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Experimental release of hand-reared wolf pups in Tver region (Russia): food habits, movement patterns and fear of humans.

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Abstract:

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Nyckelord

Keyword:

Canis lupus, diet, GPS-Argos telemetry, hand-reared wolf pups, movement patterns, reintroduction, scat-analysis.

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1 Abstract

Studying the reintroduction of hand-raised wolves may embrace several interests such as deepening knowledge on wolf biology and allowing a controlled release in isolated populations in need of genetic influx. Studies on hand-raised wild animals, showing successful reintroduction, suggested that young released wolves might be able to survive in the wild without previous fastidious training. Most of their survival behaviours would be instinctive. In this study, nine young wolves were reintroduced in Tver region (Russia) and followed in order to evaluate their fear of humans, their movement patterns, thanks to GPS-Argos collars fitted to three of the animals, and assess their diet via four methods of scats analysis. We analyzed 46 wolf scats collected from August 2010 to January 2011. We determined the frequency of occurrences of items per scats and per items, and used the Relative Estimated Bulk to estimate the biomass of prey species consumed. Statistics were conducted to test for significance of method comparisons. The results showed that half of the wolves remained near the enclosure weeks to months after release, occasionally leaving the vicinity. The individual wolves behaved differently, they adopted various movement patterns and had diverse home ranges (from 15 km² to 40 km²). Released wolves preyed more on ungulates, especially moose and on other wild mammals such as mountain hare. They also sporadically hunted domestic animals and regularly consumed vegetal matter along with smaller animals as alternative prey. Finally, all scat-analysis methods significantly assessed ($p < 0.01$) the relative importance of the main food types.

Key words: *Canis lupus*, diet, GPS-Argos telemetry, hand-reared wolf pups, movement patterns, reintroduction, scat-analysis.

2 List of abbreviations

GPS – Global Positioning System

FO – Frequency of Occurrence

ID – Identification of the collar worn by the wolf

PTT – Platform Transmitting Terminal

REB – Relative Estimated Bulk

St P. – Saint Petersburg city

NP – National Park

3 Introduction

Reintroduction of wild animals

Reintroduction of wild animals is a tool for biodiversity conservation (Nilsen et al. 2007, Seddon 2007). Nowadays many vertebrate species are threatened due to the high human activity. Therefore the reintroduction of endangered species can help prevent extinction. Moreover, reintroducing wild animals is not limited to endangered species; it is also a major concern to maintain top-down regulation (Terborgh et al. 1999) and sustain healthy populations with enough gene flux. Many projects of reintroduction, concerning a wide variety of species, exist all over the world.

Most reintroductions neither prepare nor train the animals before release (Kleiman 1989), but some do. Indeed, the golden lion tamarins (*Leontopithecus rosalia*) were trained to improve their foraging ability and orientation skills prior to reintroduction, the red wolves (*Canis rufus*) were prepared for hunting (first by exposure to carcasses and then to live prey), and Swift foxes (*Vulpes velox*) were preadapted to wild food items (diet of road kill) (Kleiman 1989). However,

the efficiency of such training has rarely been evaluated. The golden lion tamarin survival rates did not differ between the trained and untrained groups (Kleiman 1989), and providing red wolves with carcasses was more cost-effective and practical than giving live prey (Phillips et al. 2003). The amount and type of training depends above all on the species and the goal of the release (Kleiman 1989), although it is not well known which species-specific behaviour requires learning. However, evidence can help to evaluate which behaviour may require consequent or reduced learning. Orphan cheetahs (*Acinonyx jubatus*) without previous wild life experience are part of a reintroduction program in Namibia (Conradie 2005). The chance given to the cats to re-adapt to life in the wild is based on the belief that their inherent instincts and hunting skills will suffice (Conradie 2005). Indeed, the mechanisms and patterns of prey catching and killing in Felidae require movement of the prey as an essential stimulus to elicit the attack (Fox 1969). It has been reported that chemicals from the prey may trigger attack and feeding especially in lower vertebrate and invertebrate species (Fox 1969). Fox (1969) reported that hand-raised canids such as coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), grey foxes (*Urocyon cinereoargenteus*) as well as Arctic foxes (*Alopex lagopus*) reacted to the movement of the prey which was a stimulus for orientation, approach and chase. Similarly, wolf predation behaviour would be instinctive (Becker et al. 2010, Landry 2004). According to Klein (1995 cited by Mech & Boitani 2003), wolves bred in captivity without any previous experience, can hunt and kill wild prey and survive once released in the wild, exactly like domestic cats and dogs may instinctively do when needed. Mexican wolves (*Canis lupus baileyi*) reintroduced in Arizona in 1998, already started to kill deer within the first three weeks after their release (Parsons -pers. comm.). Indeed, several studies also support the fact that the strong stimulus provoking the attack reaction is the prey movement, which may also be reinforced by vocalization (Fox 1969, Landry 2004, Becker et al. 2010). Fox (1969) showed that, as young as four weeks of age, hand-raised wolf pups responded immediately to the prey movement by orienting and following. Moreover, pups show very early in their development playing behaviours through fighting and chasing games by pushing the hips and shoulders like adults do for hunting, even without having been raised by their mother (Landry 2004). Becker and her colleagues (2010) observed the feeding habits of twenty-two hand-raised pups from 1993 to 2008. They found that pups were able to find their own food (foraging on the ground, collecting fruit, etc...) and hunt (smaller to larger prey) without any external help from parents or adults (Becker et al. 2010).

Prey-killing patterns seemed to be present very early in the life of canids. After a period of experience depending on the species, catching, carrying, killing and eating sequences were present for all species at the term of their fourth month (Fox 1969). It is also through the early exploratory behaviour that canids learn where to find a prey, how to approach, efficiently catch and kill (Fox 1969). Wolves benefit to some degree from « social help » when learning with adults and being organized as a pack. Probably, the efficiency of hunting is improved while travelling with adults and imitating them especially for hunting large ungulates (Fox 1969). Nevertheless, play chasing and bringing down a conspecific in wolves and coyotes, may be action patterns to catch large prey in adulthood (Fox 1969). It is thanks to observation and by trial and error that young canids will acquire their experience (Landry 2004, Becker et al. 2010, Fox 1969).

Wolf reintroduction

Wolf reintroduction has been done in several countries: grey wolves (*Canis lupus*) in Yellowstone National Park in 1995-1996 (Northern Rocky Mountains, USA) as well as in Idhao,

the Red wolf (*Canis rufus*) in Northern Carolina from 1987 to 1989 (Peterson 2007, Wayne and Gittleman 1995), and the Mexican grey wolf (*Canis lupus baileyi*) in the mountains of the Southwest USA in 1998. There was also a preliminary evaluation of possible reintroduction in Scotland (Nilsen et al. 2007, Boitani 2000).

The grey wolf is a social animal that lives in packs (at least two individuals) usually including the breeding couple and their offspring (Mech 1970, 1999, Landry 2004). Taking care of the pups is one of the most important tasks for the pack: all members participate in feeding, education and protection. The loners, or dispersers, are often the yearlings looking for new territory to colonize or for another existing pack to join, replacing a missing reproductive individual (Rothman & Mech 1979, Fritts & Mech 1981).

Although the wolf is mainly a predator of wild ungulates (Ballard et al. 1987), it is also an opportunist with a generalized diet (Salvador & Abad 1987). Depending on local availability, wolves usually prey on mid-sized wild ungulates such as red deer (*Cervus elaphus*), reindeer (*Rangifer tarandus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) (Ballard et al. 1987, Nowak et al. 2005). In boreal conifer forests, moose (*Alces alces*) may be an important prey species for wolves as well (Peterson et al. 1984). Wolves can also eat smaller prey (e.g. rodents, frogs, fish, insects) and vegetal matter (Stahler et al. 2006). Moreover, they may use anthropogenic food sources such as garbage or prey on domestic animals that are present in their territory (Fritts & Mech 1981, Salvador & Abad 1987, Theuerkauf 2003, Nowak et al. 2005).

Despite various wolf reintroduction programs, there have been very few studies of human-raised wolf reintroduction (Badridze in 2003 other than the four human-raised wolves from Detroit Zoo that were released on Isle Royale in 1952: Peterson 2007). The study of human-raised wolf pups for release in the wild is interesting for several reasons: it may provide information about the success of specific rearing methods of animals for release, provide opportunities to deepen knowledge of wolf biology and behaviour, and suggest methods to use for a controlled (diseases and health control) release in populations that need genetic influx (i.e. isolated wild populations or zoo populations). On the other hand, hand-raising wild animals is probably one of the most challenging aspects of wildlife reintroduction: it requires commitment and needs to be approached carefully and responsibly. The longer-term implications and special needs of young animals must be taken into account. Hand-raised animals can become imprinted and develop behavioural problems if not handled correctly. Young animals undergo very rapid development and growth, thus, correct handling, nutrition and facilities are very important (Trendler 2005). The main points cited by Pazhetnov et al. (1999), maximum freedom and minimum human contact are essential. Klinghammer and Goodman (1987) add that any undesirable effects of imprinting can be avoided by hand-raising the animals in groups instead of alone. Wolf pups often show first flight reaction during their third week and, after some days, will tend to approach humans and this independently of the way they are raised (Zimen 1987). Zimen (1987) showed also that wolf pups raised with littermates usually demonstrate social preferences for other wolves later on. According to him, reducing the need to seek human contact in these pups will lead to increase fear. In an experiment of hand-raised dog puppies and wolf pups in social situations with humans, it has been shown that in contrast to dog puppies, wolf pups seemed to be prone to avoidance (Gacsi et al. 2005, Topál et al. 2005), even if differences in individual temperament existed (Boissy 1995, Zimen 1987) that appeared to be genetic (Zimen 1987). Individual fear reactions would be consistent through different challenging situations and

over time (Boissy 1995). Behavioural observations of a hand-reared male Timber Wolf revealed high caution towards unknown persons and objects and extreme avoidance towards new objects. The wolf was more distant to people than were hand-reared dogs (Fentress 1967). Another study concluded that wolf pups contrary to dog puppies do not show the specific patterns of attachment towards a specific human (Topál et al. 2005). Avoidance or socialization processes seem to depend on age and development stages of the animal. If wolves are not socialized to humans before 21 days old they become so fearful that human socialization will be very difficult and will require a lot of effort if done later on (Klinghammer & Goodman 1987).

