.0	0.0
Microtus mongolicus	0.7	0.2	0.9	0.3	0.0	0.0
Microtus spec	24.1	2.2	29.2	2.9	6.5	0.7
Arvicolidae indeterminable	2.2	0.1	1.9	0.1	3.2	0.1
Birds	13.1	0.4	14.2	0.6	9.7	0.1
Coturnix japonica	0.7	0.1	0.9	0.1	0.0	0.0
Emberizidae indeterminable	0.7	< 0.1	0.9	0.1	0.0	0.0
Aves indeterminable	11.7	0.3	12.3	0.3	9.7	0.1
Fishes	2.2	< 0.1	0.9	< 0.1	6.5	< 0.1
Reptiles	0.7	< 0.1	0.9	< 0.1	0.0	0.0
Insects	10.2	< 0.1	8.5	< 0.1	16.1	0.1
Carabidae indeterminable	0.7	< 0.1	0.9	< 0.1	0.0	0.0
Tenebrionidae indeterminable	0.7	< 0.1	0.9	< 0.1	0.0	0.0
Coleoptera indeterminable	0.7	< 0.1	0.9	< 0.1	0.0	0.0
Orthoptera indeterminable	8.0	< 0.1	5.7	< 0.1	16.1	0.1
Plants	3.6	< 0.1	4.7	< 0.1	0.0	0.0
Prunus padus	2.9	< 0.1	3.8	< 0.1	0.0	0.0
Plantae indeterminable	0.7	< 0.1	0.9	< 0.1	0.0	0.0

Data are expressed as frequency of occurrence (FO%) and biomass (BM%) using the biomass calculation described by Goszczynski (1974)

padus). No remnants of livestock were detected within the analyzed wolf scats in this study.

The seasonal evaluation of the wolf diet should be assessed considering the low sample size. In summer and in winter samples, the Siberian roe deer was the most consumed prey species (> 40%). Small mammals were the most common prey item in summer (frequency of occurrence 44.3%, biomass 7.4%) and of less importance in winter. Red deer was the third most consumed prey species in summer (frequency of occurrence 22.6%, biomass 20.7%) and almost absent in winter. In winter, insects of the order Ortopthera were the second most common prey category (16.1%). Fishes occurred more often in winter (6.5%) than in summer. Winter samples were mainly dominated by two prey species, the Siberian roe deer and wild boar.

Ivlev's Electivity Index highlighted a significant positive selection of the Siberian roe deer by wolves ($D = 0.34$), whereas the wild boar was significantly negatively selected ($D = -0.42$). The index value of the red deer was 0.13.

General knowledge on food habits of the Mongolian wolf is based primarily on reports of nomadic herders and lead to the conclusion that wolves in Mongolia mainly feed on livestock. Eregdenedagva et al. (2016) painted an impressive picture of historical and present conflicts between livestock-keeping nomads and wolves. Even the few existing studies on the feeding ecology of wolves in Mongolia revealed a high consumption of livestock (Hovens and Tungalaktuja 2005; Nakazawa et al. 2008; Van Duyne et al. 2009). They all stated a livestock occurrence in scats of up to 70%, with domestic horses being the main prey species. On the other hand, the present results revealed a wildlife consumption of 100%, and thus, this study highlighted an unexpected lack of livestock.

The scat analysis suggested a high predation on wild ungulates, which represent the principal prey of wolves in the study area. This is consistent with studies conducted worldwide (Mech and Boitani 2003; Sidorovich et al. 2003; Ansorge et al. 2006; Barja 2009; Mattioli et al. 2011; Lanszki et al. 2012; Wagner et al. 2012; Barber-Meyer and Mech 2016; Newsome et al. 2016; Bassi et al. 2020; Figueiredo et al. 2020; Trbojević et al. 2020). The Siberian roe deer constituted the most important prey species in the study area. It was the most consumed prey item and was positively selected by wolves. Although wolves mainly feed on the most abundant large ungulate species in most parts of their range (Jędrzejewski et al. 2000), a high consumption of roe deer has also been reported by studies conducted e.g. in Ukraine (Bibikow 1990), Spain (Barja 2009), Italy (Mattioli et al. 2004; Meriggi et al. 2015), Portugal (Figueiredo et al. 2020), Estonia (Valdmann et al. 1998) and Germany (Ansorge et al. 2006; Wagner et al. 2012). Wild boar was the second most consumed prey of wolves in Khonin Nuga. It was negatively selected by wolves due to its defensive behavior (Jędrzejewski et al. 2002). A high consumption and negative selection of wild boar was reported from various studies across Europe (Mattioli et al. 2004; Lanszki et al. 2012; Wagner et al. 2012; Meriggi et al. 2015; Figueiredo et al. 2020). Red deer ranked third, which corresponded with findings from Germany (Ansorge et al. 2006; Wagner et al. 2012), Western Poland (Nowak et al. 2011), Portugal (Figueiredo et al. 2020), Spain (Barja 2009) and Italy (Meriggi et al. 2015), whereas in Bialowieza primeval forest and the Beskid Mountains in Poland, red deer was mostly the main prey of wolves (Jędrzejewski et al. 2002). Following wild ungulates, small mammals represent the second most consumed prey category, considering both frequency of occurrence and consumed biomass. Studies carried out in Mongolia (Hovens and Tungalaktuja 2005), Inner Mongolia (Honghai et al. 1998), Russia (Heptner et al. 1998), Belarus (Sidorovich et al. 2003), Estonia (Valdmann et al. 1998), Poland (Jędrzejewski et al. 2002), and Italy (Ciucci et al. 1996; Meriggi et al. 2015) stated a minor consumption of small mammals. Although lagomorphs were consumed in low quantities, they represented one of the most important buffer prey of wolves (Meriggi et al. 2015; Newsome et al. 2016). Consistent observations were made by studies in Inner Mongolia (Honghai et al. 1998; Yan et al. 2006), Belarus (Sidorovich et al. 2003), Estonia (Valdmann et al. 1998), Poland (Jędrzejewski et al. 2002), and Italy (Ciucci et al. 1996; Meriggi et al. 2015).

