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Original investigation

Responses of wolf feeding habits after adverse climatic events in central-western Belarus<sup>☆</sup>Vadim Sidorovich<sup>a</sup>, Annik Schnitzler<sup>b,\*</sup>, Christophe Schnitzler<sup>c</sup>, Irina Rotenko<sup>a</sup>, Yulia Holikava<sup>a</sup><sup>a</sup> Institute of Zoology, National Academy of Sciences of Belarus, Akademicheskaya Street, 27, Minsk 220072, Belarus<sup>b</sup> LIEC—UMR 7360 CNRS, University of Lorraine, Metz, France<sup>c</sup> LISEC EA 2310, Faculté des Sciences du Sport, Strasbourg, France

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## ABSTRACT

Many studies have investigated the ecology of wolf populations of Eurasia, showing that although wolves are mostly opportunistic in seeking meso-large enough mammalian prey, they can also be selective, depending on local availability of prey and their population biomass. Yet prey preferences of the wolf have been poorly evaluated in situations of complex predator/prey systems because such ecological situations are extremely rare in Europe. In particular, the role of beaver is poorly known due to the extreme decline in its range and population over the last few centuries.

We conducted a 15-year study (1999–2014) of wolf *Canis lupus* diet in the Naliboki forest of central-western Belarus to determine the dietary responses of the wolf population in a context of a rich prey supply (beaver 650 inds/100 km<sup>2</sup>, elk 47 inds/100 km<sup>2</sup>, red deer 98 inds/100 km, roe deer 398 inds/100 km<sup>2</sup>, wild boar 234 inds/100 km<sup>2</sup>). The bison, although present, is not preyed on. We compared the seasonal and annual diet variations of both wolf adults and pups, by scat analysis and hair identification. In winter 2012–2013, the winter was quite harsh with a long period of snow, which severely affected the roe deer and wild boar populations. Five severe summer droughts also occurred (1999, 2001, 2002, 2004 and 2013), greatly decreasing the water level in rivers and canals. We took advantage of these stressful events to evaluate the diet responses of the wolves.

In “normal” years, we identified 11 food categories, essentially beaver and medium-sized ungulates (66%), and large ungulates to a lesser extent (9% in summer, 20% in winter). The adults were found to selectively supply pups with beaver, probably because of its easy transportability. Beaver consumption also increased during summer droughts when water levels were very low. After the harsh winter of 2012–2013, which was followed by a sharp decline in medium-sized prey, we observed a shift in the winter diet breadth of the wolves towards greater consumption of both large wild ungulates and small carnivores. We concluded that:

1. Beaver is a functional element in wolf ecology, as a primary food for adults and pups;
2. A large range of available prey species is important to maintaining a viable wolf population in cases of extreme climatic events.

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<sup>☆</sup> Vadim Sidorovich designed the study, carried out almost all the fieldwork needed to build the dataset (i.e. collected scats together with Irina Rotenko, did census of wolves, beaver and wild ungulates), tested the hypotheses and provided the framework of the manuscript. Annik Schnitzler wrote the manuscript and checked it for consistency and inferences, and took part in the fieldwork in the late stage of the study from 2013 onward. Christophe Schnitzler performed the statistical analysis. Yulia Holikava took part in the fieldwork in the late stage of the study from 2011 onward (analysis of about a quarter of the scats).

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## Introduction

Since Murie's (1944) pioneering work on the diet strategies of wolves (*Canis lupus* Linnaeus, 1758), many studies have continued to investigate the wolf populations of Eurasia (Okarma, 1995; Okarma et al., 1995; Zlatanova et al., 2014) and North America (Mech and Boitani, 2003). All these studies have shown that although wolves are mostly opportunistic in seeking big enough mammalian prey, they can also be more selective, depending on the regional specificities of the prey and their population biomass. Wolves have also been observed to chase prey of many sizes when

they encounter them by chance in order to meet their nutritional requirements.

The primary prey species are large wild ungulates (red deer *Cervus elaphus*, elk *Alces alces*, reindeer, *Rangifer tarandus* in the boreal zone) and medium-sized ungulates (roe deer *Capreolus capreolus*, wild boar *Sus scrofa*), with a preference for large sizes.

In Europe, red deer is often preferred to wild boar and roe deer in the Bialowieza forest of Poland (Okarma et al., 1995; Jedrzejewska et al., 2000; Jedrzejewski et al., 2002), and elk is preferred to wild boar in the forests of Scandinavia and the Baltic countries (Olsson et al., 1997; Kübarsepp and Valdmann, 2003; Zlatanova et al., 2014). In North America, elk is preferred to white-tailed deer (*Odocoileus virginianus*) (Frenzel, 1974; Messier and Crête, 1985). In southern European regions, red deer is preyed on in proportions similar to those of roe deer and wild boar when all are present in abundance (Meriggi et al., 2011, 2015). In other regions, wild boar or roe deer is the selected prey (Capitani et al., 2004; Zunna et al., 2009). Large mammals are easily preyed on at latitudes where winters are long and snowy because they are particularly vulnerable in deep snow (Huggard, 1993) and starvation at the end of a long winter deteriorates their physical condition. Wild boar is often selected over red deer in southern Europe when the latter are comparatively less abundant than the former (Capitani et al., 2004; Mattioli et al., 2004).