Few studies on reintroduction of hand-raised wild animals report the release success or failure (Kleiman 1989). The release is considered a success when the released animals are able to survive on their own: hunt successfully, become self-sufficient, avoid human activities, acquire the behaviour repertoire of their species (van Dijk 2005, Grundmann 2006) and reproduce (Cayford & Percival 1992). The existing population is thus enhanced with fresh genes (van Dijk 2005). Vladimir Bologov initiated a reintroduction program, in 1993, based on the release into the wild of one-year old orphan wolves purchased from hunters, in Russia. Different rearing methods were used (see Appendix 1) depending on the original situation, the local possibilities, and the first pups' reaction towards human and towards foster parents. 44 wolves out of 53 have been released since 1993 and 35 have survived. One of the objectives was to assess the rearing methods in relation to the success or failure of the wolves to survive after release (Laetitia Becker, PhD study).

Taking part in the PhD study, a group of nine young wolves were released, in the Spring 2010, in an area with few conspecifics and enough food, where there was a low risk of “density-dependent social intolerance”. For the first time in Russia, three of them were equipped with newly acquired GPS (Global positioning System)-Argos collars. The aim of this experimental study was to follow the wolves after their release in the wild and assess their survival chances. The focus was on their food habits, evaluated via different methods of scat analysis, and on their fear of humans; thus, their movement patterns in relation to human activity were studied. According to previous findings on successful releases, we hypothesized that the released wolves would be able to survive on their own without previous fastidious training. The wolves would have to find food, disperse, and look instinctively for unoccupied territory (Rothman & Mech 1979, Fritts & Mech 1981) where food was available.

4 Materials and methods

4.1 Study area

The study took place at the Biological Station “Chisty Les” situated 400 km north-west from Moscow, in the district of Toropets (84,000 sqkm), in the middle of taiga (see Fig. 1). The small village of Bubonitzky shelters the Biological Station, including a 35-km protected area. The district of Toropets is one of the wildest of the Tver region. 80% of the area is covered by unspoiled boreal forest (constituted essentially by the trees *Betula pendula*, *Pinus sylvestris* and *Picea abies*) with few roads and a low human density (5-10 inhabitants/sqkm) due to a steady and constant decline in the local population since 1990.

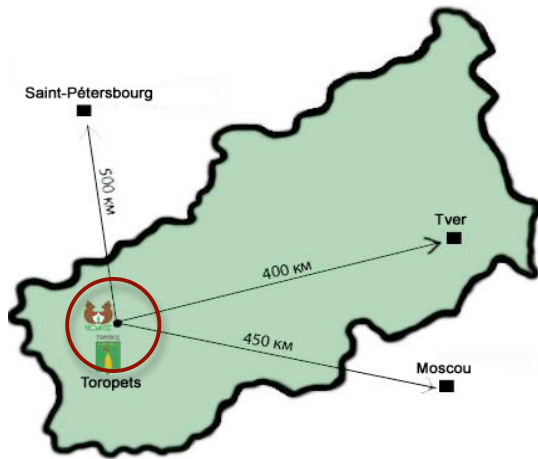


Figure 1: Localisation of the Biological Station in the Tver region, Russia.

Despite the low population density, humans are present through their activities: meat factory, timber exploitation, husbandry, traffic and hunting. Small villages and farms where the dominating livestock are hens, sheep, pigs, cows and horses, in order of importance, characterize the local community. Local people are aware of the release program and few conflicts have been experienced.

The region has a wolf density of 5.5 animals/1000 sqkm (Russian hunting office sources), and in the study area, the wolf density is quite low in comparison with previous years. Therefore, there is often vacant territory between packs. At the moment no wild wolf pack lives in the protected area.

In Russia there was a heavy persecution on wolves: 1.5 million wolves were killed between 1925 and 1990. At present, wolves are considered as pest and are still hunted all year round regardless of age or sex, using any possible method. The government is involved in this elimination campaign and gives bounties to hunters (a bounty of R1500 ~ 45 Euros- is promised per wolf, even if the government has not made any payments since 2003).

The other predator species present in the territory are brown bears (*Ursus arctos**), lynx (*Lynx lynx**), and red fox (*Vulpes vulpes**).

The main prey killed by wolves in Russia, are wild boar (*Sus scrofa**), mountain hare (*Lepus timidus**), beaver (*Castor fiber**) and racoon dog (*Nyctereutes procyonoides*). There are very few roe deer (*Capreolus capreolus**) in the region, no red deer (*Cervus elaphus*) in the study area, but moose (*Alces alces**) may also constitute as well a prey choice. They occasionally hunt mustelids such as badgers (*Meles meles*), pine marten (*Martes martes**) or weasel (*Mustela nivalis*). Other potential wolf prey species inhabiting the area include capercaillie (*Tetrao urogallus*), black grouse (*Lyrurus tetrix*), willow grouse (*Lagopus lagopus*), several anserine and passerine bird species and a variety of small rodents (*Clethrionomys spp.*, *Microtus spp.*, etc.) (Website of the Reserve, see references).

4.2 Animals studied

Three grey wolf (*Canis lupus*) females were orphaned and were given by two different hunters and the six other grey wolves (four males and two females) came from St Petersburg Zoo, Russia (see Tab. 1).

* Densities of animals present on the territory: see Appendix 2.

Table 1. Summary of the animals studied and their characteristics (ID: Identification of the collar wore by the wolf).

Animal	Birth	Features	From	Arrival at the station	ID Collar	Equipped	Released	Study period
Cleopa (female)	2009/05/10	25 kg 60 cm high	Smolenskaya oblast	2009/06/01	55107	2010/07/05	2010/05/09	2010/05/09-2010/05/26 Unknown*
Prossia (female)	2009/05/10	35 kg 68 cm high	Pskovskaya oblast	2009/07/24	98731	2010/07/15	2010/07/15	2010/07/15-2010/07/28 2010/07/28-2010/01/28
Steffi (female)	2009/05/10	33 kg 63 cm high	Pskovskaya oblast	2009/07/24	55101 - 61704 ^x	2010/05/05-2010/06/18	2010/06/18	2010/06/18-2010/09/14 2010/09/14-2010/01/28
St P. wolf 1 (female)	2009/03/25	-	St P. Zoo	2009/06	-	-	2010/05	Unknown
St P. wolf 2 (female)	2009/03/25	-	St P. Zoo	2009/06	-	-	2010/05	Unknown
St P. wolf 3 (male)	2009/03/25	-	St P. Zoo	2009/06	-	-	2010/05	Unknown
St P. wolf 4 (male)	2009/03/25	-	St P. Zoo	2009/06	-	-	2010/05	Unknown
St P. wolf 5 (male)	2010/04/10	-	St P. Zoo	2010/09	-	-	2010/09/28	2010/09/28-2011/01/28
St P. wolf 6 (male)	2010/04/10	-	St P. Zoo	2010/09	-	-	2010/09/28	2010/09/28-2011/01/28

4.3 Animals handling

4.3.1 Rearing method and locality

After their arrival at the Biological Station, the three female pups were raised following the “foster mother” method. They were introduced to an adult female (Miercoles) that behaved like their mother. It results in wild wolves that are tolerant to a human feeder. This method was also used with a previous group of pups.

The three wolves with their foster mother were kept in an enclosure of 0.7 ha within the forest, with a constant water supply.

The two males and two females from St Petersburg Zoo were raised, also after their arrival at the Biological Station, following the “feeder” method. They were kept together in groups of siblings in an enclosure of 0.7 ha within the forest and were fed by humans without direct contact, as they were wild. It may results in tolerant wolves that come to the feeder when hungry.

The two last males from St Petersburg Zoo were released at five months old, almost immediately after their arrival at the Station and were provided with regular carcasses in a special area, (mainly bones and fat) as food support for their first winter.

* When the wolf can be present in the surroundings but we do not have the certitude.

^x That wolf has been reequipped with a new collar.

4.3.2 Feeding methods and food provided to captive wolf pups

The food provided depended on pups' age and availability (animals killed, remains of hunting, meat available in slaughterhouse, fish arrival in shops).

The pups were fed dead wild animals, meat from a factory and sea fish. In addition, apples or other fruit may have been given. Indeed, these products are important for the vitamins and fibres they provide, help digestion and eradicate intestinal parasites (Mech 1970).

There were various ways to provide the food. It was just left on the ground or could also be hidden in the forest so as to stimulate the foraging behaviour of pups. The foster mother would also bring food, carrying entire pieces or regurgitating for the pups.

The food was scattered in small pieces in the enclosures and feeding was spaced as it is in the wild. The needs of wolves were also adjusted depending on the weather and the pups' body weight. The pups could also find food on their own. They were able to hunt small prey such as rodents, birds, butterflies, insects, or find them dead. They could also eat ant eggs, berries, grass, buds of pine trees, and old pieces of wood, soil, sand...which is typical for summer feeding habits in pups (Stahler et al. 2006, Becker et al. 2010).

4.3.3 Trapping method and release method

The three equipped wolves were darted with a hypodermic gun but using different tranquilizer substances (see Appendix 3) and later, they were able to awake and feel free to go out the enclosure whenever they wanted. All wolves were just released from their enclosures by opening the pens.

After release, supplemental food was provided temporarily at a central site (Miercoles enclosure) as a support for the newly released wolves as well as a control of their movements and as a primary location for potential retrapping.

4.4 Data collection

Data were collected from mid-August 2010 to the end of January 2011 with a break of 15 days in early November.

The GPS positions (thanks to satellite collars) from each equipped wolf made it possible to detect if any of the wolves inappropriately approached areas of human interest, so that counter measures could be initiated. Excrements were randomly collected and analyzed to assess their diet. In snow conditions, tracking was carried out to study their travelling routes and collect excrements as well.

4.4.1 GPS & Satellite tracking collars

The acquisition of GPS-Argos collars, newly developed for wolves, from the constructor ES-PAS (ZAO ES-PAS, Moscow, Russian Federation) allowed equipping the first Russian wolves in 2010. Thus, wolves' movements were followed and recorded using a satellite-tracking system deployed on collars fitted to animals (see Fig. 2).