Considering seasonal changes, summer samples indicated a higher prey species diversity than winter samples. Pronounced seasonal variations were observed for red deer, small mammals and fruits of the bird cherry. All of them were consumed mostly during summer, when small mammal density is highest after reproduction and fruits are available (Meriggi et al. 2015). During summer, red deer calves become more independent when joining the herd, thus making them an easy prey for wolves (Hovens and Tungalaktuja 2005). Deeper investigations on the seasonal dynamics of food habits are needed to perform solid results.

Livestock was not found in the samples of Khonin Nuga, although herds of horses and cattle were free-ranging, especially in the center of the research area (Townsend et al. 2010). These results contradict those reported by Hovens and Tungalaktuja (2005), Nakazawa et al. (2008) and Van Duyne et al. (2009). The studies were all carried out in protected areas of Mongolia, but the present study was conducted in an almost undisturbed transition zone between the mountain taiga and forest steppe, whereas previous studies were implemented in steppe habitats of Central Mongolia. The vegetation zones of mountain taiga (4%) and forest steppe (25%) cover about one third of the Mongolian territory (Hilbig 2006). Those areas are sparsely populated and livestock grazing takes place mainly in forest steppe zones. The steppes of Central

Mongolia suffer from overgrazing (Hovens and Tungalaktuja 2005), implying a high livestock density around the protected areas, whereas livestock density is relatively low at the Khonin Nuga site. Husbandry practices are similar throughout Mongolia. Large livestock (horses, cattle) is free-ranging, while small livestock (sheep, goats) is herded during daytime. Horses are often not seen for days, whereas sheep, goats, and cattle stay next to the yurts at night (Hovens and Tungalaktuja 2005; Van Duyne et al. 2009; pers. observations). The wildlife density and diversity of large wild ungulates is much higher in Khonin Nuga compared to Khustai National Park (KNP) and Bogdkhan Mountain Strictly Protected Area. Van Duyne et al. (2009) observed that the wildlife density in KNP surroundings heavily decreased with decreasing proximity to the National Park and that more horses were killed in areas further away from KNP. Even though all studies stated that livestock, especially domestic horses, is the main prey of wolves, Van Duyne et al. (2009) found that livestock was negatively selected by wolves, whereas wildlife was positively selected. Furthermore, they showed that a high percentage of wildlife in the wolf diet reduced the amount of livestock in the diet. Similarly, several studies carried out in Europe suggested that a high density and diversity of wild ungulate species could reduce livestock depredation by wolves (Barja 2009; Meriggi et al. 2015; Newsome et al. 2016; Figueiredo et al. 2020; Janeiro-Otero et al. 2020). The results of this study are broadly in line with those findings. Even in times of less available main prey (Siberian roe deer), there were at least two sufficiently abundant alternative prey species (wild boar and red deer) wolves can easily compensate with. Thus, the lack of livestock in the wolf scats of this study might indicate a sufficient supply with wildlife, so that wolves have no need to prey on livestock. However, other factors like a small pack size and mainly large livestock (horses, cattle) in the core area of the study area have to be considered as well, especially with regard to the uncertainties in wolf population information in Khonin Nuga. The relatively small sample size combined with the Rangers' observations lead to the conclusion that there might be only one established wolf pack with few individuals at the Khonin Nuga site. Accordingly, roe deer represents the less defensive and most vulnerable prey species, even if they are solitary and, thus, more difficult to track than livestock herds. Since wolves hunt on a known territory, they know where to find wild prey, which is less risky to attack than large livestock.

Nevertheless, this study provides for the first time an overview of the feeding habits of wolves in a near-natural ecosystem in a mountain taiga and mountain forest steppe region of Northern Mongolia. Further investigations are crucial for a comprehensive evaluation of wolf feeding habits and depredation patterns in Mongolia, thus there is a strong need for population and feeding ecology studies of wolves in Mongolia. Moreover, the effect of livestock management practices needs to be addressed in further studies.

In conclusion, the wide prey spectrum of the wolf in the Khentii Mountains indicates an almost untouched and healthy ecosystem with an adequate abundance of wild ungulates. In times of inaccessibility of common prey species, wolves fall back on buffer prey species such as lagomorphs or small mammals. Even though unprotected and free-ranging livestock herds occur within the research area, no evidence of livestock was found in the wolf diet. In contrary, other feeding ecological studies of wolves carried out in Mongolia (Hovens and Tungalaktuja 2005; Nakazawa et al. 2008; Van Duyne et al. 2009) state a high level of livestock predation. It is assumed that the population density of wild ungulates is high enough at the study site, so that wolves are able to satisfy their food requirements without preying on livestock. In addition, a small pack size and the presence of mainly large livestock in the core area of Khonin Nuga favor the predation of (small) wild ungulates by wolves.

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Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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