Along with ungulates, the medium-sized beaver (*Castor fiber* in Eurasia, *Castor canadensis* in North America) is also regular prey for wolves in swamps and floodplains (Rosell et al., 1996). Beaver is an interesting prey in terms of energy cost because, as a social and territorial species, it concentrates in large colonies along rivers and lakes. Compared with hoofed animals, beaver is less mobile and thus easier to catch, with predators simply waiting at its feeding places on land recognizable by scent marking (Rosell and Bergan, 1998). Its aquatic lifestyle and habit of constructing partially submerged lodges under masses of mud and sticks limit the number of predators, but the wolf alone can easily destroy the tops of these lodges and burrows. Lodge destruction is nevertheless difficult in periods of deep snow and, from Scandinavia to Russia (Valdmann et al., 1998; Andersone, 1999; Andersone and Ozolins, 2004; Zunna et al., 2009) and throughout North America (Pimlott, 1967; Mech, 1970; Floyd et al., 1978; Allen, 1994; among many authors), beaver is therefore not part of the wolf's diet in winter. In the wetlands of the mid- and southern latitudes, beaver is more vulnerable to predation, however, because deep snow periods are rarer and summers are sometimes very dry (in this case, the global water table of the forest decreases, making it easier to access beaver lodges and burrows).

The role of beaver in wolf feeding habits is nevertheless not well known because of the extreme decline in its range and population due to past human overhunting for beaver pelts and castoreum (Nolet and Rosell, 1998; Rosell et al., 2005; Halley et al., 2012). Humans have thus had an impact on the wolf diet for centuries by both displacing or extirpating wolf prey and destroying or altering habitats (De Planhol, 2004). Yet the wolf preference for larger prey has been little evaluated in situations of complex predator/prey systems. Even the studies on wolf feeding habits carried out in the Bialowieza forest of eastern Poland do not meet the conditions for investigating the naturally evolved features of wolf selection because some of the most relevant prey (elk, beaver) are rather rare (Sidorovich et al., 1996; Jedrzejewska and Jedrzejewski, 1998).

In this study, we investigated the wolf diet over 15 years (1999–2014) in the natural deciduous woodlands of central-western Belarus, which are characterized by a rich and abundant prey supply, including beaver (650 km<sup>2</sup>/100 km<sup>2</sup>) and wild ungulates (Bison *Bison bonasus*, elk, red deer, roe deer, wild boar). During the study period, we also took into account the sharp decline in medium-sized ungulates (roe deer, wild boar) following the long

and cold winter of 2013 to identify the responses in wolf diet. We thus hypothesized that the wolves would encounter difficulties in meeting their traditional food requirements in the late spring and summer of 2013 and would change their food habits. We also assumed that other shifts in the wolf diet would occur in dry summers, during which the water level decreases considerably by the end of the season. Under such conditions, wolves may have more facility killing beavers and consequently be more willing to provide this food to pups.

## Material and methods

The Naliboki forest and surroundings (2750 km<sup>2</sup>) are part of the East European plain and are located in central-western Belarus (53°55'N; 26°20'E, elevation 100–200 m asl). This is a flat zone, with gently undulating sand dunes, some moraine areas and a lot of swamped areas mostly due to inundations by beavers, and it is crossed by two large meandering rivers (Nioman and Biarezina) and tributaries (Fig. 1). Flooding occurs in the summer, autumn and winter and lasts from 20 to 40 days.

The climate is moderately continental with a mean winter temperature (December) ranging from –6 °C to –8 °C (all surface water is ice-bound). The mean temperature in June ranges from 17 °C to 19 °C. Annual rainfall ranges from 580 to 690 mm, but during the research period several summer droughts occurred (1999, 2001, 2002, 2004 and 2013), causing general drying of the drainage canals. The drought in the summer of 2002 was particularly harsh, with small watercourses nearly without water for more than two months. Winters are quite severe with a snow cover generally lasting from mid November to end March. During the particularly harsh winter of 2012–2013, an unusually deep snow cover persisted till mid-April. The study area was composed of 83% forest and 27% open areas. The open areas included a large variety of grasslands (from marshes to drier lands) that had been wild-functioning for decades after being drained and then partly (for marshes) inundated by beavers. The forest habitat-types are mixed conifer (spruce *Picea abies*-oak *Quercus robur*) older than 60 years (16%), various pine (*Pinus sylvestris*) stands (plantation, bogs) (33%), young successions of deciduous species (*Quercus*, *Tilia*) (10%), and black alder (*Alnus glutinosa*) swamps (41%).

The area was exposed to little human intervention until the Second World War, which was followed by intensive land use that, fortunately for the wildlife, nearly ended in the 1990s. In particular, drainage for peat extraction and agriculture stopped completely. The density of human settlements is low (villages and hamlets: 20 per 100 km<sup>2</sup>). Quiet areas are many in the forest because of the low penetration by local people and the specificities of local forestry. Logged areas, for example, are usually left to free succession for about eight decades, with much timber left lying. With time, the most ancient logging areas evolve into spontaneous mosaics of thickets and high grasses, intermingled with uprooted or broken trees favourable for wildlife. The tranquillity of the area was further enhanced in the 1960s by the creation of a forest reserve of about 900 km<sup>2</sup> in which hunting was prohibited. Outside the reserve, the wolf is subjected to year round control. Poaching has been limited by law in the entire forest (Sidorovich, 2011, 2016).

### Prey abundance estimates

From 2002 to 2014, we selected a range of five sampling areas (15–30 km<sup>2</sup>, totalling 140 km<sup>2</sup>) where ungulates and beavers were well represented. These sampling areas were 90% forest cover and 10% grassland and open sedge-dominated marshes. The network of drainage canal systems, streams and rivers ranged from 6 to 8 km<sup>2</sup>.

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