Figure 2. Wolf equipped in 2010 with GPS-Argos ES-PAS collar.

Locations were obtained via transmission of a high frequency signal (401,650 MHz) emitted by the beacon and sent to a low-level orbit satellite system (ARGOS), then relayed to a ground-based processing centre in Toulouse (France). The satellites go over a specific platform at approximately the same time every day.

The user received the data directly on his computer via Internet connection to ArgosServer.cls.fr thanks to Telnet program (see Fig. 3).

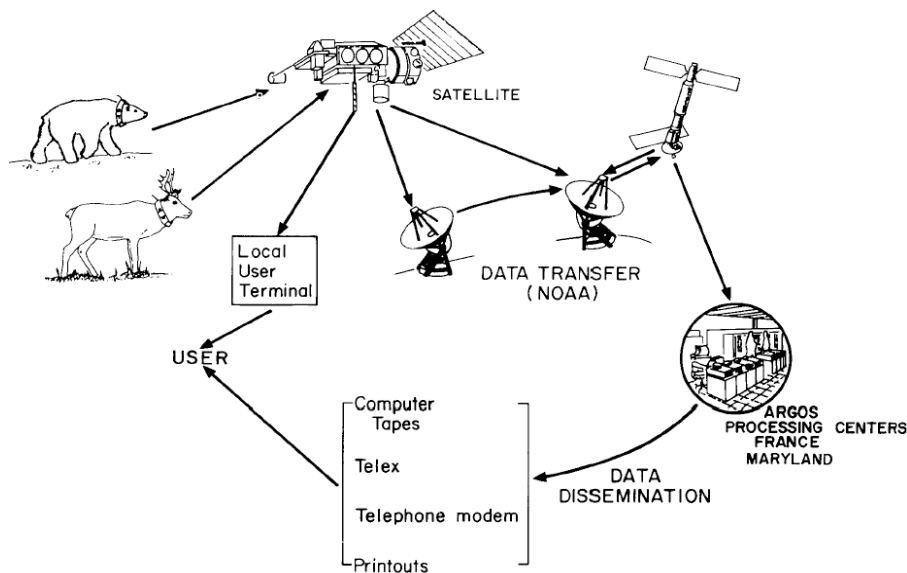


Figure 3. Overview of the Argos data collection and location system (Fancy et al. 1988).

With the present collars, the Argos system was combined with a GPS device. The GPS receptor determines the new position with regular intervals and high precision. The location is sent at the time of the emission by the Argos beacon (every one or three emissions depending on the collar programming) (see Tab. 2). The collar weighs 650 g and had an operational life of about one year (with 4 h ON / 4 h OFF).

Table 2. Collars programming

ID	Emission periods of Argos messages	Definition period of GPS locations
55101-61704	70 seconds more or less 10%	210 seconds more or less 10%
55107	120 seconds more or less 10%	120 seconds more or less 10%
98731	65 seconds more or less 10%	130 seconds more or less 10%

4.4.2 Snow tracking

Snow tracking was for following released wolves in order to find droppings and other life signs and to prevent collar failure as well.

Tracks of the released animals were followed when seen on « typical daily tours » defined prior to tracking. Indeed, three routes of different distances were identified according to the observations of wolves' movements and frequency of passages in strategic areas (rivers, streams, forest trails, etc...). They were used each time the weather allowed it, the most regularly possible and, as soon as a wolf track was found, I followed it for several kilometres until the dark.

4.4.3 Faeces collection and analysis

Wolf excrements have a diameter over or equal to 3 cm and are 5 cm to 15 cm long but can be up to 30 cm. They are composed of several cigar shaped pieces. The smell as well as the colouration is characteristic. Faeces are essentially composed of hair and bones still visible on the surface.

Scats of all the released animals were collected each time found on roads, in the fields, on travel routes used by wolves, carcass sites in the release area and by following wolf tracks in the snow. The faeces were stored in labelled plastic bags and a code was attributed. In addition to GPS locations registered with a manual GPS device, the nature of scat deposit site, scat characteristics, the date and the signs of wolf activity were also noted (see Appendix 4). The faeces were frozen prior to further treatment and analysis.

The scat was soaked in water for 24-48 hours with a few drops of dishwashing liquid to aid dissolution. Next, scats were hand separated and washed through a sieve with a mesh size of 0.5 mm in order to separate the macro components. All was rinsed with clear water into another basin. These steps could be repeated the number of times needed to obtain clear distinction of the elements. Food remains retained in the sieve (e.g. hair, bones, vegetation, seeds, skin pieces) were separated from each other using metal tongs (see Appendix 4). All was placed in an aluminium box that was stored in a hot room (around 65 degrees) for at least 24 hours to dry and conserve the components. Each macro element was arranged in a plastic bag (see Appendix 4) and conserved until further analysis.

The analysis (see Appendix 5) consisted of identifying the macro components of each scat. Hair, bones, and remains of skin found in scats were identified thanks to the particular characteristics of each animal species (e.g. colour, shape, length, thickness of the components) with the help of reference manuals (Debrot et al. 1982, Teerink 1991) and using a local reference collection developed by hunters. The macroscopic remains of vegetation, invertebrates, and birds were identified by comparison with reference material and books (Fitter et al. 1991, 1997). The microscopic fraction was discarded assuming that it came from the same macroscopic food items, in the same proportions, and that it would not significantly affect the results concerning the wolf diet (Ciucci et al. 1996).

The protocol to analyse the scat contents followed Spaulding et al. (1997). The elements were distributed in different classes according to their relative volume, visually estimated and expressed as a percentage of the volume of each scat (Fritts & Mech 1981, Ciucci et al. 1996). Hair was first examined visually concerning colour pattern, length, thickness, and thereafter the medullary pattern and cuticular scale were identified by microscope (Teerink 1991). Once identified, prey items were pooled into the following categories:

Moose/ Wild boar/ Badger/ Raccoon dog/ Beaver/ Mountain hare/ Microtinae (Small rodents)/ Non-identified mammals/ carrion/ Sheep/ Hen/ Duck/ Wild Birds (Passerine and Bird of prey)/ Insects/ Graminae/ Fruit and seeds/ Other plant items/ Others.

The latter category represents non-food items like strings, stones, leather and plastic.

When it was not possible to identify an item at the species level, we grouped those items into the category: non-identified mammals (Reynolds & Aebischer 1991).

Four different methods were used to assess wolf diet. Most studies on diet use different methods for analysing data (Ciucci et al. 1996, Spaulding et al. 1997, Anderson & Ozolins, 2004) due to limitations of each method in describing at the same time the quantity and the quality of components found in scats.

The frequency of occurrence (FO) was assessed and calculated as percentage of the total number of occurrence of all food items and of the total number of scats (Ciucci et al. 1996). It expressed the frequency of a food item relative to the other food items present in the scat as well as the frequency of a food item present in the total of scat collected. The frequency of the different prey items could be expressed independently by group (e.g. mammals, ungulates, mustelids) (Kelly 1991).

When the scats analysed contained more than one item, we visually estimated the fraction of each prey item found in each scat and summed these fractions to give the equivalent number of scat (n) representing a particular prey type (Floyd et al. 1978, Spaulding et al. 1997, Ciucci et al. 1996). We called it REB (Relative Estimated Bulk) as Spaulding et al. (1997) did in their study and expressed it as percentages. We did not include in the analysis the remains of a proportion <3% in order to reduce the bias of trace amounts of food items such as long hair from ungulates or feathers that might have been trapped by the stomach from an earlier meal and also to reduce the “equating of occurrences bias” (Ciucci et al. 1996, Huitu 2000). This would be when food items contributing different quantities to a scat’s volume are equated by frequency (Ciucci et al. 1996).

Biomass ingested ($n \cdot y$) was calculated thanks to the REB to override the bias associated with small prey items and when there is more than one prey type per scat (Floyd et al. 1978, Fritts & Mech 1981). To estimate the weight of live prey eaten per scat (y), we used Weaver’s (1993) equation where the independent variable (x) is the live weight (kg) of the prey recovered in the scat: $Y=0.439+0.008x$

Body mass of the live prey species was taken from literature (Corbett 1989, Aulagnier et al. 2010) and Internet sources (see references) and calculated using median function (we took the median of the data which included juvenile, adult, female, and male weights). The product ($n \cdot y$) expressed in kilograms is the total weight of each prey type consumed (i.e. biomass) by the wolves during the study period (Corbett 1989).

4.4.4 Data analysis

The GPS-Argos data were plotted in Ozi Explorer (GPS Mapping Software) and distances between points were calculated to obtain a minimum estimate of travel distance and evaluate the surface covered when the animal travelled (Home range) (Merrill & Mech 2003).

I performed Chi square tests as well to see if there was a significant difference between the number of locations received during the day and during the night, and between the number of locations received close to or outside villages.

To analyse the scat-analysis data I used the software SPSS Statistics 17.0.

When performing a chi square test to look for a significant difference between the number of locations occurring during night and day we found $p < 0.01$ ($\chi^2=6.1$, $ddl=1$, $p=0.013$), so there were significantly more locations during nights than during days when Steffi was close to villages (see Tab. 3). She got more GPS locations close to Boncharova (28 locations out of 59 locations emitted) where the number of inhabitants is higher than elsewhere, but also during the night (see Tab. 3).

Table 3. Frequency of Steffi's GPS locations emitted close to villages.

Villages	Inhabitants	Number of GPS locations emitted	During the day (7h31-20h30)	During the night (20h31-7h30)
Drosdovo	13	7	1	6
Stepashi/Rybino	11	5	1	4
Shapkino	5	2	1	1
Boncharova	248	28	11	17
Belkova	5	16	5	11
Kranosele	51	1	1	0
Total of GPS locations		59	20	39

Steffi's collar gave locations 63 days out of 89, for a mean of 1.97 locations day⁻¹ (see Tab. 4). And we did not receive any locations for 26 days in total but it was spread throughout this period. The collar would be programmed to give about 411 GPS locations day⁻¹ in the optimum situation (i.e. when the emission trial reaches the satellites within the definition period of GPS locations and is then transmitted to the processing centre thanks to a regular and frequent passage of the satellites). This is a theoretical calculation. More realistically, when the collar is placed in an open field without particular constraints, it would give 192 locations day⁻¹. During the working period of the collar 42 days were with 65 emissions of locations outside of villages (> 500m) and 39 days with 59 locations emissions close to villages (< 500m) (see Tab. 4). There was no significant difference ($p > 0.05$) between number of locations received close to or outside of villages ($\chi^2=0.3$, $ddl=1$, $p=0.59$).

Table 4. Period of collar functioning and collar efficiency for Steffi.

	Days	Number of GPS locations	GPS locations day ⁻¹
During the collar worked	89	124	
With emission	64	124	1.97
Whitout emission	25	0	
With emission out of villages	42	65	
With emission close to villages	39	59	

Prossia got 12 GPS locations in two days outside the enclosure from the 2010/07/27 to the 2010/07/28 before she lost her collar. But all those locations were close to the enclosure. She got a total of 140 locations in 14 days from the 2010/07/15 to the 2010/07/28, with a mean of 10 locations day⁻¹, but except the two last days, she stayed in the enclosure.

Prossia's collar did not give any significant difference between the number of locations emitted during the night and during the day ($p > 0.05$) ($\chi^2=0.3$, $ddl=1$, $p=0.61$). I had the opportunity later on to observe her in other areas until late September 2010 (see Fig. 5).

Cleopa got 22 GPS locations in 18 days from the 2010/05/09 to the 2010/05/26. She also stayed around the enclosure at the beginning but quickly moved farther away (see Fig. 5). Her estimated home range was 40.1 km². She travelled 30.86 km in 18 days with a mean of travel distance of 1.80 km day⁻¹. After that we lost signals from her collar and did not see her any more in the release area.

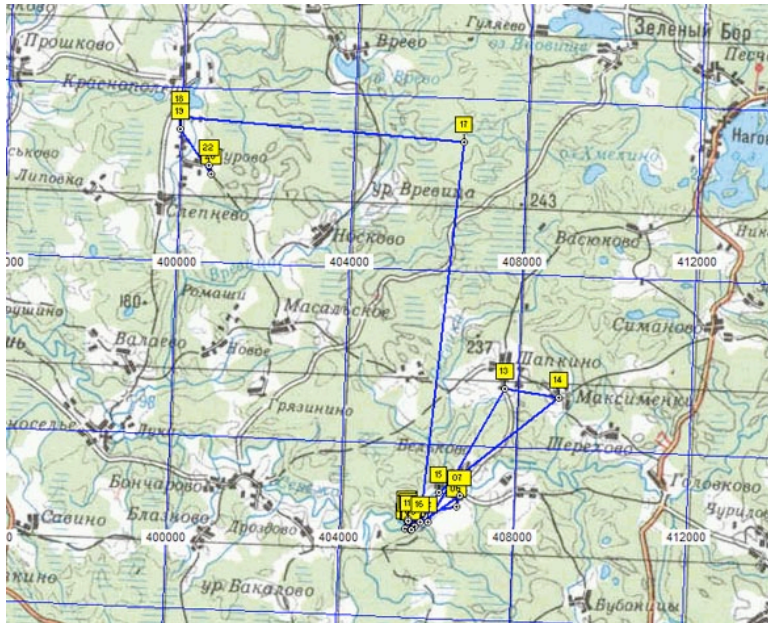


Figure 5. Cleopa's GPS locations from the 2010/05/09 to the 2010/05/26.

When performing a Chi square test to assess if there was a significant difference between the number of locations emitted during days and nights, we found $p > 0.05$ ($\chi^2=3.6$ $ddl=1$, $p=0.057$). So the difference was not significant. However the sample was too small to really talk about a tendency (see Tab. 5).

The number of GPS locations was quite similar in all villages without an apparent link to human population density (see Tab. 5).

Table 5. Frequency of Cleopa's GPS locations emitted close to villages.

Villages	Inhabitants	Number of GPS locations emitted	During the day (7h31-20h30)	During the night (20h31-7h30)
Shapkino	5	1		1
Belkova	5	3		3
Krasnopolets	51	2	1	1
Maksimienki	6	1		1
Kurovo	0	3	1	2
Total of GPS locations		10	2	8

Cleopa's collar gave locations 13 days out of 18, for a mean of 1.69 locations day⁻¹ (see Tab. 6). And we did not receive any locations for five days in total but this was spread throughout the entire period. The collar would be programmed to give about 720 GPS locations day⁻¹ in the optimum situation and we did not test this collar in an optimal field situation to make a more realistic calculation. During the 13-day total working period of the collar there were nine days with 11 emissions of locations out of villages and five days with emissions of locations close to villages (see Tab. 6). There was no significant difference ($p > 0.05$) between the number of locations received close to or outside of villages ($\chi^2=0.05$, $ddl=1$, $p=0.83$).

Table 6. Period of collar functioning and collar efficiency for Cleopa.

	Days	Number of GPS locations	GPS locations day ⁻¹
During the collar worked	18	21	
With emission	13	21	1.69
Whitout emission	5		
With emission out of villages	9	11	
With emission close to villages	5	10	

I visually observed Steffi and Prossia on several occasions from August to early October 2010 (see Fig. 7). They were seen several times preying on domestic animals such as hens and sheep, but some attacks were stopped before killing. In total 200 Euros were given as compensation for losses. Some typical urination marks (6) were found while snow tracking and all were discovered the same day for the same wolf track (see Fig. 7). I discovered a typical resting area while snow tracking several wolf trails. Food remains, markings, faeces and three beds of branches (see Appendix 5) were found (see Fig. 7).

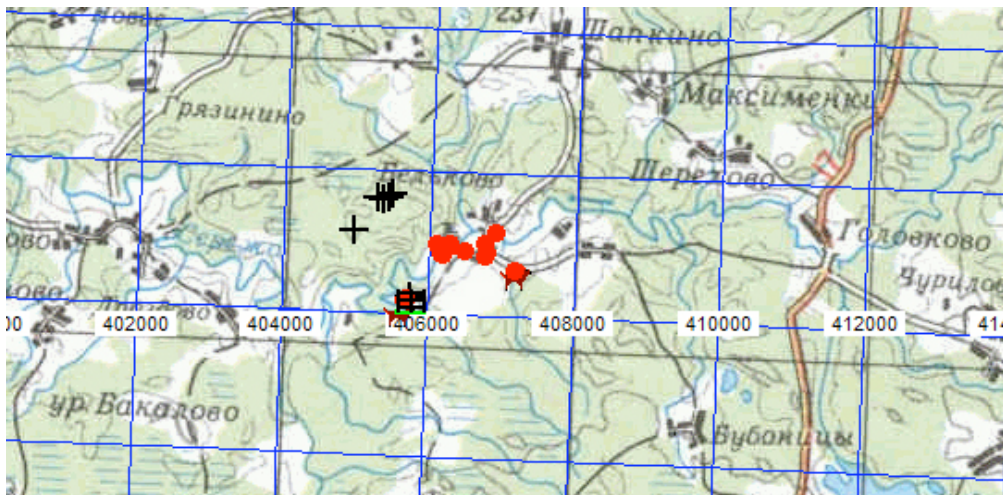


Figure 7. Visual observations of the wolves and presence clues discovered (red dots: visual observations, deer figures: winter food remains, crosses: winter urination markings).

5.2 Scats analysis data

A total of 46 wolf scats were collected from August 2010 to late January 2011 (see Appendix 6). Mean number of prey types found per scat was 1.74 with a variation from one to three prey types per scat. Most of scats contained two prey types (48.8%), 39.1% contained a single prey type and 13% contained three different prey types.

The relative importance of food items found in the scat sample was quantified by four different methods (see Tab. 7). The food items were ranked in ascending order according to the methods assessing the diet.

Table 7. Composition and evaluation of the wolves diet by four quantification methods of analysis (N scats=46)

Food items	% FO/ Scats			% FO/ Items		% REB		Biomass (Weaver)		
	N	%	Rank	%	Rank	%	Rank	Kg	%	Rank
Mountain hare (<i>Lepus timidus</i>)	18	39.13	1	19.57	1	23.98	1	5.16	14.10	3
Moose (<i>Alces alces</i>)	16	34.78	2	17.39	2	11.22	2	16.61	45.39	1
Wild boar (<i>Sus scrofa</i>)	15	32.61	3	16.30	3	6.72	5	5.68	15.53	2
Fruit, seeds (see Appendix 7)	11	23.91	4	11.96	4	5.35	7			
Sheep (<i>Ovis aries</i>)	6	13.04	5	6.52	5	8.67	3	4.46	12.20	4
Carrion	5	10.87	6	5.43	6	6.41	6			
Beaver (<i>Castor fiber</i>)	4	8.70	7.5	4.35	7.5	7.50	4	2.25	6.14	5
Hen (<i>Gallus gallus</i>)	4	8.70	7.5	4.35	7.5	1.85	10	0.39	1.06	8
Raccoon dog (<i>Nyctereutes procyonides</i>)	3	6.52	10	3.26	10	4.35	8	0.99	2.71	6
Microtinae (<i>Microtus sp.</i> , <i>Sorex sp.</i>)	3	6.52	10	3.26	10	2.72	9	0.55	1.50	7
Wild Birds (<i>Aves</i>) (Passerine, Bird of prey)	3	6.52	10	3.26	10	0.87	13	0.18	0.49	10
Unidentified mammals	2	4.35	12	2.17	12	1.15	12			
Badger (<i>Meles meles</i>)	1	2.17	13.5	1.09	13.5	1.20	11	0.30	0.83	9
Insects (<i>Coleoptera sp.</i>)	1	2.17	13.5	1.09	13.5	0.11	14	0.02	0.06	11
Duck (<i>Cairina moschata</i>)	0	0.00	15	0.00	15	0.00	15	0.00	0.00	12

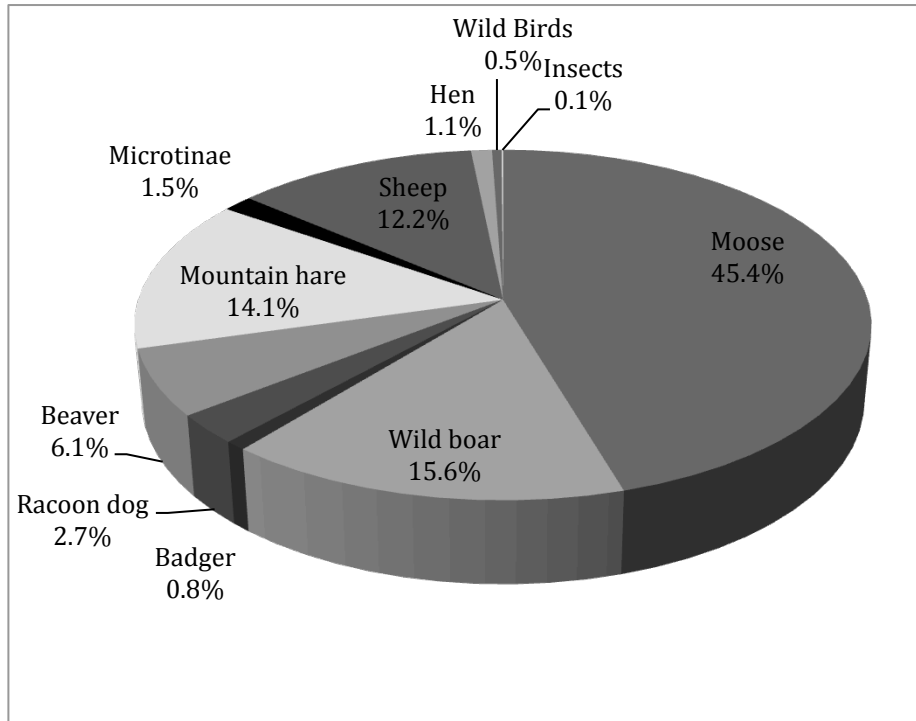


Figure 9. Percentages of biomass consumed and calculated using Weaver equation (1993).

Mammals constituted the bulk of the diet accounting for 73.9% of all occurrences ranging from 67.5% of the REB to 98.4% of the biomass ingested (see Tab. 7, Fig. 11).

The main food categories were the wild mammals (wild ungulates and medium sized mammals like mountain hares and beavers) representing 58.7% of the REB and 86.7% of the biomass eaten (see Fig. 11). Mountain hare (occupying the first rank) followed by the moose (rank 2) and the wild boar (rank 3) were the three main prey eaten by wolves with some differences in rankings for the REB and the biomass methods (see Tab. 7). Indeed, moose represented 45% of the biomass ingested (16.6 kg) the wild boar accounted for 16% (5.7 kg) and the mountain hare constituted 14% (5.2 kg) of it (see Fig. 9).

Domestic animals were of secondary importance accounting for 10.5 % of the REB and 13.3% of the biomass, occurring 10 times of 46 scats (21.7%) (see Fig. 11). Sheep was the main domestic animal prey representing 12.2% of the biomass ingested and occupying the third rank with REB method (8.7%) (see Fig. 9, Tab. 7).

Fruit and seeds frequently occurred in the scats (11 times in 46 scats: 24% of the cases) and also in comparison with other food items (12%) (see Fig. 11, Tab. 7). The graminae and other plant items (leaves, wood, *Picea abies* needles, *Sphagnum*, *Equisetum*) appeared very frequently (41% of the total food items) and represented 17% of the REB.

Carrion category regrouped mainly the carrion given as food supplement during the winter and were typically distinguished by the presence of cattle bones in the scat without any hair and the scat itself was of a particular consistence. Five scats out of 46 scats were constituted of carrion (11% of occurrences per scats but 5.4% of occurrences per items), which represented about 6.4% of the REB (see Fig. 11).

Some mammal remains recovered in scats (two times out of 46 scats) could not be identified and were categorized as unidentified mammals (see Tab. 7).

The released wolves were seen several times preying on microtinae in open field. This food type, including *Microtus sp.* and *Sorex sp.* essentially, represented 6.5% of the occurrences per scat but 1.5% of the biomass ingested (see Tab. 7, Fig. 9). They occasionally ate birds such as passerines (three times out of 46 scats) (see Tab. 7) but generally small animals (i.e. microtinae, birds, insects) represented quite a small part of their diet (3.7% of the REB and 2% of the biomass consumed) (see Fig. 11). Some other items (stones, papers, strings) were occasionally found in wolf scats (0.07% of the REB). We could notice some differences in rankings and percentages depending on the method used to assess the diet (see Fig. 11, Tab. 7) but statistics conducted showed no significant differences (see Tab. 8, 9).

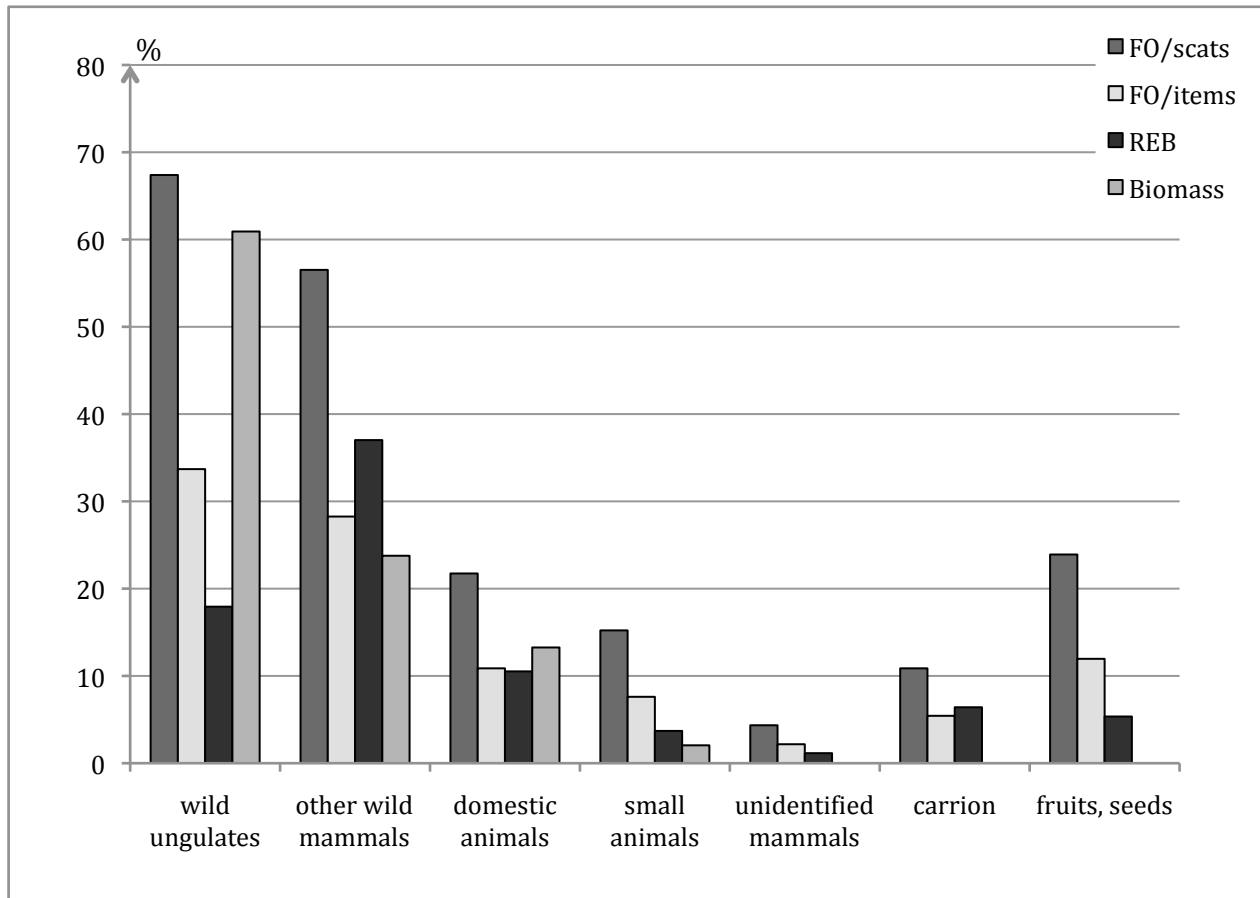


Figure 11. Main food categories in the released wolves diet assessed by four scat-analysis methods (N=46).

Accord among rankings was significant in all simultaneous and pairwise comparisons ($0.76 \leq W \leq 1.0$ and $0.90 \leq r_s \leq 1.0$, $p < 0.01$, see Tab. 8 and 9). The lowest significance was for the one involving the REB method and was higher when it was substituted by biomass model ($W = 0.76$ and $W = 0.80$ respectively, see Tab. 8).

Agreement among the different methods for rankings was particularly strong for the most important food items (i.e. rank ≤ 3 , see Tab. 7), with some variations with the biomass model (Weaver 1993) and REB method. Higher correlations between rankings were obtained in pairwise comparisons involving variants of the same method (% FO) being highest for variants

involving occurrences per items data ($r_s=1$, $P < 0.01$, $N=15$). Rankings by biomass model of Weaver (1993) correlated well with rankings relative to the other methods ($0.92 \leq r_s \leq 0.94$, $p < 0.01$, $N=12$ and $0.80 \leq W \leq 0.88$, $P < 0.01$, $N=12$, see Tab. 9, 8)

Table 8. Comparisons of scat-analysis methods to assess released wolves diet, tested by simultaneous concordance (Kendall coefficient of concordance, W)

		Correlations			
		% FO/ Scats	% FO/ Items	% REB	% Biomass
% FO/ Scats	Correlation Coefficient		1.000**	.761**	.804**
	Sig.	-	.	.000	.000
	N		15	15	12
% FO/ Items	Correlation Coefficient	1.000**		.761**	.804**
	Sig.	-	-	.000	.000
	N	15		15	12
% REB	Correlation Coefficient	.761**	.761**		.879**
	Sig.	.000	.000	-	.000
	N	15	15		12

** Correlation is highly significant at the 0.01 level ($P < 0.01$).

Table 9. Pairwise comparisons between 4 methods of scat-analysis to assess released wolves diet in Tver region (Spearman correlation coefficient, r)

		Correlations			
		% FO/ Scats	% FO/ Items	% REB	% Biomass
% FO/ Scats	Correlation Coefficient		1.000**	.899**	.915**
	Sig.	-	.	.000	.000
	N		15	15	12
% FO/ Items	Correlation Coefficient	1.000**		.899**	.915**
	Sig.	.	-	.000	.000
	N	15		15	12
% REB	Correlation Coefficient	.899**	.899**		.944**
	Sig.	.000	.000	-	.000
	N	15	15		12

** Correlation is highly significant at the 0.01 level ($p < 0.01$).

6 Discussion

6.1 Movement patterns of released wolves

Both equipped wolves travelled about 1.8 km day^{-1} for a total travel distance of 163 km in 89 days and 30.86 km in 18 days for Steffi and Cleopa, respectively. Distances and travelling estimates were minimum estimates since they were straight-line measures of itineraries of unknown lengths between locations. Therefore, two equal distances might represent different real distances and travel distance estimates (Merrill & Mech 2003). In spite of this, the travel distance estimates of each wolf was low compared to the distance (up to 80 km) that a wolf can cover in Alaska within a day (Kosak et al. 2005). However, Kosak et al. (2005) showed that the straight distances travelled by wolf females in Croatia in a day could vary from 0 m to 13.2 km with a mean of 2.5 km day^{-1} . The travel distance estimates appear to vary depending on the prey availability and the ecological conditions for finding food (Kosak et al. 2005). Smallest home ranges were described from areas where red deer was common (Okarma et al. 1998). In North America, with higher density of ungulates than in Croatia, wolves travelled on average between 1.6 km and 9.0 km day^{-1} (Kolenosky & Johnston 1967 cited by Kosak et al. 2005). In Croatia and central Italy, the distances travelled are even shorter (3.3 km day^{-1} , Abruzzo NP) due to availability of human provided food sources (Ciucci et al. 1997).

The estimated home range for the two individuals while their collars were operating was 14.7 km^2 and 40.1 km^2 for Steffi and Cleopa respectively. Usually the home range of grey wolves in summer is between $82\text{--}243 \text{ km}^2$ for established packs in southern and central Europe (Okarma et al. 1998, Kosak et al. 2005). Kosak et al. (2005) reported the summer home range of their two females: 86.2 km^2 and 56.3 km^2 . The latter was considered small compared to the average estimated and was associated with her status of reproductive female, confined to den and rendezvous sites (Kosak et al. 2005). Those figures were established for 4 to 18th months, much longer than my study. Still the home range of our two females were relatively small, especially Steffi's home range: she covered smaller area than Cleopa, however in a longer period and travelling the same distance per day. It may also be partly explained by the food availability and their attachment to the release site.

When examining wolf activity, it may be difficult to see the dawn and dusk peaks and the nocturnal activity of wolves described by scientists (Ciucci et al. 1996, Theuerkauf et al. 2003, Merrill & Mech 2003) when the GPS intervals are > 3 hours (Merrill & Mech 2003). The larger the GPS intervals, the more the travel rates are underestimated (Merrill & Mech 2003).

Despite different intervals in programming, two of the collars gave as much location data at night as during the day whether the wolves were close to villages or not, but Steffi's collar gave significantly more locations at night when she was close to villages. She also had more GPS locations close to Boncharova where the inhabitant number is however higher than in other villages. This may be due to the higher number of domestic animals as well as the smell coming from the meat factory.

Snow tracking allowed a certain amount of faeces collection and to follow the released wolves by a means other than GPS-Argos collars. In November as soon as the snow cover permitted, tracks were followed. They gave important clues about the wolves' habits such as urination marking territory boundaries or resting areas where food remains were found as well as three beds made from branches attesting of the presence of several wolves. The tracks found

often belonged to the two St Petersburg males whose prints were extremely big for their age (between 10 and 11 cm).

6.2 GPS-Argos telemetry

The collars did not work at the same time, nor in the same time period, so comparison (e.g. non-parametric statistical Kruskal–Wallis test for testing the efficiency of data collection between individuals) between the collars of the three wolves was not possible.

The collars did not give the same amount of data per wolf. Either the collar did not work long enough to obtain relevant data despite a high emission (Prossia's collar), or the collar did not work long enough and gave little data before the signal stopped (Cleopa's collar), or the collar worked some time (three months) but gave low data before it also stopped (Steffi's collar). Prossia's collar was indeed the best performing, giving ten locations per day. Unfortunately it lasted only 14 days, during which she stayed in or close to the enclosure. Actually, all wolves stayed some time around the enclosure after release. When wolves live several months in a place, with food support and social bonds with other wolves, it is expected for them to stay around for a while. A known place is safe in comparison with unknown territory (Wydeven et al. 1995). It often occurs with released animals: most of the released golden lion tamarins stayed close to the release site for weeks and months (Kleiman 1989).

The reasons the collars stopped working may be due to antenna break or battery failure. Indeed, environmental and weather conditions may influence the resistance of the system and the transmission as well. GPS location attempts may be more or less successful in some habitats than in others, depending on the forest type (Rempel et al. 1995, Johnson et al. 1998). Transmitted signals would have trouble reaching receivers through the forest canopy and might also be affected by topography, resulting in animals being undetected in some sites (North & Reynolds 1996, Cain et al. 2005), for instance in their den. Additionally, the animal behaviour might also affect the transmission efficiency (D'eon et al. 2002, Frair et al. 2004, Cain et al. 2005) in changing its activity patterns (e.g. resting, denning versus moving) and thus changing its head position, which is susceptible to affect the antenna orientation (currently being studied by a student in the field). GPS and Argos systems have proven their efficiency in numerous field studies, but more often in areas where the topography varies and offers open fields time to time, like in the USA or Africa. Coelho et al. (2007) found that signal acquisition rates were highly effective in open habitats but decreased with increasing vegetation density. Hebblewhite et al. (2007) also showed that fix rates decreased in aspen stands, closed coniferous stands but was higher on upper hills. This was the first time that wolves were equipped in Russia, where the boreal forest can be particularly dense with few open areas and where, like in other sites, some variable gaps occur between satellite passages. Janeau et al. (2001) showed that the taller the trees, the poorer the GPS performance, especially when the winter snow cover is important on the branches of coniferous trees.

The operating duration of combined GPS-Argos devices is essentially determined by the GPS fix rate and the size of the battery pack employed but also on the PTT uplink programme. For instance, a small GPS-Argos unit having a total weight of 1.7 kg, which attempts one GPS location day⁻¹ with a six-hour Argos uplink every five days, has an expected operating duration of 584 days. The latter decreases to 145 days if the number of GPS location attempts per day and the Argos uplink increase (Rodgers 2001). We must consider that this technology is relatively new and thus can undergo some premature failures (Rodgers 2001).

6.3 Scat-analysis data

Wolf scats could be confused with those of dogs or foxes, but application of the mentioned criteria of faeces characteristics in hesitant cases ruled both of these out. Even though some faeces could eventually belong to wild dispersers, we consider the number negligible (Kohira & Rexstad 1997). Moreover, the wild dispersers could have been the released wolves from previous years so in that regard, part of the same study. In addition, no wild pack faeces could have been collected due to the absence of established populations of wild wolves in the release area.

Wild diet of the released wolves

Scat-analysis methods revealed that released wolves, already at five months old for two of them, ate mainly wild mammals from large to medium size. Similarly, Pazhetnov (2005) noticed that hand-raised brown bears acquired, already at five months, the basic foraging behaviour which was efficient enough for their survival in the wild. He showed that in Russia the bears could successfully be reintroduced into their natural habitat by applying specific handling procedures.

The wild ungulates constituted a large part of this mammal consumption accounting for 61% of the biomass eaten and occurring more often in scats than other prey items (67.4%). Moose was the first choice of ungulate eaten representing 45% of the biomass ingested. Other studies reported that moose is an important prey species for wolves in boreal coniferous forest and make up the main part of the diet composition (Peterson et al. 2004, Müller 2006, Smietana 2005, Merrigi et al. 1996). However, large ungulates may be hard to hunt for single or a pair of wolves and we know that they may find remains from illegal hunting in the surroundings of the release area (Becker et al. 2010).

The other wild mammals (of medium size) making up 24% of the biomass ingested were mainly represented by mountain hares constituting 14% of the biomass, followed by beavers representing 6% of it. These prey species may be easier to find and kill especially for single or paired wolves. Actually beaver may be a vital alternative prey of wolves (Ballard et al. 1987). Mountain hare occupied the first rank of all occurrences and with REB method as well. When wolves successfully hunt an animal they may specialize in this prey (Becker et al. 2010). Becker and her colleagues (2010) observed wild yearlings hunting beavers for several months along the river after a first success.

Fruit and seeds occurred often in scats and represented 5.4% of the REB. Several scats contained for instance plum kernels, apple seeds and fruit remains and seeds of *Heracleum sp.* as well as *Ranunculaceae*. Other studies support these results and suggest that the consumption of fruit and seeds is intentional and may serve as an additional source of vitamins and minerals (Mech 1970, Andersone & Ozolins 2004, Castroviejo 1975). Indeed, when items appeared with more than 5% of the relative volume of scats and with high frequency of occurrences, they could be regarded as voluntarily consumed (Müller 2006). Although the bias of equating the occurrences of food items contributing in different quantity to scats volume was partially reduced by not considering items occurring in trace amounts (< 3%), fruit have been ranked higher by percentage of occurrences than by other methods (Ciucci et al. 1996).

We also observed a high occurrence of plant material (Graminae) especially in summer (89% of scats contained grams in summer) despite their low nutritional value. This may be due to the higher availability of plant material in summer. Grams consumption is supposed to be useful as a purgative to eliminate intestinal parasites and aid in cleaning the intestine of hair (Mech 1970,

Mech & Boitani 2003). Boitani (1982) and Castroviejo et al. (1981 cited by Salvador & Abad 1987) found a frequency of occurrence of vegetal matter from 7.3% to 16.2% and from 1.9 to 6% in Italy and Spain respectively. However, we assumed that some graminæ as well as other plant items (such as *picea abies* needles) might also be ingested by chance while wolves were feeding on the ground (Müller 2006). Leaves often appeared folded and sometimes there were entire leaves, which may fill a purgative role as well (Krief 2004, Huffman 1997, Huffman 2001). Indeed, Krief (2003), Huffman (1997, 2001) and Wrangham (1995) found in several species of great apes that folded or even entire leaves ingested and found intact in faeces had a purgative and medicinal role. Leaves act as a mechanical vermifuge, irritating the intestinal lining and promoting the expulsion of parasites (Krief 2004, Huffman 1997, Huffman 2001, Wrangham 1995).

Small animals (i.e. microtinae, insects and birds) represented a relatively low part of their diet (2% of the biomass ingested) but occurred for 15.2% in 46 scats. The higher part was attributed to the microtinae accounting for 6.5% of the occurrences per scats and for 1.5% of the small animals biomass. They may find this prey item quite easily in Summer due to their high activity. Despite the low biomass intake, it may constitute alternative prey, as well as birds (Mech & Boitani 2003, Müller 2006, Huitu 2000). As a general result from other studies, wolf preferences and utilization of diverse prey items are influenced by prey densities and seasonal availability (Spaulding et al. 1997, Müller 2006). Most studies found significant differences between the Summer and Winter diet compositions with variations in prey selection and kill rates (Müller 2006, Stahler et al. 2006). Unfortunately we could not evaluate the potential seasonal variation for prey preferences due to a lack of data for the Winter period (N=35 scats for Summer and N=11 for Winter). Scats were not equally easy to discover in all seasons most likely due to changes in wolf behaviour (Reynolds & Aebischer 1991).

Birds appeared in trace amounts a total of two times compared with three times in non-trace amounts. Duck appeared only in trace amount (< 3%) and the same phenomenon happened with insects (occurring three times in trace amounts compared with one time in non-trace amount). Compared to other prey, avian and insect remains are more easily fragmented and therefore may be washed out during the sieving process (Reynolds & Aebischer 1991, Huitu 2000). Thus, the relative importance of such items may have been underestimated.

Carrion (cattle and pig bones and fat only) essentially given as food support during Winter occurred in five out of 46 scats and represented up to 6.4% of the REB due to the consequent volume taken of bones. We did not evaluate the equivalent biomass ingested because it would not be relevant to calculate the live weight of cattle and pigs when wolves had had only a small part of the entire animal.

Livestock depredation and fear of humans

Wolves are opportunistic therefore anthropogenic food sources (i.e. garbage) and domestic animals can also be used when wolves live close to human settlements (Fritts & Mech 1981, Salvador & Abad 1987, Theuerkauf 2003, Nowak et al. 2005).

Indeed, some other items (stones, papers, strings) were occasionally found in wolf scats but probably ingested by accident when foraging on garbage.

In this study, domestic animals represented 13.3% of the biomass ingested with the main proportion attributed to sheep accounting for 12%. Studies of wild wolf populations in European and Asiatic countries revealed that domestic animals could represent an important part of their diet when wild prey species lacked (Kusak et al. 2005, Mech & Boitani 2003). Smietana (2005)

found that up to 16% of the biomass consumed in Winter by wild Polish wolves was constituted of domestic animals. Cattle and horses were the most preyed animals by those wolves and represented up to 12% of the biomass consumed in Autumn and 13.4% in Winter. Andersone and Ozolins (2004) also demonstrated that domestic animal carrion represented 13% of the wolf diet in Latvia.

The attacks on domestic animals were conducted mainly by two of the released wolves, Steffi and Prossia. Steffi especially, was sometimes observed very close to villages: two locations were measured at three and four meters from farms and several locations were around thirty meters. Wolves can be highly tolerant of human activity and live very close to human settlements by habituation (Theuerkauf 2003, Wam 2002). However, they usually fear humans since an early age (from their third week) probably because wolves have been largely persecuted, which may have resulted in the selection of the more fearful animals (Boissy 1995). According to Boitani (2000), wolves are rarely found where the human density is above 30 up to 40 persons per square kilometers. Also hand-reared brown bears demonstrated fear reactions in all cases when they were presented to new unknown stimulus. They were very cautious (Pazhetnov 2005). These cubs were released at the age of seven months and were successfully adapted (61 animals out of 81). Similarly, two 4,5 month old captive-born bears (coming from Kazan “Zoo-Botanical Garden”) were also released without difficulties and developed strong avoidance of humans (Pazhetnov 2005). Wam (2002) tested the tolerance to humans of 125 wolves in south-central Scandinavia. In 123 trials the wolf ran quickly away when approached and the mean tolerance distance was 257 m, but varied greatly (47 – 488 m) due to different factors (Wam 2002). Though, some exceptions exist: Arctic wolves have never been hunted and seem « neutral » towards humans, without aggressivity nor fear (Landry 2004).

Steffi, from an early age, seemed to be the boldest wolf of those released. Yet, both Steffi and Prossia were raised together with Miercoles and did not show any abnormal behaviour before release. However when the two pups were few months old, in order to treat their illnesses, they had to be penned separately, accessible to humans. According to Klinghammer and Goodman (1987), if a wolf pup is removed and kept away from other conspecifics during first three months of life, it will remain socialized to human. The early social contact to humans would suppress wolf fear (Zimen 1987). Zimen (1987) stated that early development of fear and flight reactions normally prevents any social contact and bonding with other species unless those first reactions are overridden. Although in his study, only extremely socially deprived pups receiving intensive care from humans became. Zimen (1987) also showed that later, pups finally reared with their littermates and larger conspecifics, developed social preference for other wolves and showed no longer socialization to humans. Although Steffi and Prossia were raised the same way and had similar experiences we noticed behaviour differences. In the enclosure Prossia was shyer, hiding in holes, avoiding humans while Steffi was bolder and showed some approach tendencies. Later when encountering humans or killing livestock these temperaments were distinguishable. Large individual differences in reaction to threats (Zimen 1987) may be explained by genetic and environmental influences (Boissy 1995). Individual rehabilitated brown bears also displayed differing reactions to humans (Djuro 2005). A genetic component in reactivity to humans has been found in several domestic species (poultry, pigs, sheep and dogs) (Goddard & Beilharz 1984, Dickson et al. 1970, Hemsworth et al. 1990, Jones 1986, Jones & Waddigton 1992). The influence of genetic factors on psychobiological reactivity seems to be consistent in different adverse situations and also over time (Brush et al. 1985 cited by Boissy 1995). In addition, earlier

learning works together with that genetic background to modulate the emotional reactivity of each individual (Jones 1986). Genetic inclinations and developmental experiences might shape the individual tendency to be fearful, anxious or confident and might thus explain the different behaviours displayed by Prossia and Steffi in reaction to humans.

Attacks were grouped in the Summer months (in August and September) and seemed to stop after several human interventions and shots to scare them. In Georgia, wolves for reintroduction were conditioned to avoid humans by giving an electric shock via a collar when a person was introduced in the enclosure (van Dijk 2005). In Russia, as soon as the first snow falls all animals were kept inside for the Winter months, so attacks no longer happened. Indeed Liberg (2006) noticed that domestic animals consumption occurs only when animals are pastured or graze freely during the Summer months. Depredation seems to be seasonal and local in several countries (Meriggi et al. 1991, 1996). In Russia, farmers as well as people in general leave their animals free to roam, at times near forests, which may attract wolves. Wolves select the easiest prey, providing the largest amount of biomass per successful kill (Müller 2006).

Scat-analysis methods

Concordance and correlation coefficients resulting from the simultaneous and pairwise comparisons demonstrated that the analysis methods ranked food items quite likely, especially for high ranked food items (ranks 1-3). We nevertheless observed some differences in those rankings between REB, biomass and percentage of occurrence methods. REB method ranked the sheep at the third rank instead of the wild boar with other methods and evaluated other wild mammals higher than wild ungulates. With biomass method, the high ranks slightly changed too (inversion of the first ranks), maybe due to the influence of the important live weight of large prey species such as moose and wild boar compared to the live weight of mountain hare. Biomass model is likely to assigned higher ranks to large mammals (i.e. ungulates, sheep, etc.) and lower ranks to small animals (i.e. insects, microtinae, wild birds, etc.) than the other methods do (Ciucci et al. 1996). Some sources of difference between methods might be due to the quantification process. The percentage of occurrence method accounted for the presence of an item whereas the two other methods (REB and biomass) also account for the amount of the item in the scat sample (Ciucci et al. 1996). Thus the quantity of small animals consumed may be overrepresented by percentage of occurrence method compared with larger animals (Mech 1970, Floyd et al. 1978, Huitu 2000). Percentage of occurrence method takes into account prey items contributing various amounts by volume to a scat equally and not in their respective proportions (Huitu 2000). The latter as well as REB method undergo biases due to changes in surface/volume proportion in prey of different sizes (Ciucci et al. 1996).

Wild ungulates biomass might be overestimated if wolves have only eaten small pieces of the animal or carcasses remains from hunters instead of the entire animal. It is known that wolves often do not consume prey entirely in a single meal (Miller et al. 1985, Kruuk pers. comm. cited by Ciucci et al. 1996). Moreover, the live weight of prey might not reflect the reality as they were estimated median values of juvenile, adult, female and male weight of the animals and not adjusted weights calculated from proportions of juveniles, adults, females and males actually eaten (Corbett 1989). The biomass model took in consideration neither the part taken from scavengers nor the possible poor physical condition of the prey (Ciucci et al. 1996). We did not estimate the age of the prey, its healthy condition neither if it resulted of a wolf-kill or other causes of death because of the methods employed to identify food items in scats.

Wild ungulates proportions might be underestimated by the REB method compared to the REB of other wild mammals (17.9% compared to 37% relatively). We did not find that often hair and bones of wild ungulates in high quantity (six scats out of 46 scats contained more than 50% of ungulates hair). This may be due to a difference in digestibility of different prey sizes and of prey types (Lockie 1959, Weaver & Hoffman 1979). Large prey may be higher digestible than smaller ones, for which entire prey is ingested with all hair and bones then recovered more easily in scats. The important volume that took thin and dense hare and beaver furs recovered in scats (up to 90% of the relative volume in some scats) may play a role. The way in which the wolf eats its prey may certainly be a source of bias as well as the order in which the prey are eaten (Lockie 1959). Individual wolf may meet differential digestibility, especially of bone remains (Kelly 1991). For instance, the digestive system of young wolves is less efficient compared to the one of adults (Reynolds & Aebischer 1991).

Finally, it is relevant to stress that methods differ in sort: all methods except biomass model, measures undigested food remains in scats whereas biomass estimates relative importance of food items in terms of actual live prey ingested (Ciucci et al. 1996). The great differences between rankings by REB or biomass and percentage of occurrences involve particularly food items (small animals, fruit and seeds and medium-sized mammals) whose remains were structurally diverse and weigh not as much of large mammal remains (Ciucci et al. 1996). In addition, structural bias can occur within the same food type like in mammalian prey where it could be related to difference in the relative proportions of hair and bones recovered in scats (Ciucci et al. 1996). Thus, interpretation of statistical comparisons of the different rankings should be careful. This considered, we might however highlight that differences among rankings for particular food items did not significantly influence the overall assessment of the diet. Indeed, the relative importance of the main food types (i.e. wild mammals, wild ungulates, domestic animals, etc.) was revealed by all methods. Ciucci et al. (1996) as well as Spaulding et al. (1997) found similar results.

6.4 Improvements for future research and perspectives

Research on the released wolves' survival should continue to be improved to obtain more results. GPS-Argos collar technology might be improved by making more studies on equipped captive animals but also in different fieldwork conditions to be able to make adjustments (battery duration, antenna shape). Assessment of the diet using biomass model should be complemented by providing detailed information about the amount of prey consumed by wolves and lost to scavengers, about the prey's age and physical conditions (Ciucci et al. 1996). Moreover, food habits of wild wolves of the same region may be used to compare and identify items difficult to recognize and quantify in the released wolves diet. Analysis of scats data might be biased due to the precarious conditions of analysis and classification errors of two confusable scat components (e.g. mountain hare and domestic cat fur) may have occurred (Reynolds & Aebischer 1991). Both collection and analysis could be ameliorated by getting better technical equipment and by making a pilot study to ensure that the material provided answers to the questions asked in the study. In addition, the data collection should cover a longer period, at least 12 months. Another aspect that should be taken into consideration before release is the temperament of each individual wolf in order to determine the capacity of the animal to survive in the wild and to definite the proper area for release considering the human risk (risk for both, humans and their livestock, and for wolves encountering humans). After all, it will be crucial that such study continue to answer questions about future dispersion and survival rate as well as about the reproduction of the released wolves.

Although we do not know to what extent the released wolves hunted or foraged on carcasses of large prey, in terms of foraging activity they succeeded in finding wild food and killing medium-sized mammals. These findings will hopefully contribute in some extent to the development of new methods of preparing hand-reared wolves for successful reintroduction in the wild without creating conflicts with local human communities. The local wolf population is probably not in need of additions from captive sources (indeed, wolf number remains stable), but elsewhere additions may be useful. E.g. the Swedish authorities have decided to artificially introduce a maximum of twenty wolves to the inbred Swedish wild wolf population within the coming five years. It has been suggested that these wolves be captured as adults in Finland and be relocated by air transport (Olle Liberg, pers. comm.). Another option could be to release wolves from wild strains brought up in captivity. The advantage with the latter method is that the health status of the wolves would be known, thus avoiding the risk of introducing potentially lethal diseases. Lastly, if the method is proved to be reproducible for other canids, it could help other endangered canid species around the world.

7 Conclusions

Although GPS-Argos collars proved their efficiency in diverse habitats, all three collars underwent some unknown issues and failed to give a large amount of movement patterns data for released wolves in Russia. We noticed differences between efficiency and operating duration of the collars, which resulted in an unequal data collection among wolves. However, we still could estimate the travel routes and home ranges of two of the wolves. They both travelled 1.8 km per day but had a home range of 14.7 km² and 40.1 km², probably depending on the individual wolf behaviour and on ecological conditions for finding food.

We did not find significant differences between the number of locations occurring during days and nights, except for one wolf that got more locations at night when she was close to villages. Two of the wolves came to villages to prey on domestic animals until human intervention occurred and Winter arrived. Genetic inclination and past environmental influences may explain the individual tendency to be confident even in threatening situations.

Snow tracking allowed us to continue following the released wolves and to collect scats to assess their diet. Half of the wolves stayed in the surrounding of the release area for some weeks or months, occasionally leaving the vicinity.

Regardless of the relatively low amount of scats, scat-analysis revealed that released wolves mainly preyed on wild mammals from medium to large size. Wild ungulates represented a great part of this consumption and moose stood for the first choice as usually happens in boreal forests. Other wild mammals were of high importance as well, with mountain hare occupying the first position of occurrences and REB. Domestic animals, mainly sheep, also constituted a relative part of the wolf diet, neither more nor less than in some wild populations. The vegetal matter (fruit and seeds, grams) occurring often in scats should be regarded as partly intentional and may serve as vitamin and mineral sources and purgative. Small animals, especially small rodents, also occurred quite often which, despite their low biomass representation, may be used as alternative prey.

Some differences in rankings occurred among methods due to their difference in sort and in quantification procedure. Each method may undergo biases and has thus to be cautiously interpreted. But, simultaneous and pairwise comparisons demonstrated that differences among rankings for particular food items did not significantly influence the overall assessment of the

diet. The relative importance of the main food types was revealed by all methods. Frequencies of occurrence and Relative Estimated Bulk still give a qualitative evaluation of the diet and facilitate comparisons with other studies. Biomass model offers a quantitative and biologically meaningful assessment of the wolf diet.

We can conclude that the released wolves succeeded in foraging, finding food in the wild and killing medium-sized mammals to some large ungulates without prior specific training.

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Appendixes

Appendix 1. *Different rearing methods of wolf pups.*

The “tutor” method consists in human feeding the pups since the first day, from milk bottles if necessary. It may result in tame wolves that consider the tutor as their pack leader.

The “feeder” method relies on human feeding the pups without direct contact, as they are wild. It may result in tolerant wolves that come to the feeder when hungry.

“Within a pack” consists in introducing the pups to a wolf’s sibling. It results in wild pups that are tolerant to an observer.

Finally the “foster” method relies on adult wolves that take care of the pups when introduced into the group. Foster wolves are often human reared wolves to have a sort of control on the pups that they rear, and they did not themselves have pups before. The pups may result in wild wolves that are a bit tolerant to humans (observer).

Appendix 2. *Densities of species present in Tver region.*

Species	Density (animals present in the region/1000sqkm)
Ursus arctos	18,57
Lynx lynx	16
Vulpes vulpes	106
Sus scrofa	185 (in the study area)
Lepus timidus	1197
Castor fiber	186
Capreolus capreolus	14,37
Alces alces	142
Martes martes	139 (in the study area)

Appendix 3. *Substances used for darting the collared animals.*

Animal	Anesthetic used (name and dose)
Cleopa	Zoletil 0.7 ml + Domitor 0.7 ml
Prossia	Zoletil 0.7 ml + Xylosine 0.5 ml
Steffi	Zoletil 1 ml + Domitor 0.6 ml (first time) Zoletil 0.7 ml + Xylosine 0.5 ml (second time)

Appendix 4. *Protocole of scats pre-analysis*

Looking for excrements:



Fresh scat (humid)



Scat of more than a month



Collecting the scat



Cleaning/ordering process before analysis:



Washing and rinsing by hand



Separation of the macro components with tongs



Disposition of all components in an aluminium box and kept in a warm room for 24 hours minimum (drying and conservation processes). Each component is finally ordered in a plastic bag for analysis purpose.

Appendix 5. Scat-analysis (model of the typical classification realised)

Ex. N° 27

Analysis : 01 /16 /2011

Mammals : 50 - 75%



Bones : 5 - 25 %



Vegetation :

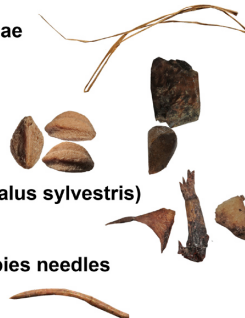
Graminae

Leaves

Seed

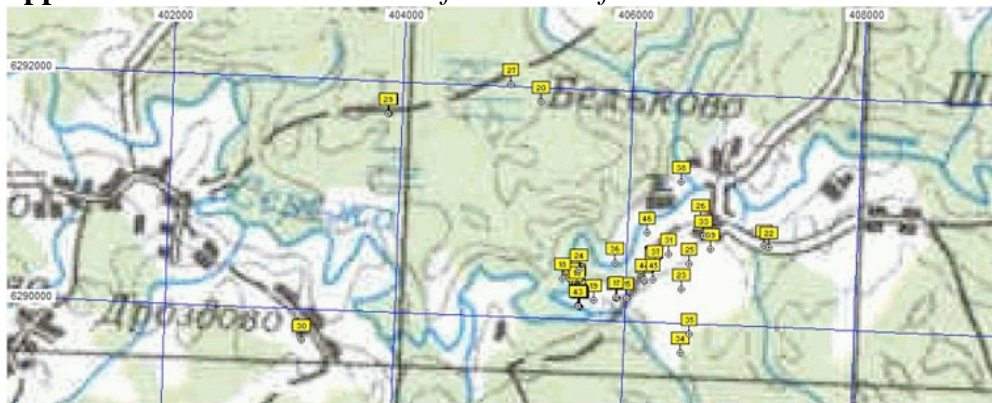
Fruit (malus sylvestris)

Picea abies needles



Total :	
Type	Sp %
- Micromammals :	75%
- Graminae :	3%
- Seeds & fruits.	20%
- Other plants :	2%

Appendix 6: Locations where the faeces were found.



Appendix 7. *Details of fruit and seeds items found in scats.*

Fruit	Seeds
Apple (<i>Malus sylvestris</i>)	Apple (<i>Malus sylvestris</i>)
Rowan (<i>Serbus aucuparia</i>)	Rowan (<i>Serbus aucuparia</i>)
	Cucurbitacea
	Ranunculaceae
Plum (<i>Prunus</i>)	Plum (<i>Prunus</i>)
	Sweet cicely (<i>Myrrhis odorata</i>)
Hogweed (<i>Heracleum sp.</i>)	Hogweed (<i>Heracleum sp.</i>)